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ORIGINAL ARTICLE

Osteology and myology of the cephalic region and pectoral girdle of *Pimelodus blochii*, comparison with other pimelodines, and comments on the synapomorphies and phylogenetic relationships of the Pimelodinae (Ostariophysi: Siluriformes)

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Abstract
The cephalic and pectoral girdle structures of the pimelodin *Pimelodus blochii* (*Pimelodus* group) are described and compared to those of representatives of the two other main pimelodin groups, namely *Calophysus macropterus* (*Calophysus* group) and *Pseudoplatystoma fasciatum* (*Sorubim* group), and of a representative of the peculiar pimelodin genus *Hypophthalmus*, *H. edentatus*, and several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Pimelodinae. Three new, additional potential synapomorphies to support the monophyly of the Pimelodinae are pointed out: (1) presence of a 'muscle 1 of the mandibular barbels' running from the antero-ventro-mesial surface of the cartilaginous plates carrying these barbels to the dentaries; (2) presence of a muscle tensor tripodis running from the posterior surface of the neurocranium to the dorsal surface of the swimbladder near the tripus; and (3) presence of a 'drumming muscle of the swimbladder' running from the parapophyses of the fourth vertebra and, eventually, the posterior surface of the neurocranium, to the antero and antero-ventral surface of the swimbladder. The subfamilies Pimelodinae, Heptapterinae and Pseudopimelodinae seem to constitute a monophyletic assemblage, thus contradicting the commonly accepted idea that the family Pimelodidae is a polyphyletic clade.

Keywords: *Catfish, cephalic region, comparative morphology, mycology, osteology, pectoral girdle, phylogeny, Pimelodinae, Pimelodidae,* Pimelodus, *Siluriformes*

Introduction

The Siluriformes, or catfishes, found in North, Central and South America, Africa, Europe, Asia and Australia, with fossils inclusively found in Antarctica, constitute a highly diversified, cosmopolitan group, which, with more than 2700 species, is one of the most diverse Vertebrate taxa (Teugels 2003). Among the 35 siluriform families (Ferraris & de Pinna 1999), the Pimelodidae, with more than 300 species, is one of the largest and most diverse Neotropical groups (e.g., de Pinna 1998; Shibatta 2003). In reality, most authors nowadays consider that such a diversity is due to the fact that the family Pimelodidae is a heterogeneous assemblage comprising 'three major well-defined monophyletic groups, currently ranked as subfamilies, the Pimelodinae, Heptapterinae, and Pseudopimelodinae' that do not form a monophyletic 'Pimelodidae' clade (de Pinna 1998: 313).

Among these three subfamilies, the Pimelodinae, defined by two synapomorphies, namely 'an elongated articulation surface on lateral ethmoid for palatine' and 'the presence of an hypertrophied pair of processes on the dorsal surface of premaxilla', and comprising 32 genera, is the largest and the most diverse one (de Pinna 1998: Figure 16). However, although the anatomy of pimelodines has been the subject of some published studies (e.g., Starks 1926; Alexander 1965; Chardon 1968; Ghiot 1978; Howes 1983; Azpelicueta 1998; Lundberg et al. 1991; Arratia 1992; Ladich & Fine 1994; Ladich & Bass 1998; Ladich 2001), most of these concerned mainly osteological structures of the cranium. Therefore, some important aspects of the morphology of this vast group of catfishes are still little known (e.g., their cranial muscles, or the structures associated with their mandibular barbels, only described with some detail by Alexander 1965; Ghiot 1978; Howes 1983) or practically unknown (e.g., the muscles of the

pectoral girdle). This not only complicates the study of the functional morphology of the pimelodines, but also restricts considerably the data available to infer the synapomorphies and/or the phylogenetic relationships of these catfishes.

In this work I describe the myological and osteological structures of both the cephalic region and the pectoral girdle of the pimelodin *Pimelodus blochii* Valenciennes 1840 (Bloch 1782) ('*Pimelodus*-group'), and compare these structures with those of representatives of the two other main pimelodin subgroups, namely *Calophysus macropterus* (Lichtenstein 1819) ('*Calophysus*-group') and *Pseudoplatystoma fasciatum* (Linnaeus 1766) ('*Sorubim*-group'), as well as of a representative of the 'quite peculiar' pimelodin genus *Hypophthalmus*, *H. edentatus* Spix and Agassiz, 1829 (see de Pinna 1998). This comparison, together with the comparison between these taxa and several other pimelodid and non-pimelodid catfishes allows a discussion on the synapomorphies and the phylogenetic relationships of the Pimelodinae.

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 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). 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 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 ineac* 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, 1 (alc). *Hemicetopsis candiru* USNM 167854, 1 (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 ebriensis* 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 zammaronoi* 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 inexspectata* 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: *Batrachoglanis raninus* USNM 226136, 3 (alc). *Calophysus macropterus* USNM 306962, 1 (alc); LFEM, 1 (alc). *Goeldiella eques* USNM 066180, 2 (alc). *Hepapterus mustelinus* USNM 287058, 2 (alc). *Hypophthalmus edentatus* USNM 226140, 1 (alc); LFEM, 1 (alc). *Microglanis cottoides* USNM 285838, 2 (alc). *Pimelodus blochii* LFEM, 4 (alc), 1 (alc). *Pseudoplatystoma fasciatum* USNM 284814, 2 (alc). *Rhamdia guatemalensis* USNM 114494, 2 (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). *Pseudeutropius brachypopterus* 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 yarreli* 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 banneaui* LFEM, 2 (alc). *Trichomycterus immaculatus* USNM 301015, 2 (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 recent papers (Diogo et al. 2001a; Diogo & Chardon 2003), with respect to the skeletal components of the suspensorium I follow Diogo et al. (2001a). The myological nomenclature is based mainly on Winterbottom (1974), but for the different adductor mandibulae sections, Diogo and Chardon (2000a) is followed, for reasons explained in Gosline (1989) and Diogo and Chardon (2000a). In relation to the muscles associated with the mandibular barbels, Diogo and Chardon (2000b) is followed. Concerning the nomenclature of the pectoral girdle bones and muscles, Diogo et al. (2001b) is followed.

Pimelodus blochii

Osteology. Os mesethmoideum. Situated on the anterodorsal surface of the neurocranium (Figure 1), with each of its antero-ventro-lateral margins ligamentously connected to the premaxilla.

Os lateroethmoideum. The lateral ethmoid is an irregular, large bone (Figure 1) presenting a markedly elongated articulatory facet for the autopalatine. The ethmoid cartilage, situated ventrally to both the lateral ethmoid and the mesethmoid, is well-developed, with its anterior portion being markedly extended anteriorly and almost reaching the posterior surface of the premaxillae.

Os praevomerale. Well-developed bone with reduced anterolateral arms and without ventral tooth-plates.

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

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

Os parasphenoideum. The parasphenoid 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 (Figure 1) are large bones that constitute a great part of the cranial roof. They are largely separated by a well-developed fontanel.

Os sphenoticum. Significantly smaller than the pterotic (Figure 1), it constitutes, together with this bone, a well-developed, deep articulatory facet for the hyomandibulo-metapterygoid.

Os pteroticum. Well-developed, irregularly-shaped bone situated posteriorly to the sphenotic (Figure 1).

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

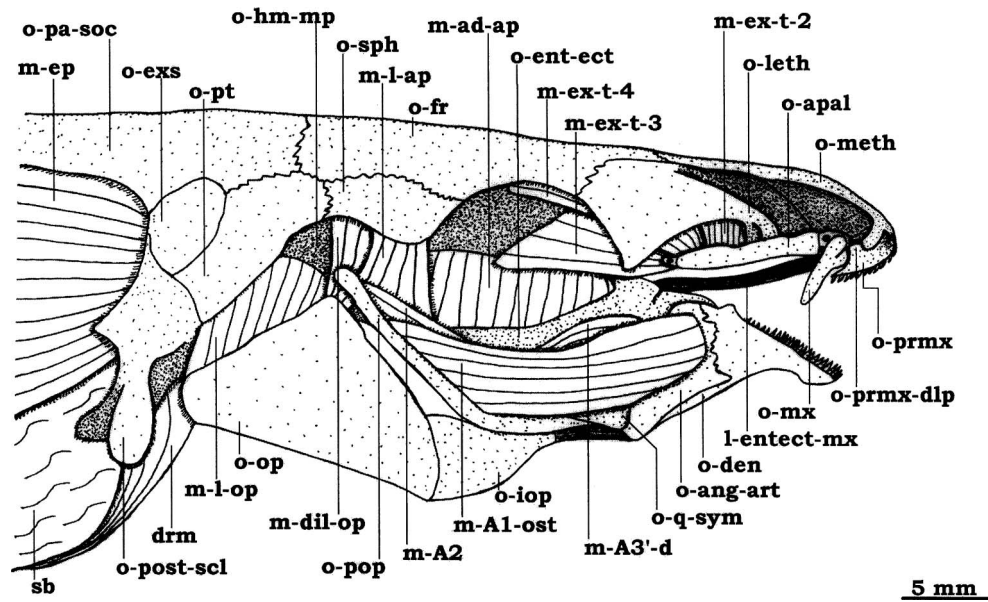*Os epioccipitale.* Situated on the posterior surface of the neurocranium.

Figure 1. Lateral view of the cephalic musculature of *Pimelodus blochii*. All the muscles are exposed. DRM drumming muscle, L-ENTECT-MX ligamentum entoectopterygoideo-maxillare, M-A1-OST M-A2 M-A3'-D sections of musculus adductor mandibulae, M-AD-AP musculus adductor arcus palatini, M-DIL-OP musculus dilatator operculi, M-EP musculus epaxialis, M-EX-T-2 M-EX-T-3 M-EX-T-4 sections of musculus extensor tentaculi, M-L-AP musculus levator arcus palatini, M-L-OP musculus levator operculi, O-ANG-ART os angulo-articulare, O-APAL os autopalatinum, O-DEN os dentale, O-ENT-ECT os ento-ectopterygoideum, O-EXS os extrascapulare, O-FR os frontale, O-HM-MP os hyomandibulo-metapterygoideum, O-IOP os interoperculare, O-LETH os latero-ethmoideum, O-METH os mesethmoideum, O-MX os maxillare, O-OP os operculare, O-PA-SOC os parieto-supraoccipitale, O-POP os praeoperculare, O-POST-SCL os posttemporo-supracleithrum, O-PRMX os praemaxillare, O-PRMX-DLP dorsolateral process of os praemaxillare, O-PT os pteroticum, O-Q-SYM os quadrato-symplecticum, O-SPH os sphenoticum, SB swimbladder.

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

Os extrascapulare. Small bone (Figure 1) situated on the postero-dorso-lateral surface of the neuro-cranium, between the posttemporo-supracleithrum, the pterotic and the parieto-supraoccipital.

Os basioccipitale. Well-developed, unpaired bone, forming the posteriormost 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 (Figure 1) constituting the postero-dorso-median surface of the cranial roof. It bears an enlarged, posteriorly pointed, triangular postero-median process.

Os angulo-articulare. This bone (Figure 1), together with the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible. Postero-ventrally, the angulo-articular is ligamentously connected to both the interopercular bone and the posterior ceratohyal. Posterodorsally, it presents an articulatory facet for the quadrate-symplectic.

Os dentale. The posterodorsal margin of the toothed (Figure 1) dentary forms, together with the anterodorsal margin of the angulo-articular, a well-developed dorsal process (processus coronoideus).

Os coronomeckelium. Small bone lodged in the medial surface of the mandible. Posterodorsally

it bears a crest for attachment of the adductor mandibulae A3'-d.

Os praemaxillare. Well-developed bone presenting a prominent dorsolateral process (Figure 1: o-prmx-dlp) for the attachment of a short, but strong, ligament connecting this bone to the maxilla. Ventrally, the premaxilla bears a well-developed tooth-plate with numerous small teeth having their tips slightly turned backward (Figure 1).

Os maxillare. The maxilla is a small bone (Figure 1) presenting two well-developed proximal heads and being connected by means of a short but strong ligament to the premaxilla (see above) and by means of a strong, long ligament to the ento-ectopterygoid. As in most catfishes, the maxillary barbels are supported by the maxillary bones.

Os autopalatinum. The autopalatine (Figure 1) is a rod-like anteroposteriorly elongated bone with its posterior portion slightly expanded dorsoventrally. Its posterior end is capped by a small cartilage and its anterior end is tipped by a somewhat well-developed cartilage with two antero-lateral concavities, which accept the two proximal heads of the maxilla. Medially, the autopalatine articulates, by means of a markedly elongated articulatory surface, with the lateral ethmoid.

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 (e.g., McMurrich 1884; Starks 1926; De Beer 1937; Gosline 1975; Howes 1983, 1985; Arratia 1992; Howes & Teugels 1989; Diogo et al. 2001a; Diogo & Chardon 2003). As referred before, for the several reasons explained in detail in recent papers (Diogo et al. 2001a; Diogo & Chardon 2003), the nomenclature used here to describe these elements will strictly follow that presented by Diogo et al. (2001a). The hyomandibulo-metapterygoid (Figure 1) is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercular bone.

Os sesamoideum 1. Well-developed, boomerang-shaped. It is attached, by means of two thick ligaments, to the ento-ectopterygoid and to the lateral ethmoid.

Os sesamoideum 2. Narrow, elongated bone with its posterodorsal surface attached, *via* connective tissue, to the dorsolateral surface of the sesamoid bone 1 of the suspensorium, and its anterodorsal surface connected, by means of a short and thin ligament, to the ventral surface of the autopalatine. The sesamoid bone 3 (see Diogo et al. 2001a) is absent.

Os entopterygoide-ectopterygoideum. Well-developed (Figure 1), with its anterior surface being slightly bifurcated. Posteriorly, the ento-ectopterygoid is sutured with both the hyomandibulo-metapterygoid and the quadrate-symplectic. Anteriorly, it is connected, by means of two long, strong ligaments to both the maxilla (Figure 1) and the sesamoid bone 1 of the suspensorium (Figure 1: it should be noted that the ligament between this latter bone and the ento-ectopterygoid is covered, in this figure, by the muscle extensor tentaculi).

Os quadrato-symplecticum. The quadrate-symplectic (Figure 1) presents a well-developed anterior articulatory surface to articulate with the posterodorsal surface of the angulo-articular.

Os praeoperculare. Long and thin bone (Figure 1) firmly sutured to both the hyomandibulo-metapterygoid and the quadrate-symplectic.

Os operculare. The opercular bone (Figure 1) is a large, roughly triangular structure attached ventrally, by means of connective tissue, to the interopercular bone. It presents a well-developed, dorso-ventrally elongated anterodorsal articulatory surface for the hyomandibulo-metapterygoid.

Os interoperculare. Its anterior surface is ligamentously connected to the postero-ventral margin of the mandible (Figure 1). The interopercular bone is attached medially by means of massive connective tissue to the lateral surface of the posterior ceratohyal.

Os interhyale. Small-bone ligamentously connected to the hyomandibulo-metapterygoid dorsally and to the posterior ceratohyal ventrally.

Os ceratohyale posterior. Well-developed, somewhat triangular bone connected by means of two strong ligaments to the postero-ventral edge of the mandible and to the interhyal, respectively.

Os ceratohyale anterior. Elongated, stout 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.

Os hypohyale dorsale. These are small bones situated dorsally to the ventral hypohyals.

Os parurohyale. The parurohyal is a large, irregular bone lying medially behind the two ventral hypoyals and presenting a well-developed, posteriorly pointed triangular posterior process.

Os posttemporo-supracleithrum. This bone (Figure 1), together with 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.

Os cleithrum. The cleithrum (Figure 2) is a large, well-ossified stout structure presenting a prominent
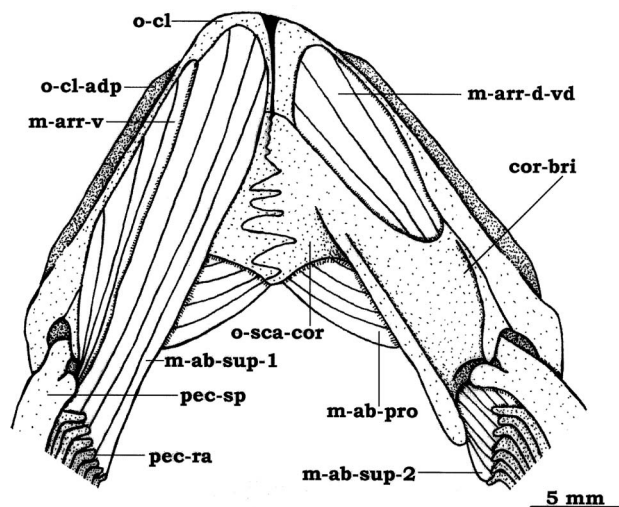

Figure 2. Ventral view of the pectoral girdle musculature of *Pimelodus blochii*. On the left side all the muscles are exposed, on the right side the arrector ventralis as well as the section 1 of the abductor superficialis were removed. COR-BRI coracoid bridge, M-AB-PROF musculus abductor profundus, M-AB-SUP-1 M-AB-SUP-2 sections of musculus abductor superficialis, M-ARR-D-VD ventral division of musculus arrector dorsalis, M-ARR-V musculus arrector ventralis, O-CL os cleithrum, O-CL-ADP anterodorsal projection of os cleithrum, O-SCA-COR os scapulo-coracoide, PEC-RA pectoral rays, PEC-SP pectoral spine.

anterodorsal projection of laminar bone (Figure 2: o-cl-adp) and forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It contacts its counterpart in the antero-medial line *via* connective tissue and bears a deep crescentic, medially faced groove that accommodates the dorsal condyle of the well-developed pectoral spine. The humeral process of the cleithrum is well-developed.

Os scapulo-coracoideum. This is an elongated bony plate (Figure 2) suturing with the cleithrum along its antero-lateral edge. Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge (Figure 2: cor-bri), which extends ventrally to the ventro-lateral surface of the cleithrum, suturing with an antero-ventral ridge of this bone. Mesially, the scapulo-coracoid joins its counterpart in an interdigitation of several strong serrations. Postero-laterally, it bears two condyles, which articulate respectively with the pectoral spine and the complex radial (see Mo 1991). There is a well-developed meso-coracoid arch.

Myology.

Musculus adductor mandibulae. The adductor mandibulae A1-ost (see Diogo & Chardon 2000a) originates on the preopercular bone and the quadrate-symplectic and inserts on the dorsolateral surface of the angulo-articular (Figure 1). The A2 (Figure 1), which lies dorso-mesially to the A1-ost, runs from the preopercular bone and the hyomandibulo-metapterygoid to the medial surface of the dentary. The adductor mandibulae A3′ is divided into a dorsal and a ventral part. The dorsal one (A3′-d) (Figure 1: m-A3′-d) originates on the hyomandibulo-metapterygoid and inserts tendinously on the coronomeckelian bone, while the ventral one (A3′-v) originates on the quadrato-symplectic and inserts on the medial surface of the angulo-articular. The adductor mandibulae A3″, situated mesially to the A3′, runs from the hyomandibulo-metapterygoid and the quadrato-symplectic to the mesial surface of the angulo-articular. Lastly, the adductor mandibulae Aω, which is well-developed, attaches anteriorly on the mesial surface of both the dentary and the angulo-articular and posteriorly on the tendon of the A2.

Musculus levator arcus palatini. The levator arcus palatini (Figure 1) is situated medially to the adductor mandibulae A3′. It originates on the sphenotic and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (Figure 1) runs from the parasphenoid, pterosphenoid and orbitosphenoid to the hyomandibulo-metapterygoid and the ento-ectopterygoid.

Musculus levator operculi. It originates on both the ventro-lateral margin of the pterotic and the postero-dorso-lateral surface of the hyomandibulo-metapterygoid and inserts on the dorsal surface of the opercular bone (Figure 1).

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 bone.

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. The dilatator operculi (Figure 1) originates on the pterosphenoid, frontal and sphenotic and inserts on the anterodorsal margin of the opercular bone.

Musculus extensor tentaculi. This muscle is divided into four bundles. The extensor tentaculi 1 runs from the lateral ethmoid to both the postero-ventral and the postero-mesial surfaces of the autopalatine. The extensor tentaculi 2 (Figure 1) originates on the lateral ethmoid and inserts on the posterodorsal surface of the autopalatine. The extensor tentaculi 3 (Figure 1) runs from the lateral ethmoid and the orbitosphenoid to the postero-ventral margin of the autopalatine. Lastly, the extensor tentaculi 4 (Figure 1) originates on both the orbitosphenoid and the lateral ethmoid and inserts on the posterodorsal surface of the autopalatine.

Musculus protractor hyoidei. This muscle (Figure 3) has 3 parts. The pars ventralis, in which are lodged both the cartilages associated with the internal and external mandibular barbels (Figure 3: c-in-mnd-t; c-ex-mnd-t) and the large cartilaginous plate carrying these barbels (Figure 3: cp-mnd-b) (see Ghiot 1978; Diogo & Chardon 2000b), originates on the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis (Figure 3). The pars lateralis runs from the posterior ceratohyal to the ventro-medial face of the dentary (Figure 3). The pars dorsalis runs from the anterior ceratohyal to the anterodorsal surface of the dentary. It should be noted that the cartilaginous plate carrying the mandibular barbels of the right side of the fish (which corresponds to the left side of Figure 4) situates ventrally to the cartilaginous plate carrying the mandibular barbels of the opposite side (i.e. of the left side of the fish, which corresponds to the right side of Figure 4), thus covering a significant part of this latter structure in ventral view (Figure 4).
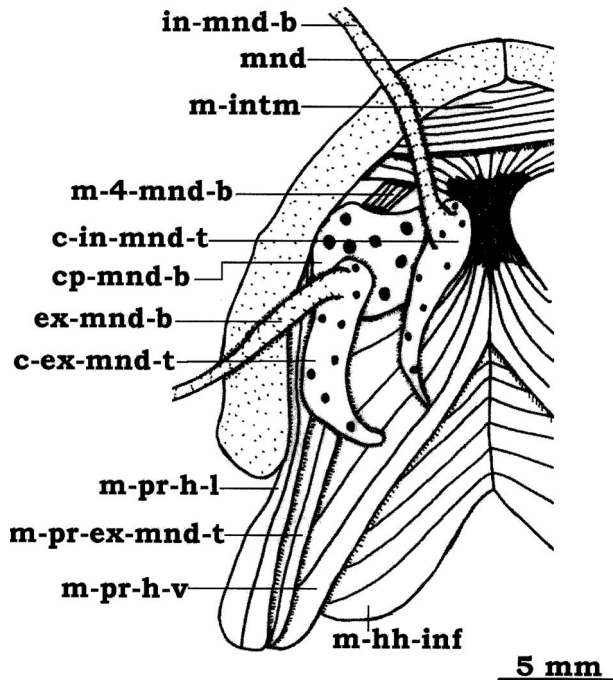
Figure 3. Ventral view of the cephalic musculature of *Pimelodus blochii*. All the muscles are exposed. C-IN-MND-T cartilago internus mandibularis tentaculi, C-EX-MND-T cartilago externus mandibularis tentaculi, cp-mnd-b cartilaginous plate carrying the mandibular barbels, EX-MND-B IN-MND-B external and internal mandibular barbels, M-4-MND-B muscle 4 of the mandibular barbels, M-HH-INF musculus hyohyoideus inferior, M-INTM musculus intermandibularis, MND mandible, M-PR-EX-MND-T musculus protractor externi mandibularis tentaculi, M-PR-H-L M-PR-H-V pars lateralis and ventralis of musculus protactor hyoideus.
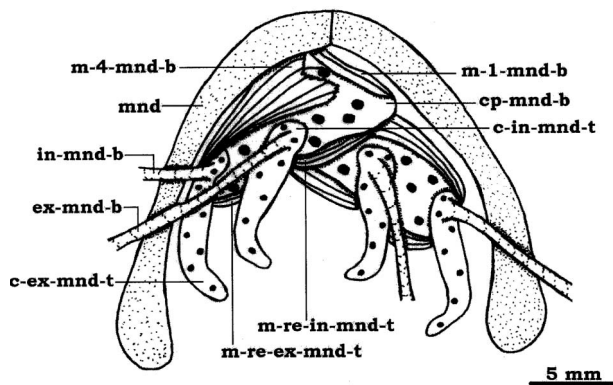

Figure 4. Ventral view of the cephalic musculature of *Pimelodus blochii*. The intermandibularis the protractor hyoidei the hyoideus inferioris and the protractor externi mandibularis tentaculi were removed. In addition a part of the plates carrying the mandibular barbels was also removed in order to expose the muscle 4 of the mandibular barbels. C-IN-MND-T cartilago internus mandibularis tentaculi, C-EX-MND-T cartilago externus mandibularis tentaculi, CP-MND-B cartilaginous plate carrying the mandibular barbels, EX-MND-B IN-MND-B external and internal mandibular barbels, M-1-MND-B M-4-MND-B muscles 1 and 4 of the mandibular barbels, MND mandible, M-RE-EX-MND-T musculus retractor externi mandibularis tentaculi, M-RE-IN-MND-T musculus retractor interni mandibularis tentaculi.

Musculus retractor externi mandibularis tentaculi. Small muscles situated dorsally to the cartilaginous plates carrying the mandibular barbels (Figure 4). They run from the anterodorsal surface of the moving part (see Diogo & Chardon 2000b) of the cartilages associated with the outer mandibular barbels to the posterodorsal surface of these cartilaginous plates.

Musculus retractor interni mandibularis tentaculi. These small muscles are also situated dorsally to the large cartilaginous plates carrying the mandibular barbels (Figure 4). They run from both the dorso-medial surface of these plates and the anterodorsal surface of the dentaries to the anterodorsal surface of the moving part of the cartilages associated with the internal mandibular barbels.

Musculus protractor externi mandibularis tentaculi. Well-developed, elongated muscles (Figure 3) originating on the anterior ceratohyals and inserting on the anterodorsal surface of the moving part of the cartilages associated with the outer mandibular barbels. It is important to note in addition to the protractor and the two retractor muscles of the mandibular barbels described above, which are present in a large number of catfishes (Diogo & Chardon 2000b), the presence of two additional, small paired muscles associated with these barbels. These are the 'muscle 1 of the mandibular barbels' (Figure 1: m-1-mnd-b), which runs from the dentaries to the cartilaginous plates carrying the mandibular barbels, and the 'muscle 4 of the mandibular barbels' (Figure 4: m-4-mnd-b), which runs from these cartilaginous plates and the dentaries to the proximal surface of the outer mandibular barbels (with respect to the nomenclature of these muscles, see Diogo & Chardon 2000b).

Muscle intermandibularis. Small muscle joining the two mandibles (Figure 3).

Musculus hyohyoideus inferior. Thick muscle (Figure 3) 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, as well as the most external branchiostegal ray with the opercle of that side.

Musculus sternohyoideus. It runs from the posterior portion of the parurohyal to the anterior portion of the cleithrum.

Musculus arrector ventralis. It runs from the cleithrum to the ventral condyle of the pectoral spine (Figure 2).

Musculus arrector dorsalis. This muscle, dorsal to the arrector ventralis and the abductor superficialis, is differentiated into two well-developed divisions. The ventral division (Figure 2: m-arr-d-vd), situated on the ventral surface of the pectoral girdle, originates on the ventral margin of the cleithrum 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. This well-developed muscle (Figure 2) 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 (Figure 2: 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 (Figure 2: m-ab-sup-2), situated dorsally to the larger one, runs from the lateral edge of the scapulo-coracoid to the anterodorsal margin of the ventral part of the pectoral fin rays.

Musculus adductor superficialis. This muscle situates 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 anterodorsal 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 radials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus protractor pectoralis. Well-developed muscle running from the ventral surfaces of both the pterotic and the posttemporo-supracleithrum to the anterodorsal surface of the cleithrum.

Musculus tensor tripodis. The tensor tripodis (see, e.g., Bridge & Haddon 1894; Ladich & Fine 1994; Ladich & Bass 1998; Ladich 2001) is a small muscle situated posteriorly to the protractor pectoralis and running from the posterior surface of the parieto-supraoccipital to the dorsal surface of the swimbladder near the tripus. Although it is not a cranial muscle, it is worthwhile to notice the presence of another muscle also directly associated with the swimbladder, the drumming muscle (Figure 1: drm) (see Ladich & Fine 1994; Ladich & Bass 1998; Ladich 2001), which runs from the anterior and antero-ventral surfaces of this latter structure to the well-developed parapophysis of the fourth vertebra.

Calophysus macropterus

The principal differences between the structures of the cephalic region and pectoral girdle of this species and those of *P. blochii* are that in *C. macropterus*: (1) the posterior process of the parieto-supraoccipital process is not as developed as in *P. blochii*; (2) a great part of the fibers of the muscle adductor hyomandibularis are mixed to those of the adductor operculi; (3) the coronoid process is still more developed than that of *P. blochii*; (4) the humeral process of the cleithrum is undifferentiated; (5) in *C. macropterus* the cartilaginous plate carrying the mandibular barbels of the left side of the fish lies ventrally, and not dorsally, to the cartilaginous plate carrying the mandibular barbels of the right side of the fish; and (6) the pectoral spine is significantly thinner and less developed than that of *P. blochii*.

Pseudoplatystoma fasciatum

The principal differences between the structures of the cephalic region and pectoral girdle of *P. blochii* and those of *P. fasciatum* are that in this latter species: (1) the cartilaginous plates carrying the mandibular barbels of the different sides of the fish do not overlap with each other; (2) the humeral process is significantly less developed than that of *P. blochii*; (3) the coracoid bridge is significantly thinner than it is in *P. blochii*; (4) the postero-lateral surface of the scapulo-coracoid presents a well-developed, circular foramen to receive the anterior condyle of the pectoral spine when this spine is abducted; (5) the coronoid process is significantly less developed than that of *P. blochii*; (6) there is a muscle retractor tentaculi running from the antero-lateral surface of the suspensorium to posterior surface of the maxilla; (7) the hyomandibulo-metapterygoid and the ento-ectopterygoid do not contact, being widely separated by the quadrato-symplectic; (8) the interopercular bone presents a prominent, markedly developed, thin anterior process for the attachment of the ligament between this bone and the angulo-articular; (9) the drumming muscle does not only originate on the parapophysis of the fourth vertebra, but also on the neurocranium, namely on the parieto-supraoccipital and the exoccipital; (10) the sesamoid bone 2 of the suspensorium is missing, but there is an additional tooth-plate between the ento-ectopterygoid and the autopalatine, as well as teeth on the ventral surface of the ento-ectopterygoid; (11) the lateral surface of the premaxilla is markedly pointed posteriorly; (12) contrarily to *P. blochii*, in *P. fasciatum* there is a prevomerine tooth-plate; and (13) the posterior process of the parieto-supraoccipital process is not as developed as in *P. blochii*.

Hypophthalmus edentatus

The principal differences between the structures of the pectoral girdle and cephalic region of *H. edentatus* and those of *P. blochii* are that in the former species: (1) the muscle intermandibularis is significantly smaller than that of *P. blochii*; (2) each one of the two cartilaginous plates carrying the mandibular barbels is somewhat divided into three main parts, but these parts are firmly connected, forming a single compact structure; (3) the posterior ceratohyal, the anterior ceratohyal and the ventral hypohyal are very thin, elongated bones, thus forming a markedly thin, elongated hyoid arch; (4) the lateral surface of the postero-ventral part of the cleithrum is pierced by a large, circular foramen that receives the dorsal condyle of the pectoral spine, with this condyle being, thus, visible in a lateral view of the pectoral girdle; (5) the coracoid bridge is significantly thinner than it is in *P. blochii*; (6) the humeral process of the cleithrum is undifferentiated; (7) the ventral division of the muscle arrector dorsalis is situated in the dorsal surface, and not in the ventral one, of the pectoral girdle; (8) the pectoral spine, as well as the coronoid process, are significantly less developed than that of *P. blochii*; (9) the mandible is edentate, and much more elongated anteroposteriorly than that of *P. blochii*; (10) the adductor mandibulae A3″ does not originates only on the suspensorium, but on both the suspensorium and the neurocranium; (11) the interopercular bone presents a prominent, markedly developed, thin anterior process for the attachment of the ligament between this bone and the angulo-articular; (12) the sesamoid bone 1 of the suspensorium is markedly smaller than that of *P. blochii*, and the sesamoid bone 2 of the suspensorium is missing; (13) there is a muscle retractor tentaculi connecting the suspensorium to the maxilla; (14) the dorsomedial limb of the posttemporo-supracleithrum is firmly sutured, and not only ligamentously attached, to the neurocranium; (15) the extrascapular is missing; (16) the posterior process of the parieto-supraoccipital process is not as developed as in *P. blochii*; and (17) contrarily to *P. blochii*, in *H. edentatus*, the premaxillae are edentate.

Discussion

In a recent overview of the phylogeny and systematics of the subfamily Pimelodinae, de Pinna (1998) listed two synapomorphies to support the monophyly of this subfamily (de Pinna 1998: Figure 16): (1) 'elongated articulation surface on lateral ethmoid for autopalatine'; and (2) 'presence of an hypertrophied pair of processes on the dorsal surface of premaxilla, between which the proximal portion of the maxilla fits'. The author's phylogenetic analysis, which included 440 characters and 87 terminal taxa representing all the extant catfish families (Diogo 2004), not only confirmed these two synapomorphies, but also pointed out three other features that seemingly represent pimelodin synapomorphies, which are described below.

Presence of a 'muscle 1 of the mandibular barbels'. Plesiomorphically catfishes lack a 'muscle 1 of the mandibular barbels' (Diogo & Chardon 2000b; Diogo & Vandewalle 2003). However in all pimelodines examined, and exclusively in these catfishes there is a 'muscle 1 of the mandibular barbels' running from the antero-ventro-mesial surface of the cartilaginous plates carrying the mandibular barbels to the dentaries (see, e.g., Figure 4).

Presence of a muscle tensor tripodis. Plesiomorphically catfishes lack a muscle tensor tripodis (Ladich & Fine 1994; Ladich & Bass 1998; Ladich 2001). However, such a muscle, running from the posterior surface of the neurocranium to the dorsal surface of the swimbladder near the tripus (see, e.g., Ladich 2001: Figure 2), is present in all pimelodines examined in the present study, with exception to *Hypophthalmus edentatus*. The derived position of *Hypophthalmus* within the Pimelodinae (de Pinna 1998: Figure 16), associated with the presence of the tensor tripodis in the other pimelodines examined and its absence in non-pimelodin catfishes, strongly suggests that the presence of this muscle constitutes a Pimelodinae synapomorphy. The absence of this muscle in *Hypophthalmus* is seemingly due to a secondary loss (Diogo 2004), which could be associated with the fact that in the members of this genus, contrarily to most other pimelodines, the swimbladder is almost completely encapsulated by the well-developed parapophyses of the complex vertebra.

Presence of a 'drumming muscle' of the swimbladder. The presence of a 'drumming muscle' of the swimbladder (see, e.g., Ladich & Fine 1994; Ladich & Bass 1998; Ladich 2001) running from the parapophyses of the fourth vertebra and, eventually (e.g., in *Calophysus macropterus*) from the posterior surface of the neurocranium, to the antero and antero-ventral surfaces of the swimbladder, is a derived feature that is present in all pimelodines examined (see, e.g., Figure 1) except *Hypophthalmus edentatus* and that is absent in non-pimelodin catfishes. Therefore, the presence of this muscle seemingly also constitutes a synapomorphic feature, secondarily lost in the highly derived genus *Hypophthalmus* (Diogo 2004), to support the monophyly of the Pimelodinae.

But probably the more important aspect of the author's results is that they support the monophyly of the family Pimelodidae as a whole, that is, of the clade

including the subfamilies Pimelodinae, Pseudopimelodinae and Heptapterinae, thus contradicting the nowadays commonly accepted view that the Pimelodidae is a polyphyletic, unnatural assemblage (see Introduction). In fact, the author's phylogenetic analysis (Diogo 2004) pointed out four characters that constitute, very likely, synapomorphies of a clade formed by the pimelodines, the heptapterines and the pseudopimelodines, two of which are uniquely present in these three groups among catfishes. These four characters are described below.

Presence of a 'muscle 4 of the mandibular barbels'. Plesiomorphically catfishes lack a 'muscle 4 of the mandibular barbels' (Diogo & Chardon 2000b; Diogo & Vandewalle 2003). However, in all pimelodids examined, and in no other catfishes studied examined by the author or described in the literature, there is a 'muscle 4 of the mandibular barbels' connecting the proximal surface of the external mandibular barbels to the antero-ventro-lateral surface of the cartilaginous plates carrying the mandibular barbels and to the antero-mesial surfaces of the dentaries (see, e.g., Figure 4).

Presence of 'cartilaginous plates carrying the mandibular barbels'. As the presence of a 'muscle 4 of the mandibular barbels', the presence of 'cartilaginous plates carrying the mandibular barbels' (see, e.g., Ghiot 1978; Diogo & Chardon 2000b) is a derived feature present in the pimelodines, pseudopimelodines and heptapterines examined (see, e.g., Figures 3 and 4), and in no other catfishes studied by the author or described in the literature.

Origin of the muscle levator operculi on both the hyomandibulo-metapterygoid and the pterotic. Plesiomorphically in catfishes the muscle levator operculi originates exclusively on the neurocranium, namely on the pterotic (Diogo & Vandewalle 2003). However, in the pimelodines, heptapterines and pseudopimelodines examined, a great part of the fibers of this muscle also originate on the postero-dorso-lateral surface of the hyomandibulo-metapterygoid (see, e.g., Figure 1). The origin of the levator operculi on both the neurocranium and the hyomandibulo-metapterygoid is a very rare feature among catfishes, being only present, apart from the pimelodids, in a few catfishes such as plotosids, cranoglanidids, schilbids and silurids (Diogo & Vandewalle 2003). As these latter four groups are seemingly more closely related to other catfish taxa than to pimelodines, heptapterines and/or pseudopimelodines (Mo 1991; de Pinna 1998; Diogo et al. 2002a; Diogo 2004), this character also supports the monophyly of the Pimelodidae.

Anterior portion of ethmoid cartilage markedly extended anteriorly. One other derived character that seemingly supports the monophyly of this family is the markedly anterior extension of the anterior portion of the ethmoid cartilage, which almost reaches the posterior surface of the premaxillaries. Contrarily to the vast majority of the Siluriformes, in which the anterior portion of the ethmoid cartilage does not extend far beyond the anterior margin of the lateral ethmoids (see, e.g., Mo 1991; Diogo & Chardon 2000c), in the pimelodines, pseudo-pimelodines and heptapterines examined this cartilage is markedly extended anteriorly, almost reaching the posterior margin of the premaxillaries; such a feature is, again, extremely rare among catfishes, only being found so far apart from the pimelodines in the austroglanidids claroteins and schilbids (see, e.g., Diogo & Chardon 2000c: Figures 5 and 6). As these three groups are seemingly more closely related to certain other catfish groups than to pimelodines, heptapterines and/or pseudopimelodines (Mo 1991; de Pinna 1998; Diogo et al. 2002a; Diogo 2003, 2004), this character constitutes one more argument on behalf of the monophyly of the family Pimelodidae.

Of the four characters discussed above, the first two characters particularly constitute very strong evidence to support the monophyly of the Pimelodidae, as they concern noticeable, distinct, easily recognised features that are *exclusively* present in pimelodids. As noted de Pinna (1998), the uniform, exclusive presence of a well-defined, distinct feature in a certain catfish group is extremely rare in a taxon as large and diverse as the Siluriformes. As referred above, this hypothesis contradicts the somewhat commonly accepted view nowadays that the Pimelodidae constitute a polyphyletic assemblage. However, it should not be forgotten that the only published work where this view was actually explicitly stated, i.e. where it was provided a phylogenetic hypothesis proposing that the three pimelodid subfamilies are more closely related to other catfish groups than to each other, was that of de Pinna (1998). And, as de Pinna's 1998 work does not describe the characters that supported that phylogenetic hypothesis (de Pinna 1998 refers to an unpublished PhD thesis by the same author), there are in reality no published characters to support such a view and, thus, to confront with the arguments given in the present study.

The evidence presented above to support the monophyly of the family Pimelodidae is clearly related to the inclusion of characters that are not usually included in works concerning catfish phylogeny, such as, for example, those concerning the structures associated with the mandibular barbels or the cranial muscles. As other papers recently published by the author and colleagues (e.g., Diogo & Chardon 2000b; Diogo et al. 1999, 2000a,b, 2001b,c, 2002a,b; Oliveira et al. 2002; Diogo 2003, 2004; Diogo & Vandewalle 2003), the present study thus stresses that the analysis

of such features, and, particularly of the configuration of the cranial and pectoral girdle musculature, could reveal useful data for disclosing not only the phylogenetic relationships between different catfish groups, but also the synapomorphies and/or autapomorphies of these groups.

Acknowledgements

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