

On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium

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ABSTRACT. There has been much controversy concerning the identity of the components of the suspensorium in Siluriformes (catfishes). This confusion has implications not only for comparative morphology, but also for phylogenetic studies. The identity of the suspensorium components in catfish is reviewed here on the basis of: 1) dissections of numerous catfishes, including members of the most primitive group (Diplomystidae), and morphological descriptions in the literature; 2) developmental and paleontological data available; 3) functional morphology; and 4) comparisons with other member of the Ostariophysi, as well as with other teleosts. Our observations and comparisons indicate that catfish suspensorium consists of: 1) a hyomandibula+metapterygoid compound, which corresponds to the hyomandibula plus metapterygoid of other teleosts; 2) a symplectic+quadrate compound, which corresponds to the symplectic+quadrate of other teleosts; 3) an ectopterygoid+ectopterygoid compound, which corresponds to the entopterygoid plus ectopterygoid of other teleost. The small bones present in several catfishes between the anterior portions of the pars quadrata, the palatine, and the ethmoideal region are considered to be sesamoid ossifications.

KEY WORDS: catfish, comparative anatomy, cranium, evolution, ethmoideal region, homologies, morphology, Ostariophysi, suspensorium, Siluriformes, suspensorium.

INTRODUCTION

The division of the suspensorium into rostral (the palatine alone) and caudal (the other skeletal elements) units is a major synapomorphy of catfish (FINK & FINK, 1981; ARRATIA & SCHULTZE, 1991; ARRATIA, 1992). This frees the palatine-maxillary system from the more posterior elements, thereby allowing ample movements of the maxillary barbels (ALEXANDER, 1965; GOSLINE, 1975; DIOGO & CHARDON, 2000a; in press). The division is ontogenetically present from the first appearance of the splanchnocranium cartilages (KINDRED, 1919; ARRATIA, 1987; 1990; 1992; HOWES & TEUGELS, 1989; SURLEMONT & VANDEWALLE, 1990; KOBAYAKAWA, 1992; VANDEWALLE et al., 1993; 1995a; 1997; ADRIAENS & VERRAES 1998; etc.) and is probably required functionally by the early respiratory pattern of the larva (VANDEWALLE et al., 1985).

The division results in the lack of an anterior support for the large posterior portion of the suspensorium and the need for compensatory mechanisms, which are probably correlated with numerous synapomorphies in the suspen-

sorium of different catfish lineages. Noteworthy differences between taxa involve several ligaments and small bones between the fore end of the pars quadrata, the palatine, and the ethmoideal region (GOSLINE, 1975).

There are usually three large bones (not including the preopercular) and some small bones in the pars quadrata, instead of five or six large bones present in that region in the other teleosts. The determination of the identity of the components of the pars quadrata of catfish has long been a matter of controversy. Despite a series of excellent contributions on the topic (see, for example, REGAN, 1911; STARKS, 1926; FINK & FINK, 1981; HOWES, 1983; 1985; ARRATIA, 1987; 1990; 1992; HOWES & TEUGELS, 1989), comparative and developmental arguments have not yet resulted in a satisfactory consensus as to the identity of the involved ossifications.

In most papers, including ARRATIA's 1992 well-documented review, the three large bones of the pars quadrata are considered as the hyomandibula, quadrate, and metapterygoid; with the symplectic considered to be totally absent; the smaller anterior bones are interpreted as either the ectopterygoid and/or entopterygoid or as sesamoid bones. ARRATIA's (1992) opinions appear, how-

ever, subtler and adapted to particular cases, as will be demonstrated in the discussion. However, many authors have alternative interpretations, of which three are particularly interesting. HOWES (1983) hypothesises that, in catfish, the hyomandibula of authors corresponds to the hyomandibula and metapterygoid of other teleosts, and that the so-called metapterygoid is the result of the fusion of the ecto- and entopterygoid sensu stricto, with the small bones being sesamoid ossifications. HOWES (1985) suggests that the hyomandibula is the result of the fusion of the hyomandibula sensu stricto and the metapterygoid, with the so-called metapterygoid being the entopterygoid, and the small bones representing sesamoid ossifications. HOWES & TEUGELS (1989) consider that the metapterygoid of authors is homologous to a part of the metapterygoid fused with an ecto- and an entopterygoid. The smaller anterior bones are interpreted as sesamoids and/or fragments of the dermal pterygoids.

On the basis of 1) careful dissections of numerous catfishes, including the most primitive ones (Diplomystidae: see EIGENMANN, 1890; REGAN, 1911; ALEXANDER, 1965; CHARDON, 1968; LUNDBERG & BASKIN, 1969; GOSLINE, 1975; FINK & FINK, 1981; ARRATIA, 1987; 1992; MO, 1991; DE PINNA, 1993; 1998; DIOGO & CHARDON, 2000bc; DIOGO et al., 2000b; in press; etc.) and the morphological descriptions in the literature, 2) available developmental and paleontological data, 3) functional morphology and 4) comparisons with other members of the Ostariophysi, as well as with other teleosts, we shall try to propose a comprehensive hypothesis about the homologies of the skeletal components of catfish suspensorium.

MATERIAL AND METHODS

The examined specimens are from the collection of our laboratory (LFEM), the “Musée Royal de l’Afrique Centrale” of (Tervuren: MRAC), the “Université Nationale du Bénin” (Kotonou: UNB), the “Muséum National D’Histoire Naturelle” (Paris: MNHN) and the National Museum of Natural History (Washington: USNM). Anatomical descriptions are made after dissection of fresh, alcohol-fixed or trypsin-cleared and alizarine-stained (following TAYLOR & VAN DYKE’s 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The cleared and stained (c+s), fresh (fre) or alcohol-fixed (alc) condition of the studied fishes in the list below, is given in parentheses following the number of specimens dissected.

The following specimens were dissected:

Amphilius brevis Boulenger, 1902 (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c+s). *Amphilius jacksonii* Boulenger, 1912 (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* Boulenger, 1900 (Doumeidae): MNHN 1961-0600, 1 (alc); *Arius herzegbergii* (Bloch, 1794) (Ariidae): LFEM, 1 (fre). *Arius heudelotii* Valenciennes, 1840 (Ariidae):

MRAC P.56259, 1 (alc); MRAC P.56260, 1 (alc); MRAC P.56261, 1 (alc); *Arius latiscutatus* Günther, 1864 (Ariidae): MRAC 90-057-P-995, 1 (alc). *Auchenoglanis biscutatus* (Geoffroy St. Hilaire, 1809) (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagre marinus* (Mitchill, 1815) (Ariidae): LFEM, 1 (alc); LFEM, 1 (c+s). *Bagrus bayad* (Pfaff, 1933) (Bagridae): LFEM, 1 (alc); LFEM, 1 (c+s). *Bagrus docmac* (Forsskal, 1775) (Bagridae): LFEM, 2 (alc); MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (c+s); UNB, 2 (fre). *Belonoglanis tenuis* Boulenger, 1902 (Doumeinae): MRAC P.60494, 1 (alc). *Clariallabes melas* Boulenger, 1887 (Clariidae): LFEM, 2 (alc). *Clarias gariepinus* (Burchell, 1822) (Clariidae): LFEM, 2 (alc); LFEM, 2 (c+s); MRAC 93-152-P-1356, 1 (alc). *Chrysichthys auratus* (Geoffroy St. Hilaire, 1809) (Claroteidae): LFEM, 2 (c+s); UNB, 2 (alc); UNV, 3 (fre). *Chrysichthys cranchii* (Leach, 1818) (Claroteidae): LFEM, 1 (alc); LFEM, 2 (fre); LFEM, 1 (c+s). *Chrysichthys nigrodigitatus* (Lacepède, 1803) (Claroteidae): UNB, 2 (alc); UNB, 3 (fre); UNB, 2 (c+s). *Doumea typica* Sauvage, 1879 (Doumeidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152, 1 (alc). *Diplomystes chilensis* (Molina, 1782) (Diplomystidae): LFEM, 2 (alc). *Genidens genidens* (Valenciennes, 1840) (Ariidae): LFEM, 2 (alc). *Hemibagrus wycki* (Bleeker, 1858) (Bagridae): LFEM, 1 (alc); LFEM, 1 (c+s). *Heterobranchius longifilis* Valenciennes, 1840 (Clariidae): LFEM, 2 (alc). *Ictalurus punctatus* (Rafinesque, 1818) (Ictaluridae): LFEM, 5 (alc). *Mochokus niloticus* Joannis, 1835 (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Hamilton, 1822) (Bagridae): LFEM, 1 (alc). *Neosilurus rendahli* (Whitley, 1928) (Plotosidae): USNM 173554, 2 (alc). *Paraphilius trichomycteroides* Pellegrin, 1907 (Amphiliidae): LFEM, 2 (alc). *Paraplotosus albilabris* (Valenciennes, 1840) (Plotosidae): USNM 173554, 2 (alc). *Phractura brevicauda* Boulenger, 1911 (Doumeidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c+s). *Phractura intermedia* Boulenger, 1911 (Doumeidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias* Geoffroy St. Hilaire, 1809 (Pimelodidae): LFEM, 2 (alc), LFEM, 3 (fre); LFEM, 2 (c+s). *Plotosus lineatus* Valenciennes, 1840 (Plotosidae): USNM 200226, 2 (alc). *Pseudomystus bicolor* (Fowler, 1934) (Bagridae): LFEM, 1 (alc), LFEM, 1 (c+s). *Schilbe intermedius* Rüppell, 1832 (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* Linnaeus, 1758 (Siluridae): LFEM, 2 (alc).

LIST OF ABBREVIATIONS

“ADPT”	“additional pterygoid”
ATLP	additional tooth-plate
AF-	articular facet
AF-I	f. a. neurocranium-autopalatinum
C-	cartilago ...
C-APAL-A	c. autopalatinus anterior
C-APAL-P	c. autopalatinus posterior
ECT-TE	ectopterygoid teeth
ISUT	incomplete suture
L-	ligamentum ...
L-ANG-“Q”	l. angulo- “quadratum”
L- “ECT”-APAL	l. “ectopterygoideum”-autopalatinum
L-ENT-VM	l. entopterygoideo-vomerale
L-“ENT”-APAL	l. “entopterygoideum”-autopalatinum

L-“ENT”-LETH	l. “entopterygoideo”-lateroethmoideum
L-“ENT”-VM	l. “entopterygoideo”-vomere
L-“ENT”-PRMX-VM	l. “entopterygoideo”-praemaxillovomere
L-“MP”-APAL	l. “metapterygoideo”-autopalatinum
L-“MP”-“ENT”	l. “metapterygoideo”-“entopterygoideum”
L-“MP”-MX	l. “metapterygoideo”-maxillare
L-“MP”-OSPH-LETH	l. “metapterygoideo”-orbito-lateroethmoideum
L-“MP”-PRMX-LETH	l. “metapterygoideo”-praemaxillo-lateroethmoideum
L-“MP”-PRMX-VM	l. “metapterygoideo”-praemaxillovomere
L-“MP”-VM	l. “metapterygoideo”-vomere
L-PRMX-MX	l. praemaxillo-maxillare
L-“Q”-“MP”	l. “quadrato”-“metapterygoideum”
L-“Q”-PRMX	l. “quadrato”-praemaxillare
M-	musculus ...
M-AD-AP	m. adductor arcus palatini
M-EX-T	m. extensor tentaculi
M-RE-T	m. retractor tentaculi
MND	mandible
“MP”-TE	“metapterygoid” teeth
MX-B	maxillary barbel
O-	os ...
O-APAL	o. autopalatinum
O-ECT	o. ectopterygoideum
O-“ECT”	o. “ectopterygoideum”
O-ENT	o. entopterygoideum
O-“ENT”	o. “entopterygoideum”
O-HM	o. hyomandibulare
O-“HM”	o. “hyomandibulare”
O-IOP	o. interoperculare
O-LETH	o. latero-ethmoideum
O-METH	o. mesethmoideum
O-MP	o. metapterygoideum
O-“MP”	o. “metapterygoideum”
O-MX	o. maxillare
O-OP	o. operculare
O-OSPH	o. orbitosphenoidium
O-PARA	o. parasphenoidium
O-POP	o. praepoperculare
O-PRMX	o. praemaxillare
O-PROT	o. prooticum
O-PSPH	o. pterosphenoidium
O-PT	o. pteroticum
O-Q	o. quadratum
O-“Q”	o. “quadratum”
O-SPH	o. sphenoticum
O-SPOP	o. suprapraepoperculare
O-VM	o. vomere
O-SY	o. symplecticum
T-M-EX-T	tendon of the musculus extensor tentaculi
VM-TLP	vomerine tooth-plate

RESULTS

We herein describe the suspensorium of representatives of eight catfish families. Recent studies (HE, 1998; HE et

al., 1999; DIOGO & CHARDON, in preparation), have shown that the “Amphiliidae” as previously delimited are non monophyletic, and that, thus, the subfamilies “Doumeinae” and “Amphiliidae” should be raised to the family level; therefore, the Amphiliidae and Doumeidae of the present study correspond, respectively, to the former “Amphiliinae” and “Doumeinae”). Significant differences between the configuration of the suspensorium of these species and that of other species of the same families are noted.

In the descriptions, we follow the most commonly accepted nomenclature (see, REGAN, 1911; DAVID, 1936; HARRY, 1953; NAWAR, 1955; TILAK, 1961; 1963ab; 1964; 1965; ALEXANDER, 1965; JAYARAM, 1966; 1968; 1971; GOSLINE, 1975; FINK & FINK, 1981; 1996; GAUBA, 1969; SKELTON, 1981; SKELTON et al., 1984; SCHAEFER, 1987; 1990; KOBAYAKAMA, 1989; 1992; MO, 1991; DE PINNA, 1993; 1996; 1998; DE VOS, 1995; VANDEWALLE et al., 1997; HE, 1998; REIS, 1998; HE et al., 1999; NG & KOTTELAT, 1999; etc.). The visual information presented in the figures has preponderance over the text, which will thus be brief.

Diplomystes chilensis Molina, 1782 (Diplomystidae)

Diplomystids are the catfishes richest in archaic characters and thus are considered to be the sister group of all the other siluriforms (EIGENMANN, 1890; REGAN 1911; ALEXANDER 1965; CHARDON 1968; LUNDBERG & BASKIN 1969; GOSLINE 1975; FINK & FINK 1981; 1996; ARRATIA, 1987; 1992; MO 1991; DE PINNA, 1993; 1996; etc.). In *Diplomystes chilensis* (Figs 1, 2), the articulation between the suspensorium and the neurocranium is particularly elongated anteroposteriorly on the prootic, pterotic, sphenotic, and pterosphenoid (Fig. 1). The “quadrato” is triangular, being linked with the “hyomandibula” and the “metapterygoid” by cartilage (Fig. 1). Two ligaments originate from the forked anterior end of the “metapterygoid”, and attach respectively to the vomer (Fig. 2A) and to the palatine (Fig. 2B). Only on the right side of the dissected specimens is there an “entopterygoid”, which is imbedded in the ligament that attaches to the vomer (Fig. 2B). In both sides of these specimens the ligament that attaches to the palatine has some fibers in common with the other ligament and with a tendon of the extensor tentaculi muscle, and contains the “ectopterygoid” bone and an “additional pterygoid” (Fig. 2B).

There are some slight discrepancies between our observations and the literature. ALEXANDER (1965: fig. 4A) does not mention the ligament between the “metapterygoid” and the palatine, nor the two “pterygoids” (“ectopterygoid” and “additional pterygoid”) embedded in it. FINK AND FINK (1981: fig. 11) omit the same ligament and describe only two small bones anteriorly to the metapterygoid. ARRATIA’s (1987: fig. 6B) descriptions are

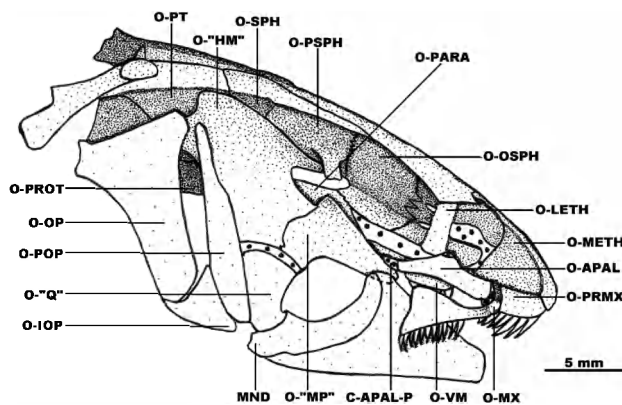
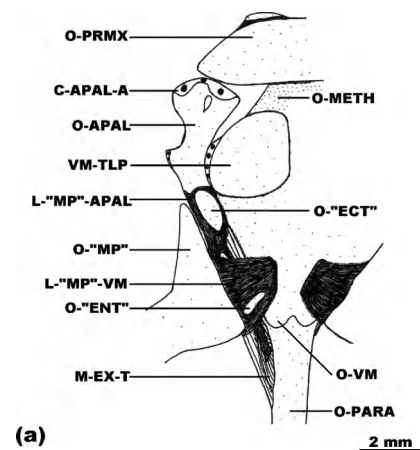


Fig. 1. – Lateral view of the skull of *Diplomystes chilensis*. Infraorbital series and mandibular teeth were removed. Ligaments are not represented.

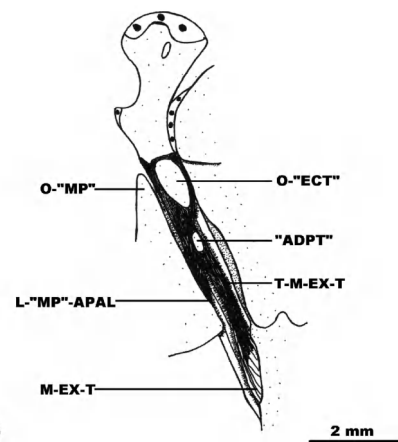
much closer to our observations, since, although she does not figure the ligament between the “metapterygoid” and the palatine, she does mention in the text an “additional pterygoid” linked with the palatine by a short ligament.

***Chrysichthys nigrodigitatus* Lacépède, 1803**
(Claroteidae)

The “hyomandibula” articulates with the pterotic and sphenotic (Fig. 3). The “quadrate” is associated with the “hyomandibula” and “metapterygoid” by cartilage and bony sutures (Fig. 3). The “metapterygoid” is strongly bifurcated anteriorly (Fig. 4A). Its anterolateral portion bears teeth ventrally and is linked to the vomer and to the premaxilla by a thick ligament in which a small toothed plate is imbedded (Fig. 4A). This is also the case in *Chrysichthys cranchii*, but not in *Chrysichthys auratus*,



(a)



(b)

Fig. 2. – Ventral view of the anterior region of the suspensorium of *Diplomystes chilensis*. (A) Vomerine and premaxillary teeth were removed. (B) “Entopterygoid” and ligament between the “metapterygoid” and the vomer were removed.

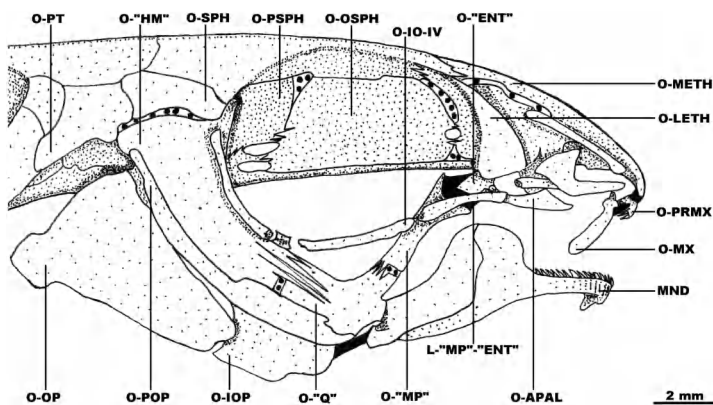
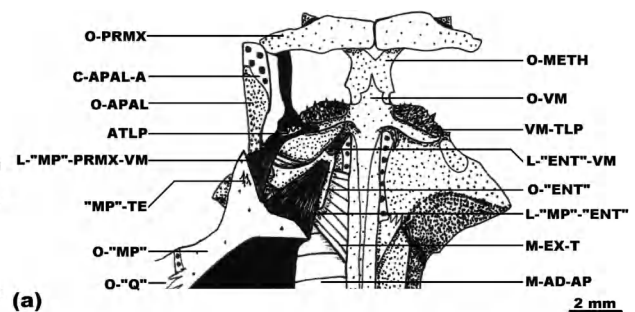
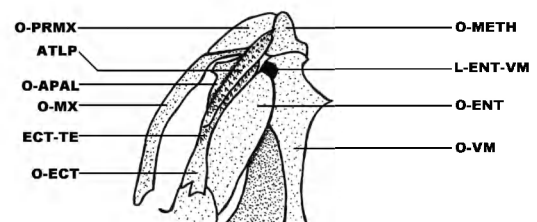


Fig. 3. – Lateral view of the skull of *Chrysichthys nigrodigitatus*. Primordial ligament, palatine cartilage and ligament between the “metapterygoid”, vomer and premaxillary were removed.



(a)



(b)

Fig. 4. – Ventral view of the anterior region of the suspensorium of: (A) *Chrysichthys nigrodigitatus*. Premaxillary teeth were removed. (B) *Hoplias* species (modified from ROBERTS, 1969: the nomenclature used here follows that used in the original illustration).

which lacks “metapterygoid” teeth, or in *Auchenoglanis biscutatus*, in which both these teeth and the small toothed plate are absent. The “entopterygoid” is associated, by means of two ligaments, with the anteromedial part of the

“metapterygoid” and the vomer (Figs 4A, 5A). The “ectopterygoid” is firmly attached to the “entopterygoid” and is associated with the palatine by a short, thin ligament (Fig. 5A).

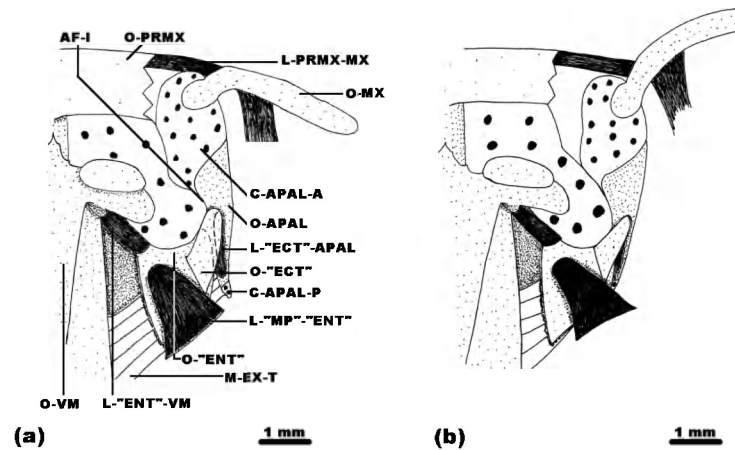


Fig. 5. – Ventral view of the palatine-maxillary system of *Chrysichthys cranchii*. The premaxillary was cut off to show the movements associated with this system. Vomerine and premaxillary teeth, as well as the ligament between the “metapterygoid”, vomer and premaxillary were removed. (A) The maxillary is adducted. (B) The maxillary is abducted.

Neosilurus rendahli Valenciennes, 1840 (Plotosidae)

The “hyomandibula” articulates with both the pterotic and sphenotic (Fig. 6). In the two specimens of *Neosilurus rendahli* dissected, but not in the other plotosid species studied, there is a prominent incomplete suture in the anterodorsal margin of the “hyomandibula” (Fig. 6). The “quadrate” is associated with the “hyomandibula” by cartilage and to the “metapterygoid” by cartilage and a bony suture (Fig. 6). Anteroventrally, the “quadrate” is associ-

ated with the posterior margin of the lower jaw by means of a large, strong ligament (Fig. 6). The antero-mesial edge of the “metapterygoid” is firmly attached to both the antero-lateral surface of the orbitosphenoid and the postero-lateral surface of the lateral ethmoid by means of a very short, strong ligament (Fig. 6). Anterolaterally, the “metapterygoid” is also strongly connected, by means of a very short ligament, with the large “entopterygoid” (Fig. 6). However, the roughly dentate aspect of both the anterior and the posterior surfaces of, respectively, the “metapterygoid” and the “entopterygoid”, associated to the very small gap existing between these bones, makes the ligamentous connection between them seem rather as a bony suture. The “ectopterygoid” is absent. The anterior margin of the “entopterygoid” is firmly attached by massive ligamentous tissue to the postero-lateral surface of the vomer.

Bagrus docmak Forsskal, 1775 (Bagridae)

The “hyomandibula” articulates with both the sphenotic and pterotic and is linked to the “quadrate” by a cartilaginous band. The “metapterygoid” lies anterodorsally to the “quadrate” and is joined to it by cartilage and a short bony suture. The “entopterygoid” is attached by ligaments to the anteromedial part of the “metapterygoid” and to the lateral ethmoid (Fig. 7). The “ectopterygoid” is firmly attached medially to the “entopterygoid” and laterally, by a short ligament, to the palatine (Fig. 7). A long, thin ligament joins the anterolateral end of the “metapterygoid” to the maxilla (Fig. 7). In addition, there

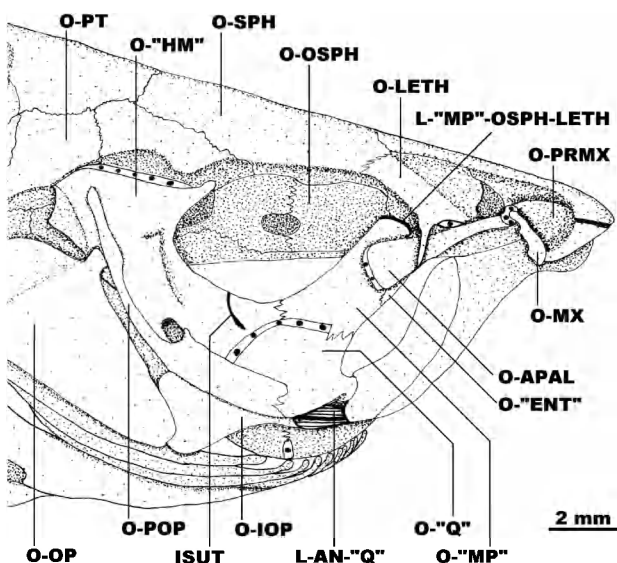


Fig. 6. – Lateral view of the skull of *Neosilurus rendahli*. Primordial ligament and infraorbital series were removed.

is a long, strong ligament between the upper surface of the “metapterygoid” and the posterior margin of the palatine.

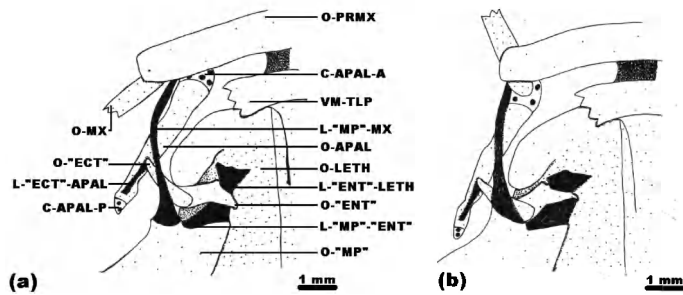


Fig. 7. – Ventral view of the palatine-maxillary system of *Bagrus docmak*. The vomerine tooth-plate was cut off to show the movements associated with this system. Vomerine and premaxillary teeth were removed. (A) The maxillary is adducted. (B) The maxillary is abducted.

***Clarias gariepinus* Burchell, 1822**
(Clariidae)

The “hyomandibula” articulates with the pterotic and sphenotic. The very broad “quadrate” is attached to the “hyomandibula” by bony sutures and to the “metapterygoid” by bony sutures and a small, ventral cartilage band (Fig. 8). The large “entopterygoid” is linked to other bones by five ligaments (Fig. 9): 1) its posterior portion to the anteromesial edge of the “metapterygoid” by a very

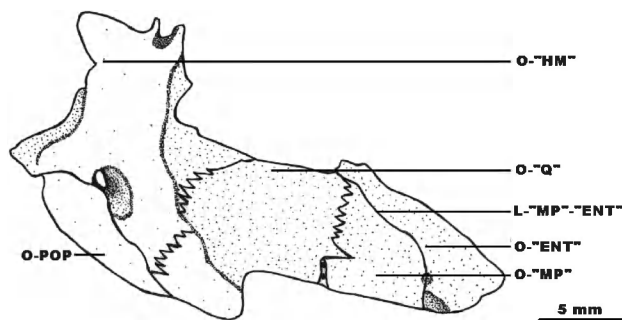


Fig. 8. – Medial view of the suspensorium (palatine not included) of *Clarias gariepinus*.

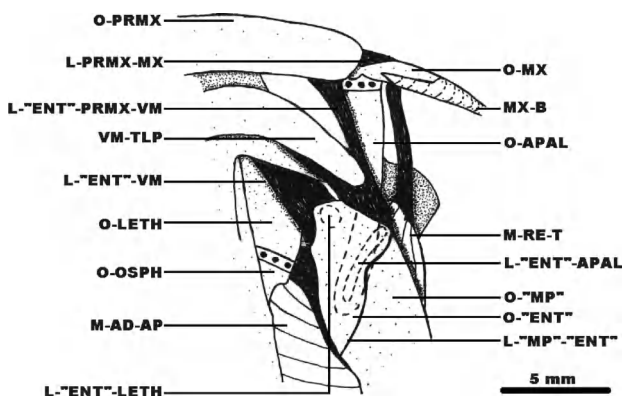


Fig. 9. – Ventral view of the anterior region of the suspensorium of *Clarias gariepinus*. Vomerine and premaxillary teeth are not represented.

short, strong ligament; 2) its anterior part to the vomer by a thick ligament; 3) its antero-dorsal border to the lateral ethmoid by a short ligament; 4) its posterodorsal extremity to the palatine by a thin ligament; and 5) its anterolateral edge to the vomer and the premaxilla by a long, massive ligament. The “entopterygoid” of *Clariallabes melas* is much smaller than that of *Clarias gariepinus*, and is firmly associated with the anterolateral, and not with the anteromesial (see above) edge of the “metapterygoid”.

***Amphilius brevis* Boulenger, 1902**
(Amphiliidae)

In this species the articulation between the suspensorium and both the sphenotic and pterotic is particularly elongate (Fig. 10). The “quadrate” is associated to the “hyomandibula” and to the “metapterygoid” by bony sutures and cartilage (Fig. 10). The “metapterygoid” is deeply forked anteriorly (Fig. 10). This is also the case in *Amphilius jacksosii*, but not in *Paramphilius trichomycteroides*, in which the “metapterygoid” is a broad, rectangular bone without an anterior bifurcation. The anterolateral margin of the “metapterygoid” is attached by a long, thick ligament to both the lateral ethmoid and the premaxilla (Fig. 10). Its anteromedial portion is firmly linked to the “entopterygoid” by a very short, strong ligament (Fig. 10), and to the “entopterygoid” and the lateral ethmoid by massive ligamentous tissue.

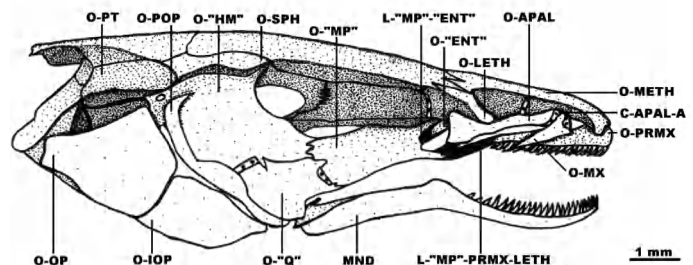


Fig. 10. – Lateral view of the skull of *Amphilius brevis*. Infraorbital series was removed. Only the ligaments associated with the suspensorium are represented.

***Arius heudelotii* Valenciennes, 1840**
(Ariidae)

The “hyomandibula” articulates with the pterotic and sphenotic. It bears a prominent, thick lateral crest to which a medial section of the adductor mandibulae muscle attaches. The “quadrate” is associated with the “hyomandibula” by cartilage and to the “metapterygoid” by bony sutures. The “metapterygoid” is somewhat bifurcate anteriorly (Fig. 11). The “entopterygoid” is a small, triangular bone, which is joined, by means of two long, thick ligaments, with the anterolateral margin of the “metapterygoid” and the anteroventral margin of the vomer (Fig. 11). The main part of the ligament between the “entopterygoid” and the vomer is located dorsal to the

well-developed vomerine tooth-plate (Fig. 11). The small, boomerang-shaped “ectopterygoid” is firmly articulated with the “entopterygoid” medially (Fig. 11). Laterally, this little bone is strongly connected by means of connective tissue to the posterior edge of the palatine (Fig. 11). The configuration of the “entopterygoid” of *Genidens genidens* is quite different from that of the “entopterygoid” of *Arius heudelotii*, and of the other ariid species studied, being a long, thin bone significantly larger than the “ectopterygoid”.

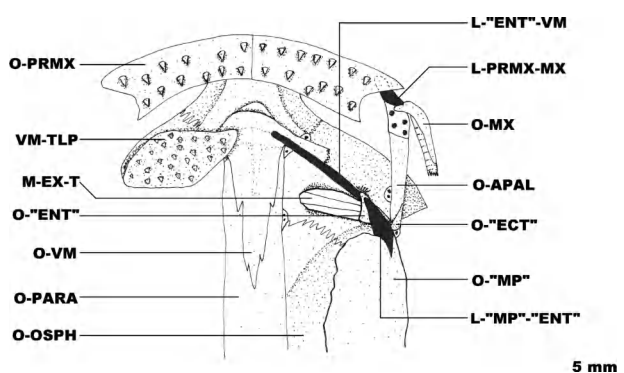


Fig. 11. – Ventral view of the anterior region of the suspensorium of *Arius heudelotii*. In the right side, the vomerine tooth-plate was removed.

***Phractus brevicauda* Boulenger, 1911
(Doumeidae)**

The “hyomandibula” articulates with the sphenotic and pterotic (Fig. 12). The “quadrate” has a large number of pores (true holes). It is connected to the “hyomandibula” by a long cartilaginous strip (Figs 12, 13), to the premaxillary by a long, thick ligament and to the “metapterygoid” by massive connective tissue bands (Fig. 13). The “entopterygoid” is firmly attached to the “metapterygoid” and to the vomer by short, strong ligaments (Fig. 13). The “metapterygoid” is small, being much smaller than the “entopterygoid” (Figs 12, 13). However, it is more devel-

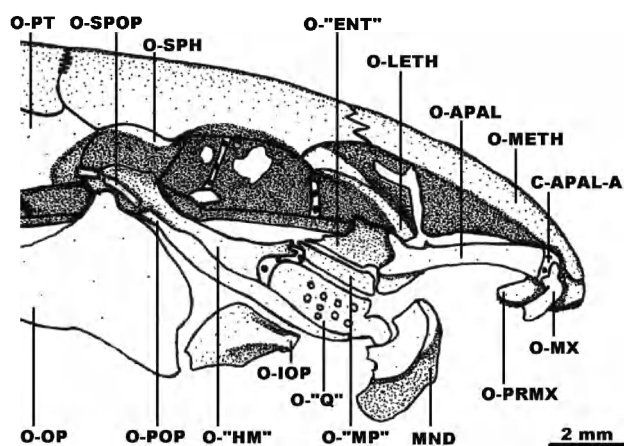


Fig. 12. – Lateral view of the skull of *Phractus brevicauda*. Infraorbital series was removed. Ligaments are not represented.

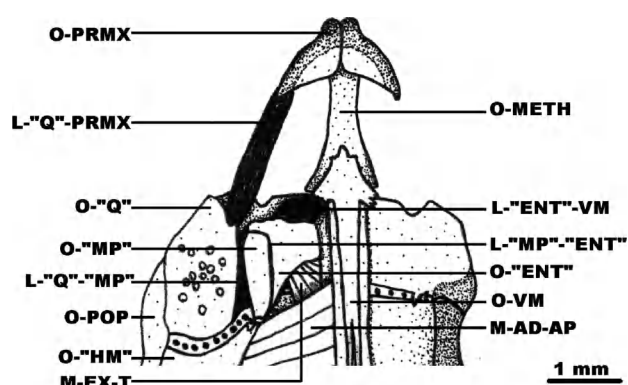


Fig. 13. – Ventral view of the anterior region of the suspensorium (palatine not included) of *Phractus brevicauda*. Premaxillary teeth are not represented.

oped than that of the specimen of *Andersonia leptura* dissected, in which the “metapterygoid” is a very small, oval bone.

DISCUSSION

In order to ascertain the true homologies of the ossifications of the suspensorium in catfish we compared the studied catfishes with other Siluriformes, other ostariophysans and even other teleosts. The comparison between catfishes and gymnotiforms, in particular, has proved very interesting. The gymnotiforms are considered to be the closest relatives of the siluriforms (FINK & FINK 1981; 1996; ARRATIA, 1992). The components of the suspensorium in gymnotiforms are easily homologised with those of other teleosts (CHARDON & DE LA HOZ, 1973; 1974; 1977; DE LA HOZ, 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; DE LA HOZ & CHARDON, 1984; ARRATIA & SCHULTZE, 1991; ARRATIA, 1992), with the exception of the so-called “entopterygoid”, which may represent the entopterygoid or the ectopterygoid or both (DE LA HOZ, 1974) (see below).

The suspensorium of one of the most archaic gymnotiforms, *Sternopygus macrurus* (Bloch & Schneider, 1801) (CHARDON & DE LA HOZ, 1974; 1977; DE LA HOZ, 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; DE LA HOZ & CHARDON, 1984; but see GAYET et al., 1994; ALBERT & FINK, 1996; ALBERT & CAMPOS DA PAZ, 1998, for a different view), and the South-American trichomycterid catfish *Trichomycterus areolatum* (Valenciennes, 1846) are very similar (Fig. 14), with: 1) a cartilaginous band (A) between two bones; 2) an inverted Y-shaped formation (B) in the middle of the suspensorium; and 3) only one bone (C) situated anterodorsal to this formation and extending up to half the length of the palatine.

Three differences are, however, noteworthy:

- 1) The A cartilage of *Sternopygus* (Fig. 14A) is prolonged by a clear separation (D) between two bones (hyomandibula and metapterygoid) (DE LA HOZ & CHARDON, 1984). In *Trichomycterus*, there is only a

partial suture between the bones at the same level (see, for example, Fig. 15C), and this is only observed in some species (as, e.g., *Trichomycterus roigi* Arratia & MenuMarque, 1984: see fig. 15C and ARRATIA & MENUMARQUE, 1984) of this genus (ARRATIA & CHANG 1975; ARRATIA et al., 1978; ARRATIA & MENUMARQUE, 1981; 1984; ARRATIA, 1987; 1990; 1992). Complete sutures were however described at the same location in malapterurids (Fig. 15D) (HOWES, 1985) and some diplomystids (see, for example, Fig. 15A, B) (ARRATIA, 1987).

- 2) In *Sternopygus*, the suspensorium is linked to the neurocranium by an ossified ligament (E), which terminates dorsally in very short fibres (Fig. 14A) (DE LA HOZ & CHARDON, 1984), while *Trichomycterus* (Fig. 14B), like many other catfishes (MO, 1991; ARRATIA, 1992), has these bones joined by a non-ossified ligament (ARRATIA, 1990). However, these ligaments seem to be homologous (see DE LA HOZ, 1974), and the almost total ossification of the ligament in some gymnotiforms is an unusual situation in this group (CHARDON & DE LA HOZ, 1974; DE LA HOZ, 1974).
- 3) *Sternopygus*, like all Gymnotiformes (CHARDON & DE LA HOZ, 1974; 1977; DE LA HOZ, 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; DE LA HOZ & CHARDON, 1984), has a symplectic completely separate from the quadrate (F) (Fig. 14A). In *Trichomycterus* (Fig. 14B), a single ossification occupies the position of these two bones, without any visible separation at the level F. This separation is also lacking in all other cat-

fishes (see, for example, Figs 1, 3, 6, 10, 16) except, perhaps (see below), *Malapterurus* (Fig. 15D) (HOWES, 1985).

The above comparison strongly suggests the following homologies for the hitherto discussed skeletal parts of the suspensorium of catfish: [1] their “hyomandibula” (Fig. 14B) represents the hyomandibula+metapterygoid of other teleosts (Fig. 14A); [2] their “quadrate” (Fig. 14B) represents the quadrate+symplectic of the other teleosts (Fig. 14A); [3] their “metapterygoid” (Fig. 14B) corresponds to the “entopterygoid” of gymnotiforms (Fig. 14A). However, as mentioned before, the identity of the “entopterygoid” of the gymnotiforms is somewhat uncertain. In fact, REGAN (1911) called this bone the “mesopterygoid” (=“entopterygoid”) without providing evidence to support its homology with the entopterygoid of other teleosts. This nomenclature was followed by other authors (CHARDON & DE LA HOZ, 1973; 1974; 1977; DE LA HOZ, 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; ARRATIA & SCHULTZE, 1991; ARRATIA, 1992; DE LA HOZ & CHARDON, 1984; etc.), but some of them (e.g. CHARDON & DE LA HOZ 1973; DE LA HOZ, 1974) pointed out that this bone has features typical of the entopterygoid (e.g. ligamentous connection with the neurocranium; relation with the adductor arcus palatini), ectopterygoid (e.g. antero-dorsal relation with the palatine) and entopterygoid+ectopterygoid (spatial position) of other ostariophysine fishes. We are unable, at the present, to determine the identity of the “entopterygoid” in the Gymnotiformes. However, our own observations,

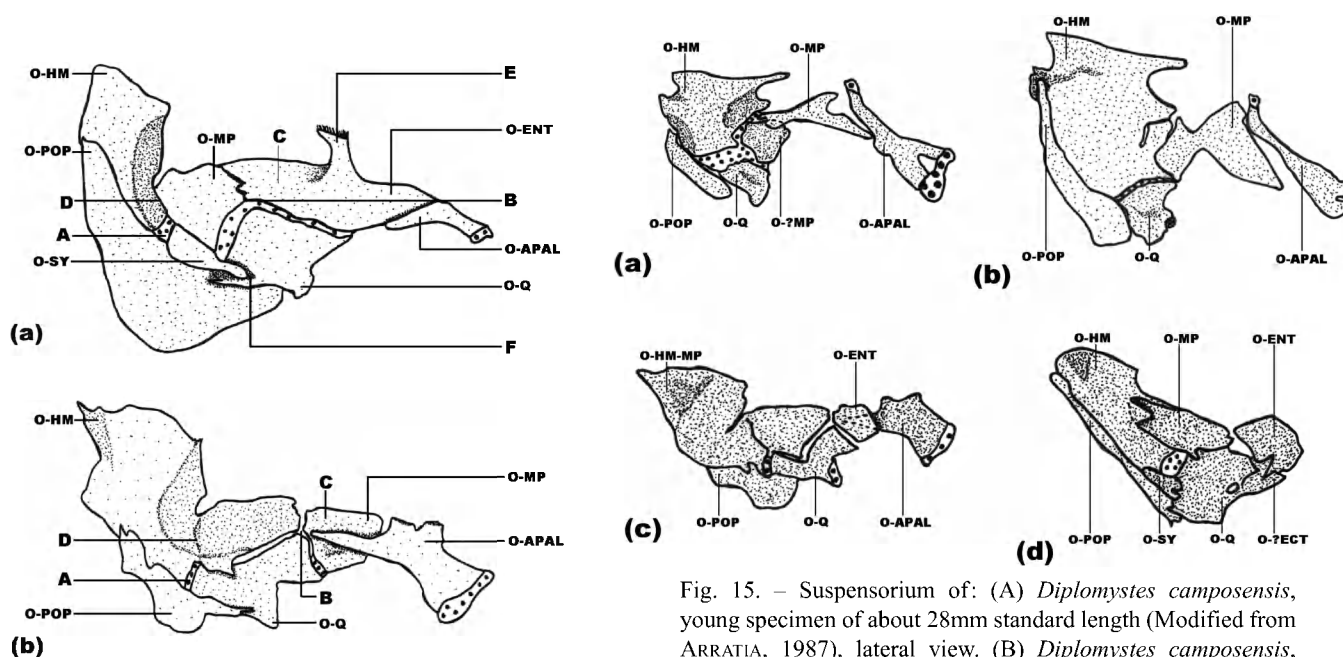


Fig. 14. – Lateral view of the suspensorium of: (A) *Sternopygus macrurus* (modified from DE LA HOZ & CHARDON, 1984). (B) *Trichomycterus areolatum* (modified from ARRATIA, 1990). The nomenclature used here follows that used in the original illustrations.

Fig. 15. – Suspensorium of: (A) *Diplomystes camposensis*, young specimen of about 28mm standard length (Modified from ARRATIA, 1987), lateral view. (B) *Diplomystes camposensis*, large specimen (modified from ARRATIA, 1987), lateral view. (C) *Trichomycterus roigi* (modified from ARRATIA & MENUMARQUE, 1984), dorsal view. (D) *Malapterurus electricus* (modified from Howes 1985), lateral view (the palatine is not represented). The nomenclature used here follows that used in the original illustrations.

together with the anatomical, paleontological and developmental data available in the literature on siluriforms and other groups of fishes, indicate that the “metapterygoid” of the catfish corresponds, very likely, to the entopterygoid+ectopterygoid of other teleosts, and that the small anterior bones present in most catfish (see, for example, Figs 2, 4A, 5, 7) are, in fact, sesamoid ossifications (see below). Further arguments are now presented in favour of this hypothesis.

Hyomandibula and metapterygoid

(1) The metapterygoid of teleosts results from the ossification of the posterodorsal part of the palatoquadrate, thus dorsally and somewhat posteriorly relative to the quadrate (see, for example, STARKS, 1926; DE BEER, 1937; BERTMAR, 1959; DAGET, 1964; HUNT VON HERBING et al., 1996; VERRAES, 1977). It remains in the same position in almost all adults (see, for example, STARKS, 1926; GREGORY, 1933; DE BEER, 1937; WEITZMAN, 1962; DAGET, 1964; OSSE, 1969; ROBERTS, 1969; DE LA HOZ, 1974; TAVERNE, 1974; VANDEWALLE, 1975; GIJSEN & CHARDON, 1976; MAGO-LECCIA, 1978; DE LA HOZ & ALDUNATE, 1994), with the exception of very few cases, such as some specialised clupeids such as *Engraulis encrasicolus* (Linnaeus, 1758) (RIDEWOOD, 1904: fig. 135A). In the course of postembryonic development the palatoquadrate fuses and associates with the hyosymplectic, so that the ossifying metapterygoid contacts the future hyomandibula from which it remains separated by a cartilaginous strip, a suture, or a combination of both (DAGET, 1964). So, given the position of the metapterygoid in these related groups and primitive teleosts, the true metapterygoid of catfish seems to correspond to the anterior part of the so-called “hyomandibula”. The fusion between these two bones may be a consequence of the fact that in catfish the pars quadrata and the hyosymplectic are fused (see, for example, KINDRED, 1919; ARRATIA, 1987; 1990; 1992; HOWES & TEUGELS, 1989; SURLÉMONT & VANDEWALLE, 1990; KOBAYAKAWA, 1992; VANDEWALLE et al., 1993; 1995a; 1997; ADRIAENS & VERRAES, 1998; etc.) from the first appearance of the chondrocranium cartilages.

The fact that this true metapterygoid is united by cartilage to the true entopterygoid+ectopterygoid (see below) could lead to the erroneous interpretation that both bones are enchondral and, thus, that the entopterygoid+ectopterygoid cannot be a dermal compound, as hypothesised above. In fact the cartilage is, probably, the remnant of the pterygoid process of the pars quadrata. Such a cartilage remains present in some adult ostariophysan fishes, such as, for example, *Chanos chanos* (Forsskal, 1775) (Gonorynchiformes), *Opsariichthys uncirostris* Temminck & Schlegel, 1846 (Cypriniformes), *Xenocharax spilurus* Günther, 1867 (Characiformes) and *Sternopygus macrurus* (Gymnotiformes) (see, for example, FINK & FINK, 1981) as well as in some other adult teleosts (see, for example, DAGET, 1964).

(2) In some juvenile *Diplomystes camposensis* Arratia, 1987 (ARRATIA, 1987) a broad, completely independent bone, which lies in the same position and presents the same configuration as the metapterygoid of other teleosts (see above), is present between the “hyomandibula”, “metapterygoid” and “quadrate” (Fig. 15A: compare, for example, with Fig. 14A). ARRATIA (1987) stated that “it does not seem to result from fracture of one of the above (“hyomandibula”, “metapterygoid” and “quadrate”) mentioned bones”. In adult specimens, this bone may be completely independent (ARRATIA, 1987: fig. 25C), but may be partially fused with the “hyomandibula” as well (ARRATIA, 1987). In this last case, only a partial suture is present between these two bones (Fig. 15B). Similar sutures also occur in some trichomycterids (see, for example, Fig. 15C) (ARRATIA & CHANG, 1975; ARRATIA et al., 1978; ARRATIA & MENUMARQUE, 1981; 1984; ARRATIA, 1987; 1990; 1992), plotosids (see, for example, Fig. 6), and malapterurids (see, for example, Fig. 15D) (HOWES, 1985). The fact that these partial or complete sutures appear in a position very similar to those between the hyomandibula and the metapterygoid of other teleosts (Fig. 15: compare with Fig. 14A) strongly supports the hypothesis that the so-called “hyomandibula” of catfish corresponds, in fact, to the hyomandibula plus metapterygoid of non-siluriform teleosts.

(3) *Chrysichthys nigrodigitatus*, like some other claroteids (see, for example, SKELTON et al., 1984: fig. 15A; MO 1991: fig. 54), some pimelodids (see, for example, ARRATIA, 1992: figs 35B, 36A) and some schilbeids (see, for example, TILAK, 1961: figs 7, 8) has a toothed “metapterygoid” (Fig. 4a). The teleost metapterygoid is enchondral and, thus, does not bear dermal toothplates (JOLLIE, 1986). ARRATIA (1992) suggested therefore that this toothed bone is “the metapterygoid fused with a dermal toothplate”. As a toothed “metapterygoid” is present in some species of three not closely related catfish families (see, for example, MO, 1991; DE PINNA, 1993), ARRATIA’s suggestion requires that the “metapterygoid”+dermal toothplate compound arose at least three times among catfishes, which seems unlikely since the development of such a compound is quite unusual in teleosts (TAVERNE, 1974). The explanation for the toothed “metapterygoid” of some siluriforms seems to be, thus, that this bone is not the true enchondral metapterygoid, but rather a dermal bone (toothed ectopterygoids and entopterygoids are widely distributed in teleosts: see TAVERNE, 1974).

(4) Some authors have also expressed opinions, convergent with our hypothesis:

STARKS (1926), in a study dedicated to the ethmoideal region of several fishes, suggested that in siluriforms “the metapterygoid, if represented at all, may be incorporated with the pterygoid, but may well be incorporated with the hyomandibula”.

HOEDEMAN (1960), in a work on the development of the skull of some callichthyids, suggested that in catfish the

“hyomandibula is ontogenetically fused to the metapterygoid” and that the so-called “metapterygoid” is a dermal bone.

In an extensive work concerning some problems related to catfish anatomy, HOWES (1983: fig. 24) hypothesised that the so-called “hyomandibula” of siluriforms could be the hyomandibula plus metapterygoid of other teleosts.

In his extensive work on the anatomy and phylogeny of catfish, MO (1991) pointed out that “comparing the hyomandibula of siluroids with those of non-siluroid fishes, it is very likely that a large portion of the metapterygoid has joined to the hyomandibula at its lower dorso-medial margin in siluroids”.

VANDEWALLE et al. (1993: fig. 2), in an embryological study concerning the suspensorium of *Clarias gariepinus* (Burchell, 1822) interpreted the so-called “metapterygoid” (Figs 8, 9) as dermal bone since “its ossification seems external to and independent of the processus pterygoquadrato” (VANDEWALLE et al., 1997). The dermal origin of the “metapterygoid” of this species was also suggested by POLL (1942).

Entopterygoid and ectopterygoid

It was pointed out above that in catfish the so-called “metapterygoid” is a dermal bone, and that the true metapterygoid is fused with the hyomandibula. We interpret this dermal bone as the entopterygoid+ectopterygoid of other teleosts, since:

(1) As mentioned, for example, by ALEXANDER (1965), HOWES (1983) and ARRATIA (1990; 1992), the “metapterygoid” in catfish occupies the position of the ectopterygoid and entopterygoid in other teleosts. In fact, this similarity is not restricted to the spatial position, but also extends to both the shape of the bone and its relations with other cranium components. The “metapterygoid” is bifurcated anteriorly in most generalised catfishes (see, for example, Figs 3, 4a, 11, 15a, b, 16b, and also TAVOLGA, 1962: Plates 9, 17; ALEXANDER, 1965: fig. 6; HOWES, 1983: figs 23, 24; SKELTON et al., 1984: fig. 4, 14; KOBAYAKAWA, 1989: figs 6, 27, 35; MO, 1991: figs 4, 44, 45, 48; ARRATIA, 1992: figs 16, 22, 25, 27, 33, 35, 36) but also in some specialised groups, as, for example, some amphiliids (Fig. 10) and callichthyids (ALEXANDER, 1965: fig. 15). This configuration is similar to that of the entopterygoid+ectopterygoid of some characiforms (see, for example, ROBERTS, 1969: fig. 18; GIJSEN & CHARDON, 1976: fig. 5; FINK & FINK, 1981: fig. 10A; MIQUELARENA & ARÁMBURU, 1983: fig. 6; ARRATIA, 1992: fig. 10A), cypriniforms (see, for example, VANDEWALLE, 1975: figs 2, 12; TAVERNE & DE VOS, 1997: fig. 6), gonorynchiforms (see, for example, ARRATIA, 1992: fig. 4d) and some “fossil Ostariophysi” – e.g. *Lusitanichthys characiformis* Gayet, 1981 (GAYET, 1985: figs 17, 20) and *Ramallichthys orientalis* Gayet, 1982 (GAYET, 1982: fig. 10). Moreover, the anteromedial and the anterolateral

extremities of the “metapterygoid” of catfish have the same anatomical relations as, respectively, the entopterygoid and the ectopterygoid of other teleosts (see, for example, DAGET, 1964): the anteromedial margin is linked by a ligament to the neurocranium and the anterolateral tip is situated ventral to the posterior end of the palatine (see, for example, Figs 4A, 10). Therefore, the anteromedial and anterolateral margins of the “metapterygoid” of catfish seem to correspond, respectively, to the anterior tips of the entopterygoid and ectopterygoid of other teleosts, and, thus, this bone seem to be, in fact, an ento-ectopterygoid compound.

(2) *Chrysichthys nigrodigitatus*, like many other catfishes (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; ALEXANDER, 1965; GOSLINE, 1975; ARRATIA, 1987; 1992; etc.) possesses an additional tooth-plate (some catfish have more than one) between the anterior portion of the so-called “metapterygoid” and the ethmoideal region (Fig. 4A). The identity of these tooth plates has been a subject of controversy. Some authors (JAYARAM 1966; 1968; 1971; SKELTON, 1981; SKELTON et al., 1984; ARRATIA, 1987; 1992; etc.) suggest that such tooth plates are associated with the palatine. Others (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; GOSLINE, 1975; FINK & FINK, 1981) interpret them as structures associated with the vomer and to the anterolateral margin of the “metapterygoid”. In *C. nigrodigitatus* the tooth plate is embedded in a long ligament between the premaxilla, the vomer, and the toothed anterolateral tip of the “metapterygoid” (Fig. 4A). The similarity between this configuration and that of some characiforms, as, for example, *Hoplias*, is remarkable (Fig. 4A, B). In fact, *Hoplias* (ROBERTS, 1969) has a tooth-plate associated to the toothed anterior portion of the ectopterygoid and to the premaxillary (Fig. 4B). This noticeable resemblance to the noted catfish condition, associated with the fact that such tooth-plates are present in a large number of characiforms (SAGEMEHL, 1885; STARKS, 1926; WEITZMAN, 1962, 1964; ROBERTS, 1969; FINK & FINK 1981; etc.), in some species of archaic or generalised catfish families – e.g. Diplomystidae, Ariidae, Pimelodidae, Claroteidae, Austroglanidae, Cranoglanididae, Bagridae and Schilbeidae – (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; GOSLINE, 1975; JAYARAM, 1966; FINK & FINK, 1981; SKELTON, 1981; ARRATIA, 1987; 1992; MO, 1991; etc.), and in *Hypsidoris farfonensis* Lundberg and Case, 1970, a fossil catfish from the Eocene (GRANDE, 1987), supports our suggestion that the anterolateral portion of the “metapterygoid” of catfish is homologous to the anterior tip of the ectopterygoid of other teleosts.

(3) HOWES (1983) reported that in *Pinirampus pirinampu* (Spix & Agassiz, 1829) and *Hypophthalmus edentatus* Spix & Agassiz, 1829, two South-American catfish, the usually called “metapterygoid” has “a sharply demarcated ventral portion that articulates with the (so-called) quadrate, whilst the dorsal portion articulates with the (so-called) hyomandibula process” (Fig. 16B). This observa-

tion led him to hypothesise that the “metapterygoid” is, in fact, the result of a fusion – which, in the particular case of *P. pirinampu* is incomplete (see Fig. 16B) – between the ectopterygoid and entopterygoid of other teleosts.

(4) GRANDE (1987), in his reconstruction of *Hypsidoris farsonensis*, a fossil catfish from the Eocene of the Green River formation, reported an “entopterygoid” sutured with a “metapterygoid” (Fig. 16a). However, as ARRATIA (1992) argued, this “condition is unlikely, when you compare it with other primitive siluroids” (see, for example, *Diplomystes chilensis*; Fig. 2A). ARRATIA (1992) proposed two alternative hypotheses: 1) that the two bones are not really sutured; 2) that GRANDE’s “entopterygoid” is, in fact, a fragment of the so-called “metapterygoid”. However, both of her hypotheses are questionable. First, even if we allow that GRANDE misinterpreted the presence of a suture between the two bones (which is not the case: see below), it seems unlikely that his “entopterygoid” is homologous to the true entopterygoid, since it does not have the same position and anatomical relations as the latter ossification (Fig. 16A). In reality, this “entopterygoid” has the typical features of the ectopterygoid of other teleosts (the spatial relation between its anterior portion and the posterior tip of the palatine, for example) (Fig. 16A). Moreover, it clearly corresponds to the antero-lateral portion of the “metapterygoid” of other catfishes (compare, for example, Fig. 16A to Figs 3, 4A, 10, 15A). With respect to ARRATIA’s second hypothesis, a post-mortem, incidental fracture of the “metapterygoid”, resulting in the separation of two parts that present, respectively, the same spatial position and relations as the ectopterygoid and entopterygoid of other teleosts (see above), seems very improbable, especially since a similar fracture is also present in some living catfishes (see above). Moreover, a quite similar, complete fracture is equally present in *Astephus antiquus* (Leidy, 1873), a fossil ictalurid catfish that also occurs in the Eocene of the Green River formation (see GRANDE & LUNDBERG, 1988: Fig. 10). We thus agree with GRANDE’s (1987) suggestion that the two parts corresponding to his “metapterygoid” and “entopterygoid” (see Fig. 16A) are, in fact, separated by a suture, and we interpret them as the true entopterygoid and the true ectopterygoid, respectively.

(5) Some opinions, not mentioned above, are convergent with our hypothesis:

After studying the development of the pterygoid bones of some catfishes, HOWES & TEUGELS (1989) pointed out that the true metapterygoid “persists in adult siluroids only as a densely ossified area of the palatoquadrate arch and not as a laminar ossification” and that the so-called “metapterygoid” is composed in great part by the entopterygoid and ectopterygoid of other teleosts.

Sesamoid bones

(1) In *Diplomystes chilensis*, the three anterior small bones of the suspensorium are clearly sesamoid ossifications related to ligaments and, in no way, vestigial bones (Fig. 2). In fact, if we compare them to those of other studied catfishes, it is clear that the larger anterior bones present in some more specialised siluriforms are the result of progressive ossification of these ligaments. The small “entopterygoids” of the generalised *Chrysichthys nigrodigitatus* (Fig. 4A) and *Bagrus docmak* (Fig. 7A) and the relatively wide “entopterygoids” of the specialised *Amphilius brevis* (Fig. 10), *Clarias gariepinus* (Fig. 9) and *Phractus brevicauda* (Fig. 13), for example, are clearly the result of progressive ossification of the “metapterygoid”-neurocranium ligament, which, in *Diplomystes chilensis*, is only slightly ossified (Fig. 2A: “entopterygoid”). This hypothesis is strongly supported by developmental data: a) in a detailed embryological study ADRIAENS & VERRAES (1998) show that the so-called “entopterygoid” of one of the above-mentioned species (e.g. *Clarias gariepinus*) is, in reality, a sesamoid ossification of the ligament between the “metapterygoid” and the vomer; b) after studying the development of some silurids, KOBAYAKAWA (1992) stated that the “entopterygoid” “has ligaments on both its anterior and posterior sides from the onset of its ossification (...), it appears as a small, rod-shaped bone connected by ligaments with the (so-called) metapterygoid posteriorly and the ventral surface of the lateral ethmoid anteriorly”; and c) according to ARRATIA (1990) “the “entopterygoid” in *Nematogenys* arises as an ossification of the ligament extending between the (so-called) metapterygoid and lateral ethmoid, and, late in ontogeny, with the vomer”.

(2) The “ectopterygoid” and “entopterygoid” of catfish begin to develop anteriorly to the pterygoid process of the pars quadrata (see, for example, KOBAYAKAWA, 1992: figs 9, 10; VANDEWALLE et al., 1993: fig. 2; 1995a: figs 9B, 10B; 1997: figs 7B, 8B), while in most teleosts the ectopterygoid and the entopterygoid develop on the processus pterygoideus (see, for example, DE BEER, 1937; DAGET, 1964; BERTMAR, 1959). There is, thus, a difference between the place of origin of the anterior small bones in catfishes and that of the ectopterygoid and entopterygoid in other teleosts.

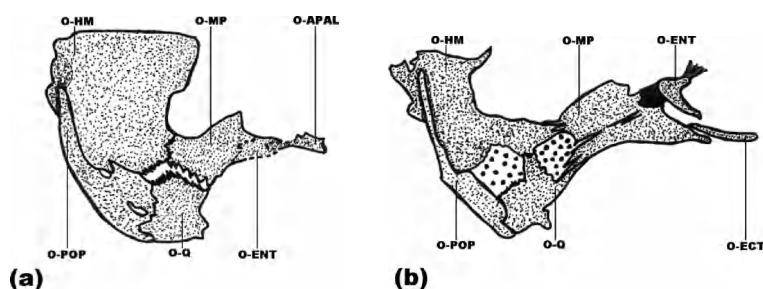


Fig. 16. – Lateral view of the suspensorium of: (A) *Hypsidoris farsonensis*, fossil catfish from the Eocene (modified from GRANDE, 1987). (B) *Pinirampus pirinampu* (modified from HOWES, 1983) (the palatine is not represented). The nomenclature used here follows that used in the original illustrations.

(3) The so-called “ectopterygoid” and “entopterygoid” of the examined catfish (see, e.g., Figs 2, 4A, 5, 7, 9, 13), as well as those of other siluriforms (see, for example, the descriptions of TILAK, 1963a: figs 6, 15, 21; 1965: figs 13, 14; GAUBA, 1969: fig. 16; HOWES, 1983: figs 23, 24; SRINIVASA RAO & LAKSHMI, 1984: fig. 9B; HOWES & TEUGELS, 1989: fig. 8; ARRATIA, 1990: fig. 12; 1992: figs 25B, 28A, D, 29, 33, 34; MO, 1991: figs 14, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49; KOBAYAKAWA, 1992: fig. 4; DIOGO et al., 1999: figs 3, 4; 2000a: fig. 3) are always associated with ligaments.

(4) HOWES & TEUGELS (1989) clearly show that the two anterior bones of the suspensorium of a 72 mm *Pimelodus blochii* Cuvier & Valenciennes, 1840 result from ossifications in the ligament joining the palatine to the lateral ethmoid, which is already conspicuous in a 40 mm specimen. According to these authors, the “entopterygoid” and “ectopterygoid” of catfish are sesamoid bones and/or fragments of the “metapterygoid”.

(5) If the small bones present in the anterior portion of the suspensorium of some catfish are interpreted as reduced or vestigial pterygoids (entopterygoid and/or ectopterygoid), it is expected that they would generally be larger in primitive families than in specialised ones. However, in such primitive catfishes such as diplomystids (see, for example, Fig. 2) and the fossil *Hypsidoris farsonensis* (see, for example, Fig. 16A) these bones are very small or absent, whereas they are not as reduced in generalised siluriforms such as bagrids (see, for example, Fig. 7 and MO, 1991: figs 14, 40, 41, 42, 43, 46, 47; DIOGO et al., 1999: figs 3, 4), claroteids (see, for example, Fig. 4A, 5 and MO: figs 44, 45, 48), pimelodids (see, for example, Fig. 16A and ALEXANDER, 1965: fig. 6; HOWES, 1983: fig. 24; ARRATIA, 1992: fig. 35A, 36), schilbeids (see, for example, ALEXANDER, 1965: fig. 13; DE VOS, 1995: fig. 91), silurids (see, for example, KOBAYAKAWA, 1989: figs 14, 27, 35; 1992: Fig. 4), cranoglanidids (see descriptions of MO, 1991), malapterurids (see, for example, HOWES, 1985: fig. 13), austroglanids (see descriptions of MO, 1991) and ariids (see, for example, Fig. 11 and TILAK, 1965: fig. 14; SRINIVASA RAO & LAKSHMI, 1984: fig. 9). In certain more specialised catfishes, such as clariids (see, for example, Fig. 9 and DAVID, 1936: fig. 4C; TILAK, 1963b: fig. 4), amblycipitids (see, for example, MO, 1991: 28), amphiliids (see, for example, Fig. 10 and HARRY, 1953: fig. 10), doumeids (see, for example, Figs 12, 13 and DIOGO et al., 2000a: fig. 1, 3) and sisorids (see, for example, TILAK, 1963a: figs 6, 21; GAUBA, 1969: fig. 16) these bones are much larger, being sometimes as broad (or even broader) as the so-called “metapterygoid”. It is unlikely that, basally among catfishes, the “ectopterygoid” and “entopterygoid” had become reduced or even lost, and, subsequently, re-acquired a large size in some more derived catfish. It is rather more probable that these bones are, in fact, sesamoid ossifications that had begun to develop in some primitive catfishes, and became progressively larger in some siluriform lineages. These ossi-

fications are, probably, functionally related to the decoupling of the palatine from the rest of the suspensorium, as well as to the specialisation of the palatine-maxillary system. In fact, the shape of the sesamoid bones and associated ligaments in the suspensorium of siluriforms seems to be closely associated with the different types of palatine-maxillary system of these fishes. Thus, for example, in siluriforms with a “rocking” palatine-maxillary system (where the abduction of the maxillary is associated with a medial displacement of the back of the palatine: see GOSLINE, 1975) these structures are disposed so as to allow a pronounced medial movement of the rear end of the palatine (see, for example, Fig. 5 A→B), while in catfishes with a “sliding” palatine-maxillary system (where the abduction of the maxillary is associated with a posterior displacement of the palatine: see GOSLINE, 1975), in contrast, their configuration allows a large posterior displacement of this bone (see, for example, Fig. 7 A→B).

(6) Some opinions, not mentioned above, convergent with our hypothesis:

McMURRICH (1884) interpreted the small bone “lying behind and within the posterior extremity of the palatine” in *Ictalurus catus* Linnaeus, 1758 as a sesamoid bone, which he called “bone number 4”.

HOWES (1983, 1985) pointed out that the so-called “entopterygoid” and “ectopterygoid” of catfish are, probably, sesamoid bones.

ARRATIA (1987) stated: “... the position of this bone (“ectopterygoid”) in diplomystids is not homologous with that of the ectopterygoid in other teleosts. This small pterygoid appears as an additional element of the series and it could represent a neomorphic feature”. Concerning the other small bone present in the anterior portion of the suspensorium of some diplomystids, which corresponds to the “additional pterygoid” we figure in *Diplomystes chilensis* (Fig. 2B), she commented: “... it cannot be interpreted as belonging to the pterygoid series. I interpret it as a neomorphic feature”.

According to ARRATIA (1992) the “pterygoid bones in most catfish are highly specialised sesamoid elements, connected by ligaments to cranial bones or other bones of the suspensorium (...) or additional bones whose function is unclear”.

Quadrato and symplectic

(1) A ‘typical’ teleostean quadrato has a posterior notch in which the symplectic inserts on the lateral side (see, for example, TAVERNE, 1974: fig. 4). The inferior arm of the notch, which probably represents the quadratojugal (DEVILLERS, 1958), is lacking in some teleosts, as, for example, some clupeids (see, for example, RIDWOOD, 1904: figs 124, 132). As for the symplectic, it remains cartilaginous in some mormyriiforms (TAVERNE, 1974) and clupeiforms (RIDWOOD, 1904). However, both the quadrato and the symplectic are present and well ossified

in the Gonorynchiformes (CHARDON & DE LA HOZ, 1974: figs 2, 3, 4, 5, 6; MAGO-LECCIA, 1978: fig. 12; FINK & FINK, 1981: fig. 12; ARRATIA, 1992: fig. 12A, B, D), Cypriniformes (see, for example, VANDEWALLE, 1975: figs 1, 2, 12; ARRATIA, 1992: fig. 8B; TAVERNE & DE VOS, 1997: fig. 6), Characiformes (see, for example, GIJSEN & CHARDON, 1976: fig. 5; ARRATIA, 1992: fig. 10A), Gymnotiformes (see, for example, fig. 14A and ARRATIA, 1992: fig. 12A, B, D) and “fossil Ostariophysi” (see, for example, GAYET, 1982: fig. 10; 1985: figs 2, 19, 20). Catfish have neither a notch nor a distinct symplectic – HOWES (1985) described a “symplectic” in the African catfish *Malapterurus electricus* (Gmelin, 1879) (see Fig. 15D), but this statement was questioned by ARRATIA (1992) – and it is thus plausible that the symplectic is incorporated into the quadrate, filling the notch. In fact, it is difficult to explain the disappearance of the quadrate notch and also the similar shape of the “quadrate” of catfishes and the quadrate+symplectic of other teleosts (see, for example, Fig. 14) if we accept that the “disappearance” of the symplectic in catfish is simply a function of the non-ossification of this element (see below). As in the case of the fusion between the hyomandibula and the metapterygoid (see above), the fusion between the quadrate and symplectic is probably related to the fact that in catfish the pars quadrata and the hyosymplectic are fused from the first appearance of the chondrocranium cartilage.

(2) Most authors (McMURRICH, 1884; HARRY, 1953; TILAK, 1961; 1963ab; 1964; 1965; SKELTON, 1981; SKELTON et al., 1984; HOWES, 1983; MO, 1991; ARRATIA, 1992; ADRIAENS & VERRAES, 1998; etc.) consider that an ossified symplectic is absent in catfish, and interpret the cartilage between the “hyomandibula”, preopercular and “quadrate” (see, for example, Figs 3, 10, 14B) as the remnant of the symplectic cartilage present early in ontogeny, and, thus, as the homologue of the symplectic of other teleosts. However, this cartilage differs from the typical symplectic by its position. Moreover, both the cartilage and the symplectic (which is always situated anteriorly to the cartilage) are present in gymnotiforms (see, for example, Fig. 14A and CHARDON & DE LA HOZ, 1974: figs 2, 3, 4, 5, 6; MAGO-LECCIA, 1978: fig. 12; FINK & FINK, 1981: fig. 12; ARRATIA, 1992: fig. 12a, b, d), characiforms (see, for example, WEITZMAN, 1964: fig. 7; FINK & FINK, 1981: fig. 10), cypriniforms (see, for example, VANDEWALLE, 1975: figs 1, 2; FINK & FINK, 1981: fig. 9; ARRATIA, 1992: fig. 4A), gonorynchiforms (see, for example, FINK & FINK, 1981: fig. 8; ARRATIA, 1990: fig. 2; 1992: fig. 4D) as well as in a large number of other teleosts (see, for example, RIDGEWOOD, 1904: figs 123, 132; CHARDON & VANDEWALLE, 1971: fig. 2; VANDEWALLE, 1971: figs 6, 11; VANDEWALLE et al., 1995b: fig. 2), which implies that these structures can not be, in any way, homologous (compare Fig. 14A to Fig. 14B) [if two structures A and B are present at the same time in a certain species X, it

cannot be considered that these two structures are homologous within two different species Y and Z: see, for example, GOULD, 1989; HALL, 1994; BEAUMONT, 1998).

General conclusions

The suspensorium of catfish is divided into the separate palatine and a posterior portion composed of the hyomandibulo-metapterygoid, the quadrato-symplectic and the ento-ectopterygoid (see Fig. 17). The smaller anterior bones are sesamoid ossifications. Despite the great diversity in the size and shape of these sesamoid bones (see above), three major types can be distinguished (toothed plates are not considered here) (see Fig. 17): 1) *sesamoid bone 1 of the suspensorium*, which corresponds to the so-called “entopterygoid”, being associated, by means of ligaments, to the neurocranium (usually the vomer, lateral ethmoid and/or orbitosphenoid) anteriorly and to the ento-ectopterygoid posteriorly; 2) *sesamoid bone 2 of the suspensorium*, which corresponds to the so-called “ectopterygoid”, being usually situated ventral to the palatine and, in most cases, linked to it by a short ligament; 3) *sesamoid bone 3 of the suspensorium*, which corresponds to the “additional pterygoid” figured in *Diplomystes chilensis* (Fig. 2B). It is present only in some diplomystids and is situated between the sesamoid bones 1 and 2, being imbedded in the ligament between the ento-ectopterygoid and the palatine.

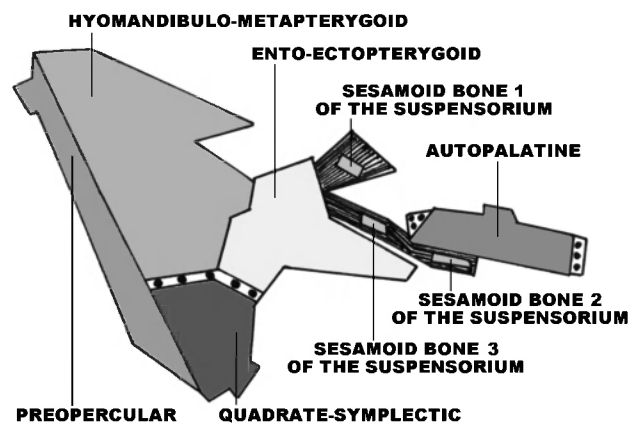


Fig. 17. – Scheme of the suspensorium of *Diplomystes chilensis* illustrating our interpretation of catfish suspensorial bones.

That hypothesis results from data from a variety of sources including comparative morphology, functional morphology, ontogeny, phylogeny and palaeontology, and results in a renewed nomenclature for the bones of the catfish suspensorium. It should be remembered that it was the misinterpretation of the catfish suspensorium that caused (and still causes) great confusion around this subject. It is hoped that the present work will contribute to an emergence from such confusion and facilitate future comparative and phylogenetic studies.

- DE PINNA, M.C.C. (1998). Phylogenetic relationships of neotropical Siluriformes: Historical overview and synthesis of hypotheses. In: MALABARNA L.R., R.E. REIS, R.P. VARI, Z.M. LUCENA & C.A.S. LUCENA (eds), *Phylogeny and classification of neotropical fishes*, Edipucrs, Porto Alegre: 279-330.
- DEVILLERS, C. (1958). Le crâne des poissons. In: GRASSÉ, P. (ed.), *Agnathes et Poissons, anatomie, éthologie, systématique*, Masson et Cie, Paris: 551-687.
- DE VOS, L. (1995). A systematic revision of the African Schilbeidae (Teleostei: Siluriformes). *Ann. Mus. R. Afr. Centr.*, 271: 1-414.
- DIOGO, R. & M. CHARDON (2000a). Anatomie et fonction des structures céphaliques associées à la prise de nourriture chez le genre *Chrysichthys* (Teleostei: Siluriformes). *Belg. J. Zool.*, 130: 21-27.
- DIOGO, R. & M. CHARDON (2000b). Homologies among different adductor mandibulae sections of teleostean fishes, with special regard to catfishes (Teleostei: Siluriformes). *J. Morphol.*, 243: 193-208.
- DIOGO, R. & M. CHARDON (2000c). The structures associated with catfish (Teleostei: Siluriformes) mandibular barbels: origin, anatomy, function, taxonomic distribution, nomenclature and synonymy. *Neth. J. Zool.*, 50: 455-478.
- DIOGO, R. & M. CHARDON (in press). The adaptive transformation of the palatine-maxillary system in catfish: Toward freedom and increased mobility for a major sensory device, the maxillary barbel. In: KAPOOR, B.G. (ed.), *Sensory Biology of Jawed Fishes – New Insights*, Oxford & IBH Publishing and Science Publishers, New Delhi and New Hampshire.
- DIOGO, R., P. VANDEWALLE & M. CHARDON (1999). Morphological description of the cephalic region of *Bagrus docmac*, with a reflection on Bagridae (Teleostei: Siluriformes) autapomorphies. *Neth. J. Zool.*, 49: 207-232.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2000a). On the anatomy and function of the cephalic structures in *Phractus* (Siluriformes: Amphiliidae), with comments on some striking homoplasies occurring between the Doumeinae and some loricaroid catfishes. *Belg. J. Zool.*, 130: 117-130.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2000b). The origin and transformation of the palatine-maxillary system of catfish (Teleostei: Siluriformes): an example of macroevolution. *Neth. J. Zool.*, 50: 373-388.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (in press). On the osteology and myology of catfish pectoral girdle, with a reflection on catfish (Teleostei: Siluriformes) plesiomorphies. *J. Morphol.*
- EIGENMANN, C. (1890). The evolution of the catfish. *Zoe*, 11: 10-15.
- FINK, S.V. & W.L. FINK (1981). Interrelationships of ostariophysan fishes (Teleostei). *Zool. J. Linnean Soc.*, 72: 297-353.
- FINK, S.V. & W.L. FINK (1996). Interrelationships of ostariophysan fishes (Teleostei). In: STIASNY, M.L.J., PARENTI, L.R. & JOHNSON, G.D. (eds), *Interrelationships of Fishes*, Academic Press, New York: 209-249.
- GAUBA, R.K. (1969). The head skeleton of *Glyptosternum reticulatum* McLelland & Griffith. *Monitore Zool. Ital.*, 3: 1-17.
- GAYET, M. (1982). Considération sur la Phylogénie et la Paléobiogéographie des Ostariophysaires. *Geobios*, 6: 39-52.
- GAYET, M. (1985). Contribution à l'Etude Anatomique et Systématique de l'Ichthyofaune Cénomaniennne du Portugal. *Comun. Serv. Geol. Portugal*, 71: 91-118.
- GAYET, M., F.J. MEUNIER & F. KIRSCHBAUM (1994). *Ellisella kirschbaumi* Gayet & Meunier, 1991, gymnotiforme fossile de Bolivie et ses relations phylogénétiques au sein des formes actuelles. *Cybium*, 18: 273-306.
- GIJSEN, L. & M. CHARDON (1976). Muscles et ligaments céphaliques, splanchnocrâne et quelques possibilités de mouvements dans la tête d'*Hoplerythrinus unitaenatus* (Spix) (Teleostei, Ostariophysi, Characoidei). *Ann. Sc. Nat. Zool. Paris*, 18: 251-274.
- GOSLINE, W.A. (1975). The palatine-maxillary mechanism in catfishes with comments on the evolution and zoogeography of modern siluroids. *Occ. Pap. Calif. Acad. Sci.*, 120: 1-31.
- GOULD, S. J. (1989). The heart of terminology. *Nat. Hist.*, 97: 24-31.
- GRANDE, L. (1987). Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes) with a reassessment of its phylogenetic relationships. *J. Vert. Paleont.*, 7: 24-54.
- GRANDE, L. & J.G. LUNDBERG (1988). Revision and redescription of the genus *Astephus* (Siluriformes: Ictaluridae) with a discussion of its phylogenetic relationships. *J. Vert. Paleont.*, 8: 139-171.
- GREGORY, W.K. (1933). Fish skulls. A study of the evolution of natural mechanisms. *Trans. Am. Philos. Soc.*, 23: 75-481.
- HALL, B.K. (1994). *Homology, the Hierarchical Basis of Comparative Biology*. Academic, New York.
- HARRY, R.R. (1953). A contribution to the classification of the family Amphiliidae with descriptions of collections from Cameroon. *Rev. Zool. Bot. Afr.*, 47: 178-232.
- HE, S. (1998). *Phylogénie et Biogéographie des Sisoridae et des Amphiliidae (Pisces: Siluriformes): deux familles de Poissons-Chats torrenticoles*. PhD. Thesis, Muséum National d'Histoire Naturelle (Paris).
- HE, S., M. GAYET & F.J. MEUNIER (1999). Phylogeny on the Amphiliidae (Teleostei: Siluriformes). *Ann. Sci. Nat.*, 20: 117-146.
- HOEDEMAN, J.J. (1960). Studies on callichthyid fishes: 4. Development of the skull in *Callichthys* and *Hoplosternum* (1) (Pisces: Siluriformes). *Bull. Aquat. Biol.*, 1: 73-84.
- HOWES, G.J. (1983). Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei, Siluroidei). *Bull. Br. Mus. Nat. Hist. (Zool.)*, 45: 1-39.
- HOWES, G.J. (1985). The phylogenetic relationships of the electric family Malapteruridae (Teleostei, Siluroidei). *J. Nat. Hist.* 19: 37-67.
- HOWES, G.J. & G.G. TEUGELS (1989). Observations and homology of the pterygoid bones in *Corydoras paleatus* and some other catfishes. *J. Zool. (Lond.)*, 219: 441-456.
- HUNT VON HERBING, I., T. MIYALE, B.K. HALL & R.G. BOUTILIER (1996). Ontogeny of feeding and respiration in larval Atlantic cod *Gadus morhua* (Teleostei, Gadiformes): I. Morphology. *J. Morphol.*, 227: 15-35.
- JAYARAM, K.C. (1966). Contributions to study of the fishes of family Bagridae. 2. A systematic account of the African genera with a new classification of the family. *Bull. Inst. Fond. Afr. Noire*, 28: 1064-1139.
- JAYARAM, K.C. (1968). Contributions to study of the bagrid fishes (Siluroidea: Bagridae). 3. A systematic account of the

- Japanese, Chinese, Malayan and Indonesian genera. *Treubia. Mus. Zool. Bogoriense*, 27: 287-386.
- JAYARAM, K.C. (1971). Contributions to study of the bagrid fishes. 6. The skeleton of *Rita gogra* (Sykes). *J. Zool. Soc. India*, 22: 117-145.
- JOLLIE, M. (1986). A primer of bone names for the understanding of the actinopterygian head and pectoral girdle skeletons. *Canadian J. Zool.*, 64: 365-379.
- KINDRED, J. (1919). The skull of *Ameiurus*. *Illinois Biol. Mono.*, 5: 1-120.
- KOBAYAKAWA, M. (1989). Systematic Revision of the Catfish Genus *Silurus*, With Description of a New Species from Thailand and Burma. *Japan. J. Ichthyol.*, 36: 155-186.
- KOBAYAKAWA, M. (1992). Comparative Morphology and Development of Bony Elements in the Head Region in Three Species of Japanese Catfishes (*Silurus*: Siluridae; Siluriformes). *Japan. J. Ichthyol.*, 39: 25-36.
- LUNDBERG, J.G. & J.N. BASKIN (1969). The caudal skeleton of the catfishes, order Siluriformes. *Am. Mus. Novitates*, 2398: 1-49.
- MAGO-LECCIA, F. (1978). Los peces de la familia Sternopygidae de Venezuela. *Acta Sci. Venez.* 29, Suppl. 1: 1-89.
- McMURRICH, J.P. (1884). On the osteology of *Amiurus catus* (L.) Gill. *Zool. Anz.*, 168: 296-299.
- MIQUELARENA, A.M. & R.H. ARÁMBURU (1983). Osteología y lepidología de *Gymnocharacinus bergi* (Pisces Characidae). *Limnobiós*, 2: 491-512.
- MO, T. (1991). Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zoologicae*, 17: 1-216.
- NAWAR, G. (1955). On the anatomy of *Clarias lazera*: I. Osteology. *J. Morphol.*, 94: 551-586.
- NG, H.H. & M. KOTTELAT (1999). *Hyalobagrus*, a new genus of miniature bagrid catfish from Southeast Asia. *Ichthyol. Explor. Freshwaters*, 9: 335-346.
- OSSE, J.W.M. (1969). Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.*, 19: 289-392.
- POLL, M. (1942). Note sur l'ostéologie de *Dolichallabes microphthalmus* Poll et remarques sur l'évolution des Clariidae. *Ann. Soc. R. Zool. Belg.*, 3-4: 222-235.
- REGAN, C.T. (1911). The classification of the teleostean fishes of the order Ostariophysi – 2. Siluroidea. *Ann. & Mag. N. Hist.*, 8: 37-577.
- REIS, R.E. (1998). Anatomy and phylogenetic analysis of the neotropical callichthyid catfishes (Ostariophysi, Siluriformes). *Zool. J. Linnean. Soc.*, 124: 105-168.
- RIDEWOOD, W.G. (1904). On the cranial osteology of the Clupeoid fishes. *Proc. Zool. Soc. Lond.*, 29: 448-493.
- ROBERTS, T.R. (1969). Osteology and relationships of characoid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenolucius* and *Acestrorhynchus*. *Proc. Cal. Acad. Sci.*, 36: 91-500.
- SAGEMEHL, M. (1885). Beiträge zur vergleichenden Anatomie der Fische, III. Das Cranium der Characiniden nebst allgemeine Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomen-familien. *Morphol. Jahrb.*, 10: 1-119.
- SCHAEFER, S.A. (1987). Osteology of *Hypostomus plecostomus* (Linnaeus), with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). *Contrib. Sci.*, 394: 1-31.
- SCHAEFER, S.A. (1990). Anatomy and relationships of the scoloplacid catfishes. *Proc. Acad. Nat. Sci. (Phil.)*, 142: 167-210.
- SKELTON, P.H. (1981). The description and osteology of a new species of *Gephyroglanis* (Siluriformes, Bagridae) from the Olifants River, south west Cape, south Africa. *Ann. Cape Prov. Mus. (Nat. Hist.)*, 13: 217-250.
- SKELTON, P.H., L. RISCH & L. DE VOS (1984). On the generic identity of the *Gephyroglanis* Catfishes from Southern Africa (Pisces, Siluroidei, Bagridae). *Rev. Zool. Afr.*, 983: 337-361.
- SRINIVASA RAO, K. & K. LAKSHMI (1984). Head skeleton of the marine catfish *Arius tenuispinis* Day (Osteichthyes: Siluriformes, Ariidae). *J. Morphol.*, 118: 221-238.
- STARKS, E.C. (1926). Bones of the ethmoid region of the fish skull. *Stanford Univ. Publications*, 4: 139-338.
- SURLEMONT, C. & P. VANDEWALLE (1990). Développement postembryonnaire du squelette et de la musculature de la tête de *Clarias gariepinus* (Pisces, Siluriformes) depuis l'éclosion jusqu'à 6.8 mm. *Canadian J. Zool.*, 69: 1094-1103.
- TAVERNE, L. (1974). Ostéologie d'*Elops* Linné, C., 1766 (Pisces, Elopiformes) et son intérêt phylogénétique. *Acad. R. Belg.*, 41: 1-96.
- TAVERNE, L. & L. DE VOS (1997). Ostéologie et morphologie d'un bariliné nouveau du bassin de la Malagarasi (système du Lac Tanganyika): *Opsaridium splendens* sp.n. (Teleostei, Cyprinidae). *J. Afr. Zool.*, 111: 281-300.
- TAVOLGA, W.N. (1962). Mechanisms of sound production in the ariid catfishes *Galeichthys* and *Bagre*. *Bull. Am. Mus. Nat. Hist.*, 124: 5-30.
- TAYLOR, W.R. & G.C. VAN DYKE (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybiurn*, 9: 107-119.
- TILAK, R. (1961). The osteocranium and the Weberian apparatus of *Eutropiichthys vacha* (Ham.) and *Eutropiichthys murus* (Ham.): a study of inter-relationship. *Zool. Anz.*, 167: 413-430.
- TILAK, R. (1963a). The osteocranium and the Weberian apparatus of the fishes of the family Sisoridae (Siluroidea): A study in adaptations and taxonomy. *Z. Wiss. Zool.*, 168: 281-320.
- TILAK, R. (1963b). Relationships between the osteocranium and the Weberian apparatus in two Indian catfishes of the genus *Clarias* (Clariidae). *Copeia*, 1963: 623-629.
- TILAK, R. (1964). The osteocranium and the Weberian apparatus of the family Schilbeidae. *Proc. Zool. Soc. Lond.*, 143: 1-36.
- TILAK, R. (1965). The comparative morphology of the osteocranium and the Weberian apparatus of Tachysuridae (Pisces: Siluroidei). *J. Zool. (Lond.)*, 146: 150-174.
- VANDEWALLE, P. (1971). Comparaison ostéologique et myologique de cinq cichlidae Africains et Sud-Américains. *Ann. Soc. R. Zool. Belg.*, 4: 259-292.
- VANDEWALLE, P. (1975). Contribution à l'étude anatomique et fonctionnelle de la région céphalique de *Gobio gobio* (Pisces, Cyprinidae). 3. Les os, les muscles et les ligaments. *Forma et Functio*, 8: 331-360.
- VANDEWALLE, P. (1977). Particularités anatomiques de la tête de deux Poissons Cyprinidés *Barbus barbus* (L.) et *Leuciscus leuciscus* (L.). *Bull. Acad. R. Belg.*, 5: 469-479.

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REFERENCES

- ADRIAENS, D. & W. VERRAES (1998). Ontogeny of the Osteocranium in the African Catfish, *Clarias gariepinus* Burchell (1982) (Siluriformes: Clariidae): ossification Sequence as a Response to Functional Demands. *J. Morphol.*, 235: 183-237.
- ALBERT, J.S. & W.L. FINK (1996). *Sternopygus xingu*, a new species of electric fish from Brazil (Teleostei: Gymnotoidei), with comments on the phylogenetic position of *Sternopygus*. *Copeia*, 1996: 85-102.
- ALBERT, J.S. & R. CAMPOZ-DA-PAZ (1998). Phylogenetic systematics of gymnotiformes with diagnoses of 58 clades: a review of available data. In: MALABARNA L.R., R.E. REIS, R.P. VARI, Z.M. LUCENA & C.A.S. LUCENA (eds), *Phylogeny and classification of neotropical fishes*, Edipucrs, Porto Alegre: 410-446.
- ALEXANDER, R.M. (1965). Structure and function in catfish. *J. Zool. (Lond.)*, 148: 88-152.
- ARRATIA, G. (1987). Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonn. Zool. Monogr.*, 24: 1-120.
- ARRATIA, G. (1990). Development and diversity of the suspensorium of trichomycterids and comparison with loricarioids (Teleostei: Siluriformes). *J. Morphol.*, 205: 193-218.
- ARRATIA, G. (1992). Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonn. Zool. Monogr.*, 32: 1-148.
- ARRATIA, G. & A. CHANG (1975). Osteología de *Pygidium areolatum* Valenciennes, 1848 (peces Siluriformes, Trichomycteridae). *Publ. Ocasional. Mus. Nac. Hist. Nat. Chile*, 18: 1-12.
- ARRATIA, G., A. CHANG, S. MENUMARQUE & G. ROJAS (1978). About *Bullockia* n. gen. and *Trichomycterus mendozensis* n.sp: revision of the family Trichomycteridae (Pisces, Siluriformes). *Stud. Neotrop. Fauna & Envir.*, 13: 157-194.
- ARRATIA, G. & S. MENUMARQUE (1981). Revision of the freshwater catfishes of the genus *Hatcheria* (Siluriformes, Trichomycteridae) with commentaries on ecology and biogeography. *Zool. Anz.*, 207: 88-111.
- ARRATIA, G. & S. MENUMARQUE (1984). New catfishes of the genus *Trichomycterus* from the high Andes of South America (Pisces, Siluriformes) with remarks on distribution and ecology. *Zool. Jb. Syst.*, 111: 493-520.
- ARRATIA, G. & H.-P. SCHULTZE (1991). Development and homology of the palatoquadrate within osteichthyans. *J. Morphol.*, 208: 1-8.
- BEAUMONT, A. (1998). La notion d'homologie. *Bull. Soc. Zool. Fr.*, 123: 311-321.
- BERTMAR, G. (1959). On the ontogeny of the chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zool.*, 40: 203-364.
- CHARDON, M. (1968). Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann. Mus. R. Afr. Centr.*, 169: 1-273.
- CHARDON, M. & P. VANDEWALLE (1971). Comparaison de la région céphalique chez cinq espèces du genre *Tilapia*, dont trois incubateurs buccaux. *Ann. Soc. R. Zool. Belg.*, 101: 3-24.
- CHARDON, M. & E. DE LA HOZ (1973). Notes sur le squelette, les muscles, les tendons et le cerveau des Gymnotoidei. *Ann. Sc. Nat. Zool. Paris*, 15: 1-10.
- CHARDON, M. & E. DE LA HOZ (1974). Towards an improved classification of the gymnotoid fishes by the use of splanchnocranium characters. *Ichthyologia*, 6: 15-25.
- CHARDON, M. & E. DE LA HOZ (1977). Remarques anatomiques et fonctionnelles à propos du suspensorium et de la série operculaire chez *Sternopygus macrurus* et *Engenmania virescens* (Teleostei Gymnotoidei). *Ann. Soc. R. Zool. Belg.*, 106: 177-191.
- DAGET, J. (1964). Le crâne des Téléostéens. *Mém. Mus. Natn. Hist. Nat.*, 31: 163-341.
- DAVID, L. (1936). *Uegitglanis*, Silure aveugle de la Somalie italienne. Chainon entre Bagrides et Clariides. *Rev. Zool. Bot. Afr.*, 3: 369-388.
- DE BEER, G. R. (1937). *The development of the vertebrate skull*. Clarendon Press, Oxford.
- DE LA HOZ, E. (1974). *Définition et classification des poissons Gymnotoidei sur la base de la morphologie comparée et fonctionnelle du squelette et des muscles*. PhD Thesis, University of Liège.
- DE LA HOZ, E. & M. CHARDON (1984). Skeleton, muscles, ligaments and swim-bladder of a gymnotid fish, *Sternopygus macrurus* Bloch & Schneider (Ostariophysi Gymnotoidei). *Bull. Soc. R. Sci. Liège*, 53: 9-53.
- DE LA HOZ, E. & R. ALDUNATE (1994). El sistema hioideo-mandibular de *Cheirodon* (Ostariophysi, Characidae): una innovación funcional. *Ann. Mus. Hist. Nat. Valparaíso*, 22: 83-90.
- DE PINNA, M.C.C. (1993). *Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysi)*. PhD Thesis, University of New York.
- DE PINNA, M.C.C. (1996). A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae and Amblycipitidae, with a hypothesis on the relationships of the neotropical Asprendidae (Teleostei, Ostariophysi). *Fieldiana (Zool)*, 84: 1-82.

- VANDEWALLE, P., C. SURLEMONT, P. SANNA & M. CHARDON (1985). Interprétation fonctionnelle de modifications du splanchnocrâne pendant le développement post-embryonnaire de *Clarias gariepinus* (Téléostéens, Siluriformes). *Zool. Jahrb. Anat.*, 113: 91-100.
- VANDEWALLE, P., C. SURLEMONT & M. CHARDON (1993). About the early larval development of the anterior suspensorial ossifications of *Clarias gariepinus* (Burchell, 1822). *Zool. Anz.*, 231: 11-19.
- VANDEWALLE, P., P. LALEYE & B. FOCANT (1995a). Early development of cephalic bony elements in *Chrysichthys auratus*. *Belg. J. Zool.*, 125: 329-347.
- VANDEWALLE, P., P. SAINTIN & M. CHARDON (1995b). Structures and movements of the buccal and pharyngeal jaws in relation to feeding in *Diplodus sargus*. *J. Fish Biol.*, 46: 623-656.
- VANDEWALLE, P., I. GLUCKMANN, E. BARAS, F. HURIAUX & B. FOCANT (1997). Postembryonic development of the cephalic region in *Heterobranchus longifilis*. *J. Fish Biol.*, 50: 227-253.
- VERRAES, W. (1977). Postembryonic ontogeny and functional anatomy of the ligamentum mandibulo-hyoideu and the ligamentum interoperculo-mandibulare, with notes on the opercular bones and some other cranial elements in *Salmo gairdneri* Richardson, 1836 (Teleostei: Salmonidae). *J. Morphol.*, 151: 111-119.
- WEITZMAN, S. H. (1962). The osteology of *Brycon meeki*, a generalised characid fish, with an osteological definition of the family. *Stanford Ichthyol. Bull.*, 8: 1-77.
- WEITZMAN, S. H. (1964). Osteology of and relationships of south American characid fishes of subfamilies Lebiasininae and Erythrinae with special reference to subtribe Nannostomina. *Proc. US Natn. Mus.*, 116: 127-170.

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