On the anatomy and function of the cephalic structures in *Phractura* (Siluriformes: Amphiliidae), with comments on some striking homoplasies occurring between the Doumeinae and some loricaroid catfishes

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ABSTRACT. The morphology and function of the cephalic structures related to the feeding mechanism – movements of the mouth, suspensorium, opercular series, hyoid arch, maxillary barbels and mandibular barbels – was studied in two catfish species of the genus *Phractura* (Amphiliidae: Doumeinae), *P. intermedia* and *P. brevicauda*. For comparison, other species of the family Amphiliidae, as well as a large number of other catfishes, were also studied. The morpho-functional analysis pointed out that *Phractura*, as well as the other doumeins, present several unusual morphological modifications, which are very likely related to two main functional specialisations: the ability to attach the body to the substrate with an oral sucker, and the ability to scrape this substrate. The comparison with other siluriforms revealed an impressive number of morpho-functional homoplasies occurring between the African doumeins and the South-American callichthyids, scoloplacids, astroblepids and loricariids.

KEY WORDS: Amphiliidae, catfish, Doumeinae, ecomorphology, evolution, feeding mechanisms, functional morphology, homoplasies, *Phractura*, Siluriformes.

INTRODUCTION

The Siluriformes, with their already described 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: 10).

Among the 34 siluriform families, the African family Amphiliidae – which is subdivided in two subfamilies, Amphiliinae (*Amphilius* and *Paramphilius*) and Doumeinae (*Andersonia*, *Belonoglanis*, *Doumea*, *Phractura* and *Trachyglanis*) –, is surely one of the less studied (HE, 1997). Despite the large number of papers concerning catfish anatomy (REGAN, 1911; KINDRED, 1919; ALEXANDER, 1965; GAUBA, 1966; 1970; JAYARAM,

1966; 1970; CHARDON, 1968; GOSLINE, 1975; HOWES, 1983ab; 1985; JAYARAM & SINGH, 1984; LUNDBERG & MCDADE, 1986; FAGADE, 1980; ARRATIA, 1987; 1990; 1992; BORNBUSCH, 1991a,b; MO, 1991; DE VOS, 1995; ADRIAENS & VERRAES, 1994; 1997a,b,c; DIOGO et al., 1999b; etc.), the only ones in which the morphology of amphiliids is described with some detail are those of REGAN (1911), HARRY (1953), CHARDON (1968), SKELTON (1986), SKELTON et al. (1984), HE (1997), DIOGO & CHARDON (1998; 1999; in press-a,b) and DIOGO et al. (1999a). Moreover, as these descriptions are restricted to the osteology and external aspect of these fishes, their myology, arthrology and functional morphology are unknown. This complicates any attempt to study the phylogenetic relationships between the amphiliid genera and also between the different catfish families.

The aim of this study is to describe the anatomy (osteology, myology and arthrology) and function of the cephalic structures, particularly those related to the feeding mechanism (movements of the mouth, suspensorium, opercular series, hyoid arch, maxillary barbels and mandibular barbels), in the amphiliid *Phractura*, in order

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to pave the way for further anatomical, functional, ecological, ethological and phylogenetical studies on amphiliids, as well as to improve our global knowledge on catfish biology.

MATERIAL AND METHODS

The specimens studied (Table I) are from the private collection of the Laboratory of Functional and Evolutionary Morphology of Liège (LFEM), from the "Musée Royal de l'Afrique Centrale" of Tervuren (MRAC), from the "Université Nationale du Bénin" (UNB), from the "Muséum National D'Histoire Naturelle" of Paris (MNHN) and from the National Museum of Natural History of Washington (USNM). 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. Functional hypotheses are based on anatomical evidence, biomechanical principles and manipulation of the dissected specimens.

TABLE 1

Specimens studied in the present work, their mode of conservation and their provenience (LFEM: private collection of the Laboratory of Functional and Evolutionary Morphology, Liège; MNHN: "Muséum National D'Histoire Naturelle", Paris; MRAC: "Musée Royal de l'Afrique Centrale", Tervuren; UNB: "Université Nationale du Bénin", Cotonou; USNM: National Museum of Natural History, Washington).

Amphiliidae	*Andersonia leptura* Boulenger 1900	Alcohol	MNHN 1961-0600
	Amphilius brevis Boulenger, 1902	Alcohol	MRAC 89-043-P-403
	Belonoglanis tenuis Boulenger 1902	Alcohol	MRAC P.60494
	Paramphilius trichomycteroides Pellegrin, 1917	Alcohol	LFEM
	Doumea typica Sauvage, 1879	Alcohol	MRAC 93-052-p-152
	Phractura brevicauda Boulenger, 1911	Alcohol	MRAC 90-057-P-5145
	Phractura brevicauda Boulenger, 1911	Alizarine	MRAC 92-125-P-386
	Phractura intermedia Boulenger, 1911	Alcohol	MRAC 73-016-P-5888
	Trachyglanis minutus Boulenger 1902	Alcohol	LFE
Ariidae	*Arius gigas* Boulenger, 1891	Alcohol	LFEM
Austroglanidinae	*Austroglanis sclateri* Boulenger, 1901	Alcohol	LFEM
Bagridae	*Bagrus docmak* Forsskall, 1775	Alcohol	MRAC 86-07-P-512
	Hemibagrus wickii Bleeker, 1858	Alcohol	LFEM
	Pseudomystus bicolor Fowler, 1934	Alcohol	LFEM
Callichthyidae	*Callichthys callichthys* Linnaeus, 1758	Alcohol	LFEM
Clariidae	*Clarias gariepius* Burchell, 1822	Alcohol	MRAC 93-152-P-1356
	Heterobranchus longifilis Valenciennes, 1840	Alcohol	LFEM
Claroteidae	*Auchenoglanis occidentalis* Cuvier & Valenciennes, 1840	Alcohol	MRAC 73-010-P-3536
	Chrysichthys auratus Geoffroy Saint-Hilaire, 1809	Alcohol	UNB
	Clarotes laticeps Rüppell, 1829	Alcohol	MRAC 73-13-P-980
	Liauchenoglanis thomasi Boulenger, 1916	Alcohol	MRAC 73-010-P-3540
	Parauchenoglanis ansorgii Boulenger, 1911	Alcohol	LFEM
Diplomystidae	*Dyplomystes chilensis* Molina, 1782	Alcohol	LFEM
Loricariidae	*Lithoxus fimbriatus*, Steidachner 1917	Alcohol	LFEM
Plotosidae	*Plotosus lineatus* Thunberg, 1787	Alizarine	USNM 200226
Pimelodidae	*Pimelodella serrata* Eigenmann, 1917	Alcohol	LFEM
Shilbeidae	*Shilbe intermedius* Rüppell, 1832	Alcohol	MRAC 90-30-P-24
Trichomycteridae	*Trichomycterus guianensis* Eigenman, 1909	Alcohol	LFEM

LIST OF ABBREVIATIONS

af-	articulatory facet …
af-I	a.f. neurocranium-autopalatinum
af-II	a.f. neurocranium-hyomandibulare
af-III	a.f. anguloarticulare-quadratum
af-IV	a.f. operculare-hyomandibulare
af-V	a.f. interoperculare-ceratohyale
afo	anterior fontanel
c-	cartilago …
c-apal-a	c. autopalatinus anterior

c-Meck-ho	c. Meckeli: horizontal portion
c-ex-mnd-b-mp	c. externus mandibularis tentaculi: mobile part
c-ex-mnd-b-sp	c. externus mandibularis tentaculi: supporting part
fr-V-VII	trigemino-facialis foramen
l-	ligamentum …
l-an-ch	l. angulo-ceratohyale
l-an-iop	l. angulo-interoperculare
l-ent-vm	l. entopterygoideo-vomerale
l-meth-apal	l. mesethmoideo-autopalatinum

l-meth-prmx	l. mesethmoideo-praemaxillare
l-prmx-apal	l. praemaxillo-autopalatinum
l-prmx-mx	l. praemaxillo-maxillare
l-puh-hh	l. parurohyalo-hypohyale
l-q-prmx	l. quadrato-praeomaxillare
m-	musculus …
m-A1-OST-1	m. adductor mandibulae A1 (Ostariophysi): section 1
m-A1-OST-2	m. adductor mandibulae A1 (Ostariophysi): section 2
m-A2	m. adductor mandibulae A2
m-A3	m. adductor mandibulae A3
m-ad-mnd	m. adductor mandibulae
m-ad-ap	m. adductor arcus palatini
m-ad-op	m. adductor operculi
m-dil-op	m. dilatator operculi
m-dp-in-mnd-b	m. depressor interni mandibularis tentaculi
m-ex-t	m. extensor tentaculi
m-ex-t-1	m. extensor tentaculi: section 1
m-ex-t-2	m. extensor tentaculi: section 2
m-ex-t-3	m. extensor tentaculi: section 3
m-hh-inf	m. hyohyoideus inferior
m-intt	m. intertentacularis
m-l-ap	m. levator arcus palatini
m-l-op	m. levator operculi
m-obl-inf	m. obliquus inferioris
m-pr-h	m. protractor hyoidei
m-pr-h-l	m. protractor hyoidei pars lateralis
m-pr-h-v	m. protractor hyoidei pars ventralis
m-pr-ex-mnd-b	m. protractor externi mandibularis tentaculi
m-re-ex-mnd-b	m. retractor externi mandibularis tentaculi
m-re-in-mnd-b	m. retractor interni mandibularis tentaculi
m-re-t	m. retractor tentaculi
m-sh	m. sternohyoideus
mnd	mandible
mnd-b-ex	external mandibular barbel
o-	os …
o-ang-art	o. angulo-articulare
o-apal	o. autopalatinum
o-boc	o. basioccipitale
o-ch-a	o. ceratohyale anterior
o-ch-p	o. ceratohyale posterior
o-cl	o. cleithrum
o-com	o. coronomeckelium
o-den	o. dentale
o-ent	o. entopterygoideum
o-eoc	o. exoccipitale
o-epot	o. epioticum
o-fr	o. frontale
o-hh	o hypohyale
o-hm	o. hyomandibulare
o-iop	o. interoperculare
o-leth	o. latero-ethmoideum
o-meth	o. mesethmoideum
o-mp	o. metapterygoideum
o-mx	o. maxillare
o-op	o. operculare
o-osph	o. orbitosphenoideum
o-para	o. parasphenoideum
o-pop	o. praeoperculare
o-post-scl	o. posttemporo-supracleithrum
o-prmx	o. praemaxillare
o-prot	o. prooticum
o-psph	o. pterosphenoideum
o-pt	o. pteroticum
o-puh	o. parurohyale
o-q	o. quadratum
o-soc	o. supraoccipitale
o-soc-pp	o. supraoccipitale: posterior process
o-sph	o. sphenoticum
o-vm	o. vomerale
pap	papillae
pfo	posterior fontanel
r-br-VI	branchiostegal ray VI

RESULTS

With the exception of the external aspect, the differences between the two species of *Phractura* (Boulenger, 1900) studied, *P. brevicauda* (Boulenger, 1911) and *P. intermedia* (Boulenger, 1911), are not significant. Therefore, our description will be based on *P. brevicauda*. The visual information given in the figures have the preponderance over the textual one, and, thus, this latter will be brief.

Osteology

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

Os mesethmoideum. Unpaired (Figs 1, 2, 3). It is connected to the palatine and to the premaxillary by two small ligaments (Fig. 4).

Os lateroethmoideum. Paired. With a lateral articulatory facet for the palatine (Figs 1, 3).

Os vomerale. Unpaired. In the shape of T, but with very small antero-lateral processes (Fig. 3).

Os orbitosphenoideum. Paired. Posterior to the lateral ethmoid (Figs 1, 3, 5).

Os parasphenoideum. Unpaired. The longest bone of the cranium (Fig. 3).

Os pterosphenoideum. Paired, posterior to the orbitosphenoid (Figs 1, 3).

Os sphenoticum. Paired. It presents, together with the pterotic, an articulatory facet for the hyomandibula (Figs 1, 3).

Os pteroticum. Paired. Well-developed bone associated posteriorly to the posttemporo-supracleithrum (Figs 1, 2, 3).

Os prooticum. Paired. The foramen of the trigemino-facial nerve complex is situated between this bone, the pterosphenoid and the parasphenoid (Fig. 3).

Os epioticum. Paired. Well-developed, situated on the posterior surface of the neurocranium (Figs 1, 3).

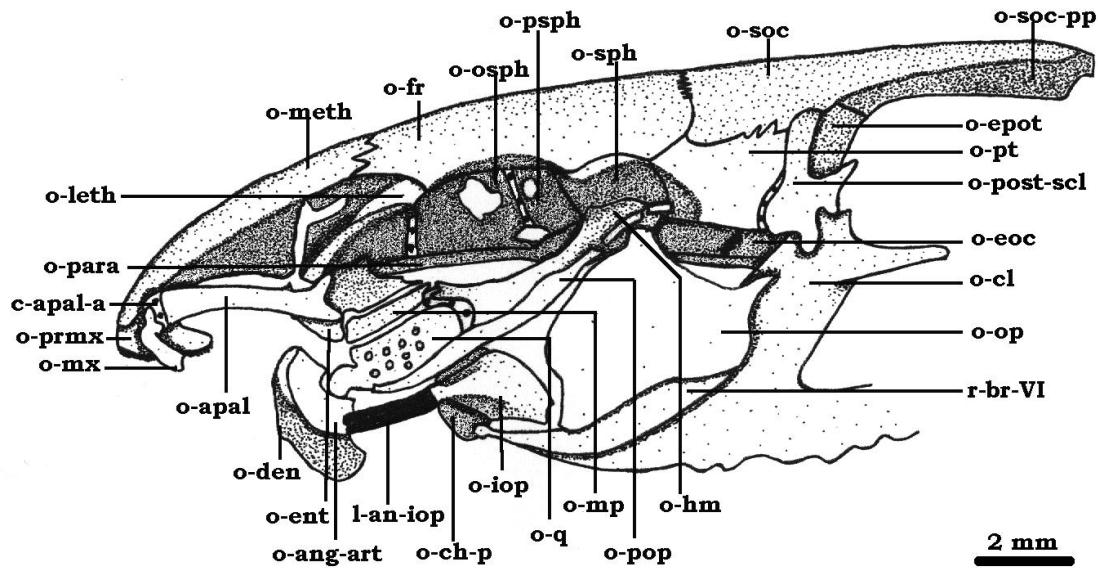*Os exoccipitale.* Paired. Situated laterally to the basioccipital (Fig. 3).

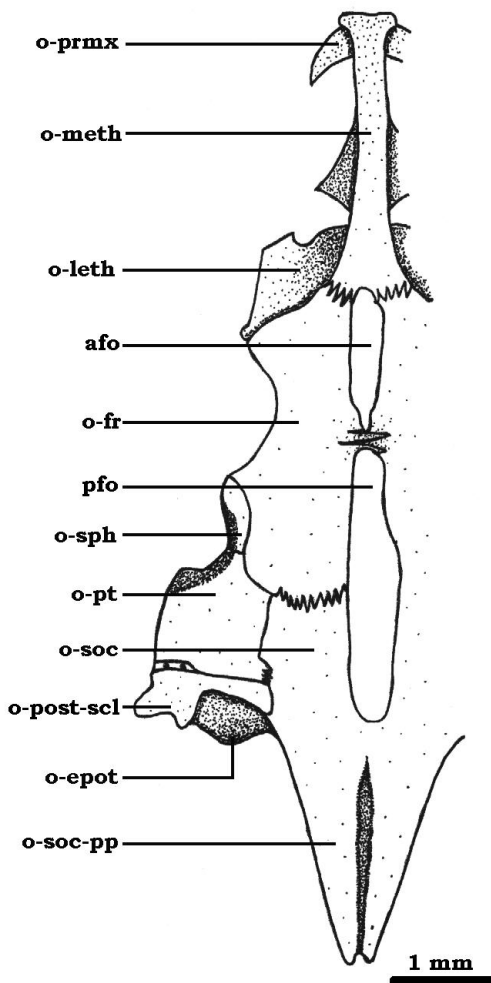Fig. 1. – Lateral view of the skull of *Phractura brevicauda*. Infraorbital series removed.

Fig. 2. – Dorsal view of the neurocranium of *Phractura brevicauda*.

Os basioccipitale. Unpaired. It presents two well-developed ventro-lateral processes associated by means of a thick ligamentous tissue with the ventro-medial limbs of the posttemporo-supracleithrum (Fig. 3). It also presents two postero-ventral processes, which join to similar processes of the first vertebra (Fig. 3).

Os frontale. Paired. The two frontals are largely separated by the well-developed anterior and posterior fontanels, and suture with each other medially only halfway along their length *via* a bony bridge, which separates the fontanels (Fig. 2).

Os supraoccipitale. Unpaired. Large bone with a long posterior process (Figs 1, 2). The posterior fontanel extends on its anterior surface (Fig. 2).

Os posttemporo-supracleithrum. Paired. Its dorso-mesial limb is firmly connected with the pterotic, epiotic and supraoccipital. The extrascapular, normally associated with this limb, is missing (Figs 1, 3). Its thin ventro-mesial limb is firmly attached to the basiocccipital by a strong and short ligament (Fig. 3). Its ventro-lateral limb is forked, forming an articulating groove for the upper edge of the cleithrum (Fig. 1). A prominent posterior process (Figs 1, 2) is present on the postero-dorsal surface of the posttemporo-supracleithrum.

Os operculare. Paired. Broad bone (Figs 1, 6 A) antero-dorsally articulated with the hyomandibular by means of two articulatory surfaces (Fig. 6 A). Its ventral edge is quite far from the suspensorial bones (Fig. 1).

Os interoperculare. Paired. It presents a well-developed mesial articulatory surface for the posterior ceratohyal (Figs 6 C, 7). Its fore end is connected to the back of the mandible by a long, strong ligament (Figs 1, 6 C, 7).
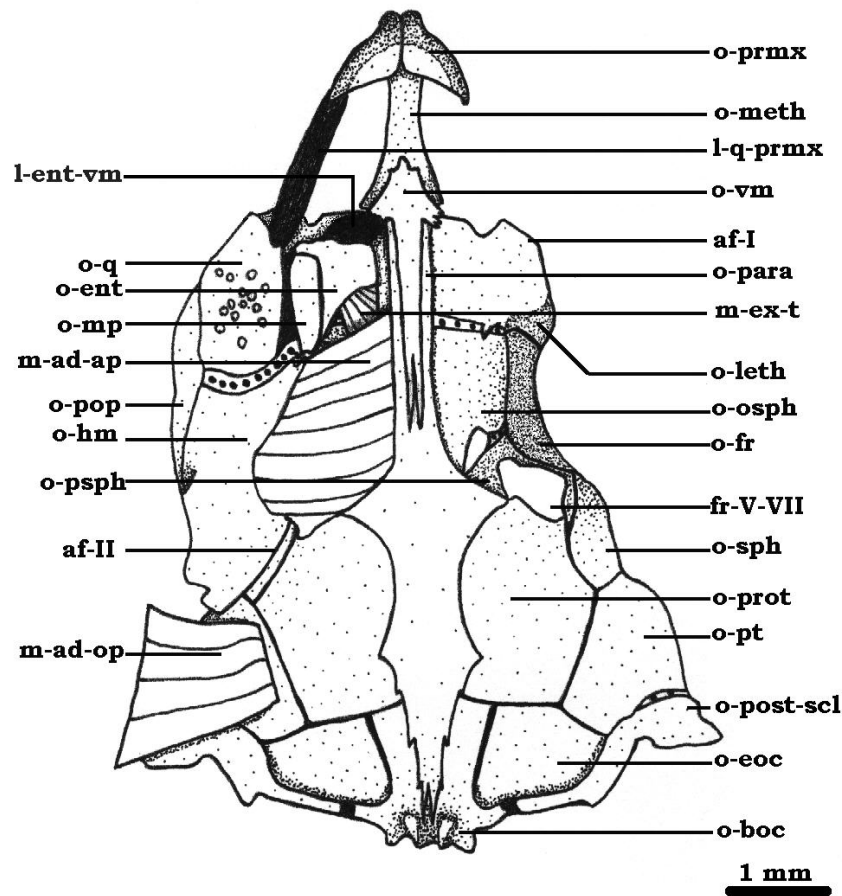
Fig. 3. – Ventral view of the neurocranium of *Phractura brevicauda*. On the left side the suspensorium,
the adductor arcus palatini, the adductor operculi and the extensor tentaculi are also illustrated.

Os praeoperculare. Paired. Long and thin bone firmly attached to the hyomandibula and to the quadrate (Figs 1, 3).

Os hyomandibulare. 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 endless controversies (MCMURRICH, 1884; DE BEER, 1937; HOEDEMAN, 1960ab; GOSLINE, 1975; ARRATIA et al., 1978; ARRATIA & MENUMARQUE, 1981; 1984; HOWES, 1983ab; 1985; ARRATIA, 1987; 1990; 1992; HOWES & TEUGELS, 1989; etc.). We hope to bring the solution in an extensive and detailed article actually proposed for publication. However, for the time being, we will describe the suspensorium bones by their most accepted names (see ARRATIA, 1992). The paired hyomandibulas articulate dorsally with the paired pterotics and sphenotics (Fig. 3).

Os quadratum. Paired. Its fore end presents a well-developed anterior articulatory facet for the angulo-articular (Fig. 1) and is connected, by means of a long, strong ligament to the premaxillary (Fig. 3). Its posterior surface is separated from the hyomandibular by means of a large cartilage (Figs 1, 3). Mesially it is firmly attached, by means of a very short ligament, to the metapterygoid and

entopterygoid bones (Fig. 3). It presents a large number of pores in all its surface (Figs 1, 3).

Os metapterygoideum. Paired. Small, rectangular bone firmly attached to the entopterygoid by means of a very short ligament (Fig. 3).

Os entopterygoideum. Paired. The paired entopterygoids are broader than the metapterygoids (Figs 1, 3). The fore end of each entopterygoid presents a short, strong ligament that attaches to each antero-lateral process of the vomer (Fig. 3). The ectopterygoids are absent.

Os autopalatinum. Paired. It articulates with the maxillary and the lateral ethmoid, respectively, by its anterior cartilage and by its postero-medial surface (Fig. 1). Its fore end is associated, by means of short ligaments, to the antero-ventro-lateral surface of the mesethmoid and to the postero-dorsal edge of the premaxillary (Fig. 4). Posteriorly, the palatine is bifurcated (Figs 1, 5).

Os maxillare. Paired. They support the paired maxillary barbels.

Os praemaxillare. Paired. Both premaxillaries present a well-developed postero-lateral process (Figs 1, 2, 3, 8),
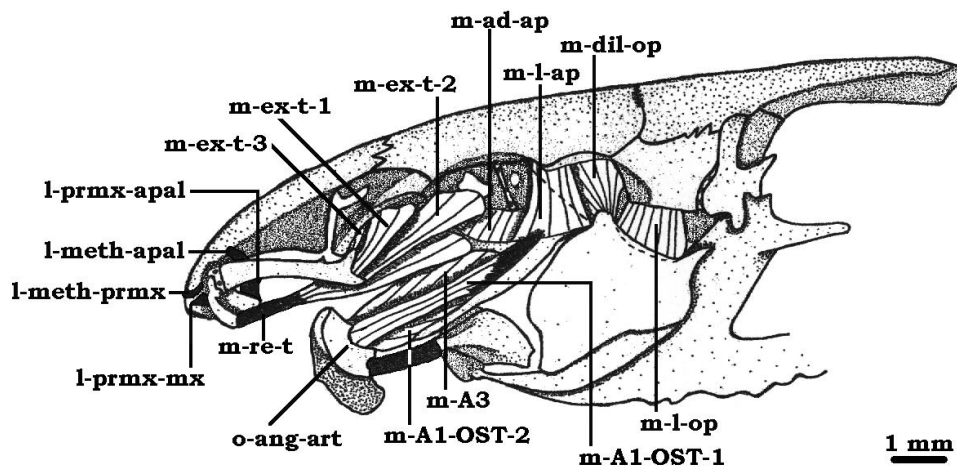
Fig. 4. – Lateral view of the cephalic musculature of *Phractura brevicauda*.

forming an inverted U-shaped complex (Figs 2, 3, 8). Each of them is dorsally linked by a strong ligament to the proximal extremity of the paired maxillaries (Fig. 4) and bears ventrally a large tooth-plate (Fig. 1).

Os angulo-articulare. Paired. This bone, together with the dentary, coronomeckelian and Meckel cartilage, constitute the mandible (Fig. 9B). The rear end of the angulo-articular presents an articulatory surface for the quadrate (Fig. 9B) and is linked to the interopercular and to the posterior ceratohyal by two long, strong ligaments (Fig. 7).

Os dentale. The paired 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. 8). The fore end of each dentary is deeply incurvated ventrally and presents only two small teeth, which confers to the mandible a very peculiar shape (Fig. 9B, C, D).

Os coronomeckelium. Paired. Small bone lodged in the medial surface of the mandible. Posteriorly it bears a crest for attachment of the jaw muscle (Fig. 9A).

Os ceratohyale posterior. Paired. The ceratohyale posterior, ceratohyal anterior and hypohyal bones have a very peculiar shape. The ceratohyale posterior is a quadrangular bone linked by ligaments to the fore end of the mandible (Fig. 7) and to the mesial surface of the suspensorium. Postero-laterally it articulates with the interopercular (Fig. 7).

Os ceratohyale anterior. Paired. Together with the posterior ceratohyal it supports the branchiostegal rays (Fig. 7).

Os hypohyale. Paired. Well-developed bone (Fig. 7).

Os parurohyale. The parurohyal (see ARRATIA & SCHULTZE, 1990) is a single shuttle-like bone lying medially behind the symphysis of the two hypohyals and con-

nected to these bones by means of two short and thick ligaments (Fig. 7).

Myology

The myological nomenclature is mainly based on WINTERBOTTOM (1974). However, for the different adductor mandibulae subdivisions, we follow DIOGO & CHARDON (2000b), since recent works have pointed out that, with respect to these subdivisions, WINTERBOTTOM'S (1974) nomenclature presents serious limitations (see
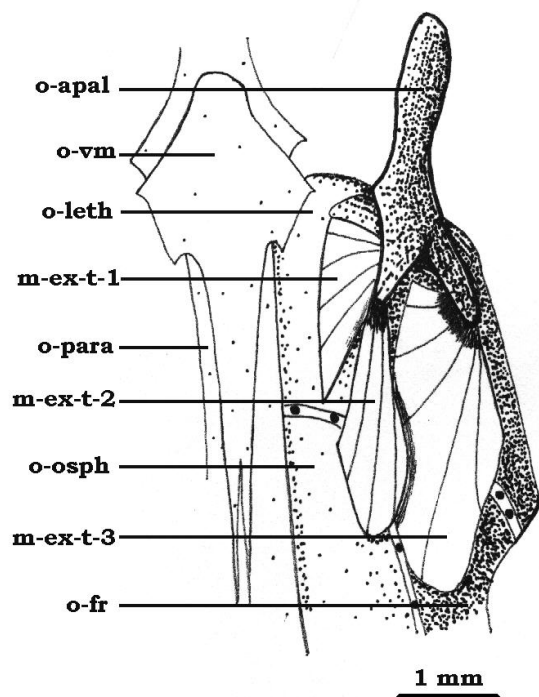

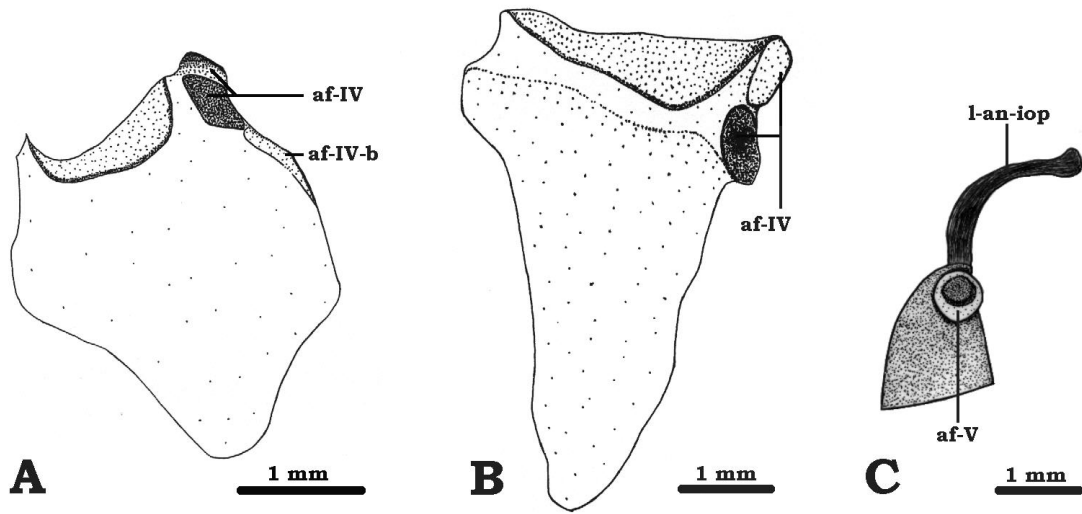Fig. 5. – Palatine and extensor tentaculi of *Phractura brevicauda*, ventral view.

Fig. 6. – (A) Opercular of *Phractura brevicauda*, medial view. (B) Opercular of *Diplomystes chilensis*, medial view. (C) Interopercular of *Phractura brevicauda*., medial view.
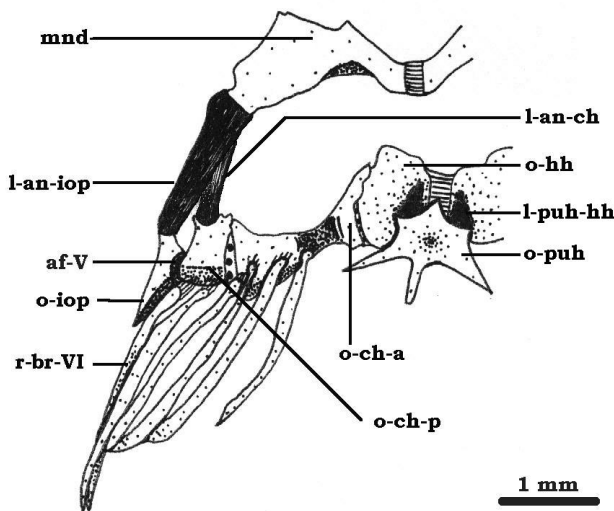

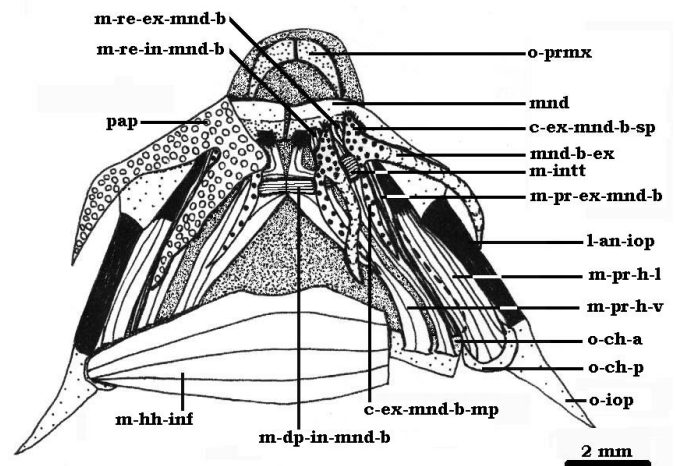Fig. 7. – Ventral view of the splanchnocranium of *Phractura brevicauda*.

Fig. 8. – Ventral view of the cephalic musculature of *Phractura brevicauda*. On the right side, the skin enveloping the mandibular barbels was removed and the hyohyoideus inferior was cut.

GOSLINE, 1989; DIOGO & CHARDON, 2000b). In relation to the muscles associated with the mandibular barbels, which were not studied by WINTERBOTTOM (1974), we follow DIOGO & CHARDON (in press-b).

Musculus adductor mandibulae. Paired. The configuration of the adductor mandibulae is rather simple. The A1-OST is sub-divided into a lateral A1-OST-1 and a medial A1-OST-2 part (Figs. 4, 9A). The A1-OST-1 originates on the preopercular and the A1-OST-2 on the preopercular and quadrate (Fig. 4). They insert on the dorso-lateral surface of the angulo-articular (Figs 4, 9A). The A2, which lies medially to the A1-OST, attaches caudally on the pre-opercular and rostrally on the medial surface of the mandible (Fig. 9A). The deeper bundle of the adductor mandibulae, A3, runs from the preopercular, hyomandibu-

lar and quadrate (Fig. 4) to the coronomeckelian bone (Fig. 9A). The Aω is lacking.

Musculus levator arcus palatini. Paired. It originates on the ventro-lateral surfaces of the frontal and sphenotic and inserts on the dorso-lateral face of the hyomandibula (Fig. 4).

Musculus dilatator operculi. Paired. Thick muscle medial to the levator arcus palatini (Fig. 4). It originates on the ventral surfaces of the frontal, sphenotic and pterotic and on the lateral surface of the pterosphenoid and inserts on the antero-dorsal face of the opercular (medial to the preopercular but lateral to the articulatory facet of the opercular for the hyomandibula) (Fig. 4).

Musculus levator operculi. Paired. Very thin muscle dorsally linked to the ventro-lateral surface of the pterotic

and ventrally associated to the dorsal face of the opercular (Fig. 4).

Musculus adductor operculi. Paired. Situated medially to the levator operculi, it originates on the ventro-medial surface of the pterotic (Fig. 3) and inserts on the dorso-medial surface of the opercular.

Musculus adductor arcus palatini. The paired adductores arcus palatini extend from the lateral sides of the orbitosphenoid, pterosphenoid and parasphenoid to the medial sides of the hyomandibula (Figs 3, 4).

Musculus extensor tentaculi. Paired. This muscle is differentiated in four sections. The extensor tentaculi 1 originates on the lateral ethmoid and inserts, by means of a thin tendon, on the postero-medial face of the palatine (Figs 4, 5). The extensor tentaculi 2 originates on the orbitosphenoid and inserts tendinously on the postero-ventro-mesial process of the palatine (Figs 4, 5). The extensor tentaculi 3 extends from the lateral ethmoid and from the ventral surface of the frontal to the postero-dorso-lateral process of the palatine, to which it is linked by means of a thin tendon (Figs 4, 5).

Musculus retractor tentaculi. Paired. Well-developed muscle running from the external surface of the hyomandibular to the maxillary (Fig. 4).

Musculus protractor hyoidei. Paired. This muscle presents three parts. The pars ventralis, originating on the ceratohyal anterior and inserting on the dentary, is differentiated into two bundles associated, respectively, with the cartilages of the external and internal mandibular barbels (Fig. 8). The pars dorsalis originates on the ventral side of the ceratohyals and inserts tendinously on the dentary. The pars lateralis originates on the antero-ventral surface of the posterior ceratohyal and inserts, by means of a strong tendon, on the ventro-medial face of the dentary (Fig. 8).

Musculus hyohyoideus inferior. Paired. Thick muscle attached laterally on the ventral surface of the ceratohyals and medially on a medial aponeurosis (Fig. 8).

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

Musculus retractor externi mandibularis tentaculi. Paired. Small muscle running from the moving part of the cartilage associated with the outer mandibular barbel to the dentary (Fig. 8).

Musculus retractor interni mandibularis tentaculi. Paired. Small muscle that originates on the moving part of the cartilage associated with the internal mandibular barbel and inserts on the dentary (Fig. 8).

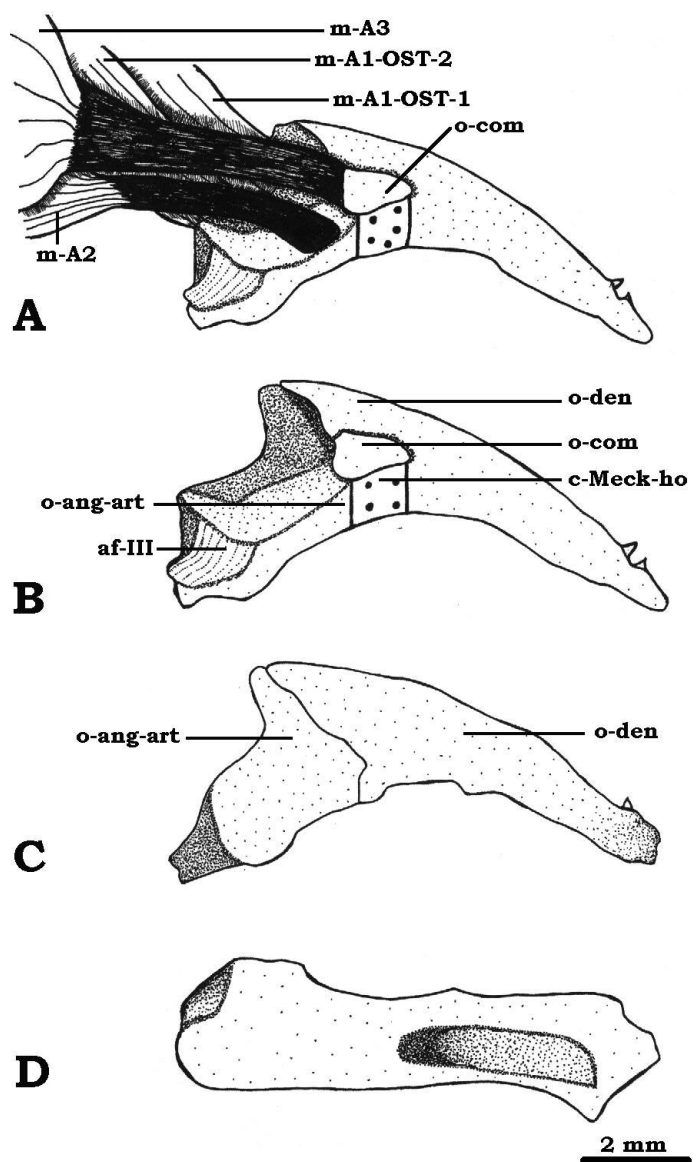*Musculus protractor externi mandibularis tentaculi*. Paired. Long muscle extending from the anterior and pos-

Fig. 9. – *Phractura brevicauda*. (A) Mandible and adductor mandibulae, medial view. (B) Mandible, medial view. (C) Mandible, lateral view. (D) Mandible, ventral view.

terior ceratohyals to the moving part of the cartilage associated with the external mandibular barbel (Fig. 8).

Musculus intertentacularis. Paired. Very small muscle running from the mesial face of the cartilage associated with the external mandibular barbel to the lateral face of that associated with the internal one (Fig. 8).

Musculus depressor interni mandibularis tentaculi. Paired. Small muscle extending from a medial aponeurosis to the mesial surface of the cartilage associated with the internal mandibular barbel (Fig. 8).

DISCUSSION

In this chapter we will firstly present a hypothesis on the function of the cephalic structures related to the feed-

ing mechanisms – movements of the mouth, suspensorium, opercular series, hyoid arch, maxillary barbels and mandibular barbels – in the doumein *Phractura*. Afterwards, we will focus on the striking functional and morphological homoplasies occurring between the Doumeinae and the callichthyid, scoloplacid, astroblepidae and loricariid catfishes.

Function of the cephalic structures related to the feeding mechanisms in Phractura

Opening of the mouth. The mechanism of mouth opening is illustrated in Fig. 10. *Phractura* has a ventrally placed mouth (Figs 1, 8) modified into a sucking disk, with a large number of labial papillae (Fig. 8). The opening of the mouth is realized by movements of both the premaxilla and the mandible (Fig. 10 A→B).

The movement of the premaxilla is associated to the palatine-maxillary system. The contraction of the extensor tentaculi muscle pulls the back of the palatine dorsomedially, what provokes – by means of the "rocking" articulation between this bone with the lateral ethmoid (see GOSLINE, 1975; DIOGO & CHARDON, 2000a) – a ventro-lateral displacement of the anterior extremity of the palatine (Fig. 10 A→B). As this extremity is firmly associated by a large, strong ligament to the posterior edge of the premaxilla (Fig. 4), this edge is also displaced ventrally, thus protracting the premaxilla (Fig. 10 A→B). Although a slightly mobile premaxilla is not unusual in catfishes (see ALEXANDER, 1965; GOSLINE, 1975; SCHAEFER & LAUDER, 1986; 1996; DIOGO & CHARDON, 2000a), a highly protractile premaxilla like that of *Phractura* (Fig. 10 A→B) is only found in the Scoloplacidae, Callichthyidae, Astroblepidae and Loricariidae (SCHAEFER & LAUDER, 1986; SCHAEFER, 1990; MO, 1991). Like in *Phractura* (Fig. 10 A→B), in the scoloplacids, callichthyids, astroblepids and loricariids the protraction of the premaxilla is related with the palatine-maxillary system, namely with the ventral displacement of the fore end of the palatine (see ALEXANDER, 1965; GOSLINE, 1975; VANDEWALLE et al., 1986).

The lowering of the mandible is associated to the retraction of the pectoral girdle. When the obliquus inferioris muscles are contracted, the girdle is retracted, which, through the sternohyoideus, provokes the retraction (without ventral displacement, due to absence of the interhyal: see ADRIAENS & VERRAES, 1994) of the mesial part of the hyoid arch (Fig. 10 A→B). This retraction, by means of the protractor hyoidei muscle and the membranous connection between the mandible and the hyoid arch, promotes the lowering of the mandible (Fig. 10 A→B). This mechanism is one of the four typical mechanisms of mandible depression in catfishes (DIOGO & CHARDON, 2000a). However, the other three typical mechanisms (first and third hyoid mechanisms and opercular mechanism) of lowering of the mandible described by DIOGO & CHARDON (2000a) seem to be lost in *Phractura*.

In fact, in *Phractura*, the peculiar configuration of the ceratohyal posterior and of the interopercular (Fig. 7), and principally the well-developed articulatory surface between these two bones (Figs 6C, 7), only allow a rocking movement of the interopercular against the ceratohyal posterior (see below). Therefore, the interopercular cannot be retracted nor rotated dorsally, and, thus, the opercular and the third hyoid mechanism described by DIOGO & CHARDON (2000a) cannot be performed. This hypothesis is supported by the fact that in *Phractura* the levator operculi (which promotes the opercular mechanism of mandible lowering in teleosts) is abnormally thin, seeming to be a vestigial, almost useless muscle. Curiously, in the scoloplacids, astroblepids and loricariids, catfishes that, like *Phractura*, also have a highly protractile premaxilla and a ventrally placed mouth modified into a sucking disk, these two mechanisms are also lost, but for a different reason: the mandibulo-interopercular ligament is absent (SCHAEFER & LAUDER, 1986; SCHAEFER, 1990). The peculiar configuration of the interopercular (Figs 6C, 7) and of all the hyoid arch (Fig. 7), the well-developed interoperculo-ceratohyal articulation (Figs 6C, 7) and the fact that, contrarily to most catfish, the angulo-ceratohyal ligament originates on the anterior (and not postero-dorsal) edge of the ceratohyal posterior (Fig. 7), prevent *Phractura* to perform the first hyoid mechanism described by DIOGO & CHARDON (2000a).

When the premaxilla is protracted and the mandible is lowered at the same time, the mouth is completely opened and can thus adhere to the substrate (Fig. 10 A→B). As in the astroblepids and the loricariids (SCHAEFER & LAUDER, 1986; VANDEWALLE et al., 1986) the high mobility of both the upper and lower jaws probably confers to *Phractura* the possibility to attach to many different types of substrates. After the attachment to the substrate (Fig. 10 A→B), slight movements of the upper (retraction/protraction) and lower (raising/lowering) jaws – which are probably independent, since in *Phractura* the upper and lower jaws are morphologically and functionally uncoupled (see DIOGO et al., 1999a) –, will promote the scraping of the substrate (see Fig. 10B). At the moment, no data on the trophic characteristics of *Phractura*, or of any other Doumeinae, are available (the Amphiliinae present many morpho-functional differences in relation to the Doumeinae – see HARRY, 1953; HE, 1997; DIOGO & CHARDON, 1998; 1999; 2000a –, and, thus, it would be incorrect to make any extrapolation between the trophic characteristics of the members of the two subfamilies). So, the question whether *Phractura* presents the same food habits as those of the other scraping catfishes, namely of the loricarids (detritus, algae) or of the astroblepids (generalist omnivores) (SCHAEFER & LAUDER, 1986), or presents any other type of feeding habit, cannot be answered yet.

Closing of the mouth. The closure of the mouth is realized by the retraction of the premaxilla and the raising of the mandible (Fig. 10 B→A). Premaxilla retraction is performed by the contraction of the antagonist of the exten-
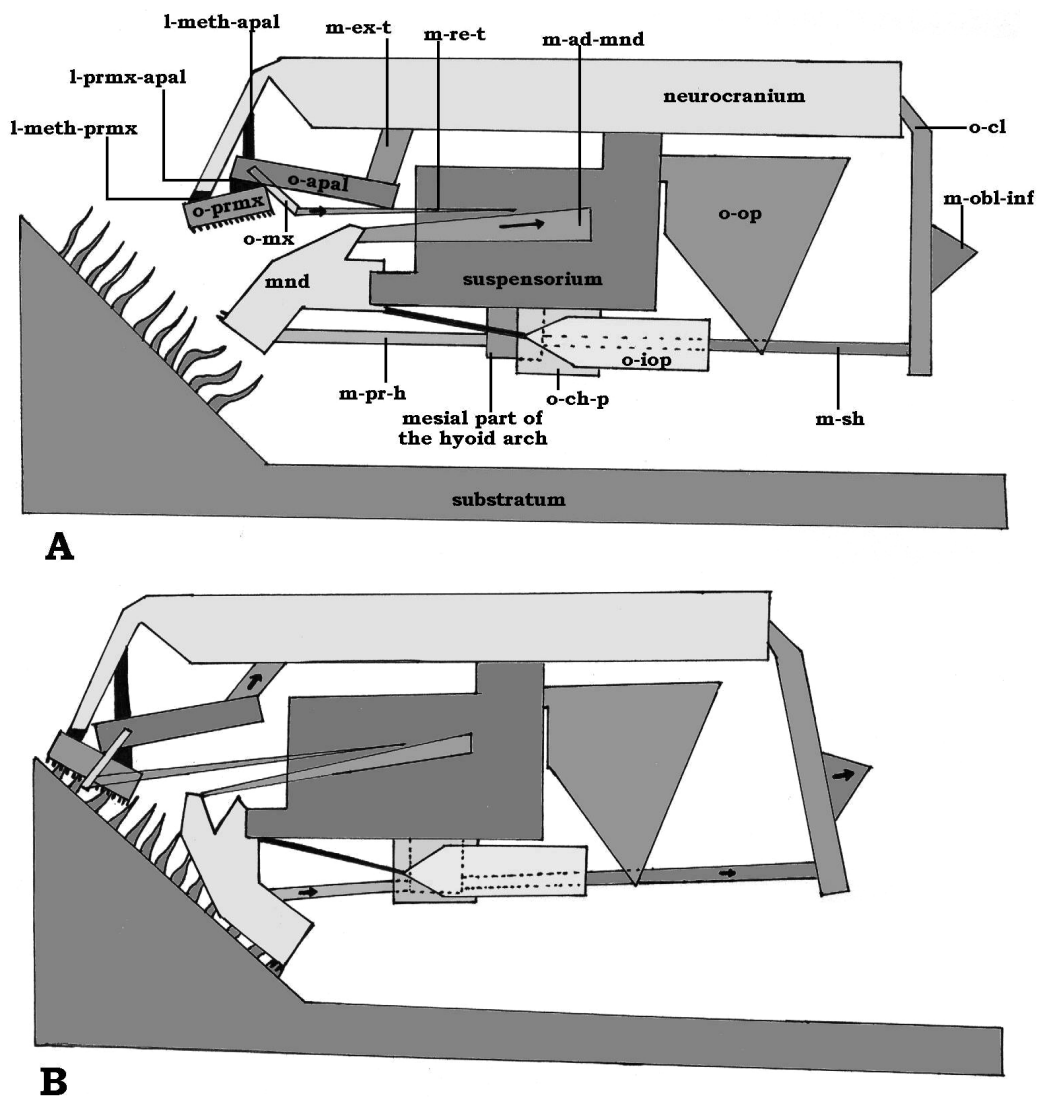
Fig. 10. – Scheme illustrating our hypothesis concerning the mechanisms of mouth closure and mouth opening in *Phractura brevicauda*. (A) The premaxilla is retracted (due to contraction of the retractor tentaculi) and the mandible is raised (due to contraction of the adductor mandibulae). (B) The premaxilla is protracted (due to contraction of the extensor tentaculi) and the mandible is lowered (due to contraction of the obliquus inferioris and/or sternohyoideus and/or protractor hyoidei).

sor tentaculi, the retractor tentaculi, which retracts the maxillary, provoking a dorsal displacement of the fore end of the palatine and, consequently, of the back of the premaxillary (Fig. 10 B→A). This seems also to be the case in the callichthyids, but not in the scoloplacids, astroblepids and loricariids, in which the retraction of the high-mobile premaxillary could be provoked directly by the contraction of specialised muscles directly inserted onto this bone (see HOWES, 1983b; SCHAEFER & LAUDER, 1986; VANDEWALLE et al., 1986; SCHAEFER, 1990). The raising of the mandible is realized by the contraction of the adductor mandibulae (Fig. 10 B→A). The two other typical mechanisms of mandible lifting described by DIOGO & CHARDON (2000a) are lost in *Phractura*.

Abduction of the suspensorium. The mechanism of suspensorium abduction is similar to that of most other catfishes (see DIOGO & CHARDON, 2000a). However, the fact that, of all the catfishes studied by us, *Phractura* is

that with a thinner levator arcus palatini, associated with the fact that it is also the only one that does not present an antero-dorsal hyomandibular articulatory spine for the neurocranium (Fig. 1), seems to indicate that in this genus the abduction of the suspensorium is not as important as in most other catfishes. This hypothesis is in agreement with HUGHES (1970). According to this author, in bottom-living fishes (like *Phractura*) the suction pump mechanism is far more important in aquatic respiration than the pressure pump system. For this suction pump mechanism, no extensive abduction of the suspensorium, no elevation of the neurocranium and no depression of the of the hyoid bars are needed. Instead, a negative pressure is generated in the opercular cavity mainly through the dilatation of the opercular cavity (which is particularly important in *Phractura*: see below), thus provoking the sucking of the water from the orobranchial cavity, through the gills, into the opercular cavity.

Adduction of the suspensorium. The mechanism of suspensorium adduction is similar to that of most other catfishes, with the exception that in *Phractura* the contraction of the adductor operculi and the adduction of the suspensorium are not functionally coupled (see DIOGO & CHARDON, 2000a), since the adductor operculi does not insert on the hyomandibular (Fig. 3).

Dilatation of the opercular cavity. As in the other catfishes (see DIOGO & CHARDON, 2000a), the dilatation of the opercular cavity is performed by the contraction of the dilatator operculi. However, a detailed analysis of some peculiar features of the opercular series of *Phractura* seems to indicate that the dilatation of the opercular cavity is a particularly important cephalic mechanism in this genus. This hypothesis is supported by HUGHES' (1970) assumption that in bottom living fishes the suction mechanism is far more important that the pressure pump system (see above). The peculiar features of the opercular series are: 1) compared to other catfishes, in *Phractura* (Fig. 1) the back of the opercular bone lies relatively far from the articulatory surface between this bone and the hyomandibular, not only due to the abnormal width of the opercular bone, which is much larger than that of most other catfishes, but also to the fact that the ventral part of this bone lies abnormally far from the hyomandibular; 2) in *Phractura* there are two (Fig. 6A, B), and not one, articulatory surfaces of the opercular for the hyomandibular; 3) the interopercular presents a peculiar articulatory surface for the ceratohyal posterior (Figs 6C, 7), which allows a large lateral displacement of the back of the former: it is thus likely that both the opercular and the interopercular, and not only the former, would contribute to the dilatation of the opercular cavity when the dilatator operculi muscle contracts; 4) in *Phractura* the adductor operculi only inserts on the opercular (Fig. 3), and not on the opercular and the hyomandibular, as is the case in most other catfish studied by us (see DIOGO & CHARDON, 2000a), what increases the mobility between these two bones; 5) the dilatator operculi and the adductor operculi of *Phractura* are very thick, well-developed muscles.

Adduction of the operculum. As in the other catfishes (see DIOGO & CHARDON, 2000a), the adduction of the opercular bone is performed by the contraction of the adductor operculi.

Abduction of the maxillary barbel. The mechanism of maxillary barbel abduction is quite similar to that of *Chrysichthys* (see DIOGO & CHARDON, 2000a: Fig. 5C→D). So, when the extensor tentaculi muscle (Figs 4, 5) is contracted, the back of the palatine is pulled dorso-mesially, what, by means of the "rocking" articulation (see GOSLINE, 1975) between the lateral-ethmoid and the palatine, provokes a ventro-lateral displacement of the fore end of the palatine and, thus, the abduction of the maxillary and its associated barbel (see DIOGO & CHARDON, 2000a: Fig. 5C→D). As in many other specialised catfishes, besides maxillary barbel abduction, the extensor tentaculi could also promote the depression (by

means of the contraction of the extensor tentaculi 2) and the elevation (by means of the contraction of the extensor tentaculi 3) of the maxillary barbel (see DIOGO & CHARDON, 1999; in press-a; DIOGO et al., 1999a).

Adduction of the maxillary barbel. As in many other specialised catfishes, the adduction of the maxillary barbel is promoted by the contraction of the retractor tentaculi (see ALEXANDER, 1965; GOSLINE, 1975; HOWES, 1983ab; 1985; DIOGO & CHARDON, 1999; in press-a; etc.), being functionally uncoupled from the movements of the lower jaw (see DIOGO & CHARDON, 1999; in press-a; DIOGO et al., 1999a).

Movements of the mandibular barbels. The movements of the mandibular barbels of Phractura are similar to those of *Chrysichthys*, which are described in detail by DIOGO & CHARDON (2000a).

Homoplasies occurring between the Doumeinae and some loricarioid catfishes

Our morpho-functional analysis pointed out that *Phractura* is a peculiar catfish presenting several unusual morphological modifications, which are probably related to two main functional specilizations: the ability to attach the body to the substrate with an oral sucker, and the ability to scrape this substrate. In order to appraise the phylogenetic and systematic significance of these morphological modifications and functional specialisations, it was decided to study the other genera of Amphiliidae, as well as many other catfish genera, and to compare our results with those available in the literature. Our observations and comparisons with other amphiliid genera indicate that the main morpho-functional specialisations present in *Phractura* are not confined to members of this genus, but are, in reality, also present in the other doumeins (but not in the Amphiliinae, which, together with the Doumeinae, compose the family Amphiliidae: DIOGO & CHARDON, in preparation). In addition, our observations and comparisons with non-amphiliid catfishes (either studied by us or described in the literature) revealed an impressive number of morpho-functional homoplasies occurring between the African doumeins and the South-American callichthyid, scoloplacid, astroblepid and loricariid catfishes (given the scarce data available on higher-level phylogeny of the siluriformes, it is impossible to discriminate whether these homoplasies are the result of a convergence or of an evolutionary parallelism). These homoplasies could be divided in five types: 1) the homoplasies shared by the doumeins, the callichthyids, scoloplacids, astroblepids and loricariids and other specialised catfishes; 2) the homoplasies shared by the doumeins and the callichthyids, scoloplacids, astroblepids and loricariids; 3) the homoplasies shared by the doumeins and the callichthyids and scoloplacids; 4) the homoplasies shared by the doumeins and the scoloplacids, astroblepids and loricariids; 5) the homoplasies shared by the doumeins and the astroblepids and loricariids.

The main homoplasies shared by the doumeins, the callichthyids, scoloplacids, astroblepids and loricariids and other specialised catfishes are: 1) *Presence of a retractor tentaculi muscle.* The functional consequence of this character is that the maxilla, and, thus, the maxillary barbel, could be retracted directly by the contraction of the retractor tentaculi, rather than indirectly by the closure of the mouth and/or the elasticity of the tissues involving the palatine-maxillary system (see ALEXANDER, 1965; GOSLINE, 1975; HOWES, 1983a; DIOGO & CHARDON, in press-a). The differentiation of a retractor tentaculi muscle, which is present in most specialised catfishes, from the adductor mandibulae occurred independently in different catfish lineages (see HOWES, 1983a; DIOGO & CHARDON, 2000b; in press-a); 2) *Absence of the extrascapular bone.* The disappearance of this bone has occurred independently in several catfish lineages (CHARDON, 1968; ARRATIA, 1987). The functional consequence of this character, which is present in most specialised catfishes, seems to be the ankilosis between the posterior region of the neurocranium, the pectoral girdle and the anterior vertebra (CHARDON, 1968); 3) *Mesethmoid without anterolateral cornua.* This character, which has very likely evolved independently in different catfish lineages (MO, 1991), is probably related to a larger mobility of the premaxillary; 4) *Articulatory surface of the palatine for the neurocranium situated in the posterior portion of the palatine.* This character has very likely evolved independently in different catfish lineages and is probably related to a larger efficacity of the palatine-maxillary system (DIOGO & CHARDON, 1998; DIOGO et al., 1999); 5) *Depression of the coronoid process and disappearance of the adductor mandibulae Aw and of the vertical portion of Meckel's cartilage.* These characters have very likely evolved independently in different catfish lineages and are probably associated with the dorso-ventral depression of the mandible, which is probably linked to the adaptation to a benthic life style (by means of a flattening of the skull) (DIOGO & CHARDON, 2000b).

The main homoplastic character shared by the doumeins and the callichthyids, scoloplacids, astroblepids and loricariids is the *highly protractile premaxillary.* Although a slightly, or even moderate (in some plotosids, for example) mobile premaxilla is not unusual in catfishes (see ALEXANDER, 1965; GOSLINE, 1975; SCHAEFER & LAUDER, 1986; DIOGO & CHARDON, 2000a), a highly protractile premaxilla like that of the doumeins (see Fig. 10 A→B) is only found in the Scoloplacidae, Callichthyidae, Astroblepidae and Loricariidae (SCHAEFER, 1990; MO, 1991). This character is however homoplastic, not only since the morphological relation (ligaments, connective tissue) between the mesethmoid and the premaxillary in the doumeins is quite different from that of the scoloplacids, callichthyids, astroblepids and loricariids, but also since these South-American catfishes are more closely related with the trichomycterids and the nematogenyids than with any other catfishes (see, for

example, SCHAEFER, 1990). The highly protractile premaxillary is probably associated with the capacity to scrape the substrate.

The main homoplastic character shared by the doumeins and the callichtyids and scoloplacids is the *mandible with few or no teeth.* With exception of the specimens of the genera *Trachyglanis* and *Phractura*, which present very few teeth on the lower jaw, the doumeins studied by us possess an edentate mandible. The lower jaw of the Scoloplacidae bears usually only four to six minute teeth (SCHAEFER, 1990), and that of the Callichthyidae bears usually very few teeth, whereas two genera of this family, *Corydoras* and *Brochis*, possess an edentate mandible (REIS, 1998). The functional significance of this homoplastic character is not clear.

The main homoplastic character shared by the doumeins and the scoloplacids, astroblepids and loricariids is the *loss of the opercular mechanism of lower jaw depression.* The morphological features associated to this functional modification in the doumeins (well-developed articulatory surface of the interopercular for the ceratohyal posterior, etc.) are quite different from those related with the same modification in the scoloplacids, astroblepids and loricariids (loss of the mandibulo-interopercular ligament) (see above). This homoplastic character could be associated to a more important dilatation of the opercular cavity, what could be related to a benthic life style (see above).

The main homoplasies shared by the doumeins and the astroblepids and loricariids are: 1) *Ventrally placed mouth modified into a sucking disk.* This homoplastic character (see, for example, SCHAEFER, 1990) is characteristic of the doumeins, astroblepids and loricariids, although it also occurs in some mochokids and in some sisorids (SCHAEFER, 1990). Its functional consequence is to confer to the fish the possibility to attach to the substrate (see Fig. 10A→B). 2) *Ligamentous connection between the palatine and the ethmoidal region.* In the astroblepids (SCHAEFER, 1990), loricariids (VANDEWALLE et al., 1986) and doumeins, the ethmoidal region is connected to the palatine by means of ligaments. However, this connection is realised in a quite different way in each of these groups. In the doumeins, a thick, short ligament (see Fig. 4) links the anterior region of both the palatine and the mesethmoid. In the loricariids these two bones are also ligamentously linked, but by means of a thin, long ligament (see VANDEWALLE et al., 1986). Finally, in the astroblepids the connection between the ethmoidal region and the palatine is realised by a ligament that runs from the palatine to the lateral ethmoid, and not to the mesethmoid (SCHAEFER, 1990). Although it is difficult to decide whether the ligaments present in the Astroblepidae and the Loricariidae are homologous or not, the close phylogenetic relationship between these catfishes and the other loricaroids (CHARDON, 1968; HOWES, 1983b; SCHAEFER & LAUDER, 1986; SCHAEFER, 1990; MO, 1991; etc.) clearly indicates that these ligaments are, in no way, homologous with those of the doumeins. The functional consequence of this character is not clear.

General conclusions

This study reveals that *Phractura*, as well as the other doumeins, present several unusual morphological modifications, which are probably related to two main functional specilizations: the ability to attach the body to the substrate with an oral sucker, and the ability to scrape this substrate. These morpho-functional specialisations are strikingly similar to those of the callichthyid, scoloplacid, astroblepid and loricariid catfishes, and particularly with those of the two latter groups, which also present the ability to attach to the substrate and to scrape it. However, this study reinforces the idea that most morphological homoplasies, even those that are quite similar, could be discriminated if analysed in a careful, detailed way. It is also stressed that several morphological modifications could be related with a sole functional specialisation. It his hoped that our results could be useful in future evolutionary, functional, morphological, ecological, ethological, systematic and phylogenetic studies concerning not only the amphiliids, but also the catfishes in general.

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