

On the osteology and myology of the cephalic region and pectoral girdle of *Liobagrus reini* Hilgendorf, 1878, with a discussion on the phylogenetic relationships of the Amblycipitidae (Teleostei: Siluriformes)

Rui Diogo, Michel Chardon and Pierre Vandewalle

Laboratory of Functional and Evolutionary Morphology, Bat. B6,
University of Liège, B-4000 Sart-Tilman (Liège), Belgium

ABSTRACT. The cephalic and pectoral girdle structures of *Liobagrus reini* are described in detail and compared with those of *Amblyceps mangois*, as well as of several other catfishes, as the foundation for a discussion on the phylogenetic relationships of the Amblycipitidae. Our observations and comparisons support de Pinna's (1996) phylogenetic hypothesis, according to which the Amblycipitidae, plus the Akysidae, Sisoridae, Erethistidae and the Aspredinidae, form a monophyletic clade, the superfamily Sisoroidea. In addition, our observations and comparisons pointed out a potentially new amblycipitid synapomorphy, namely: the hypobranchial foramen of the parurohyal is markedly enlarged, with the length of the foramen being superior to half of the length of the main body of the parurohyal.

KEY WORDS : Akysidae, Amblycipitidae, catfish, cephalic region, comparative morphology, *Liobagrus*, myology, pectoral girdle, phylogeny, Siluriformes.

INTRODUCTION

The Siluriformes is "one of the economically important groups of fresh and brackish water fishes in the world: in many countries, member species form a significant part of inland fisheries; several species have been introduced into fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade" (TEUGELS, 1996). The Amblycipitidae, with only three genera (*Liobagrus* Hilgendorf, 1878 *Amblyceps* Blyth, 1858 and *Xiurenbagrus* Chen & Lundberg, 1994) and 15 species is one of the smallest families of catfishes (CHEN & LUNDBERG, 1994). The phylogeny and systematics of the Amblycipitidae were recently revised by CHEN & LUNDBERG (1994). According to these authors, the genus *Xiurenbagrus* is the sister-group of a clade formed by the genus *Liobagrus* and the genus *Amblyceps*, with these three genera being, in turn, the sister-group of a clade containing the two akysid genera, *Akysis* and *Parakysis* (although CHEN & LUNDBERG referred to a monogeneric family Akysidae and to a monogeneric family Parakysidae, the genera *Akysis* and *Parakysis* are nowadays included in a single family, the Akysidae: see FERRARIS & DE PINNA, 1999). Such a sister-group relationship between the Amblycipitidae and the Akysidae was, however, contradicted in a later study by DE PINNA (1996). In fact, according to DE PINNA (1996), the Amblycipitidae is not the sister-group of the Akysidae, but instead the sister-group of a clade formed by this latter family, the Sisoridae, the Aspredinidae and the Erethistidae, with all the five fami-

lies forming the superfamily Sisoroidea, a hypothesis posteriorly reiterated by DE PINNA (1998).

It is worthy of note that, despite the large number of studies concerning siluriform morphology (e.g., REGAN, 1911; GAUBA, 1962, 1966, 1968, 1969; MAHAJAN, 1963, 1966ab, 1967ab; ALEXANDER, 1965; CHARDON, 1968; GOSLINE, 1975; GHIOT, 1978; GHIOT et al., 1984; ARRATIA, 1987, 1990, 1992; ARRATIA & SCHULTZE, 1990; MO, 1991; HE, 1996; DIOGO et al., 1999, 2000, 2001ab; DIOGO & CHARDON, 2000abc; etc.) the only few, somewhat detailed morphological descriptions of the amblycipitid catfishes published so far are those of TILAK (1967), CHARDON (1968), CHEN & LUNDBERG (1994) and DE PINNA (1996). Moreover, as these descriptions are almost exclusively restricted to the osteology and external anatomy of the amblycipitids, some important aspects of the morphology of these fishes, such as, for example, the configuration of both the muscles and the ligaments of the cephalic region and the pectoral girdle, or the configuration of the structures associated with their mandibular barbels, are practically unknown. This not only complicates the study of the functional morphology of the amblycipitids, but also restricts considerably the data available to infer the synapomorphies and the phylogenetic relationships of these catfishes (see DE PINNA, 1996).

The aim of this work is to describe in detail the bones, cartilages, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of the amblycipitid *Liobagrus reini* Hilgendorf, 1878, and to compare these structures with those of a representative of one of the two other amblycipitid genera, namely *Amblyceps mangois* (Hamilton, 1822), as well as of several other catfishes, as the foundation for a discussion on the phylogenetic relationships of the Amblycipitidae.

MATERIAL AND METHODS

The fishes studied are from the collection of our laboratory (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), from the University of Gent (UG) 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 DYKE's 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsin-cleared and alizarine-stained (c&s) or alcohol fixed (alc) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

Acanthodoras catophractus (Doradidae): USNM 034433, 1 (alc). *Ageneiosus vittatus* (Auchenipteridae): USNM 257562, 1 (alc). *Ailia colia* (Shilbidae): USNM 165080, 1 (alc). *Akysis leucorhynchus* (Akysidae): USNM 109636, 2 (alc). *Amblyceps mangois* (Amblycipitidae): USNM 109634, 2 (alc). *Amiurus nebolosus* (Ictaluridae): USNM 246143, 1 (alc); USNM 73712, 1 (alc). *Amphilius brevis* (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c&s). *Anadoras weddellii* (Doradidae): USNM 317965, 1 (alc). *Andersonia leptura* (Amphiliidae): MNHN 1961-0600, 2 (alc); *Arius hertzbergii* (Ariidae): LFEM, 1 (alc). *Arius heudelotii* (Ariidae): LFEM, 4 (alc). *Aspredo aspredo* (Aspredinidae): USNM 226072, 1 (alc). *Auchenipterus dentatus* (Auchenipteridae): USNM 339222, 1 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagarius yarrelli* (Sisoridae): USNM 348830, 2 (alc); LFEM, 1 (c&s). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrichthys macropterus* (Bagridae): USNM 230275, 1 (alc). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (c&s). *Belonoglanis tenuis* (Amphiliidae): MRAC P.60494, 2 (alc). *Bunocephalus knerii* (Aspredinidae): USNM 177206, 2 (alc). *Calophysus macropterus* (Pimelodidae): USNM 306962, 1 (alc). *Centromochlus hecheilii* (Auchenipteridae): USNM 261397, 1 (alc). *Cetopsis coecutiens* (Cetopsidae): USNM 265628, 2 (alc). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 2 (c&s). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 2 (c&s). *Clariallabes melas* (Clariidae): LFEM, 2 (alc). *Clarias garipepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Conta conta* (Erethistidae): LFEM, 2 (alc). *Cranoglanis boudierus* (Cranoglanididae): LFEM, 2 (alc). *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Doras punctatus* (Doradidae): USNM 284575, 1 (alc). *Doumea typica* (Amphiliidae): MRAC 93-041-P-1335, 1 (alc). *Erethistes pusillus* (Erethistidae): USNM 044759, 2 (alc). *Franciscodoras marmuratus* (Doradidae): USNM 196712, 2 (alc). *Gagata cenia* (Sisoridae): USNM 109610, 2 (alc). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Glyptosternon reticulatum* (Sisoridae): USNM 165114, 1 (alc). *Glyptothorax fukiensis* (Sisoridae): USNM 087613, 2 (alc). *Goeldiella eques* (Pimelodidae): USNM 066180, 1 (alc). *Hara filamentosa* (Erethistidae): USNM 288437, 1 (alc). *Helicophagus leptorhynchus* (Pangasiidae): USNM 355238, 1 (alc). *Helogenes marmuratus* (Cetopsidae): USNM 264030, 1 (alc). *Hemibagrus nemurus* (Bagridae): USNM 317590, 1 (alc); *Hemiceptopsis candiru* (Cetopsidae): USNM 167854, 1 (alc). *Hepapterus mustelinus* (Pimelodidae): USNM 287058, 2 (alc). *Heterobranchius longifilis* (Clariidae): LFEM, 2 (alc). *Heteroneustes fossilis* (Heteropneustidae): USNM 343564, 2 (alc); USNM 274063, 1 (alc); LFEM, 2 (alc). *Hypophthalmus edenta-*

tus (Pimelodidae): USNM 226140, 1 (alc). *Ictalurus punctatus* (Ictaluridae): USNM 244950, 2 (alc). *Laiides hexanema* (Shilbidae): USNM 316734, 1 (alc). *Leptoglanis rotundiceps* (Amphiliidae): MRAC P.186591-93, 3 (alc). *Liobagrus reini* (Amblycipitidae): USNM 089370, 2 (alc). *Loricaria cataphracta* (Loricariidae): LFEM, 1 (alc). *Microglanis cottoides* (Pimelodidae): USNM 285838, 1 (alc). *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Nematogenys inermis* (Nematogenyidae): USNM 084346, 1 (alc). *Nothoglanidium thomasi* (Claroteidae): LFEM, 2 (alc). *Parakysis anomalopteryx* (Akysidae): USNM 230307, 2 (alc). *Paramphilius trichomycteroides* (Amphiliidae): LFEM, 2 (alc). *Pangasius larnaudii* (Pangasiidae): USNM 288673, 1 (alc). *Pangasius sianensis* (Pangasiidae): USNM 316837, 2 (alc). *Paraplotosus albilabris* (Plotosidae): USNM 173554, 2 (alc). *Phractura brevicauda* (Amphiliidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c&s). *Phractura intermedia* (Amphiliidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias* (Pimelodidae): LFEM, 2 (alc); USNM 076925, 1 (alc). *Plotosus lineatus* (Plotosidae): USNM 200226, 2 (alc). *Pseudeutropius brachyopterus* (Shilbidae): USNM 230301, 1 (alc). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (c&s). *Pseudopimelodus raninus* (Pimelodidae): USNM 226136, 2 (alc). *Pseudoplatystoma fasciatum* (Pimelodidae): USNM 284814, 1 (alc). *Rhamdia guatemalensis* (Pimelodidae): USNM 114494, 1 (alc). *Rita chrysea* (Bagridae): USNM 114948, 1 (alc). *Schilbe intermedius* (Shilbidae): MRAC P.58661, 1 (alc). *Silurranodon auritus* (Shilbidae): USNM 061302, 2 (alc). *Silurus asotus* (Siluridae): USNM 130504, 2 (alc). *Synodontis clarias* (Mochokidae): USNM 229790, 1 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc). *Trachyglanis incae* (Amphiliidae): MRAC P.125552-125553, 2 (alc). *Uegitglanis zammaronoi* (Clariidae): MRAC P-15361, 1 (alc). *Wallago attu* (Siluridae): USNM 304884, 1 (alc). *Xylophius magdalenae* (Aspredinidae): USNM 120224, 1 (alc). *Zaireichthys zonatus* (Amphiliidae): MRAC 89-043-P-2243-2245, 3 (alc).

RESULTS

In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region follows basically that of ARRATIA (1997). However, for the several reasons explained in detail in our recent papers (DIOGO et al., 2001a; DIOGO & CHARDON, in press), with respect to the skeletal components of the suspensorium we follow DIOGO et al. (2001a). The myological nomenclature is based mainly on WINTERBOTTOM (1974), but for the different adductor mandibulae sections, DIOGO & CHARDON (2000a) is followed. In relation to the muscles associated with the mandibular barbels, which were not studied by WINTERBOTTOM (1974), DIOGO & CHARDON (2000b) is followed. Concerning the nomenclature of the pectoral girdle bones and muscles, DIOGO et al. (2001b) is followed.

Liobagrus reini

Osteology

Os mesethmoideum. Situated on the antero-dorsal surface of the neurocranium (Figs 1,2), with each of its antero-ventro-lateral margins ligamentously connected to the premaxillary.

Os lateroethmoideum. The lateral-ethmoid (Figs 1, 2, 3) presents a well-developed, laterally-directed articulatory facet for the autopalatine.

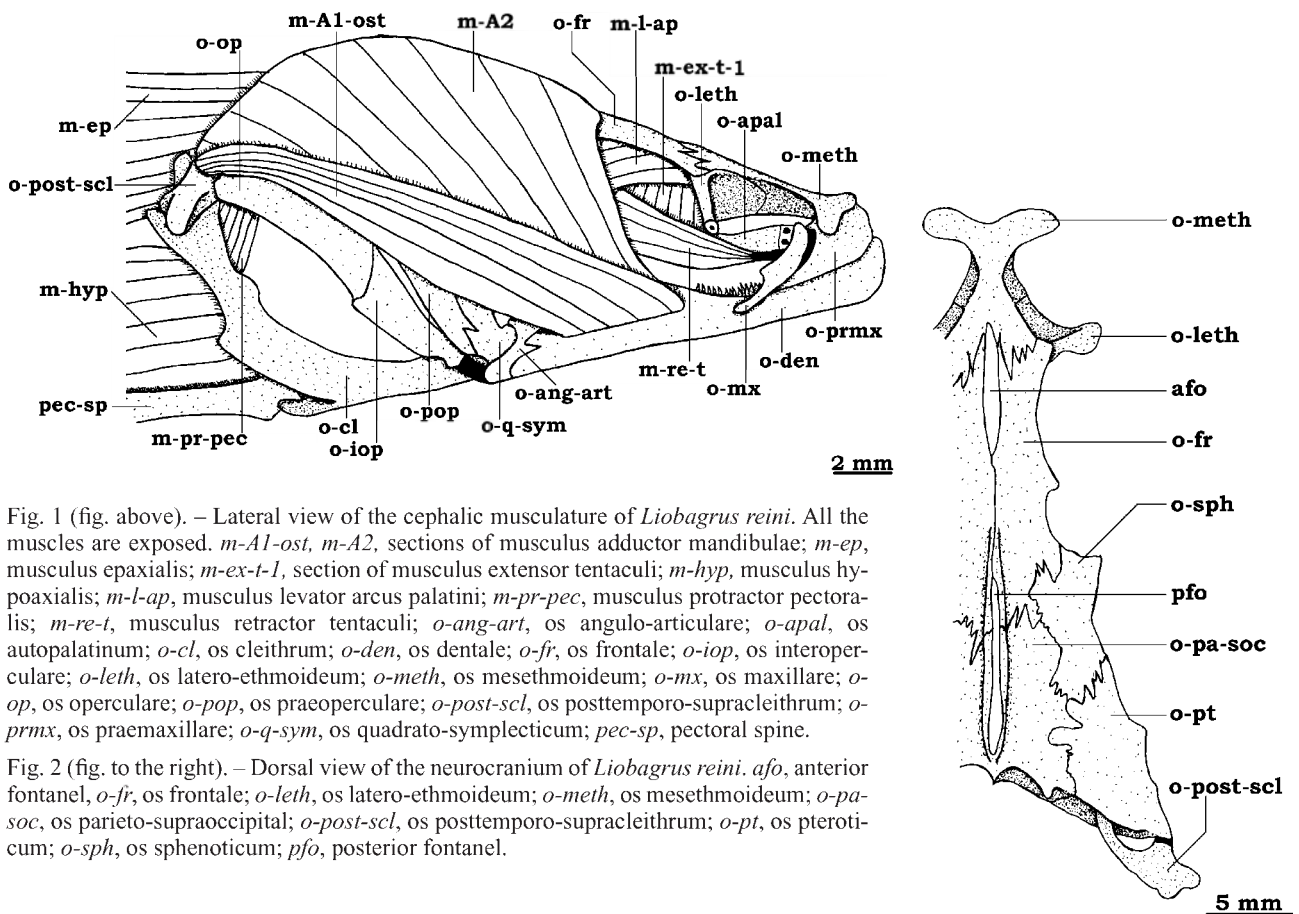


Fig. 1 (fig. above). – Lateral view of the cephalic musculature of *Liobagrus reini*. All the muscles are exposed. *m-A1-ost*, *m-A2*, sections of musculus adductor mandibulae; *m-ep*, musculus epaxialis; *m-ex-t-1*, section of musculus extensor tentaculi; *m-hyp*, musculus hypaxialis; *m-l-ap*, musculus levator arcus palatini; *m-pr-pec*, musculus protractor pectoralis; *m-re-t*, musculus retractor tentaculi; *o-ang-art*, os angulo-articulare; *o-apal*, os autopalatini; *o-cl*, os cleithrum; *o-den*, os dentale; *o-fr*, os frontale; *o-iop*, os interoperculare; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-mx*, os maxillare; *o-op*, os operculare; *o-pop*, os praeoperculare; *o-post-scl*, os posttemporo-supracleithrum; *o-prmx*, os praemaxillare; *o-q-sym*, os quadrato-symplecticum; *pec-sp*, pectoral spine.

Fig. 2 (fig. to the right). – Dorsal view of the neurocranium of *Liobagrus reini*. *afo*, anterior fontanel; *o-fr*, os frontale; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-pa-soc*, os parieto-supraoccipitale; *o-post-scl*, os posttemporo-supracleithrum; *o-pt*, os pteroticum; *o-sph*, os sphenoticum; *pfo*, posterior fontanel.

Os praeomerale. Well-developed (Fig. 3), T-shaped bone without a ventral tooth-plate.

Os orbitosphenoidem. Posterior to the lateral ethmoid, with the dorsal edge of its lateral wall being sutured with the ventral surface of the frontal.

Os pterosphenoidem. Posterior to the orbitosphenoid, covering, together with this bone, the gap between the frontals and the parasphenoid.

Os parasphenoidem. The parasphenoid (Fig. 3) is the longest bone of the cranium. It bears a pair of ascending flanges, which suture with the pterosphenoids and prootics.

Os frontale. The frontals (Figs 1, 2) are large bones that constitute a great part of the cranial roof. They are largely separated anteriorly and posteriorly by the anterior and the posterior fontanels, respectively (Fig. 2).

Os sphenoticum. Slightly smaller than the pterotic (Fig. 2), constituting, together with this bone, an articular facet for the hyomandibulo-metapterygoid.

Os pteroticum. Well-developed, irregularly-shaped bone situated posteriorly to the sphenotic (Fig. 2).

Os prooticum. Together with the pterosphenoid and the parasphenoid, it borders the well-developed foramen of the trigemino-facial nerve complex.

Os epioccipitale. Situated on the posterior surface of the neurocranium. The extrascapulars are missing.

Os exoccipitale. The well-developed exoccipitals are situated laterally to the basioccipital.

Os basioccipitale. Well-developed, unpaired bone, forming the posterior-most part of the floor of the neurocranium. Its ventro-lateral surfaces are ligamentously connected to the ventro-medial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. Large bone constituting the postero-dorso-median surface of the cranial roof, which bears a small, triangular postero-median process (Fig. 2).

Os angulo-articulare. This bone (Fig. 1), plus the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible. Postero-dorsally, the angulo-articular has an articular facet for the quadrato-symplectic. Postero-ventrally, it is ligamentously connected to both the interopercular (Figs 1, 4) and the posterior ceratohyal (Fig. 4).

Os dentale. The toothed dentary (Fig. 1) recovers the great majority of the lateral surface of the mandible. The postero-dorsal margin of the dentary forms, together with the antero-dorsal margin of the angulo-articular, a somewhat developed dorsal process (processus coronoideus).

Os coronomeckelium. Small bone lodged in the medial surface of the mandible. Postero-dorsally it bears a crest for attachment of the adductor mandibulae.

Os praemaxillare. The two premaxillaries form a U-shaped structure with its lateral tips curved posteriorly and ligamentously connected, by means of a strong, long ligament, to the antero-lateral tip of the ento-ectopterygoid (Fig. 3). Ventrally, the premaxillaries bear a well-developed tooth-plate with numerous small teeth having their tips slightly turned backward (Fig. 3).

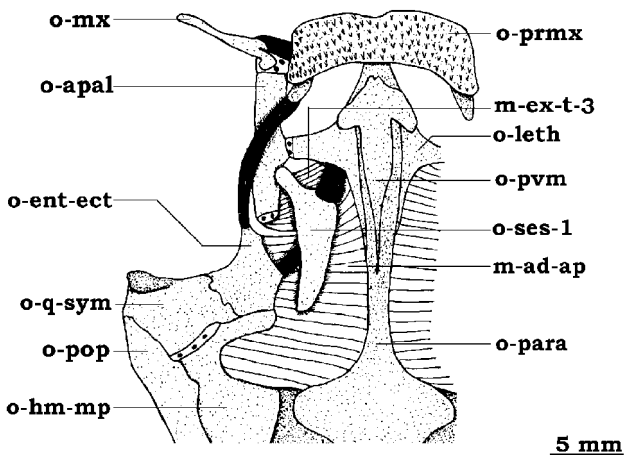


Fig. 3. – Ventral view of the neurocranium of *Liobagrus reini*. The suspensorium, palatine-maxillary system and the muscles and ligaments associated with these structures are also illustrated. *m-ad-ap*, musculus adductor arcus palatini; *m-ex-t-3*, section of musculus extensor tentaculi; *o-apal*, os autopalatinum; *o-ent*, os ento-ectopterygoideum; *o-hm-mp*, os hyomandibulo-metapterygoideum; *o-leth*, os lateroethmoideum; *o-mx*, os maxillare; *o-para*, os parasphenoideum; *o-pop*, os praeoperculare; *o-prmx*, os praeomaxillare; *o-pvm*, os praeomerale; *o-q-sym*, os quadrato-symplecticum; *o-ses-1*, sesamoidal bone 1 of the suspensorium.

Os maxillare. The well-developed, elongated maxillary is connected to the premaxillary by means of a strong, short ligament (Figs 1, 3). As in most catfishes, the maxillary barbels are supported by the maxillaries.

Os autopalatinum. The autopalatine (Figs 1, 3) is a rod-like, antero-posteriorly elongated bone with its posterior portion somewhat expanded dorso-ventrally. Its posterior end is capped by a small cartilage (Fig. 3). Its anterior end is tipped by a well-developed cartilage with two antero-lateral concavities, which accept the two proximal heads of the maxillary (Fig. 3). Medially, the autopalatine articulates, by means of a small, circular articular surface, with the lateral ethmoid (Fig. 32).

Os hyomandibulo-metapterygoideum. The homology, and, thus, the correct denomination, of this bone, as well as of the other suspensorium elements 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; DIOGO et al., 2001a; DIOGO & CHARDON, in press; etc.). As mentioned before, for the several reasons explained in detail in our recent papers (DIOGO et al., 2001a; DIOGO & CHARDON, in press), the nomenclature used here to describe these elements follows strictly that presented by DIOGO et al. (2001a). The hyomandibulo-metapterygoideum (Fig. 3) is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercular.

Os sesamoideum 1. Well-developed, 7-shaped bone attached, by means of two thick ligaments, to the ento-ectopterygoid and to the prevomer, respectively (Fig. 3). Its antero-dorso-lateral surface is weakly attached, *via* connective tissue, to the postero-ventral surface of the autopalatinum. The sesamoid bones 2 and 3 (see (DIOGO et al., 2001a)) are absent.

Os entopterygoide-ectopterygoideum. Poorly-developed, with its posterior surface being sutured with both the hyomandibulo-metapterygoideum and the quadrato-symplectic (Fig. 3). Antero-laterally, it presents a well-defined thickening for ligamentous connection with the sesamoid bone 1 of the suspensorium.

Os quadrato-symplecticum. The quadrato-symplectic (Figs. 1, 3) presents a well-developed anterior articular surface to articulate with the postero-dorsal surface of the angulo-articular.

Os praeoperculare. Long and thin bone (Figs 1, 3) firmly sutured to both the hyomandibulo-metapterygoideum and the quadrato-symplectic.

Os operculare. The opercular (Figs 1, 3) is a well-developed, roughly triangular bone attached ventrally, by means of connective tissue, to the interopercular. It presents a well-developed, dorso-ventrally elongated antero-dorsal articular surface for the hyomandibulo-metapterygoideum.

Os interoperculare. Its anterior surface is ligamentously connected to the postero-ventral margin of the mandible (Figs 1, 4). Medially, the interopercular articulates with the lateral surface of the posterior ceratohyal.

Os ceratohyale posterior. Well-developed, somewhat triangular bone connected, by means of two strong ligaments, to the postero-ventral edge of the mandible (Fig. 4) and to the medial surface of the suspensorium (the interhyal is missing), respectively.

Os ceratohyale anterior. Elongated bone that supports, together with the posterior ceratohyal, the branchiostegal rays.

Os hypohyale ventrale. The ventral hypohyals are ligamentously connected to the antero-lateral edges of the parurohyal (Fig. 4).

Os parurohyale. The parurohyal is an irregular bone presenting two well-developed postero-lateral arms and a poorly-developed postero-medial process (Fig. 4). Its hypobranchial foramen (see ARRATIA & SCHULTZE, 1990) is markedly enlarged, with the length of this foramen being superior to half of the length of the main body of the parurohyal.

Os posttemporo-supracleithrum. This bone (Figs 1, 2), plus the cleithrum and the scapulo-coracoid, constitute the pectoral girdle. Its dorso-medial limb is loosely attached to the neurocranium and its ventro-medial limb is ligamentously connected to the basioccipital. Its postero-lateral margin is deeply forked, forming an articulating groove for the upper edge of the cleithrum (Fig. 1).

Os cleithrum. The cleithrum (Figs 1, 4) is a large, stout, well-ossified structure forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially faced groove that accommodates the dorsal condyle of the well-developed pectoral spine. The two cleithra are attached in the antero-medial line via connective tissue. Antero-ventro-mesially each cleithrum bears a somewhat well-developed, antero-mesially pointed, anterior projection, with the structure formed by the association of the antero-mesial projections of both cleithra having, thus, a triangular shape (see Fig. 4). The poorly-developed humeral process of the cleithrum is surrounded posteriorly by soft tissue, which, in turn, is associated posteriorly with a long, thick ligament attached to the anterior surface of the parapophysis of the sixth vertebra.

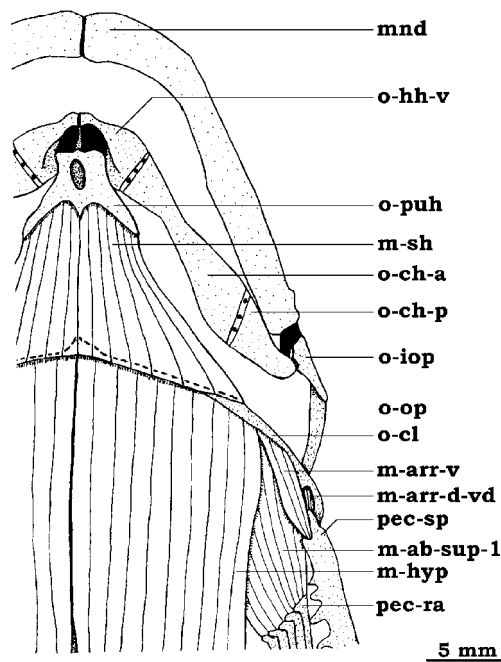


Fig. 4. – Ventral view of the cephalic region and pectoral girdle of *Liobagrus reini*. The muscles associated with the pectoral girdle are also illustrated. *m-ab-sup-1*, section 1 of musculus abductor superficialis; *m-arr-d-vd*, ventral division of musculus arrector dorsalis; *m-arr-v*, musculus arrector ventralis; *m-hyp*, musculus hypoaxialis; *mnd*, mandible; *m-sh*, musculus sternohyoideus; *o-ch-a*, os ceratohyale anterior; *o-ch-p*, os ceratohyale posterior; *o-cl*, os cleithrum; *o-hh-v*, os hypohyale ventrale; *o-iop*, os interoperculare; *o-op*, os operculare; *o-puh*, os parurohyale; *pec-ra*, pectoral rays; *pec-sp*, pectoral spine.

Os scapulo-coracoideum. Elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge. Medially it joins its counterpart in an interdigitation of several strong serrations. There is a well-developed mesocoracoid arch.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (see DIOGO & CHARDON, 2000a) originates on the pterotic, preopercular, hyomandibulo-metapterygoid and quadrate-symplectic, and inserts on the dentary (Fig. 1). The A2 (Fig. 1), which lies dorso-mesially to the A1-ost, attaches postero-dorsally on the parieto-supraoccipital, pterotic, sphenotic and frontal antero-ventrally on the dorso-medial surface of the dentary. The adductor mandibulae A3' originates on the hyomandibulo-metapterygoid and the preopercular, and inserts tendinously on the coronomeckelian bone. There is no A3'' nor A ω .

Musculus levator arcus palatini. The levator arcus palatini (Fig. 1) is a well-developed muscle situated medially to the adductor mandibulae A3'. It originates on the sphenotic, frontal and lateral-ethmoid and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (Fig. 3) runs from the parasphenoid, pterosphenoid, orbitosphenoid and lateral ethmoid to the hyomandibulo-metapterygoid, the ento-ectopterygoid and the sesamoid bone 1 of the suspensorium.

Musculus levator operculi. It originates on the lateral margin of the pterotic and inserts on the dorsal surface of the opercular.

Musculus adductor operculi. Situated medially to the levator operculi, it originates on the ventral surface of the pterotic and inserts on the dorso-medial surface of the opercular.

Musculus adductor hyomandibularis. Small muscle situated mesially to the levator operculi but laterally to the adductor operculi. It originates on the ventral surface of the pterotic and inserts on the postero-dorso-median surface of the hyomandibulo-metapterygoid.

Musculus dilatator operculi. Well-developed, originating on the pterosphenoid, frontal, sphenotic and also on the dorso-lateral surface of the hyomandibula and inserting on the antero-dorsal margin of the opercular.

Musculus extensor tentaculi. This muscle is divided into three bundles. The extensor tentaculi 1 (Fig. 1) runs from both the orbitosphenoid and the lateral ethmoid to the postero-dorsal surface of the autopalatine. The extensor tentaculi 2 originates on the lateral ethmoid and inserts on the postero-medial surface of the autopalatine. The extensor tentaculi 3 (Fig. 3) runs from the lateral ethmoid and the orbitosphenoid to the postero-ventral margin of the autopalatine.

Musculus retractor tentaculi. Well-developed muscle situated medially to the adductor mandibulae (Fig. 1). It originates on the lateral surface of the hyomandibulo-metapterygoid and inserts, by means of a thick tendon, on the maxillary.

Musculus protractor hyoidei. This muscle (Fig. 5) has three parts. The pars ventralis, in which are lodged the cartilages associated with the internal and external mandibular barbels, originates on both the anterior and posterior ceratohyals and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis (Fig. 5). The pars lateralis runs from the posterior ceratohyal to the ventro-medial face of the dentary (Fig. 5). The pars dorsalis runs from both the anterior and the posterior ceratohyals to the dentary.

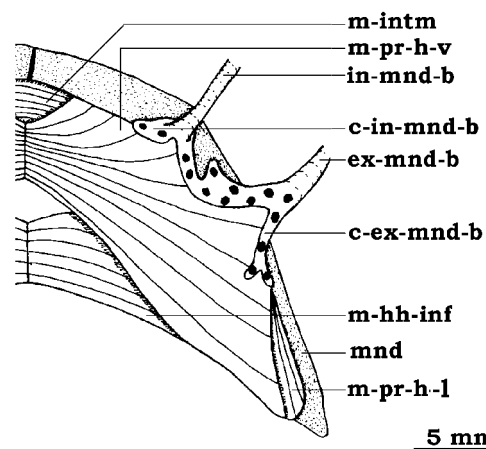


Fig. 5. – Ventral view of the cephalic musculature of *Liobagrus reini*. *c-in-mnd-b*, cartilago internus mandibularis tentaculi; *c-ex-mnd-b*, cartilago externus mandibularis tentaculi; *ex-mnd-b*, *in-mnd-b*; external and internal mandibular barbels; *m-hh-inf*, musculus hypochoideus inferior; *m-intm*, musculus intermandibularis; *mnd*, mandible; *m-pr-h-l*, *m-pr-h-v*, pars lateralis and ventralis of musculus protractor hyoideus.

Musculus retractor externi mandibularis tentaculi. Small muscle situated dorsally to the pars ventralis of the protractor hyodei and running from the dentary to the cartilage associated with the outer mandibular barbel, which is connected with the cartilage associated with the internal mandibular barbel and is markedly bifurcated posteriorly (Fig. 5).

Musculus retractor interni mandibularis tentaculi. Small muscle dorsal to the pars ventralis of the protractor hyodei. It attaches anteriorly to the dentary and posteriorly to the cartilage associated with the internal mandibular barbel.

Musculus intermandibularis. Small muscle joining the two mandibles (Fig. 5).

Musculus hyohyoideus inferior. Thick muscle (Fig. 5) attaching medially on a median aponeurosis and laterally on the ventral surfaces of the ventral hypohyal, the anterior ceratohyal and the posterior ceratohyal.

Musculus hyohyoideus abductor. It runs from the first (medial) branchiostegal ray to a median aponeurosis, which is associated with two long, strong tendons, attached, respectively, to the two ventral hypohyals.

Musculus hyohyoideus adductor. Each hyohyoideus adductor connects the branchiostegal rays of the respective side.

Musculus sternohyoideus. It runs from the posterior portion of the parurohyal to the anterior portion of the cleithrum (Fig. 5).

Musculus arrector ventralis. It runs from the cleithrum to the ventral condyle of the pectoral spine (Fig. 5).

Musculus arrector dorsalis. This muscle, dorsal to the hypoaxialis, the arrector ventralis and the abductor superficialis, is differentiated into two well-developed divisions. The ventral division (Fig. 5), situated on the ventral surface of the pectoral girdle, originates on the ventral margin of both the cleithrum and the scapulo-coracoid and inserts on the antero-lateral edge of the pectoral spine. The dorsal division, situated on the dorsal surface of the pectoral girdle, originates on the dorso-medial edge of the scapulo-coracoid and inserts on the anterior edge of the dorsal condyle of the pectoral spine.

Musculus abductor profundus. It originates on the posterior surface of the scapulo-coracoid and inserts on the medial surface of the dorsal condyle of the pectoral spine.

Musculus abductor superficialis. This muscle is differentiated into two sections. The larger section (Fig. 5: m-ab-sup-1) runs from the ventral margins of both the cleithrum and the scapulo-coracoid to the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section, situated dorsally to the larger one, runs from the lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus adductor superficialis. This muscle is situated on the posterior margin of the pectoral girdle and is divided into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from both the postero-ventro-lateral edge of the scapulo-coracoid and the dorsal surface of the proximal ra-

dials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus protractor pectoralis. Well-developed muscle (Fig. 1) running from the ventral surfaces of both the pterotic and the posttemporo-supracleithrum to the antero-dorsal surface of the cleithrum.

Amblyiceps mangois

The principal differences between the structures of the cephalic region and pectoral girdle of this species and those of *Liobagrus reini* are that in *Amblyiceps mangois*: 1) the cartilage associated with the inner mandibular barbel is pierced by a well-developed, triangular foramen; 2) the articulatory surface of the opecular for the hyomandibulo-metapterygoid is not elongated dorso-ventrally; 3) the interhyal is present; 4) the maxillary bone is not elongated proximo-distally; 5) the posterior fontanel of the neurocranium is completely surrounded by the parieto-supraoccipital, and not by both this bone and the frontal; 6) the muscle abductor profundus is significantly more developed than in *Liobagrus reini*, extending mesially to reach the postero-mesial surface of the scapulo-coracoid.

DISCUSSION

Our observations and comparisons support DE PINNA'S (1996) phylogenetic hypothesis in that the Amblycipitidae plus the Akysidae, Sisoridae, Erethistidae and Aspredinidae form a monophyletic clade, the superfamily Sisoroidea sensu DE PINNA (1996). In fact, our study not only confirmed the synapomorphies given by DE PINNA to support the monophyly of the Sisoroidea (see DE PINNA, 1996: 59-60), but also pointed out an additional synapomorphy to support this superfamily: *Presence of a well-developed, antero-mesially-pointed projection on the antero-ventro-mesial surface of the cleithrum* (Fig. 4).

Plesiomorphically in catfishes the cleithrum lacks major projections or processes on its antero-ventro-mesial surface. However, in the catfishes of the superfamily Sisoroidea, with the exception of the Aspredinidae, each cleithrum bears antero-ventro-mesially a well-developed, antero-mesially pointed, anterior projection, with the structure formed by the association of the antero-mesial projections of both cleithra having, thus, a triangular shape (see Fig. 4). The presence of such a projection clearly appears, thus, to represent a Sisoroidea synapomorphy secondarily reversed in aspredinids, since this is by far the most parsimonious hypothesis supporting the phylogenetic position of the Aspredinidae within the Sisoroidea (see DE PINNA, 1996; DIOGO et al., 2001c, 2002).

According to DE PINNA (1996), the Amblycipitidae occupy the most plesiomorphic position within the superfamily Sisoroidea, with the intra-relationships among members of this superfamily being: (Amblycipitidae + (Akysidae + (Sisoridae + (Aspredinidae + Erethistidae))). However, as noted by DE PINNA (1996: 76) himself, contrarily to the grouping of the Sisoridae, Aspredinidae and Erethistidae, which is very well supported (and was subsequently also confirmed by DIOGO et al., 2001c, 2002), the proposal of a sister-group relationship between the Akysidae and these three families is based on scarce evidence.

In fact, this proposal relied “on three synapomorphies, one of these (supratemporal fossae present) shows reversals, and the other two (supracleithrum strongly attached to skull; posterior nuchal plate with anterior process facet for articulation with anterior nuchal plate) have a number of putatively homoplastic occurrences elsewhere in siluriforms” (DE PINNA, 1996: 76). The evidence presented by DE PINNA (1996) to support a sister-group relationship between the Akysidae and the clade (Sisoridae + (Aspredinidae + Erethistidae)) was not significantly stronger than the evidence supporting the alternative, most traditional (see, e.g., REAGAN, 1911; CHEN & LUNDBERG, 1994) hypothesis of a sister-group relationship between the Akysidae and the Amblycipitidae (with the clade formed by these two families being, in turn, the sister-group of the clade formed by the Sisoridae, Erethistidae and Aspredinidae).

Our observations and comparisons confirmed the three synapomorphies provided by DE PINNA (1996) to support the grouping of the Akysidae, Sisoridae, Aspredinidae and Erethistidae, and, in addition, pointed out an additional synapomorphy to support the grouping of these four families. This additional synapomorphy is described below: *Coronoid process of the mandible exclusively formed by the dorsal margin of the dentary.*

Plesiomorphically in catfishes the coronoid process of the mandible is constituted by the dorsal surfaces of both the dentary and the angulo-articular bones. However, in the Akysidae, Erethistidae and Sisoridae the coronoid process is exclusively formed by the dorsal margin of the dentary (see, e.g., DIOGO et al., 2002: Fig. 3A). Therefore, this character appears to represent a synapomorphy of the clade constituted by the Akysidae, Sisoridae, Aspredinidae and Erethistidae, which was secondarily reversed in the aspredinids (see DIOGO et al., 2001c).

Although the present study supports, thus, DE PINNA's (1996) grouping of the Akysidae, Sisoridae, Erethistidae and Aspredinidae, we consider, as did DE PINNA, that it is important to point out that the evidence to support this grouping is scarce and that there are some conflicting characters with this hypothesis. One of these characters is the peculiar 7-shape of the sesamoid bone 1 of the suspensorium (Fig. 3). DE PINNA (1996: 70) mentioned this peculiar feature, mentioning that it was present in the amblycipitids and in *Parakysis*. However, this peculiar feature is also present in the other akysid genus, *Akysis*, as it was clearly noted by CHEN & LUNDBERG (1994: 795) and confirmed in the present study. The presence of this peculiar, derived feature in the Amblycipitidae and Akysidae genera thus conflicts with the grouping of the Akysidae with the families Sisoridae, Aspredinidae and Erethistidae. The other conflicting character concerns the bifurcation of the basal cartilages of the external mandibular barbels. Contrary to the situation in most catfishes, in both the akysids and the amblycipitids (see Fig. 5), as well as in the glyptosternin Sisoridae (see DIOGO et al., 2002: Fig. 5), the basal cartilages of the outer mandibular barbels are bifurcated posteriorly. Attending to the well-supported grouping of the Sisoridae, Aspredinidae and Erethistidae in a monophyletic clade (see DE PINNA, 1996; DIOGO et al., 2001c, 2002), the taxonomic distribution of this character would support a sister-group relationship between the Akysidae and the Amblycipitidae, with an independent, homoplastic acquisition in the glyptosternin

Sisoridae. It is also important to refer to three other characters discussed by DE PINNA (1996: 69), namely the “morphology of the first proximal pectoral radial”, the “presence of a spur-like process on the quadrate” and the “state of the humerovertebral ligament”. These refer to derived features present in the amblycipitids and in *Parakysis*, but not in *Akysis*, which, thus, could either be interpreted as independently acquired in the amblycipitids and in *Parakysis*, or as acquired in the amblycipitids plus akysids and subsequently reversed in *Akysis*. In this latter case, they would support a sister-group relationship between the families Amblycipitidae and Akysidae.

In summary, it can be said that although this study supports, with an additional synapomorphy, DE PINNA's (1996) grouping of the Akysidae, Sisoridae, Erethistidae and Aspredinidae, the phylogenetic position of the Amblycipitidae remains a problematic topic within the interrelationships of the superfamily Sisoroidea.

With respect to the synapomorphies of the Amblycipitidae, six characters were presented by DE PINNA (see DE PINNA, 1996: 60). Our observations and comparisons pointed out a quite peculiar, derived character that is found in both *Liobagrus* and *Amblyceps*, and in no other catfish examined, which, thus, could eventually constitute an additional amblycipitid synapomorphy: the hypobranchial foramen of the parurohyal is markedly enlarged, with the length of the foramen being superior to half of the length of the main body of the parurohyal (Fig. 4). However, since it was not possible to dissect an exemplar of the other amblycipitid genera, *Xiurenbagrus* (see Introduction), and since the parurohyal of *Xiurenbagrus xiurensis*, the only species of this genus, is not described in CHEN & LUNDBERG (1994), it was not possible to confirm if such a feature is, or not, present in this species. Therefore, only when a more detailed osteological description of this species becomes available will it be possible to confirm if this feature represents, or not, an unambiguous synapomorphy of the family Amblycipitidae.

ACKNOWLEDGEMENTS

We thank G.G. Teugels (MRAC), P. Lalelyè (UNB), J. Williams and S. Jewett (USNM) and P. Duhamel (MNH) for kindly providing a large part of the specimens studied in this study. A great part of this work was realised by R. Diogo at the Division of Fishes, USNM (Washington DC). We are thus especially grateful for the support, assistance and advice received from R.P. Vari and S.H. Weitzman during this period. We are also especially grateful to G. Arratia, who, through her valued close cooperation concerning the “Catfishes” book, significantly contributed, although indirectly, to the long stay of R. Diogo at the USNM. We are also pleased to acknowledge the helpful criticism, advice and assistance of L. Taverne, M. Gayet, B.G. Kapoor, F. Meunier, S. He, O. Otero, T.X. de Abreu, D. Adriaens, F. Wagemans, C. Oliveira and E. Parmentier. This project received financial support from the following grant to R. Diogo: PRAXIS XXI/BD/19533/99 (“Fundação para a Ciência e a Tecnologia”, Portuguese Federal Government).

REFERENCES

- 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. (1997). Basal teleosts and teleostean phylogeny. *Palaeo. Ichthyologica*, 7: 5-168.
- ARRATIA, G. & H-P. SCHULTZE (1990). The urohyal: development and homology within osteichthyans. *J. Morphol.*, 203: 247-282.
- 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.
- CHEN, X. & J.G. LUNDBERG (1994). *Xiurenbagrus*, a new genus of amblycipitid catfishes (Teleostei: Siluriformes), and phylogenetic relationships among the genera of Amblycipitidae. *Copeia*, 1994: 780-800.
- 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 Aspredinidae (Teleostei, Ostariophysi). *Fieldiana (Zool.)*, 84: 1-82.
- 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.
- DIOGO, R. & M. CHARDON (2000a). Homologies between different adductor mandibulae sections of teleostean fishes, with a special regard to catfishes (Teleostei: Siluriformes). *J. Morphol.*, 243: 193-208.
- DIOGO, R. & M. CHARDON (2000b). 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 (2000c). Anatomie et fonction des structures céphaliques associées à la prise de nourriture chez le genre *Chrysichthys* (Teleostei: Siluriformes). *Belg. J. Zool.*, 130: 21-37.
- DIOGO, R. & M. CHARDON (in press). On the homologies and evolutionary transformation of the skeletal elements of catfish (Teleostei: Siluriformes) suspensorium: a morpho-functional hypothesis. In: VAL A.L. & B.G. KAPOOR (eds), *Fish adaptations*, 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 docmak*, with a reflection on Bagridae (Teleostei: Siluriformes) autapomorphies. *Neth. J. Zool.*, 49: 207-232.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2000). The origin and transformation of catfish palatine-maxillary system: an example of adaptive macroevolution. *Neth. J. Zool.*, 50: 373-388.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2001a). On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium. *Belg. J. Zool.*, 131: 93-109.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2001b). On the osteology and myology of catfish pectoral girdle, with a reflection on catfish (Teleostei: Siluriformes) plesiomorphies. *J. Morphol.*, 249: 100-125.
- DIOGO, R., M. CHARDON & P. VANDEWALLE (2001c). Osteology and myology of the cephalic region and pectoral girdle of *Bunocephalus knerii*, and a discussion on the phylogenetic relationships of the Aspredinidae (Teleostei: Siluriformes). *Neth. J. Zool.*, 51: 457-481.
- DIOGO, R., M. CHARDON & P. VANDEWALLE (2002). Osteology and myology of the cephalic region and pectoral girdle of *Glyptothorax fukiensis* (Rendahl, 1925), comparison with other sisorids, and comments on the synapomorphies of the Sisoridae (Teleostei: Siluriformes). *Belg. J. Zool.*, 132: 93-101.
- FERRARIS, C.J. & M.C.C. DE PINNA (1999). Higher-level names for Catfishes (Actinopterygii: Ostariophysi: Siluriformes). *Proc. Calif. Acad. Sci.*, 51: 1-17.
- GAUBA, R.K. (1962). The endoskeleton of *Bagarius bagarius* (Ham.). part I – The skull. *Agra Univ. J. Res.*, 11: 75-90.
- GAUBA, R.K. (1966). Studies on the osteology of Indian sisorid catfishes, II. The skull of *Glyptothorax cavia*. *Copeia*, 4: 802-810.
- GAUBA, R.K. (1968). On the morphology of the skull of catfish *Pseudecheneis sulcatus*. *Zool. Anz.*, 181: 226-236.
- GAUBA, R.K. (1969). The head skeleton of *Glyptosternum reticulatum* McClelland & Griffith. *Mon. Zool. Ital.*, 3: 1-17.
- GHIOT, F. (1978). The barbel movements of three South American pimelodid catfishes. *Zool. Anz.*, 200: 1-7.
- GHIOT, F., P. VANDEWALLE & M. CHARDON (1984). Comparaison anatomique et fonctionnelle des muscles et des ligaments en rapport avec les barbillons chez deux familles apparentées de poissons Siluriformes Bagroidei. *Ann. Soc. R. Zool. Belg.*, 114: 261-272.
- GOSLINE, W.A. (1975). The palatine-maxillary mechanism in catfishes with comments on the evolution and zoogeography of modern siluroidei. *Occ. Pap. Calif. Acad. Sci.*, 120: 1-31.
- HE, S. (1996). The phylogeny of the glyptosternoid fishes (Teleostei: Siluriformes, Sisoridae). *Cybium*, 20: 115-159.
- MAHAJAN, C.L. (1963). Sound producing apparatus in an Indian catfish *Sisor rhabdophorus* Hamilton. *J. Linn. Soc. (Zool.)*, 44: 721-724.
- MAHAJAN, C.L. (1966a). Sensory canals of the head in *Sisor rhabdophorus* Hamilton. *Trans. Am. Micr. Soc.*, 85: 548-555.
- MAHAJAN, C.L. (1966b). *Sisor rhabdophorus* – A study in adaptation and natural relationship. I. The head skeleton. *J. Zool. (Lond.)*, 149: 365-393.
- MAHAJAN, C.L. (1967a). *Sisor rhabdophorus* – A study in adaptation and natural relationship. II. The interrelationships of the gas bladder, Weberian apparatus, and membranous labyrinth. *J. Zool. (Lond.)*, 151: 417-432.
- MAHAJAN, C. L. (1967b). *Sisor rhabdophorus* – A study in adaptation and natural relationship. III. The vertebral column, median fins and their musculature. *J. Zool. (Lond.)*, 152: 297-318.
- MO, T. (1991). Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zoologicae*, 17: 1-216.
- REGAN, C.T. (1911). The classification of the teleostean fishes of the order Ostariophysi: 2. Siluroidea. *Ann. & Mag. Nat. Hist.*, 8: 553-577.
- TAYLOR, W.R. & G.C. VAN DYKE (1985). Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 2: 107-119.
- TEUGELS, G.G. (1996). Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): an overview. *Aquat. Living Resour.*, 9: 9-34.
- TILAK, R. (1967). The osteocranium and the Weberian apparatus of *Amblyceps mangois* (Hamilton) (Pisces: Siluroidei) in relation to taxonomy. *Zool. Anz.*, 178: 61-74.
- WINTERBOTTOM, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. (Phil.)*, 125: 225-317.

Received: July 5, 2002

Accepted: December 4, 2002