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Osteology and myology of the cephalic region and pectoral girdle of *Cetopsis coecutiens* Spix & Agassiz, 1829, comparison with other cetopsids, and comments on the synapomorphies and phylogenetic position of the Cetopsidae (Teleostei : Siluriformes)

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ABSTRACT. The cephalic and pectoral girdle structures of the cetopsid *Cetopsis coecutiens* (Cetopsinae) are described and compared with those of another species of the subfamily Cetopsinae, *Hemicetopsis candiru*, and of one species of the single genus of the subfamily Helogeninae, *Helogenes marmoratus*, as well as of several other catfishes. Our observations and comparisons support Mo's 1991 and de Pinna's 1998 phylogenetic hypothesis, according to which the cetopsids occupy a rather basal position within the Siluriformes. In addition, our observations and comparisons pointed out three new, additional characters to diagnose the family Cetopsidae, namely : 1) presence of a muscle 6 of the mandibular barbels; 2) medial branchiostegal rays long and stout; 3) mandibular barbels originate on the posteroventral surface of their irregularly shaped basal cartilages.

KEY WORDS : catfish, cephalic region, Cetopsidae, *Cetopsis*, comparative morphology, pectoral girdle, phylogeny, Siluriformes.

INTRODUCTION

The Siluriformes, or catfishes, with about 437 genera and more than 2700 species, represent about 32% of all freshwater fishes (TEUGELS, 2003). Although some controversy and several uncertainties remain concerning the higher-level phylogeny of the Siluriformes (DE PINNA, 1998; DIOGO, 2003), some studies (MO, 1991; DE PINNA, 1998) suggest that the cetopsids occupy a markedly basal position within the non-diplomystid siluriforms (the Diplomystidae are considered as the most plesiomorphic catfishes : REGAN, 1911; ALEXANDER, 1965; ARRATIA, 1987, 1992; MO, 1991; DE PINNA, 1998; DIOGO & CHARDON, 2000bc; DIOGO et al., 2000b, 2001ab; etc.). Therefore, information on the cetopsid catfishes could probably be very useful for understanding the evolution and phylogeny of the Siluriformes. However, the anatomy of the family Cetopsidae, which includes the subfamilies Cetopsinae and Helogeninae (DE PINNA & VARI, 1995), is relatively poorly known. In fact, despite the large number of works concerning catfish anatomy (REGAN, 1911; ALEXANDER, 1965; CHARDON, 1968; GOSLINE, 1975; LUNDBERG 1975, 1982; HOWES, 1983ab, 1985; ARRATIA, 1987, 1990, 1992; MO, 1991; BORNBUSCH, 1995; DIOGO et al., 1999, 2000ab, 2002; DIOGO & CHARDON, 2000abc; etc.), the only published papers dealing with the morphology of cetopsids are those of CHARDON (1968), LUNDBERG (1975), DE PINNA & VARI (1995), LUNDBERG & PY-DANIEL (1994) and FERRARIS (1996). Moreover, the descrip-

tions given in these papers are usually brief and incomplete. In fact, the configuration of some osteological structures of the cetopsids (as, e.g., those of the pectoral girdle) are poorly known, and the myology of these fishes is practically unknown.

The aim of this work is to describe the bones, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of a species belonging to the type genus of the Cetopsidae, *Cetopsis coecutiens* Spix & Agassiz, 1829 (Cetopsinae). We will compare these structures with those of another species of this subfamily, namely *Hemicetopsis candiru* (Spix & Agassiz, 1829), and of one species of the single genus of the subfamily Helogeninae, *Helogenes marmoratus* Günther, 1863, as well as of members from the other siluriform families. This will thus serve as a foundation for a discussion on the synapomorphies and phylogenetic position of the Cetopsidae.

MATERIAL AND METHODS

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale de Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National d'Histoire Naturelle of Paris (MNHN), from the National Museum of Natural History of Washington (USNM), and from the South African Institute for Aquatic Biodiversity (SAIAB) and the Albany Museum of Grahamstown (AMG). Ana-

tomical 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 alcohol fixed (alc), trypsin-cleared and alizarine-stained (c&s), or simply alizarine-stained (s) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

Akysidae : *Akysis baramensis* LFEM, 2 (alc). *Akysis leucorhynchus* USNM 109636, 2 (alc). *Parakysis anomalopteryx* USNM 230307, 2 (alc); LFEM, 1 (alc).

Amblycipitidae : *Amblyceps caecutiens* LFEM, 2 (alc). *Amblyceps mangois* USNM 109634, 2 (alc). *Liobagrus reini* USNM 089370, 2 (alc).

Amphiliidae : *Amphilius brevis* MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c&s). *Andersonia leptura* MNHN 1961-0600, 2 (alc). *Belonoglanis tenuis* MRAC P.60494, 2 (alc). *Doumea typica* MRAC 93-041-P-1335, 1 (alc). *Leptoglanis rotundiceps* MRAC P.186591-93, 3 (alc). *Paramphilius trichomycteroides* LFEM, 2 (alc). *Phractura brevicauda* MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c&s). *Phractura intermedia* MRAC 73-016-P-5888, 1 (alc). *Trachyglanis inae* MRAC P.125552-125553, 2 (alc). *Zaireichthys zonatus* MRAC 89-043-P-2243-2245, 3 (alc).

Ariidae : *Arius hertzbergii* LFEM, 1 (alc). *Arius heudelotii* LFEM, 4 (alc). *Bagre marinus* LFEM, 1 (alc); LFEM, 1 (c&s). *Genidens genidens* LFEM, 2 (alc).

Aspredinidae : *Aspredo aspredo* USNM 226072, 1 (alc). *Aspredo sicuephorus* LFEM, 1 (alc). *Bunocephalus knerii* USNM 177206, 2 (alc). *Xyliphius magdalenae* USNM 120224, 1 (alc).

Astroblepidae : *Astroblepus phelpis* LFEM, 1 (alc); USNM 121127, 2 (alc).

Auchenipteridae : *Ageneiosus vittatus* USNM 257562, 1 (alc). *Auchenipterus dentatus* USNM 339222, 1 (alc). *Centromochlus hechelii* USNM 261397, 1 (alc).

Austroglanididae : *Austroglanis gilli* LFEM, 3 (alc); SAIAB 58416 (c&s). *Austroglanis sclateri* AMG, 1 (c&s); SAIAB 68917 (s).

Bagridae : *Bagrichthys macropterus* USNM 230275, 1 (alc). *Bagrus bayad* LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrus docmak* MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (c&s). *Hemibagrus nemurus* USNM 317590, 1 (alc). *Rita chrysea* USNM 114948, 1 (alc).

Callichthyidae : *Callichthys callichthys* USNM 226210, 2 (alc). *Corydoras guianensis* LFEM, 2 (alc).

Cetopsidae : *Cetopsis coecutiens* USNM 265628, 2 (alc). *Helogenes marmuratus* USNM 264030, 2 (alc). *Hemicetopsis candiru* USNM 167854, 2 (alc).

Chacidae : *Chaca bankanensis* LFEM, 3 (alc). *Chaca burmensis* LFEM, 2 (alc). *Chaca chaca* LFEM, 2 (alc).

Clariidae : *Clarias anguillaris* LFEM, 2 (alc). *Clarias batrachus* LFEM, 2 (alc). *Clarias ebiensis* LFEM, 2 (alc). *Clarias gariepinus* MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Heterobranchus bidorsalis* LFEM, 2 (alc). *Heterobranchus longifilis* LFEM, 2 (alc). *Uegitglanis zammaroni* MRAC P-15361, 1 (alc).

Claroteidae : *Auchenoglanis biscutatus* MRAC 73-015-P-999, 2 (alc). *Auchenoglanis occidentalis* LFEM, 2 (alc). *Chrysichthys auratus* UNB, 2 (alc); UNB, 2 (c&s). *Chrysichthys nigrodigitatus* UNB, 2 (alc); UNB, 2 (c&s). *Clarotes laticeps* MRAC 73-13-P-980, 2 (alc).

Cranoglanididae : *Cranoglanis bouderius* LFEM, 2 (alc).

Diplomystidae : *Diplomystes chilensis* LFEM, 3 (alc).

Doradidae : *Acanthodoras cataphractus* USNM 034433, 2 (alc). *Anadoras weddellii* USNM 317965, 2 (alc). *Doras brevis* LFEM, 2 (alc). *Doras punctatus* USNM 284575, 2 (alc). *Franciscodoras marmoratus* USNM 196712, 2 (alc).

Erethistidae : *Erethistes pusillus* USNM 044759, 2 (alc). *Hara filamentosa* USNM 288437, 1 (alc).

Heteropneustidae : *Heteropneustes fossilis* USNM 343564, 2 (alc); USNM 274063, 1 (alc); LFEM, 2 (alc).

Ictaluridae : *Amiurus nebolosus* USNM 246143, 1 (alc); USNM 73712, 1 (alc). *Ictalurus furcatus* LFEM, 2 (alc). *Ictalurus punctatus* USNM 244950, 2 (alc).

Loricariidae : *Hypoptopoma bilobatum* LFEM, 2 (alc). *Hypoptopoma inexpectata* LFEM, 2 (alc). *Lithoxus lithoides* LFEM, 2 (alc). *Loricaria cataphracta* LFEM, 1 (alc). *Loricaria loricaria* USNM 305366, 2 (alc); USNM 314311, 1 (alc).

Malapteruridae : *Malapterurus electricus* LFEM, 5 (alc).

Mochokidae : *Mochokus niloticus* MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Synodontis clarias* USNM 229790, 1 (alc). *Synodontis schall* LFEM, 2 (alc). *Synodontis sorex* LFEM, 2 (alc).

Nematogenyidae : *Nematogenys inermis* USNM 084346, 2 (alc); LFEM, 2 (alc).

Pangasiidae : *Helicophagus leptorhynchus* USNM 355238, 1 (alc). *Pangasius larnaudii* USNM 288673, 1 (alc). *Pangasius sianensis* USNM 316837, 2 (alc).

Pimelodidae : *Calophysus macropterus* USNM 306962, 1 (alc). *Goeldiella eques* USNM 066180, 1 (alc). *Hepapterus mustelinus* USNM 287058, 2 (alc). *Hypophthalmus edentatus* USNM 226140, 1 (alc). *Microglanis cottoides* USNM 285838, 1 (alc). *Pimelodus blochii* LFEM, 2 (alc). *Pimelodus clarias* LFEM, 2 (alc); USNM 076925, 1 (alc). *Pseudopimelodus raninus* USNM 226136, 2 (alc). *Pseudoplatystoma fasciatum* USNM 284814, 1 (alc). *Rhamdia guatemalensis* USNM 114494, 1 (alc).

Plotosidae : *Cnidoglanis macrocephalus* USNM 219580, 2 (alc). *Neosilurus rendahli* USNM 173554, 2 (alc). *Paraplotosus albilabris* USNM 173554, 2 (alc). *Plotosus anguillaris* LFEM, 2 (alc). *Plotosus lineatus* USNM 200226, 2 (alc).

Schilbidae : *Ailia colia* USNM 165080, 1 (alc). *Laides hexanema* USNM 316734, 1 (alc). *Pseudotropius brachypterus* USNM 230301, 1 (alc). *Schilbe intermedius* MRAC P.58661, 1 (alc). *Schilbe mystus* LFEM, 3 (alc). *Siluranodon auritus* USNM 061302, 2 (alc).

Scoloplacidae : *Scoloplax distolothrix* LFEM, 1 (alc); USNM 232408, 1 (alc).

Siluridae : *Silurus aristotelis* LFEM, 2(alc). *Silurus glanis* LFEM, 2 (alc). *Silurus asotus* USNM 130504, 2 (alc). *Wallago attu* USNM 304884, 1 (alc).

Sisoridae : *Bagarius yarrelli* USNM 348830, 2 (alc); LFEM, 1 (c&s). *Gagata cenia* USNM 109610, 2 (alc). *Glyptosternon reticulatum* USNM 165114, 1 (alc). *Glyptothorax fukiensis* USNM 087613, 2 (alc).

Trichomycteridae : *Hatcheria macraei* LFEM, 2 (alc). *Trichomycterus areolatus* LFEM, 2 (alc). *Trichomycterus banneai* LFEM, 2 (alc). *Trichomycterus immaculatus* USNM 301015, 2 (alc).

RESULTS

In this section we will describe the cephalic and pectoral girdle structures of *Cetopsis coecutiens* (Cetopsinae) and compare these structures with those of another cetopsin species, *Hemicetopsis candiru*, as well as of one representative of the single genus of the subfamily Helogeninae, *Helogenes marmoratus*. 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, 2003), with respect to the skeletal components of the suspensorium we follow DIOGO et al. (2001a). The nomenclature of the cephalic muscles is mainly based on WINTERBOTTOM (1974). However, for the different adductor mandibulae sections, we follow DIOGO & CHARDON (2000b). In relation to the muscles associated with the mandibular barbels, which were not studied by WINTERBOTTOM (1974), we follow DIOGO & CHARDON (2000c). With respect to the nomenclature of the pectoral girdle muscles, we follow DIOGO et al. (2001b).

Cetopsis coecutiens (adult specimens)

Osteology

Mesethmoid. It is situated on the anterodorsal surface of the neurocranium (Figs 1, 2). Each of its prominent anterolateral arms is ligamentously connected to the premaxilla.

Lateral ethmoid. Large bone (Fig. 1), which exhibits a laterally directed articulatory facet for the palatine. Its posterodorsolateral surface presents a prominent lateral projection that sutures with a somewhat similar lateral projection of the anterodorsolateral surface of the pterosphenoid (Fig. 1).

Prevomer. T-shaped bony plate lying underneath the ethmoidal region and presenting two prominent, posterolaterally directed anterolateral arms (Fig. 2). Anteroventrally, the prevomer bears numerous prominent teeth (Fig. 1).

Orbitosphenoid. Large bone lying posterior to the lateral ethmoid (Figs 1, 2). It does not contact the frontal (Fig. 1).

Pterosphenoid. It is posterior to the orbitosphenoid (Figs 1, 2), covering, together with this bone, the gap between the frontals and the parasphenoid.

Parasphenoid. This is the longest bone of the cranium (Fig. 2). It bears a pair of prominent ascending flanges, which suture with the pterosphenoids and prootics.

Frontal. The paired frontals are very long bones (Fig. 1). A great part of their main body forms part of the prominent dorsomedial crest of the cranial roof, on which originates part of the muscle adductor mandibulae (see below). There is no fontanel between the dorsomedian margins of the paired frontals.

Sphenotic. It bears, together with the pterotic, an articulatory facet for the hyomandibulo-metapterygoid (Fig. 2) and presents a prominent, anteriorly oriented anterodorsal process (Figs 1, 2 : sph-adp).

Pterotic. Its dorsal surface is somewhat rectangular and has about the same size as the dorsal surface of the sphenotic (Fig. 1). The pterotic has short, lateral triangular process posteriorly to its articulatory surface for the hyomandibulo-metapterygoid (Fig. 2).

Prootic. Large bone (Fig. 2). Together with the pterosphenoid, it borders the foramen of the trigemino-facial nerve complex (Fig. 2).

Epioccipital. Small bone situated on the posteroventral surface of the neurocranium, lateral to the posterior surface of the exoccipital and medial to the posterior surface of the pterotic (Fig. 2).

Exoccipital. The paired exoccipitals are small bones situated laterally to the basioccipital (Fig. 2). The posteroventromedial surfaces of the exoccipitals are firmly connected, by means of connective tissue, to the ventromedial limbs of the posttemporo-supracleithra (Fig. 2).

Basioccipital. Unpaired bone, which forms the posteriormost part of the floor of the neurocranium and presents two prominent posteroventrolateral processes (Fig. 2).

Parieto-supraoccipital. Large bone (Fig. 1) with two prominent, thin, posterolaterally directed, posterodorsolateral arms and a large, posteriorly directed posterodorsomedian process. The anteromedian surfaces of the parieto-supraoccipital are largely separated by a somewhat rectangular dorsal fontanel.

Extrascapular. Small bone situated between the dorso-medial surface of the posttemporo-supracleithrum, the posterodorsal surface of the pterotic and posterodorsolateral surface of the parieto-supraoccipital (Fig. 1).

Angulo-articular. This bone (Figs 1, 3), together with the dentary bone, coronomeckelian bone and Meckel's cartilage, constitute the mandible (Fig. 3). The anterodorsal surface of the angulo-articular, together with the posterodorsal surface of the dentary bone, form a prominent dorsal process (processus coronoideus) (Figs 1, 3), which is linked to the maxilla by means of a massive, long ligament. Posterodorsally, the angulo-articular has an articulatory surface for the quadrato-symplectic. The angulo-articular presents a prominent, circular, medially directed posteromedial process (Fig. 3 : ang-art-pmp).

Dentary bone. Anterodorsally, it presents a broad dorsolateral lamina (Fig. 3 : den-dl), which covers a considerable portion of the lateral surface of the mandibular teeth in lateral view (see Fig. 1).

Coronomeckelian bone. Small bone lodged in the medial surface of the mandible (Fig. 3). Posterodorsally it bears a crest for attachment of the adductor mandibulae A3'-d (see below).

Premaxilla. The premaxillae (Figs 1, 2) are a pair of large triangular plates lying underneath and attaching to

the mesethmoidal cornua via ligamentous tissue. Ventrally, each premaxilla bears numerous small teeth (Fig. 1) having their tips slightly turned backward.

Maxilla. It is markedly compressed proximodistally and articulates with the anterior cartilage of the autopalatine by means of a single proximal articular head (Fig. 4). As in most catfishes, the maxilla barbels are supported by the maxillae.

Autopalatine. The autopalatine (Fig. 4) is markedly compressed dorsoventrally. Its anterior end is tipped by a large cartilage (Fig. 4), which is markedly extended mesially, bordering inclusively part of the anteromedial margin of the bony portion of the autopalatine. This cartilage presents an anterolateral concavity to receive the proximal articular head of the maxilla. The posterior end of the autopalatine, which is expanded transversely, is capped by a small cartilage. Medially, the autopalatine articulates with the lateral ethmoid (Fig. 4). The autopalatine articulates mesially with the lateral ethmoid (Fig. 4).

Hyomandibulo-metapterygoid. Dorsally, this bone articulates synchondrally with both the pterotic and the sphenotic (Figs 1, 2). Anterior to this articulation, it presents a prominent, anteriorly pointed anterodorsal extension, which, however, does not articulate synchondrally with the neurocranium (Fig. 1). Laterodorsally, it presents a prominent, broad, somewhat quadrangular lateral crest for the attachment of the posterior section of the muscle levator arcus palatini (see below). Posteriorly, the hyomandibulo-metapterygoid presents a large articular facet for the opercle, which is significantly elongated dorsoventrally (Fig. 4).

Sesamoid bone 1 of suspensorium. Roughly triangular in shape (Figs 1, 2). Its dentate posterior margin is firmly attached, by means of a very short, strong ligament, to the also dentate anterolateral margin of the entopterygoideo-ectopterygoid, thus giving the impression that these two bones are partially sutured (see Fig. 2). Its anterior margin is ligamentously connected to the prevomer (Fig. 2). The sesamoid bones 2 and 3 of the suspensorium are absent.

Entopterygoideo-ectopterygoid. Posteriorly the broad, somewhat rectangular entopterygoideo-ectopterygoid (see DIOGO et al., 2001a) is connected, by a large cartilaginous band and by bony sutures, to both the quadrato-symplectic and the hyomandibulo-metapterygoid (Fig. 1).

Quadrato-symplectic. Triangular bone that articulates anteroventrally with the mandible (Fig. 1).

Preopercle. Long and large bone firmly sutured to the hyomandibulo-metapterygoid and to the quadrato-symplectic (Fig. 1).

Opercle. Very large, irregular bone, with its ventral margin being significantly broader than its dorsal margin (Fig. 1).

Interopercle. The interopercle is a broad, dorsoventrally elongated bone roughly triangular in shape (Fig. 1). Its posterior margin, which is connected to the opercle by means of connective tissue, is situated medial to this latter bone (Fig. 1). Its anterodorsal margin is linked, by means of thick ligament (Fig. 1 : l-ang-iop) to the angulo-articular. Medially, the interopercle is firmly connected, via connective tissue, to the posterolateral surface of the ceratohyal (Figs 1, 4, 5).

Interhyal. The interhyal (Fig. 2) is a small bone attached, by means of ligaments, to both the posterior ceratohyal and the medial surface of the suspensorium (hyomandibulo-metapterygoid and quadrato-symplectic).

Posterior ceratohyal. This triangular bone (Figs 1, 5) is linked by ligaments to the angulo-articular, interhyal and interopercle.

Anterior ceratohyal. Stout bone (Fig. 1) that, together with the posterior ceratohyal, supports the large branchiostegal rays, which are, including the inner ones, remarkably elongated anteroposteriorly (see Fig. 5).

Ventral hypohyal. Small bone (Fig. 1). Each ventral hypohyal contains a ventral concavity to receive one of the anterolateral edges of the parurohyal.

Dorsal hypohyal. It is a small bone. It lies dorsally to the ventral hypohyal, to which it is connected by a thin cartilage.

Parurohyal. The parurohyal (see ARRATIA & SCHULTZE, 1990) is a somewhat triangular bone with two prominent posterolateral processes and a small posteromedial process. It lies medially behind the ventromedial surfaces of the ventral hypohyals and is connected to these bones by means of two strong, thick ligaments.

Posttemporo-supracleithrum. The medial and posterior margins of the thin ventromedial limb of this large bone are firmly attached, by means of connective tissue, to the posteroventromedial surface of the exoccipital and to the anterior surface of the fourth parapophysis of the complex vertebra (Fig. 2). Its posteroventrolateral limb is forked, forming, together with the anterolateral surface of this parapophysis, an articulating groove (Fig. 2) for the upper edge of the cleithrum (see Fig. 1).

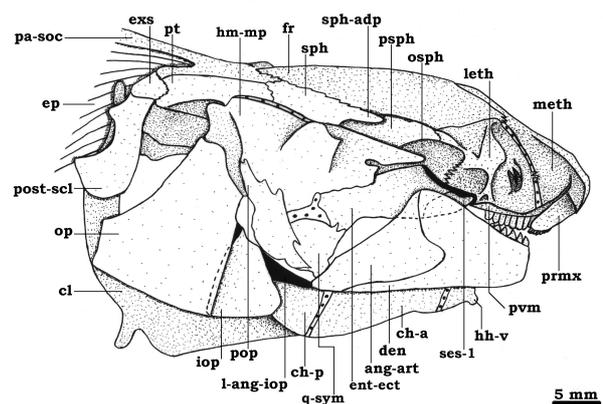


Fig. 1. – Lateral view of the cranium and pectoral girdle of *Cetopsis coecutiens*. The muscle epaxialis is also illustrated. ang-art, angulo-articular; ch-a, anterior ceratohyal; ch-p, posterior ceratohyal; cl, cleithrum; den, dentary bone; ent-ect, entopterygoideo-ectopterygoid; ep, muscle epaxialis; exs, extrascapular; fr, frontal; hh-v, ventral hypohyal; hm-mp, hyomandibulo-metapterygoid; iop, interopercle; l-ang-iop, angulo-interopercular ligament; leth, lateral-ethmoid; meth, mesethmoid; op, opercle; osph, orbitosphenoid; pa-soc, parieto-supraoccipital; pop, preopercle; post-scl, posttemporo-supracleithrum; prmx, premaxilla; psph, pterotic; pvm, prevomer; q-sym, quadrato-symplectic; ses-1, sesamoid bone 1 of suspensorium; sph, sphenotic; sph-adp, anterodorsal process of sphenotic.

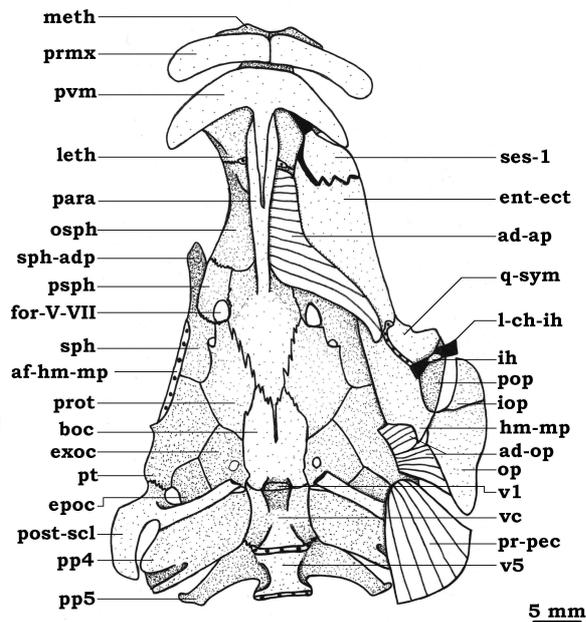


Fig. 2. – Ventral view of the neurocranium of *Cetopsis coecutiens*. On the right side the suspensorium, as well as the adductor arcus palatini, adductor operculi and protractor pectoralis, are also illustrated. Both the premaxillary and the prevomerine teeth were removed. *ad-ap*, muscle adductor arcus palatini; *ad-op*, muscle adductor operculi; *af-hm-mp*, articular facet for hyomandibulo-metapterygoid; *boc*, basioccipital; *ent-ect*, entopterygoideo-ectopterygoid; *epoc*, epioccipital; *exoc*, exoccipital; *for-V-VII*, trigemino-facialis foramen; *hm-mp*, hyomandibulo-metapterygoid; *ih*, interhyal; *iop*, interopercle; *l-ch-ih*, ceratohyalo-interhyale ligament; *leth*, lateral ethmoid; *meth*, mesethmoid; *op*, opercle; *osph*, orbitosphenoid; *para*, parasphenoid; *pop*, preopercle; *post-scl*, posttemporo-supracleithrum; *pp4*, *pp5*, parapophyses 4 and 5; *pr-pec*, muscle protractor pectoralis; *prmx*, premaxilla; *prot*, prootic; *psph*, pterosphenoid; *pt*, pterotic; *pvm*, prevomer; *q-sym*, quadrato-symplectic; *ses-1*, sesamoid bone 1 of suspensorium; *sph*, sphenotic; *sph-adp*, anterodorsal process of sphenotic; *v1*, *v5*, vertebrae 1 and 5; *vc*, complex vertebrae.

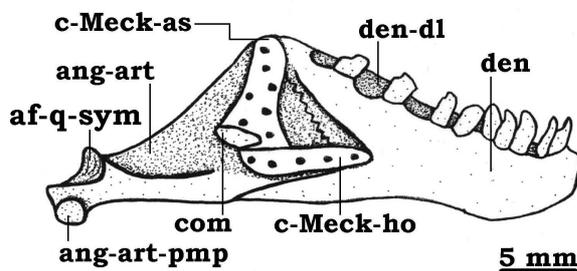


Fig. 3. – Medial view of the left lower jaw of *Cetopsis coecutiens*. *af-q-sym* articular facet for quadrato-symplectic, *ang-art* angulo-articular, *ang-art-pmp* posteromedial process of angulo-articular, *c-Meck-as*, *c-Meck-ho* ascending and horizontal portions of Meckel's cartilage, *com* coronomeckelian, *den* dentary bone, *den-dl* dorsal lamina of dentary bone.

Cleithrum. The cleithrum (Figs 1, 6) is a large, well-ossified stout structure forming the major part of the pectoral girdle and the posterior boundary of the branchial chamber. It has a single dorsal process (Fig. 6 : *cl-dp*), which articulates (Fig. 1) with both the posttemporo-supracleithrum and the fourth parapophysis of the complex vertebra. The humeral process is absent (Figs 1, 6). The two cleithra are attached in the anteromedial line via massive connective tissue.

Scapulo-coracoid. This is an elongated bony plate, of which the anteromedial and the posterolateral margins are firmly attached with the cleithrum (Fig. 6). It presents a short, thin median arm (see DIÓGO et al., 2001b), which does not reach the median line (Fig. 6), and, thus, does not suture with its counterpart medially. Anterolaterally, the scapulo-coracoid presents a prominent, anteroventrolaterally directed process, usually called the coracoid bridge (see DIÓGO et al., 2001b), which extends anteroventrally to the ventral surface of the cleithrum, fusing with a ventral ridge of this bone (Fig. 6 : *cor-bri*). This coracoid bridge is prolonged posteromesially by a prominent posteroventral laminar process (Fig. 6 : *cor-bri-pvp*). Posterolaterally, the scapulo-coracoid bears two condyles, which articulate, respectively, with the pectoral spine and the complex radial (see MO, 1991). The mesocoracoid arch (see DIÓGO et al., 2001b) is present and markedly expanded transversally.

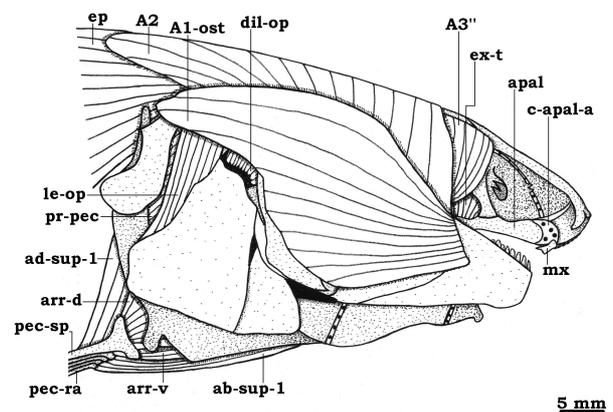


Fig. 4. – Lateral view of the cephalic and pectoral girdle musculature of *Cetopsis coecutiens*. *A1-ost*, *A2*, *A3''*, sections of muscle adductor mandibulae; *ab-sup-1*, section of muscle abductor superficialis; *ad-sup-1*, section of muscle adductor superficialis; *apal*, autopalatine; *arr-d*, muscle arrector dorsalis; *arr-v*, muscle arrector ventralis; *c-apal-a*, anterior cartilage of autopalatine; *dil-op*, muscle dilatator operculi; *ep*, muscle epaxialis; *ex-t*, muscle extensor tentaculi; *le-op*, muscle levator operculi; *mx*, maxilla; *pec-ra*, pectoral rays; *pec-sp*, pectoral spine; *pr-pec* muscle protractor pectoralis (for the other osteological structures, see abbreviations on Fig. 1).

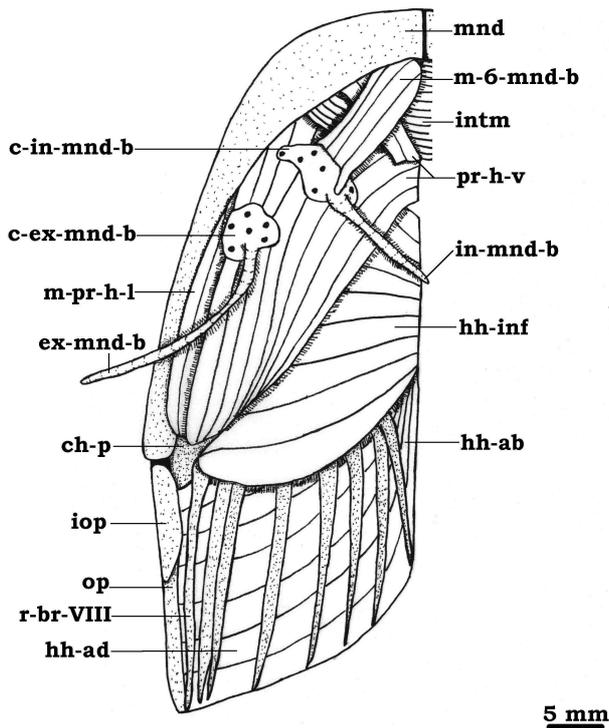


Fig. 5. – Ventral view of the cephalic musculature of *Cetopsis coecutiens*. *c-ex-mnd-b*, *c-in-mnd-b*, basal cartilages of external and internal mandibular barbels; *ch-p*, posterior ceratohyal; *ex-mnd-b*, *in-mnd-b*, external and internal mandibular barbels; *hh-ab*, muscle hyohyoideus abductor; *hh-ad*, muscle hyohyoideus adductor; *hh-inf*, muscle hyohyoideus inferior; *intm*, muscle intermandibularis; *iop*, interopercle; *m-6-mnd-b*, muscle 6 of the mandibular barbels; *mnd*, mandible; *op*, opercle; *pr-h-l*, *pr-h-v*, pars lateralis and ventralis of muscle protractor hyoideus; *r-br-VIII*, branchiostegal ray VIII.

Myology

Adductor mandibulae. The adductor mandibulae A1-ost (DIOGO & CHARDON, 2000b) originates on the parieto-supraoccipital, posttemporo-supracleithrum, extrascapular, pterotic, hyomandibulo-metapterygoid and preopercle and inserts on the lateral surface of both the dentary bone and the angulo-articular (Fig. 4). The A2 (Fig. 4), which lies dorsomesially to the A1-ost, originates on the prominent dorsomedian crest of the cranial roof formed by both the frontal and the parieto-supraoccipital and inserts, by means of a thick tendon, on the posteroventromedial surface of the dentary bone. It covers almost all the posterodorsal surface of the neurocranium (Fig. 4), and also covers the most anterior fibers of the epaxialis. However, it should be noted that there is no aponeurosis between the A2 and the epaxialis. The adductor mandibulae A3' runs from the quadrato-symplectic, hyomandibulo-metapterygoid, entopterygoideo-ectopterygoid and preopercle to both the angulo-articular and the coronomeckelian bone. The deeper bundle of the adductor mandibulae, the A3" (Fig. 4) originates on both the anterodorsal surface of the frontal and the posterodorsal surface of the lateral ethmoid and inserts, by means of a

massive tendon, to the medial surface of the angulo-articular. The A₀, which is small and situated on the mesial surface of the mandible, contacts anteriorly the tendon of the A2 and posteriorly the anteriormost fibers of the A3'.

Levator arcus palatini. This hypertrophied muscle is differentiated into posterior and anterior large sections. The posterior section originates on the dorsal surfaces of both the sphenotic, frontal and lateral ethmoid and inserts on a prominent lateral crest of the hyomandibulo-metapterygoid (see above). The anterior section runs from the dorsal surface of the lateral ethmoid to the lateral surfaces of both the hyomandibulo-metapterygoid and the entopterygoideo-ectopterygoid.

Adductor arcus palatini. It extends from the lateral sides of the parasphenoid, pterosphenoid and orbitosphenoid to the medial sides of the hyomandibulo-metapterygoid and entopterygoideo-ectopterygoid (Fig. 2).

Adductor operculi. It runs from the ventral surface of the pterotic to both the dorsomedial surface of the opercle and the posterodorsomedial surface of the hyomandibulo-metapterygoid (Fig. 2).

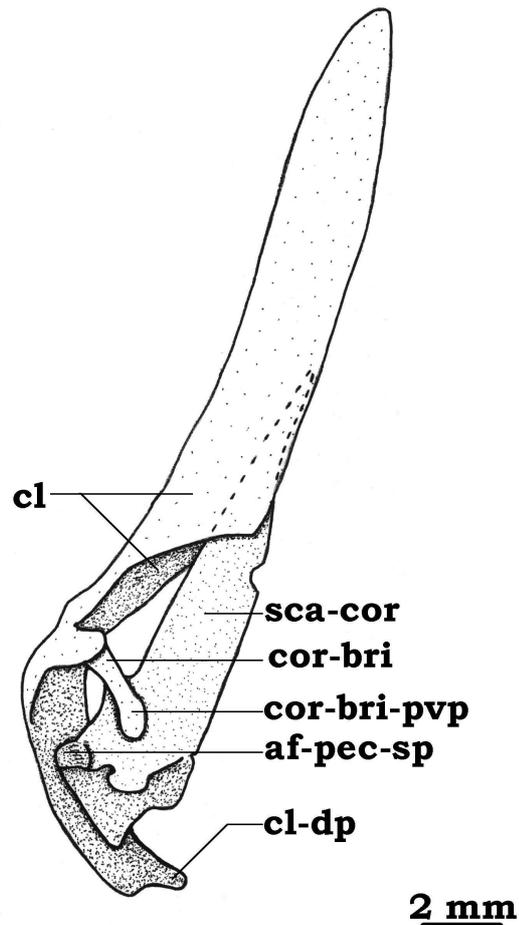


Fig. 6. – Ventral view of the pectoral girdle of *Cetopsis coecutiens*. *af-pec-sp*, articulatory surface for pectoral spine; *cl*, cleithrum; *cl-dp*, dorsal process of cleithrum; *cor-bri*, coracoid bridge; *cor-bri-pvp*, posteroventral process of coracoid bridge; *sca-cor*, scapulo-coracoid.

Dilatator operculi. Thick muscle running from the pterotic, sphenotic, frontal, pterosphenoid, orbitosphenoid and lateral ethmoid, as well as from the anterodorsal surface of the hyomandibulo-metapterygoid, to the anterodorsal edge of the opercle (medial to the preopercle but lateral to the articulatory facet of the opercle for the hyomandibulo-metapterygoid) (Fig. 4).

Levator operculi. It originates on the ventrolateral margin of the pterotic and inserts on the dorsal edge of the opercle (Fig. 4).

Extensor tentaculi. It runs from the ventromedial surface of the lateral ethmoid to the posterior portion of the autopalatine (Fig. 4).

Protractor hyoidei. This muscle has 3 parts. The pars ventralis (Fig. 5 : m-pr-h-v) lodges the large, irregular cartilages associated with the mandibular barbels, which are not differentiated into a moving and a supporting part (see DIOGO & CHARDON, 2000c), with the mandibular barbels originating on their posteroventral surfaces (Fig. 5). It runs from both the anterior and the posterior ceratohyals to the dentary bone, meeting its counterpart in a large median aponeurosis (Fig. 5). The pars lateralis (Fig. 5 : m-pr-h-l) originates on the posterior ceratohyal, inserting, by means of a thick tendon, on the ventromedial face of the dentary bone. The pars dorsalis originates tendinously on the anterior ceratohyal and inserts tendinously on the dentary bone, with some of its anterior fibers being mixed with those of the intermandibularis.

Intermandibularis. This muscle joins the two mandibles (Fig. 5).

Retractor tentaculi mandibularis interni. Small muscle lying dorsal to the muscle 6 of the mandibular barbels (see below) and running from the cartilage associated with the inner mandibular barbel to the dentary bone.

Retractor tentaculi mandibularis externi. Small muscle attaching anteriorly on the dentary bone and posteriorly on the cartilage associated with the outer mandibular barbel.

Protractor tentaculi mandibularis externi. Small muscle lying dorsal to the pars ventralis of the protractor hyoidei and running from the posterior ceratohyal to the cartilage associated with the external mandibular barbel.

Muscle 6 of the mandibular barbels. This muscle (Fig. 5 : m-6-mnd-b), which is not homologous with the muscles 1, 2, 3, 4 and 5 of the mandibular barbels described by DIOGO & CHARDON (2000c) (see below), originates on the dentary bone. It passes ventrally to both the intermandibularis, the retractor tentaculi mandibularis interni and the pars ventralis of the protractor hyoidei and inserts on the ventrolateral surface of the cartilage associated with the internal mandibular barbel.

Hyohyoideus inferior. This thick muscle (Fig. 5) attaches medially on a median aponeurosis and laterally on the ventral surfaces of the ventral hypohyal, anterior ceratohyal and posterior ceratohyal.

Hyohyoideus abductor. This muscle (Fig. 5) 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.

Hyohyoideus adductor. Each hyohyoideus adductor (Fig. 5) connects the branchiostegal rays of the respective

side, with the most lateral fibers of this muscle also attaching to the mesial surface of the opercular bone.

Sternohyoideus. It originates on the anterior region of the cleithrum and inserts on the posterior region of the parurohyal. Posteriorly, the fibers of the sternohyoideus are deeply mixed with those of the epaxialis.

Arrector ventralis. Thin, anteroposteriorly elongated muscle attaching anteriorly on both the cleithrum and the scapulo-coracoid and posteriorly on the anteroventral surface of the pectoral spine (Fig. 4).

Arrector dorsalis. The arrector dorsalis, although constituted by a single section (see DIOGO et al., 2001b) that inserts posteriorly on the anterodorsal surface of the pectoral spine (Fig. 4), is bifurcated anteriorly, with its anteroventral fibers attaching to the ventral surface of the pectoral girdle and its anterodorsal fibers attaching to the dorsal surface of the pectoral girdle.

Abductor profundus. Small muscle, it originates on the posterolateral surface of the coracoid and inserts on the anterodorsomedial surface of the pectoral spine.

Adductor superficialis. It is differentiated into two sections. The larger section (Fig. 4 : ad-sup-1) originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid, as well as on the posterior margin of the mesocoracoid arch and inserts on the anterodorsal margin of the dorsal part of the pectoral fin rays. The smaller section originates on the posterior surface of the scapulo-coracoid, the posteroventral surface of the mesocoracoid arch and the dorsal surface of the proximal radials and inserts on the anteroventral margin of the dorsal part of the pectoral fin rays.

Abductor superficialis. This muscle is also differentiated into two sections. The larger section (Fig. 4 : ab-sup-1) attaches anteriorly on the ventral face of both the cleithrum and the scapulo-coracoid and posteriorly on the anteroventral margin of the ventral part of the pectoral fin rays. The smaller section runs from both the posterolateroventral edge of the scapulo-coracoid and the ventral surface of the proximal radials to the anterodorsal margin of the ventral part of the pectoral fin rays.

Protractor pectoralis. This thick muscle (Figs 2, 4) runs from the ventral surfaces of both the pterotic, the epioccipital and the posttemporo-supracleithrum to the anterodorsal surfaces of both the cleithrum and the scapulo-coracoid.

Hemicetopsis candiru (adult specimens)

Osteology

In a general way, the configuration of the osteological structures of the pectoral girdle and cephalic region of this species resembles that of *Cetopsis coecutiens*, although there are some differences : 1) the anterolateral arms of the prevomer are considerably more expanded anteroposteriorly in *H. candiru* than in *C. coecutiens*; 2) there are two, and not only one, large fontanels on the dorsal surface of the cranial roof in *H. candiru*; 3) in *H. candiru* the dorsomedian crest of the cranial roof is not as large as in *C. coecutiens*; 4) the interopercle of *H. candiru* is considerably less expanded dorsoventrally than that of

C. coecutiens; 5) in *H. candiru* the dorsolateral lamina of the dentary bone is significantly broader than that of *C. coecutiens*, with this dorsomedial lamina covering the main part of the lateral surface of the mandibular teeth in lateral view; 6) contrarily to *C. coecutiens*, there is no posteromedian circular process of the angulo-articular in *H. candiru*.

Myology

The configuration of the cephalic and pectoral girdle muscles of *H. candiru* resembles that of *C. coecutiens*, although there are some differences between these species concerning these muscles: 1) the adductor mandibulae A2 of *H. candiru* is still more developed than that of *C. coecutiens*, covering inclusively all the lateral surface of the A3" in lateral view; 2) the levator arcus palatini is not as voluminous in *H. candiru* than in *C. coecutiens*; 3) contrarily to *C. coecutiens*, in *H. candiru* the dilatator operculi does not contact the anterodorsal surface of the hyomandibulo-metapterygoid.

Helogenes marmoratus (adult specimens)

Osteology

There are differences between the configuration of the osteological structures of the cephalic region and pectoral girdle of *H. marmoratus* and those of *C. coecutiens*: 1) the premaxilla of *H. marmoratus* (Fig. 7) is considerably more expanded anteroposteriorly than that of *C. coecutiens*; 2) anteroventrally the mesethmoid of *H. marmoratus* presents a broad, horizontal lamina (Fig. 7), which borders a significant part of the dorsal surface of the premaxilla; 3) in the examined specimens of *H. marmoratus* there is a large cartilaginous band between the posterodorsal margin of the lateral ethmoid and the anterodorsal margin of the sphenotic (see Fig. 7), and the mesethmoid is unossified posterodorsomesially; 4) the posterior arm of the T-shaped prevomer of *H. marmoratus* is significantly shorter than that of *C. coecutiens*; 5) the sesamoid bone 1 of the suspensorium of *H. marmoratus* (Fig. 7) is smaller than that of *C. coecutiens*; 6) in *H. marmoratus* there is no prominent anterodorsal expansion of the hyomandibulo-metapterygoid; 7) the articulatory surface between the hyomandibulo-metapterygoid and the opercle is not as expanded dorsoventrally in *H. marmoratus* as it is in *C. coecutiens*; 8) the parieto-supraoccipital of *H. marmoratus* (Fig. 7) is markedly compressed anteroposteriorly, and does not present, as in *C. coecutiens* (see above), two prominent, thin posterolateral arms; 9) in *H. marmoratus* there are two, and not only one, large fontanels on the dorsomedian surface of the cranial roof, and there is no median crest on the dorsomedian surface of the neurocranium; 10) in *H. marmoratus* the anterolateral teeth of the mandible are significantly larger than the remaining mandibular teeth (Fig. 7); 11) the mandible of *H. marmoratus* is significantly more compressed dorsoventrally (Fig. 7) than that of *C. coecutiens*; 12) there is no dorsolateral lamina of the dentary bone in *H. marmoratus* (Fig. 7); 13) contrary to *C.*

coecutiens, in *H. marmoratus* there is no connection (Figs 7, 8) between the posterior ceratohyal and the interopercle; 14) in *H. marmoratus* the ventromedial limb of the posttemporo-supracleithrum is firmly attached to the posterolateral surface of the basioccipital, and not to the posteroventromedial surface of the exoccipital; 15) the mesocoracoid arch of *H. marmoratus* is not significantly expanded transversally.

Myology

There are some differences between the configuration of the cephalic and pectoral girdle muscles of *H. marmoratus* and those of *C. coecutiens*: 1) the adductor mandibulae A1-ost and the adductor mandibulae A2 of *H. marmoratus* (Fig. 7) are significantly less developed than those of *C. coecutiens*; 2) the adductor mandibulae A3" is absent in *H. marmoratus*; 3) in *H. marmoratus* the levator arcus palatini does not cover part of the dorsal surface of the cranial roof; 4) contrary to *C. coecutiens*, in *H. marmoratus* the dilatator operculi does not contact the anterodorsal surface of the hyomandibulo-metapterygoid; 5) the muscle 6 of the mandibular barbels of *H. marmoratus* (Fig. 8) is significantly more expanded transversally than that of *C. coecutiens*; 6) in *H. marmoratus* the protractor externi mandibularis tentaculi (Fig. 8: pr-ex-mnd-t) lies ventral to the pars lateralis and the pars ventralis of the protractor hyoidei, thus being visible in ventral view (see Fig. 8).

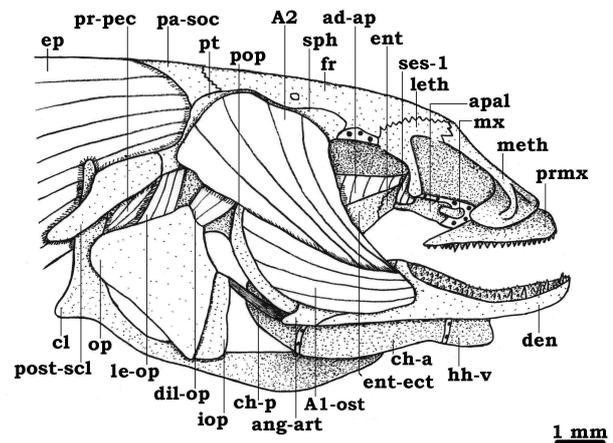


Fig. 7. – Lateral view of the cephalic musculature of *Helogenes marmoratus*. A1-ost, A2, sections of muscle adductor mandibulae; ad-ap, muscle adductor arcus palatini; ang-art, angulo-articular; apal, autopalatine; ch-a, ch-p, anterior and posterior ceratohyals; cl, cleithrum; den, dentary bone; dil-op, muscle dilatator operculi; ent-ect, entopterygoideo-ectopterygoid; ep, muscle epaxialis; ex-t, muscle extensor tentaculi; fr, frontal; hh-v, ventral hypohyal; iop, interopercle; le-op, muscle levator operculi; leth, lateral-ethmoid; meth, mesethmoid; mx, maxilla; op, opercle; pa-soc, parieto-supraoccipital; pop, preopercle; post-scl, posttemporo-supracleithrum; pr-pec, muscle protractor pectoralis; prmx, premaxilla; pt, pterotic; ses 1, sesamoid bone 1 of suspensorium; sph, sphenotic.

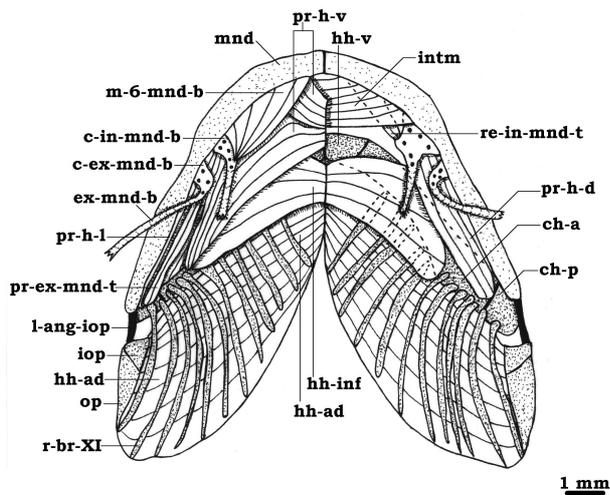


Fig. 8. – Ventral view of the cephalic musculature of *Helogenes marmoratus*. On the right side the protractor externi mandibularis tentaculi, the muscle 6 of the mandibular barbels and the pars ventralis and lateralis of the protractor hyoidei were removed. *c-ex-mnd-b*, *c-in-mnd-b*, basal cartilages of external and internal mandibular barbels; *ch-a*, *ch-p*, anterior and posterior ceratohyals; *ex-mnd-b*, external mandibular barbel; *hh-ab*, muscle hyohyoideus abductor; *hh-ad*, muscle hyohyoideus adductor; *hh-inf*, muscle hyohyoideus inferior; *hh-v*, ventral hypohyal; *intm*, muscle intermandibularis; *iop*, interopercle; *l-ang-iop*, angulo-interopercular ligament; *m-6-mnd-b*, muscle 6 of the mandibular barbels; *mnd*, mandible; *op*, opercle; *pr-ex-mnd-t*, muscle protractor externi mandibularis tentaculi; *pr-h-d*, *pr-h-l*, *pr-h-v*, pars dorsalis lateralis and ventralis of muscle protractor hyoideus; *r-br-XI*, branchiostegal ray XI; *re-in-mnd-t*, muscle retractor interni mandibularis tentaculi.

DISCUSSION

DE PINNA & VARI (1995 : 4-7) listed nine characters to support the monophyly of the Cetopsidae (including the subfamilies Cetopsinae and Helogeninae), of which eight concern the configuration of structures examined in this work, namely : *I*) “maxilla with a single proximal head”; *II*) “posterior portion of palatine depressed, expanded lateromesially”; *III*) “anterior distal cartilage of palatine extending onto mesial surface of bone”; *IV*) “anterior cartilage of palatine expanded anteriorly”; *V*) “lap joint present between opercle and interopercle”; *VI*) “attachment of interoperculo-mandibular ligament on dorsal portion of interopercle”; *VII*) “interopercle expanded along dorsoventral axis, deeper than long”; *VIII*) “metapterygoid elongate, roughly rectangular in shape” [the other character was the “shaft of second basibranchial expanded laterally, with strongly convex lateral margins”]. Our observations and comparisons not only confirmed these eight synapomorphies, but also pointed out three other characters that are found in the three cetopsid genera examined, that is, in members of the two subfamilies of the family Cetopsidae, and in no other catfish examined or described in the literature. These, thus, constitute very likely additional characters to diagnose this family :

1- Presence of a muscle 6 of the mandibular barbels. Although several catfishes have small, specialised mus-

cles directly associated with the movements of the mandibular barbels (see DIOGO & CHARDON, 2000c : 465-475), a muscle 6 of the mandibular barbels is exclusively present in the cetopsid catfishes examined (see Figs 5, 8).

2- Large, stout medial branchiostegal rays. Characteristically among catfishes the inner branchiostegal rays are relatively thin, being markedly thinner than the more lateral ones (see, e.g., TILAK, 1963 : figs 1, 12, 30; GRANDE, 1987 : fig. 5B; ARRATIA & SCHULTZE, 1990 : figs 6B, 8A, 8B, 13D; MO, 1991 : fig. 16D; DIOGO et al., 1999 : fig. 5; DIOGO & CHARDON, 2000a : fig. 4; OLIVEIRA et al., 2001 : fig. 8B; etc.). However, the helogenines (see Fig. 8), and particularly the cetopsines (see Fig. 5) examined present large, stout median branchiostegal rays.

3- Mandibular barbels originate on the posteroventral surface of their irregularly shaped basal cartilages. Characteristically in those catfishes having mandibular barbels the cartilages associated with these barbels are differentiated into an anterior, short “supporting” part and a posterior, long “moving” part (DIOGO & CHARDON, 2000c), with the mandibular barbels originating on the anteroventral surface of these cartilages (see, e.g., DIOGO & CHARDON, 2000c : fig. 1). However, in both the cetopsines (see Fig. 5) and the helogenines (see Fig. 8) examined the mandibular barbels originate on the posteroventral, and not on the anteroventral, margin of the basal cartilages, which are irregularly shaped and not differentiated into a “supporting” and a “moving” part.

So far, the only published cladistic papers dealing with the phylogenetic position of the cetopsids within the order Siluriformes were those of MO (1991) and DE PINNA (1998). Both these papers suggest that the cetopsid catfishes occupy a markedly basal position within the siluriforms. In MO's paper the cetopsids appear as the most basal non-diplomystid catfishes. The cetopsids and diplomystids are separated from the remaining catfishes by a “computer node” in MO's cladogram 1 (see MO, 1991 : fig. 4) and by the fact that in these two groups the “ramus mandibularis nerve (does not run) inside hyomandibular for a distance” (although MO considered the Cetopsidae of the present study a non-monophyletic group, both the genus *Hemicetopsis*, the remaining cetopsines and the helogenines appear in a more basal position than all the other non-diplomystid catfishes, including the fossil hypsidorids, in MO's 1991 cladograms). With respect to the work of DE PINNA (1998 : fig. 1), it suggests that the cetopsids, together with the fossil hypsidorids, are the most basal non-diplomystid catfishes. These because “they lack some synapomorphies of all other catfishes except for diplomystids and in some stances also hypsidorids”, without specifying, however, which are these synapomorphies (DE PINNA, 1998 : 292).

Our observations and comparisons strongly support the hypotheses of MO (1991) and DE PINNA (1998) concerning the phylogenetic position of the cetopsids within the Siluriformes. In fact, although the cetopsids are characterised by numerous derived, synapomorphic features (see above), they lack some apomorphic features that are present in the vast majority of the non-diplomystid catfishes, which are described below. It is important to notice that these phylogenetic results were corroborated by an explicit phylogenetic comparison of 440 morpho-

logical characters, concerning the bones, muscles, cartilages and ligaments of both the cephalic region and the pectoral girdle, in 87 genera representing all the extend catfish families (DIOGO, 2005).

Pronounced ankylosis between the cleithrum and the scapulo-coracoid. As stated by DIOGO et al. (2001b), the plesiomorphic condition for catfishes is that in which the scapulo-coracoid is just loosely ankylosed with the cleithrum. Such a plesiomorphic condition is found in diplomystids (DIOGO et al., 2001b) and cetopsids (see, e.g., Fig. 6). In the vast majority of the catfishes, including the fossil hypsidorids, there is a pronounced ankylosis between the cleithrum and the scapulo-coracoid (see DIOGO et al., 2001b).

Abductor profundus originated in the medial surface of the pectoral girdle. In catfish closest relatives, as well as in the diplomystids (DIOGO et al., 2001b) and the cetopsids, the abductor profundus, although well-developed, does not reach medially to the median line (it should be noted that, due to the state of conservation of the fossil hypsidorids reported so far, it is not possible to appraise the configuration of the adductor profundus in these catfishes). In the vast majority of the other catfishes, excluding the plotosids (DIOGO et al., 2001b) and the nematogenyids, silurids and heptapterines (pers. obs), the abductor profundus originates on the medial surface of the pectoral girdle, at the level of the interdigitations between the scapulo-coracoids (see DIOGO et al., 2001b).

Arrector dorsalis differentiated into two broad, separated sections. In diplomystid (DIOGO et al., 2001b) and cetopsid (see, e.g., Fig. 4) catfishes the muscle arrector ventralis is made up of a single mass of fibers partially bifurcated medially, a configuration that, according to DIOGO et al. (2001b) represents the plesiomorphic condition for the Siluriformes (it should be noted that, due to the state of conservation of the fossil hypsidorids reported so far, it is not possible to appraise the configuration of the adductor profundus in these catfishes). In the vast majority of the catfishes the arrector dorsalis is divided into two broad, separated sections (DIOGO et al., 2001b).

Broad scapulo-coracoid suturing medially with its counterpart. Plesiomorphically in siluriforms the scapulo-coracoid is a slender structure with a thin median process, which does not suture with its counterpart medially (BORNBUSCH, 1995; GRANDE & DE PINNA, 1998; DIOGO et al., 2001b). Such a configuration of the scapulo-coracoid is only found in the diplomystids, cetopsids (see, e.g., Fig. 6), trichomycterids, nematogenyids, astroblepids and silurids. The other catfishes, including the fossil hypsidorids, present a broad scapulo-coracoid suturing medially with its counterpart (see DIOGO et al., 2001b). According to BORNBUSCH (1995) and GRANDE & DE PINNA (1998) the slender scapulo-coracoid with no mesial suture with its counterpart present in the trichomycterids, nematogenyids, astroblepids and silurids is very likely the result of a secondary homoplastic reversion of the apomorphic situation found in the vast majority of the catfishes.

These characters, together with the papers of MO (1991) and DE PINNA (1998), strongly suggest that the Cetopsidae occupy a rather basal position within the Siluriformes. As noted by DE PINNA (1998 : 292), this “may

seem contradictory, since cetopsids are considered as highly specialised catfishes in most of the specialised literature”. In fact, the cetopsids present several peculiar apomorphic morphological features, as it is clearly indicated by the numerous cetopsid synapomorphies described in DE PINNA & VARI's 1995 study and in the present paper (see above). However, as argued by DE PINNA (1998 : 292), the presence of numerous apomorphic features in the cetopsids is not contradictory with a rather basal position of these catfishes within the Siluriformes, since it indicates, precisely, that the cetopsids “have a long history independent of that of other catfishes”.

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REFERENCES

- ALEXANDER, R.M.N. (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.
- BORNBUSCH, A.H. (1995). Phylogenetic relationships within the Eurasian catfish family Siluridae (Pisces : Siluriformes), with comments on generic validities and biogeography. *Zool. J. Linnean Soc.*, 115 : 1-46.
- CHARDON, M. (1968). Anatomie compar  e de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann. Mus. R. Afr. Centr.*, 169 : 1-273.
- DE PINNA, M.C.C. (1998). Phylogenetic relationships of neotropical Siluriformes : history overview and synthesis of hypotheses. In : MALABARBA, 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.

- DE PINNA, M.C.C. & R.P. VARI (1995). Monophyly and phylogenetic diagnosis of the family Cetopsidae, with synonymization of the Helogenidae (Teleostei : Siluriformes). *Smithsonian Contr. Zool.*, 571 : 1-26.
- DIOGO, R. (2003). Higher-level phylogeny of the Siluriformes : an overview. In : ARRATIA, G., B.G. KAPOOR, M. CHARDON & R. DIOGO (eds), *Catfishes*, Science Publishers, Enfield : 353-384.
- DIOGO, R. (2005). *Exaptations, parallelisms, convergences, constraints, living fossils, and evolutionary trends : catfish morphology, phylogeny and evolution, a practical case study for general discussions on theoretical phylogeny and macroevolution*, Science Publishers, Enfield.
- DIOGO, R. & M. CHARDON (2000a). Anatomie et fonction des structures céphaliques associées à la prise de nourriture chez le genre *Chrysichthys* (Teleostei : Siluriformes). *Belg. J. Zool.*, 130 : 21-37.
- DIOGO, R. & M. CHARDON (2000b). 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 (2000c). The structures associated with catfish (Teleostei : Siluriformes) mandibular barbels : Origin, Anatomy, Function, Taxonomic distribution, Nomenclature and Synonymy. *Neth. J. Zool.*, 50 : 455-478.
- DIOGO, R. & M. CHARDON (2003). Homologies and evolutionary transformation of the skeletal elements of catfish (Teleostei : Siluriformes) suspensorium : a morphofunctional hypothesis. In : VAL, A.L. & B.G. KAPOOR (eds), *Fish adaptations*, Science Publishers, Enfield : 273-284.
- DIOGO, R., M. CHARDON & P. VANDEWALLE (2002). Osteology and myology of the cephalic region and pectoral girdle of *Bunocephalus knerii*, and a discussion of the phylogenetic relationships of the Aspredinidae (Teleostei : Siluriformes). *Neth. J. Zool.*, 51 : 457-481.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2000a). On the anatomy and function of the cephalic structures in *Phractura* (Siluriformes : Amphiliidae), with comments on some striking homoplasies occurring between the doumeins and some loricaroid catfishes. *Belg. J. Zool.*, 130 : 117-130.
- DIOGO, R., C. OLIVEIRA & M. CHARDON (2000b). 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 : 155-171.
- 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., 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.
- FERRARIS, C.J. (1996). *Denticetopsis*, a new genus of South-american whale catfish (Siluriformes : Cetopsidae, Cetopsinae), with two new species. *Proc. Calif. Acad. Sci.*, 49 : 161-170.
- GOSLINE, W.A. (1975). The palatine-maxillary mechanism in catfishes with comments on the evolution and zoogeography of modern siluroids. *Occ. Pap. Calif. Acad. Sci.*, 120 : 1-31.
- GRANDE, L. (1987). Redescription of *Hypsidoris farsonensis* (Teleostei : Siluriformes), with a reassessment of its phylogenetic relationships. *J. Vert. Paleont.*, 7 : 24-54.
- GRANDE, L. & M.C.C. DE PINNA (1998). Description of a second species of the catfish *Hypsidoris* and a reevaluation of the genus and the family Hypsidoridae. *J. Vert. Paleont.*, 18 : 451-474.
- HOWES, G.J. (1983a). Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei : Siluroidei). *Bull. Br. Mus. Nat. Hist. (Zool.)*, 45 : 1-39.
- HOWES, G.J. (1983b). The cranial muscles of the loricaroid catfishes, their homologies and value as taxonomic characters. *Bull. Br. Mus. Nat. Hist. (Zool.)*, 45 : 309-345.
- HOWES, G.J. (1985). The phylogenetic relationships of the electric family Malapteruridae (Teleostei : Siluroidei). *J. Nat. Hist.*, 19 : 37-67.
- LUNDBERG, J.G. (1975). Homologies of the upper shoulder girdle and temporal region bones in catfishes (Order Siluriformes), with comments on the skull of the Helogenidae. *Copeia*, 1975 : 66-74.
- LUNDBERG, J.G. (1982). The comparative anatomy of the toothless blindcat, *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. *Misc. Publ. Mus. Zool., Univ. Mi.*, 163 : 1-85.
- LUNDBERG, J.G. & L. PY-DANIEL (1994). *Bathycetopsis oliveirai*, Gen. et Sp. Nov., a Blind and Depigmented Catfish (Siluriformes : Cetopsidae) from the Brazilian Amazon. *Copeia*, 1994 : 381-390.
- MO, T. (1991). Anatomy, relationships and systematics of the Bagridae (Teleostei : Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zoologicae*, 17 : 1-216.
- OLIVEIRA, C., R. DIOGO, P. VANDEWALLE & M. CHARDON (2001). Osteology and myology of the cephalic region and pectoral girdle of *Plotosus lineatus*, with comments on Plotosidae (Teleostei : Siluriformes) autapomorphies. *J. Fish. Biol.*, 59 : 243-266.
- 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. (2003). State of the art of recent siluriform systematics. In : ARRATIA, G., B.G. KAPOOR, M. CHARDON & R. DIOGO (eds), *Catfishes*, Science Publishers, Enfield : 317-352.
- TILAK, R. (1963). The osteocranium and the Weberian apparatus of the fishes of the family Sisoridae (Siluroidea) : a study in adaptation and taxonomy. *Z. Wiss. Zool.*, 169 : 281-320.
- WINTERBOTTOM, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. (Phil.)*, 125 : 225-317.

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