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Osteology and myology of the cephalic region and pectoral girdle of *Batrochoglanis raninus*, with a discussion on the synapomorphies and phylogenetic relationships of the Pseudopimelodinae and Pimelodidae (Teleostei: Siluriformes)

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Abstract—The cephalic and pectoral girdle structures of the pseudopimelodin *Batrochoglanis raninus* are described and compared to those of a representative of another pseudopimelodin genera, namely *Microglanis cottoides*, as well as to several other pimelodid and non-pimelodid catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Pseudopimelodinae. Our observations and comparisons pointed out two new, additional features that could represent potential Pseudopimelodinae synapomorphies: 1) mesethmoid markedly bifurcated anteriorly; 2) spoon-shaped autopalatine with a somewhat roundish, markedly enlarged dorso-ventrally, posterior tip. In addition, our observations and comparisons indicate that the subfamilies Pseudopimelodinae, Pimelodinae and Heptapterinae do constitute a monophyletic assemblage, and, thus, contradict the commonly accepted idea that the family Pimelodidae is a polyphyletic group.

Keywords: *Batrochoglanis*; catfish; Heptapterinae; *Microglanis*; morphology; myology; osteology; phylogeny; Pimelodidae; Pimelodinae; Pseudopimelodinae; Siluriformes.

INTRODUCTION

The Siluriformes, with approximately 438 genera and over 2750 species, represent about 33% of all freshwater fishes and are one of the economically important groups of fresh and brackish water fishes in the world (Teugels, 2003). Among the 35 siluriform families (Ferraris and de Pinna, 1999), the Pimelodidae, with more than 300 species, is one of the largest and most diverse neotropical groups (de

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Pinna, 1998; Shibatta, 2003). In fact, nowadays most authors consider that such a noticeable diversity is due to the fact that the 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). That is why de Pinna (1998), in a recent, detailed overview on the phylogeny and systematics of this clade, decided to treat these three subfamilies as separate families, although, as he noted, keeping their subfamilial names (de Pinna, 1998: 313).

Among these three subfamilies, the Pseudopimelodinae, comprising the genera *Pseudopimelodus*, *Microglanis*, *Batrachoglanis*, *Cephalosilurus* and *Lophiosilurus*, is the smallest and least studied (de Pinna, 1998; Shibatta, 2003). In fact, the only published work describing with some detail the morphology of the pseudopimelodin catfishes is that of Lundberg et al. (1991). Moreover, this description concerns mainly the osteological structures of the cranium, and, thus, some important aspects of the morphology of these catfishes are still poorly known (e.g., their cranial muscles, the structures associated with their mandibular barbels, and their pectoral girdle musculature). This not only complicates the study of the functional morphology of the pseudopimelodins, but also restricts considerably the data available to infer the synapomorphies and/or the phylogenetic relationships of these catfishes.

In this work we will describe the myological and osteological structures of both the cephalic region and the pectoral girdle of a representative of the subfamily Pseudopimelodinae, namely *Batrochoglanis raninus* (Valenciennes, 1840), and compare these structures with those of a representative of another of the five pseudopimelodin genera, namely *Microglanis cottoides* (Boulenger, 1891), as well as several other pimelodid and non-pimelodid catfishes, as a foundation for a discussion on the synapomorphies and phylogenetic relationships of the Pseudopimelodinae. It is also hoped that this study will increase the knowledge of the anatomy and phylogeny of the catfishes in general, as well as pave the way for future works regarding the comparative anatomy, evolution, functional morphology, palaeontology, eco-morphology and, particularly, the phylogeny of these fishes.

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 and 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). *Xylophius 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). *Hemisetopsis 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 boudierius* 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: *Batrochoglanis raninus* USNM 226136, 3 (alc). *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, 2 (alc). *Pimelodus blochii* LFEM, 2 (alc). *Pimelodus clarias* LFEM, 2 (alc); USNM 076925, 1 (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 anguillarlis* LFEM, 2(alc). *Plotosus lineatus* USNM 200226), 2 (alc).

Schilbidae: *Ailia colia* USNM 165080, 1 (alc). *Laides hexanema* USNM 316734, 1 (alc). *Pseudeutropius 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 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 this section we will describe the cephalic and pectoral girdle structures of the pseudopimelodin *Batrochoglanis raninus* and compare these structures with those of a representative of another pseudopimelodin genera, namely *Microglanis cottoides*. In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region basically follows that of Arratia (1997). However, for the several reasons explained in detail in our recent papers (Diogo et al., 2001a; Diogo and Chardon, 2003), with respect to the skeletal components of the suspensorium we follow Diogo et al. (2001a). The myological nomenclature is based mainly on Winterbottom (1974), but for the different adductor mandibulae sections, Diogo and Chardon (2000a) are 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) are followed. Concerning the nomenclature of the pectoral girdle bones and muscles, Diogo et al. (2001b) are followed.

Batrochoglanis raninus

Osteology

Os mesethmoideum. Situated on the antero-dorsal surface of the neurocranium (fig. 1). It is markedly bifurcated anteriorly, with each of its well-developed antero-lateral arms being ligamentously connected to the premaxilla.

Os lateroethmoideum. The lateral ethmoid is an irregular, large bone (fig. 1) articulating laterally with the autopalatine. The ethmoid cartilage, situated ventrally to both the lateral ethmoid and the mesethmoid, is highly developed, with its anterior portion being markedly extended anteriorly and almost reaching the posterior surface of the premaxillaries (fig. 1). The prevomer is missing.

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

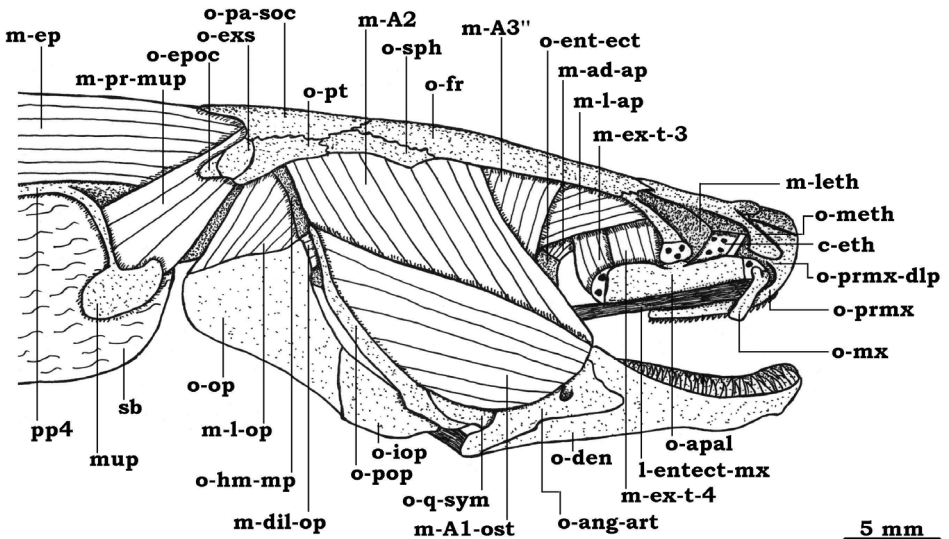


Figure 1. Lateral view of the cephalic musculature of *Batrochoglanis raninus*. All the muscles are exposed, but the ligament between the maxilla and the premaxilla, as well as the posttemporo-supracleithrum, were removed. *c-eth* cartilago ethmoideus, *l-entect-mx* ligamentum entoectopterygoideo-maxillare, *m-A1-ost*, *m-A2*, *m-A3''* 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-3*, *m-ex-t-4* sections of musculus extensor tentaculi, *m-l-ap* musculus levator arcus palatini, *m-l-op* musculus levator operculi, *m-pr-mup* musculus protractor of müllerian process, *mup* müllerian process, *o-ang-art* os angulo-articulare, *o-apal* os autopalatini, *o-den* os dentale, *o-ent-ect* os entoptyrgoideo-ectopterygoideum, *o-epoc* os epioccipitale, *o-exs* os extrascapulare, *o-fr* os frontale, *o-hm-mp* os hyomandibulo-metapterygoideum, *o-iop* os interoperculare, *o-leth* os lateroethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-op* os operculare, *o-pa-soc* os parieto-supraoccipitale, *o-pop* os praeoperculare, *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, *pp4* parapophysis of vertebra 4, *sb* swimbladder.

Os pterosphenoidum. Well-developed, roughly rectangular bone covering, together with the orbitosphenoid, the gap between the frontals and the parasphenoid.

Os parasphenoidum. 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 (fig. 1) are large bones that constitute a large part of the cranial roof. They are largely separated by a well-developed fontanel.

Os sphenoticum. With approximately the same size than the pterotic (fig. 1), the sphenotic constitutes, together with this bone, a well-developed, deep articular facet for the hyomandibulo-metapterygoid.

Os pteroticum. Well-developed, irregularly-shaped bone situated posteriorly to the sphenotic (fig. 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, postero-ventrally to the extrascapular (fig. 1).

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

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

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 (fig. 1) constituting the postero-dorso-median surface of the cranial roof. It bears an enlarged, posteriorly pointed, roughly triangular postero-median process.

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

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

Os coronomeckelium. Small bone lodged in the medial surface of the mandible. Postero-dorsally it bears a crest for attachment of the adductor mandibulae A3'-d.

Os praemaxillare. Well-developed bone with an extensive postero-lateral projection oriented posteriorly. Dorsally, it presents a prominent dorsolateral process (fig. 1: o-prmx-dlp) for the attachment of a short, but strong, ligament connecting this bone to the premaxilla. Ventrally, the premaxilla bears a well-developed tooth-plate with numerous small teeth having their tips slightly turned backward (fig. 1).

Os maxillare. The maxilla is a small bone (fig. 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 maxillaries.

Os autopalatinum. The autopalatine (fig. 1) is a spoon-like, anteroposteriorly elongated bone with a roundish, dorsoventrally expanded posterior tip. Both its anterior and posterior tips are tipped by small cartilages, with the anterior one presenting two antero-lateral concavities, which accept the two proximal heads of the maxilla. Medially, the autopalatine articulates 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 controversy (Gosline, 1975; Howes, 1983, 1985; McMurrich, 1884; Mo, 1991; Arratia, 1992; Diogo et al., 2001a; Diogo and Chardon, 2003, etc.). As stated before, for the several reasons explained in detail in our recent papers (Diogo et al., 2001a; Diogo and Chardon, 2003), the nomenclature used here to describe these elements strictly follows that presented by Diogo et al. (2001a). The hyomandibulo-metapterygoideum (fig. 1) is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercle.

Os sesamoideum 1. Well-developed, irregularly shaped bone with a markedly developed antero-lateral extension. It is attached, by means of two thick ligaments, to the ento-ectopterygoid posteriorly and to the lateral ethmoid anteriorly.

Os sesamoideum 2. Well-developed, comma-shaped bone with its dorsolateral surface attached, by means of connective tissue, to the postero-ventral surface of the autopalatine. The sesamoid bone 3 (see Diogo et al., 2001a) is absent.

Os entopterygoide-ectopterygoideum. Short bone with its a slightly bifurcated anterior surface. It is sutured with both the hyomandibulo-metapterygoideum postero-dorsally and the quadrate-symplectic postero-ventrally.

Os quadrato-symplecticum. The quadrate-symplectic (fig. 1) presents a well-developed anterior articular surface to articulate with the postero-dorsal surface of the angulo-articular. Its antero-ventral surface is pierced by a small, circular foramen.

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

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

Os interoperculare. Its anterior surface is ligamentously connected to the postero-ventral margin of the mandible (fig. 1). Medially, the interopercle is attached, by means of massive connective tissue, to the lateral surface of the posterior ceratohyal.

Os interhyale. Small-bone ligamentously connected to the hyomandibulo-metapterygoideum 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. The dorsal hypohyals are missing.

Os parurohyale. The parurohyal is a large, irregular bone lying medially behind the symphysis of the two ventral hypohyals and presenting a small posteromedian process and two well-developed postero-lateral processes.

Os posttemporo-supracleithrum. The dorso-medial limb of this well-developed bone is attached, by strong connective tissue, to both the pterotic and the extrascapular. Its stout ventro-medial limb is firmly connected by a short, strong ligament to the basioccipital. Its ventro-lateral limb is deeply forked, forming an articulating groove for the upper edge of the cleithrum. The postero-ventral surface of the posttemporo-supracleithrum is weakly attached by means of connective tissue to the antero-ventral process of the fourth parapophysis (=Müllerian process) (fig. 4: mup), which is well developed and presents a highly mobile, roughly oval ventro-lateral tip. This highly mobile Müllerian process, together with a well-developed, separate muscle, the protractor of the Müllerian process (fig. 4: m-pr-mup), running from its anterior surface to the posterior surface of the neurocranium, form an “elastic-spring-apparatus” (see e.g., Bridge and Haddon, 1894; Alexander, 1965; Chardon, 1968).

Os cleithrum. The cleithrum (fig. 2) is a large, well-ossified stout structure presenting a prominent antero-dorsal projection of laminar bone (fig. 2: o-cl-adp) and forming a large 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, irregular bony plate (fig. 2) sutured with the cleithrum along its antero-lateral edge. Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge (Diogo et al., 2001b), which extends ventrally to the ventro-lateral surface of the cleithrum, fusing 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 (Mo, 1991). There is a well-developed mesocoracoid arch.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (Diogo and Chardon, 2000a; Diogo and Vandewalle, 2003) originates on the preopercle and the hyomandibulo-metapterygoid and inserts on the dorso-lateral surface of the angulo-

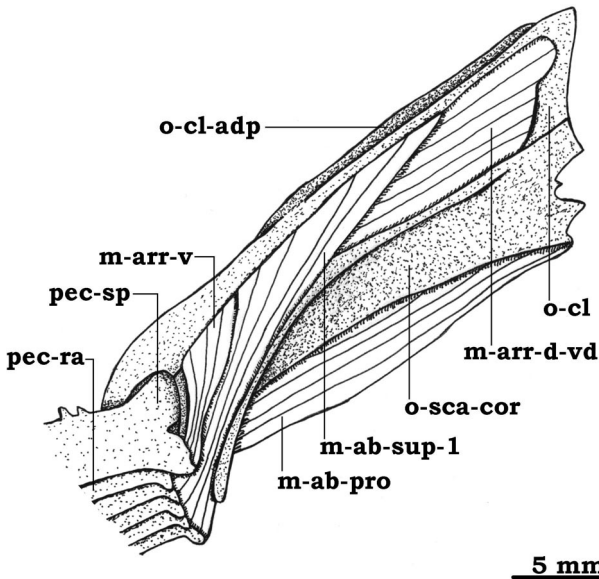


Figure 2. Ventral view of the pectoral girdle musculature of *Batrochoglanis raninus*. All the muscles are exposed. *m-ab-pro* musculus abductor profundus, *m-ab-sup-1* section of musculus abductor superficialis, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector ventralis, *o-cl* os cleithrum, *o-cl-adp* antero-dorsal projection of os cleithrum, *o-sca-cor* os scapulo-coracoide, *pec-ra* pectoral rays, *pec-sp* pectoral spine.

articular (fig. 1). The A2 (fig. 1), which lies dorso-mesially to the A1-ost, runs from the pterotic, sphenotic, preopercle and the hyomandibulo-metapterygoid to the medial surface of the dentary bone. The adductor mandibulae A3' is divided into a dorsal and a ventral part. The dorsal one (A3'-d) originates on the both the hyomandibulo-metapterygoid and the quadrate-symplectic and inserts tendinously on the coronomeckelian bone, while the ventral one (A3'-v) originates on the quadrate-symplectic and inserts on the medial surface of the angulo-articular. The adductor mandibulae A3'' (fig. 1), situated mesially to the A3', runs from the hyomandibulo-metapterygoid, the sphenotic and the frontal to the mesial surface of the angulo-articular. Lastly, the adductor mandibulae $A\omega$, 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 (fig. 1) is situated medially to the adductor mandibulae A3'. It originates on the sphenotic, frontal and lateral ethmoid and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (fig. 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 opercle (fig. 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 opercle.

Musculus adductor hyomandibularis. Well-developed 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 (fig. 1) originates on the pterosphenoid, frontal and sphenotic and inserts on the antero-dorsal margin of the opercle.

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

Musculus protractor hyoidei. This muscle (fig. 3) has three parts. The pars ventralis, in which are lodged both the cartilages associated with the internal and external mandibular barbels (fig. 3: c-in-mnd-t; c-ex-mnd-t) and the large cartilaginous plate carrying these barbels (fig. 3: cp-mnd-b) (Ghiot, 1978; Diogo and Chardon, 2000b), originates on the anterior ceratohyal and inserts on the dentary bone, meeting its counterpart in a well-developed median aponeurosis (fig. 3). The pars lateralis runs from the posterior ceratohyal to the ventro-medial face of the dentary bone (fig. 3). The pars dorsalis runs from the anterior and posterior ceratohyals to the antero-dorsal surface of the dentary bone.

Musculus retractor externi mandibularis tentaculi. Small muscles situated dorsally to the cartilaginous plates carrying the mandibular barbels (fig. 4). They run from the antero-dorsal surface of the moving part (Diogo and Chardon, 2000b) of the cartilages associated with the outer mandibular barbels to the dorsal 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 (fig. 4). They run from the antero-dorsal surface of the dentaries to the antero-dorsal surface of the moving part of the cartilages associated with the internal mandibular barbels.

Musculus protractor externi mandibularis tentaculi. Well-developed, elongated muscles (figs 3, 4) originating on the anterior ceratohyals and inserting on the antero-dorsal surface of the moving part of the cartilages associated with the outer mandibular barbels. It is important to register, 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 and Chardon, 2000b), the presence of one

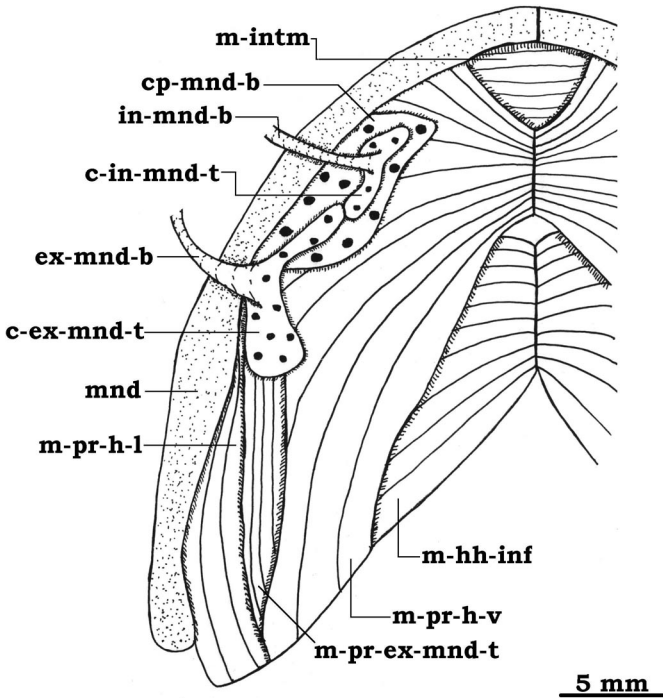


Figure 3. Ventral view of the cephalic musculature of *Batrochoglanis raninus*. All the muscles are exposed. *c-in-mnd-t* cartilago internus mandibularis tentaculi, *c-ex-mnd-t* cartilago externus mandibularis tentaculi, *cp-mnd-b* cartilaginous plate carrying the mandibular barbels, *ex-mnd-b*, *in-mnd-b*, external and internal mandibular barbels, *m-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 protractor hyoideus.

additional, paired muscle associated with these barbels. This is the ‘muscle 4 of the mandibular barbels’ (fig. 4: *m-4-mnd-b*), which contacts mesially the retractor of the external mandibular barbel and runs from the cartilaginous plates carrying the mandibular barbels and the dentaries to the proximal surface of the outer mandibular barbels (with respect to the nomenclature of this muscles, see Diogo and Chardon, 2000b).

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

Musculus hyohyoideus inferior. Thick muscle (fig. 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.

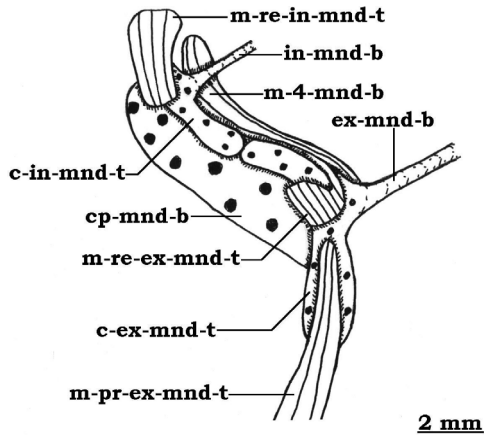


Figure 4. Dorsal view of the right cartilaginous plate carrying the mandibular barbels and its associated structures in *Batrachoglanis raninus*. *c-in-mnd-t* cartilago internus mandibularis tentaculi, *c-ex-mnd-t* cartilago externus mandibularis tentaculi, *cp-mnd-b* cartilaginous plate carrying the mandibular barbels, *ex-mnd-b*, *in-mnd-b* external and internal mandibular barbels, *m-4-mnd-b* 'muscle 4 of the mandibular barbels', *m-pr-ex-mnd-t* musculus protractor externi mandibularis tentaculi, *m-re-ex-mnd-t* musculus retractor externi mandibularis tentaculi, *m-re-in-mnd-t* musculus retractor interni mandibularis tentaculi.

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 (fig. 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 (fig. 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 highly developed muscle (fig. 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 (fig. 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, situated dorsally to the larger one, runs from the lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus adductor superficialis. This muscle 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 antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from both the postero-ventro-lateral edge of the scapulo-coracoid and the dorsal surface of the proximal 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 antero-dorsal surface of the cleithrum.

Microglanis cottoides

In a general way, the configuration of the osteological and myological structures of the pectoral girdle and cephalic region of this species resembles that of *Batrochoglanis raninus*, with the most significant differences between these species regarding these structures being that in *M. cottoides*: 1) the posteromedian process of the parurohyal is significantly more developed than that of *B. raninus*; 2) the coracoid bridge is considerably thinner than that of *B. raninus*; 3) the adductor hyomandibularis is less developed than in *B. raninus*; 4) the premaxilla does not present a markedly developed postero-lateral projection; 5) the hypoaxialis do not attach on the postero-ventral, but on the antero-ventral surface of the pectoral girdle; 6) the posterior process of the parieto-supraoccipital is longer and broader than that of *B. raninus*.

DISCUSSION

Five synapomorphies are commonly listed to support the monophyly of the subfamily Pseudopimelodinae (see Lundberg et al., 1991; de Pinna, 1998; Shibatta, 2003), namely: 1) “lateral ethmoid lacking a spine-like wing of membrane bone projecting beyond the palatine condyle”; 2) “metapterygoid foreshortened (twice or more broad than long), its dorsal fourth or more deflected inward and usually subtended by a ridge or crest”; 3) “endopterygoid and ectopterygoid broad, distinctively shaped (the former with a sharp antero-lateral process, the latter comma-shaped), and movably linked between the neurocranium from near the lateral ethmoid-orbitosphenoid suture and the palatine”; 4) “third to seventh (last) proximal radials of dorsal fin broad, and adjacent radials in full contact for their entire lengths (in large pseudopimelodines) or only narrowly separated”; 5) “dorsal hypohyal bones absent”. Our own phylogenetic analysis, which includes 440 characters and 87 terminal taxa representing all the extant catfish families (Diogo, 2004), not only confirmed these five synapomorphies, but also pointed out two other features that could eventually represent potential pseudopimelodin synapomorphies, which are described below.

Mesethmoid markedly bifurcated anteriorly. Plesiomorphically in catfishes the mesethmoid is bifurcated anteriorly, thus presenting two well-developed antero-lateral arms (Mo, 1991). However, in the two pseudopimelodin genera examined,

as well as in *Lophiosilurus* and *Pseudopimelodus* (Lundberg et al., 1991), the anterior bifurcation of this bone is even more pronounced, with its antero-mesial surface being situated posteriorly to the postero-mesial surface of the premaxillae (fig. 1). Such a pronounced bifurcation is a very rare feature among catfishes, being only present, apart from the pseudopimelodins, on a few catfishes such as chacids, silurids, ictalurids, claroteids or the amphiliid genus *Amphilius* (Diogo, 2003a). The fact that these four latter groups are very likely more closely related to other catfish groups than to the pseudopimelodines (Mo, 1991; de Pinna, 1998; Diogo et al., 2002a; Diogo, 2003a, b, 2004), associated with the fact that this character is present in all these four pseudopimelodin genera (the situation in *Cephalosilurus* could not be discerned) but absent in the non-pseudopimelodin pimelodids (see below), seems to indicate that this feature constitutes a pseudopimelodin synapomorphy.

Spoon-like autopalatine with a roundish, dorso-ventrally expanded posterior tip. As the pronounced anterior bifurcation of the mesethmoid, this derived character (Mo, 1991; de Pinna, 1998) also seems to constitute a pseudopimelodin synapomorphy, since, apart from the pseudopimelodins, it is only present in a few, phylogenetically distant (Mo, 1991; de Pinna, 1993; de Pinna, 1998; Diogo et al., 2002a; Diogo, 2003b, 2004) catfish groups, such as the doradoids or the sisoroids, and absent in both the pimelodin and the heptapterin pimelodids (see below). However, it is evidently necessary to undertake further studies on the configuration of other pseudopimelodin members to discern if this character indeed constitutes a Pseudopimelodinae synapomorphy.

However, probably one of the most important aspects of our results is that they support the monophyly of the family Pimelodidae as a whole, that is, of the clade including the subfamilies Pseudopimelodinae, Pimelodinae and Heptapterinae, thus contradicting the nowadays commonly accepted view that the Pimelodidae is a polyphyletic, unnatural assemblage (see Introduction). Our phylogenetic analysis (Diogo, 2004) pointed out five characters that probably constitute synapomorphies of a clade formed by the pimelodins, the heptapterins and the pseudopimelodins, two of which are uniquely present in these three groups among catfishes, and which, therefore, strongly support the monophyly of the family Pimelodidae. These five characters are described below.

Presence of a 'muscle 4 of the mandibular barbels'. Plesiomorphically catfishes lack a 'muscle 4 of the mandibular barbels' (Diogo and Chardon, 2000b; Diogo and Vandewalle, 2003). However, in all the pimelodids examined, and in no other catfishes studied by us or described in the literature, there is a 'muscle 4 of the mandibular barbels', which is a well-developed muscle connecting the proximal surface of the external mandibular barbels to both the antero-ventro-lateral surface of the cartilaginous plates carrying the mandibular barbels and the antero-mesial surfaces of the dentaries (fig. 4). The presence of such a noticeable, well-defined, distinct character in all the pimelodins, heptapterins and pseudopimelodines exam-

ined, and in no other catfishes studied by us or described in the literature, clearly constitutes strong evidence to support the monophyly of the Pimelodidae.

Presence of cartilaginous plates carrying the mandibular barbels. As with the presence of a 'muscle 4 of the mandibular barbels', the presence of 'cartilaginous plates carrying the mandibular barbels' (Ghiot, 1978; Diogo and Chardon, 2000b) is a derived feature present in all the pimelodines, pseudopimelodines and heptapterines examined (figs 3, 4), and in no other catfishes studied by us 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 and Vandewalle, 2003). However, in all the pimelodins, heptapterins and pseudopimelodins examined, a large part of the fibres of this muscle also originate on the postero-dorso-lateral surface of the hyomandibulo-metapterygoid (fig. 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, on a few catfishes such as plotosids, cranoglanidids, schilbids and silurids (Diogo and Vandewalle, 2003). As these four groups are probably more closely related to other catfish groups than to pimelodids (Mo, 1991; de Pinna, 1998; Diogo et al., 2002a; Diogo, 2004), this character also supports the monophyly of the Pimelodidae.

Presence of an antero-dorsal projection of laminar bone on the anterior surface of the cleithrum. Plesiomorphically catfish lack major processes or projections on the anterior surface of the cleithrum (Diogo et al., 2001b). However, in all the pimelodids examined except *Hypophthalmus edentatus*, the cleithrum presents a well-developed, antero-dorsal projection of laminar bone (fig. 2: o-cl-adp). Since such a feature is present in all pimelodids studied except this peculiar and highly derived pimelodin genus *Hypophthalmus*, and a somewhat similar feature is only present among non-pimelodid catfishes, in some members of the phylogenetically distant Doradoidea (i.e., in some mochokids, auchenipterids and doradids examined) (Mo, 1991; de Pinna, 1998; Diogo, 2003b, 2004), this character also supports the monophyly of the Pimelodidae.

Anterior portion of ethmoid cartilage markedly extended anteriorly. One other derived character that seems to constitute a Pimelodidae synapomorphy, and which therefore 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. Contrary to the vast majority of the Siluriformes, where the anterior portion of the ethmoid cartilage does not extend far beyond the anterior margin of the lateral ethmoids (Mo, 1991; Diogo and Chardon, 2000c), in all pimelodins, pseudopimelodins and heptapterins examined this cartilage

is markedly extended anteriorly, almost reaching the posterior margin of the premaxillaries (fig. 1). Such a feature is, again, extremely rare among catfishes, only being found to date, apart from the pimelodins, in the austroglanidids, claroteins and schilbids (Diogo and Chardon, 2000c: figs 5, 6). As these three groups seem to be more closely related to certain other catfish groups than to the pimelodids (Mo, 1991; de Pinna, 1998; Diogo et al., 2002a; Diogo, 2003b, 2004), this character constitutes yet one more strong argument on behalf of the monophyly of the family Pimelodidae.

The five characters discussed above thus strongly support the monophyly of the clade formed by the subfamilies Pimelodinae, Pseudopimelodinae and Heptapterinae, the family Pimelodidae as a whole. In particular, the first two characters, which concern the presence, exclusively in the pimelodids, of noticeable, distinct, easily recognised features, clearly constitute very strong evidence to support the monophyly of this family. As de Pinna (1998) noted, 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. Thus, the presence of not only one, but of two of such features in the pimelodins is clearly a very strong argument for the monophyly of the Pimelodidae. Furthermore, the taxonomic distribution of the three other characters, which refer, in any case, to rare features among catfishes (among 35 catfish families they are only present, besides the pimelodins, in three or four other specific groups), and particularly the fact that the non-pimelodins where these characters are found are, seemingly, more closely related to certain other catfishes than to pimelodins, rules out their serious consideration as a support of the monophyly of the Pimelodidae.

As mentioned above, this hypothesis contradicts the rather 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 the phylogenetic hypothesis that the three pimelodid subfamilies are more closely related to other catfish groups than to each other, was proposed, was in de Pinna (1998). And since de Pinna (1998) 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 oppose the arguments given in the present study.

The strong evidence presented above to support the monophyly of the family Pimelodidae is clearly due to the inclusion of characters that, unfortunately, are not usually included in works concerning the phylogenetic relationships among catfishes, such as the structures associated with the mandibular barbels, the pectoral girdle structures or the cranial musculature. Other studies recently published by the authors have also stressed that the analysis of such characters, and, particularly, of the configuration of the cranial and pectoral girdle musculature, could prove very useful in disclosing not only the phylogenetic relationships between different catfish groups, but also the respective synapomorphies and/or autapomorphies of

these groups (Diogo et al., 1999, 2000b, 2001b, c, 2002a, b; Diogo and Chardon, 2000b; Oliveira et al., 2002; Diogo, 2003a, 2004; Diogo and Vandewalle, 2003).

If the subfamilies Pimelodinae, Pseudopimelodinae and Heptapterinae do, therefore, constitute very probably a monophyletic assemblage, namely the family Pimelodidae, two leading questions could be asked: 1) of the three subfamilies that constitute this monophyletic assemblage, which two share a sister-group relationship; and 2) among non-pimelodin catfishes, which group seems to be more closely related to this monophyletic assemblage, the Pimelodidae? With respect to the first question, unfortunately, our results did not point to any distinct, well-defined, unambiguous synapomorphies to support any type of sister-group relationship among the three pimelodin subfamilies. This clearly seems to be a very complex issue that undoubtedly deserves special attention in future studies. However, with respect to the second question, our phylogenetic analysis strongly suggests that the South-American pimelodids are closely related to the Afro-Asiatic bagrids (Diogo, 2004). The three derived characters described below support this hypothesis.

Presence of a prominent dorsal process on the dorso-lateral surface of the premaxilla for the attachment of the well-developed ligament connecting this bone to the maxilla. Plesiomorphically, catfishes lack major dorsal processes and/or projections on the dorsal surface of the premaxilla (Mo, 1991; de Pinna, 1998; Diogo et al., 1999). However, in all bagrids, as well as in all pimelodids examined and exclusively on these catfishes, there is a prominent dorso-lateral process of the premaxilla (fig. 1: o-prmx-dlp) for the attachment of the markedly well-developed ligament connecting this bone to the maxilla. The uniform, exclusive presence of such a well-defined, distinct feature in all the pimelodids and bagrids studied thus supports a close relationship between these two catfish groups.

'Sliding' articulation between the autopalatine and the neurocranium. The vast majority of catfishes present a 'rocking' palatine-maxillary system where the abduction of the maxilla and its respective barbel is mainly associated with a significant mesial displacement of the back of the autopalatine (Alexander, 1965; Gosline, 1975; Ghiot, 1978; Diogo et al., 2000a). However, in all the bagrids, as well as in all the pimelodids examined excepting pseudopimelodins (which present a 'rocking' palatine-maxillary system), and exclusively on these catfishes, there is a true 'sliding' palatine-maxillary system (Alexander, 1965; Gosline, 1975; Ghiot, 1978; Diogo et al., 2000a), i.e. the abduction of the maxilla and its respective barbel is mainly associated with a significant posterior displacement of the back of the autopalatine. Since a true 'sliding' palatine-maxillary system is virtually absent in all non-pimelodid and non-bagrid catfishes, and since such a character is uniformly present in all the numerous bagrid and pimelodid catfishes studied except pseudopimelodins, this character probably constitutes a synapomorphic feature, secondarily lost in pseudopimelodins, to support a close relationship between bagrids and pimelodids.

Presence of a concavity or foramen on the antero-ventral surface of the quadrato-symplectic. The status of this character is similar to that regarding the 'sliding' type articulation between the autopalatine and the neurocranium. The presence of a deep concavity or foramen on the antero-ventral surface of the quadrato-symplectic is an extremely rare feature among catfishes (Mo, 1991; Arratia, 1992; Diogo et al., 2001a; Diogo and Chardon, 2003) but is commonly present in bagrids (Diogo et al., 1999) and is found in all the pimelodid catfishes examined except pimelodins. Among non-bagrid and non-pimelodid catfishes, such a feature is only sporadically present in a few, specific genera such as *Paramphilius*, *Schilbe* or *Ageiosius* (but not on the remaining genera of their respective families). Therefore, this also seems to constitute a synapomorphic feature, secondarily lost in pimelodins, which supports a close relationship between the pimelodid and the bagrid catfishes.

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