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Osteology and myology of the cephalic region and pectoral girdle of *Centromochlus heckelii*, comparison with other auchenipterids, and comments on the synapomorphies and phylogenetic relationships of the Auchenipteridae (Teleostei: Siluriformes)

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Abstract—The cephalic and pectoral girdle structures of the auchenipterid *Centromochlus heckelii* (Centromochlinae) are described and compared with those of two representatives, *Auchenipterus dentatus* and *Ageneiosus vittatus* (Auchenipterinae), of the other auchenipterid subfamily, as well as with several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic position of the Auchenipteridae. Our observations and comparisons support the idea that the Auchenipteridae and the Doradidae are sister-groups, and also that the clade formed by these two Neotropical families is closely related to the African mochokids. In addition, our observations and comparisons identified a potentially new auchenipterid synapomorphy, maxillary markedly elongated proximo-distally.

Keywords: Auchenipteridae; catfish; comparative morphology; Doradidae; Mochokidae; pectoral girdle; phylogeny; Siluriformes.

INTRODUCTION

The Siluriformes, or catfishes, with approximately 416 genera and over 2500 species, represent about 32% of all freshwater fishes (Teugels, 1996). They are “one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the

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aquarium industry where they represent a substantial portion of the world trade” (Teugels, 1996). Among the 35 catfish families (Ferraris and de Pinna, 1999), the Auchenipteridae, with about 20 genera and 70 species, constitutes a conspicuous Neotropical catfish group (de Pinna, 1998). The phylogeny and systematics of the Auchenipteridae were recently revised by de Pinna (1998). According to the cladogram provided on de Pinna’s (1998) figure 15 which, according to this author, is mostly based on the unpublished theses of Ferraris (1988) and Soares-Porto (1996), the Auchenipteridae are divided into two subfamilies, the Centromochlinae and the Auchenipterinae, with the auchenipterids being diagnosed by the following three synapomorphies: anterior rays of anal fin enlarged and thickened in adult males; maxillary barbel, when adducted, fits in a groove in the cheek integument, just ventral to eye; adducted maxillary barbel directed laterally and dorsally.

It is worthy of note that, despite the relatively large number of studies concerning siluriform morphology (e.g., McMurrich, 1884; Regan, 1911; de Beer, 1937; Gauba, 1962, 1966, 1968, 1969; Mahajan, 1963, 1966a, b, 1967a, b; Alexander, 1965; Gosline, 1975; Ghiot, 1978; Ghiot et al., 1984; Mo, 1991; Arratia, 1992; Diogo et al., 1999, 2000, 2001a, b, c, 2002a, b; Oliveira et al., 2001, 2002; etc.), the few, somewhat detailed, morphological descriptions of the auchenipterid catfishes published to date are those of Chardon (1968), Curran (1989), Royero and Neville (1997) and Soares-Porto (2001). Moreover, as these descriptions are almost exclusively restricted to the osteology and external anatomy of the auchenipterids, little is known about some important aspects of the morphology of these fishes (e.g., the configuration of their pectoral girdle) and almost nothing about others (e.g., the structures associated with their mandibular barbels, the muscles and ligaments of their cephalic region, or their pectoral girdle musculature). This not only complicates the study of the functional morphology of the auchenipterids, but also restricts considerably the data available to infer the synapomorphies and the phylogenetic relationships of these catfishes.

The aim of this work is to describe in detail the bones, cartilages, muscles and ligaments of the cephalic region (excluding the branchial apparatus) and pectoral girdle of the auchenipterid *Centromochlus heckelii* (de Filippi 1853) (Centromochlinae), and to compare these structures with those of two representatives of the other, more diverse, auchenipterid subfamily, *Auchenipterus dentatus* Valenciennes 1840 and *Ageneiosus vittatus* Steindachner 1908 (Auchenipterinae). We will also compare the structures with those of other catfishes, in particular, doradids and mochokids. The study will form the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Auchenipteridae. It is also hoped that this study will increase knowledge of the anatomy and phylogeny of the catfishes in general, as well as pave the way for future studies on the comparative anatomy, evolution, functional morphology, palaeontology, eco-morphology and, in particular, 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 University of Gent (UG) and from the National Museum of Natural History of Washington (USNM). Anatomical descriptions were 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 carried out using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsin-cleared and alizarine-stained (c&s) or alcohol-fixed (alc) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

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). *Belonoglanistenuis* 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 heckelii* USNM 261397, 1 (alc).

Austroglanididae: *Austroglanis gilli* LFEM, 3 (alc).

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 garipepinus* MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Heterobranchus bidorsalis* LFEM, 2 (alc). *Heterobranchus longifilis* LFEM, 2 (alc). *Uegitglanis zammaroni* MRAC P-15361, 1 (alc).

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

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

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

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

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

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

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

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

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

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

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

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

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

Plotosidae: *Cnidoglanis macrocephalus* USNM 219580, 2 (alc). *Neosilurus rendahli* USNM 173554, 2 (alc). *Paraplotosus albilabris* USNM 173554, 2 (alc). *Plotosus anguil-laris* 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 yarrelli* USNM 348830, 2 (alc); LFEM, 1 (c&s). *Gagata cenia* USNM 109610, 2 (alc). *Glyptosternon reticulatum* USNM 165114, 1 (alc). *Glyptothorax fukiensis* USNM 087613, 2 (alc).

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

RESULTS

In this section we will describe the cephalic and pectoral girdle structures of a representative Auchenipteridae catfish of subfamily Centromochlinae, *Centromochlus heckelii*, and compare these structures with those of two representatives of the subfamily Auchenipterinae, *Auchenipterus dentatus* and *Ageneiosus vittatus*. In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region basically follows that of Arratia (1997). However, for the many reasons explained in detail in our recent papers (Diogo et al., 2001a; Diogo and Chardon, in press), with respect to the skeletal components of the suspensorium we follow Diogo et al. (2001a). The myological nomenclature, including the musculature associated with the palatine-maxillary system, is based mainly on Winterbottom (1974), but for the different adductor mandibulae sections, Diogo and Chardon (2000a) are followed (see Gosline, 1989; Diogo and Chardon, 2000a). For those muscles associated with the mandibular barbels which were not studied by Winterbottom (1974), Diogo and Chardon (2000b) are followed. For the nomenclature of the pectoral girdle bones and muscles, Diogo et al. (2001b) are followed.

Centromochlus heckelii

Osteology

Os mesethmoideum. Unpaired bone situated on the antero-dorsal surface of the neurocranium (fig. 1: o-meth), with each of its antero-ventro-lateral margins ligamentously connected to the premaxillary.

Os lateroethmoideum. The lateral-ethmoid (fig. 1: o-leth) is an irregularly shaped bone presenting a well-developed, laterally directed articulatory facet for the autopalatine.

Os praevomerale. Well-developed, unpaired T-shaped bone without a ventral tooth-plate.

Os orbitosphenoideum. Posterior to the lateral ethmoid (fig. 1: o-osph), with the dorsal edge of its lateral wall being sutured with the ventral surface of the frontal.

Os pterosphenoideum. Posterior to the orbitosphenoid (fig. 1: o-psph), covering, together with this bone, the gap between the frontals and the parasphenoid.

Os parasphenoideum. The unpaired 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: o-fr) are large bones that constitute a large part of the cranial roof. They are largely separated by two median fontanels. There is a well-developed, deep, roughly oval fossa between the posterodorsolateral margin of the frontal, the dorsomedian surface of the sphenotic and the anterodorsolateral surface of the parieto-supraoccipital.

Os sphenoticum. Smaller than the pterotic (fig. 1: o-sph), constituting, together with this bone, an articulatory facet for the hyomandibulo-metapterygoid.

contacting a well-developed, roughly triangular, unpaired anterior nuchal plate, which is enclosed by the parieto-supraoccipital anteriorly, by a even larger, unpaired median nuchal plate posteriorly, and by the well-developed epioccipitals laterally.

Os angulo-articulare. This bone (fig. 1: o-ang-art), together with the dentary, the coronomeckelian and the highly developed Meckel's cartilage (fig. 1: c-Meck-as), constitute the mandible. Postero-dorsally, the angulo-articular has an articulatory facet for the quadrate-symplectic. Postero-ventrally, it is ligamentously connected to both the interopercular and the posterior ceratohyal.

Os dentale. The toothed dentary recovers a great part of the lateral surface of the mandible. The postero-dorsal margin of the dentary forms, together with the antero-dorsal margin of the angulo-articular, a poorly developed dorsal process (processus coronoideus) (fig. 1: o-den).

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. The well-developed, roughly rectangular premaxillaries (fig. 1: o-prmx) bear ventrally a well-developed tooth-plate with numerous small teeth having their tips slightly turned backward.

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

Os autopalatium. The autopalatine (fig. 1: o-apal) is a rod-like bone with its posterior end capped by a small cartilage and its anterior end tipped by a well-developed cartilage with two antero-lateral concavities that accept the two proximal heads of the maxillary. Medially, the autopalatine articulates, by means of a small, circular 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 controversy (McMurrich, 1884; De Beer, 1937; Hoedeman, 1960; Gosline, 1975; Howes, 1983, 1985; Arratia, 1990, 1992; Diogo *et al.*, 2001a; Diogo & Chardon, in press, etc.). As referred to above, for the many reasons explained in detail in our recent papers (Diogo *et al.*, 2001a; Diogo and Chardon, in press), the nomenclature used here to describe these elements strictly follows that presented by Diogo *et al.* (2001a). The hyomandibulo-metapterygoid (fig. 1: o-hm-mp) is a large bone presenting a markedly broad antero-dorsal spine. It articulates dorsally with both the pterotic and the sphenotic and posteriorly with the opercular.

Os sesamoideum 1. Small bone attached by means of a long, strong ligament to the ento-ectopterygoid posteriorly and by means of a thick, long ligament to the lateral ethmoid anteriorly. The sesamoid bones 2 and 3 (Diogo *et al.*, 2001a) are absent.

Os entopterygoide-ectopterygoideum. Well-developed bone (fig. 1: o-ent-ect) with its posterior surface being sutured with the quadrate-symplectic.

Os quadrato-symplecticum. The quadrate-symplectic (fig. 1: o-q-sym) presents a well-developed anterior articular surface to articulate with the postero-dorsal surface of the angulo-articular.

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

Os operculare. The opercular (fig. 1: o-op) is a well-developed, roughly triangular bone attached ventrally, by means of connective tissue, to the interopercular. It presents a well-developed, antero-dorsally elongated, articular surface for the hyomandibulo-metapterygoid.

Os interoperculare. The anterior surface of this bone (fig. 1: o-iop) is ligamentously connected to the postero-ventral margin of the mandible. Medially, the interopercular articulates with the lateral surface of the posterior ceratohyal.

Os interhyale. Small bone ligamentously connected to both the postero-dorsal surface of the posterior ceratohyal and the median surface of the hyomandibulo-metapterygoid.

Os ceratohyale posterior. Well-developed, somewhat triangular bone ligamentously connected to the postero-ventral edge of the mandible and to the medial surface of the interopercular.

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

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

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

Os parurohyale. The parurohyal is an irregular, unpaired bone with a well-developed, triangular, posteriorly pointed posteromedian process.

Os posttemporo-supracleithrum. This bone (fig. 1: o-post-scl), together with the cleithrum and the scapulo-coracoid, constitute the pectoral girdle. Its dorso-medial limb is firmly sutured to the epioccipital and the pterotic. Its ventro-medial limb is firmly sutured with the basioccipital. Its postero-lateral margin 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. 1: mup), which is well developed and highly mobile. This highly mobile Müllerian process, together with a well-developed protractor of the Müllerian process, which is divided into a larger (fig. 1: m-pr-mup-1) and a smaller (fig. 1: m-pr-mup-2) section and runs from the anterior surface of the Müllerian process to the posterior surface of the cranium, form an 'elastic-spring-apparatus' (see Bridge & Haddon, 1894; Alexander, 1965; Chardon, 1968).

Os cleithrum. The cleithrum (fig. 2: o-cl) is a large, well-ossified stout structure forming a large part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially faced groove that accommodates the dorsal condyle of the well-developed pectoral spine. The two cleithra are

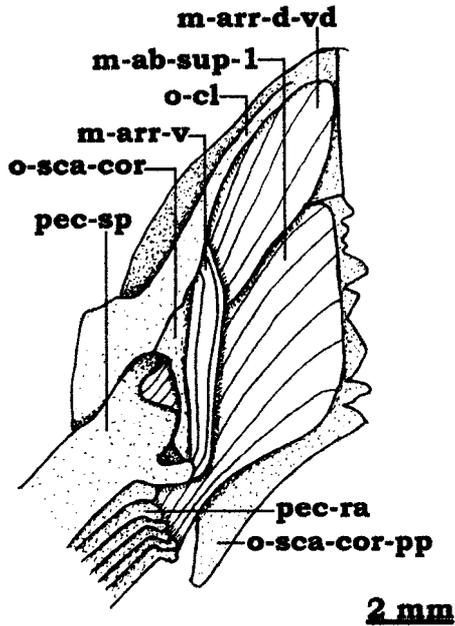


Figure 2. Ventral view of the pectoral girdle musculature of *Centromochlus heckelii*. *m-ab-sup-1* section 1 of musculus abductor superficialis, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector ventralis, *o-cl* os cleithrum, *o-sca-cor* os scapulo-coracoide, *o-sca-cor-pp* posterior process of os scapulo-coracoide, *pec-ra* pectoral rays, *pec-sp* pectoral spine.

attached in the antero-medial line via connective tissue. The humeral process is well developed.

Os scapulo-coracoideum. This is an elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge (fig. 2: *o-sca-cor*). Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge (see 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 (see Mo, 1991), and it presents a prominent, triangular, posteriorly directed posterior process (fig. 2: *o-sca-cor-pp*). The main scapulo-coracoid articular surface for the pectoral spine (see Diogo et al., 2001b) is a markedly narrow, dorsoventrally elongated structure. The mesocoracoid arch is undifferentiated.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (Diogo and Chardon, 2000a) originates (fibres) on the preopercular and the quadrate-symplectic and inserts (fibres + tendon) on the dorsolateral surface of the angulo-articular (fig. 1: m-A1-ost). The A2 (fig. 1: m-A2), which lies dorso-mesially to the A1-ost,

runs (fibres) from the preopercular and the hyomandibulo-metapterygoid to the medial surfaces of both the angulo-articular and the dentary (tendon). The adductor mandibulae A3' is divided into a dorsal and a ventral part. The dorsal one (A3'-d), originates (fibres) on the hyomandibulo-metapterygoid and quadrate-symplectic and inserts tendinously on the coronomeckelian bone, while the ventral one (A3'-v) originates (fibres) on the quadrato-symplectic and inserts tendinously on the medial surface of the angulo-articular. The adductor mandibulae A3'' (fig. 1: m-A3''), situated mesially to the A3', runs from the hyomandibulo-metapterygoid and the pterosphenoid (fibres) to the mesial surface of the angulo-articular (tendon). Lastly, the adductor mandibulae A ω runs from the mesian surface of the dentary (fibres) to the median surface of the angulo-articular (fibres), with some of its posterior fibres being mixed with the tendon of the adductor mandibulae A2.

Musculus levator arcus palatini. The levator arcus palatini (fig. 1: m-l-ap) is situated medially to the adductor mandibulae A3'. It originates (fibres) on the sphenotic and inserts (fibres) on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (fig. 1: m-ad-ap) runs from the parasphenoid, pterosphenoid and orbitosphenoid (fibres) to the hyomandibulo-metapterygoid, quadrate-symplectic and ento-ectopterygoid (fibres).

Musculus levator operculi. It originates (fibres) on the ventro-lateral margin of both the pterotic and the posttemporo-supracleithrum and inserts (fibres) on the dorsal surface of the opercular (fig. 1: m-l-op).

Musculus adductor operculi. Situated medially to the levator operculi, it runs (fibres) from the ventral surface of the pterotic to the dorso-medial surface of the opercular (fibres). There is no adductor hyomandibularis (sensu Diogo and Vandewalle, in press).

Musculus dilatator operculi. The dilatator operculi (fig. 1: m-dil-op) originates (fibres) on the pterotic, frontal and sphenotic and inserts tendinously on the antero-dorsal margin of the opercular.

Musculus extensor tentaculi. This muscle is divided into three bundles. The extensor tentaculi 1 (fig. 1: m-ex-t-1) runs from both the lateral ethmoid and the orbitosphenoid (fibres) to the postero-dorsal surface of the autopalatine (fibres). The extensor tentaculi 2 originates on the lateral ethmoid and the orbitosphenoid (fibres) and inserts on the postero-median surface of the autopalatine (fibres). Lastly, the extensor tentaculi 3 (fig. 1: m-ex-t-3) runs from the lateral ethmoid and the orbitosphenoid (fibres) to the postero-ventral margin of the autopalatine (fibres).

Musculus retractor tentaculi. Well-developed muscle (fig. 1: m-re-t) originating on the lateral surface of both the lateral ethmoid and the orbitosphenoid (fibres), and attaching on the maxilla (fibres + tendon).

Musculus protractor hyoidei. This muscle (fig. 3: m-pr-h) has three parts. The pars ventralis (fig. 3: m-pr-h-v), in which are lodged the cartilages associated with the internal and external mandibular barbels (fig. 3: c-in-mnd-t; c-ex-mnd-t), originates on the anterior ceratohyal (fibres) and inserts on the dentary (fibres), meeting its counterpart in a well-developed median aponeurosis. The pars lateralis (fig. 3: m-

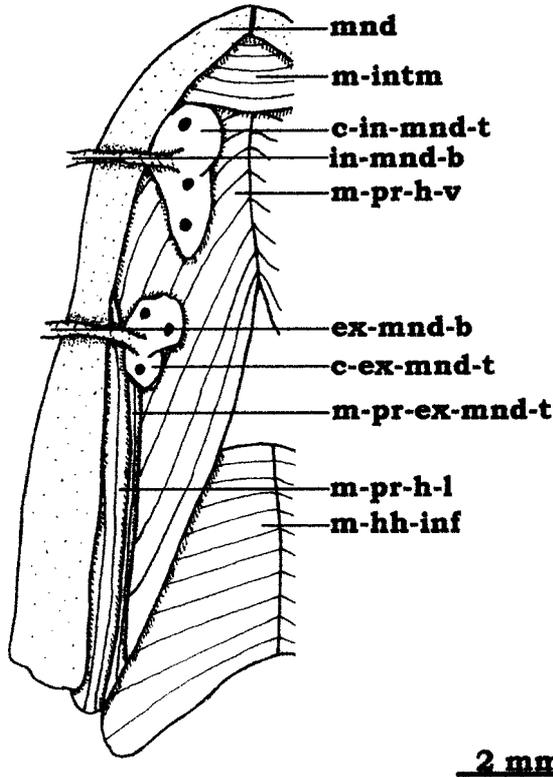


Figure 3. Ventral view of the cephalic musculature of *Centromochlus heckelii*. *c-in-mnd-t* cartilago internus mandibularis tentaculi; *c-ex-mnd-t* cartilago externus mandibularis tentaculi; *ex-mnd-b*, *in-mnd-b* external and internal mandibular barbels, *m-hh-inf* musculus hyohyoideus inferior, *m-intm* 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.

pr-h-l) runs from the posterior ceratohyal (fibres) to the ventro-medial face of the dentary (fibres + tendon). The pars dorsalis runs from both the anterior and the posterior ceratohyals (fibres) to the antero-dorsal surface of the dentary (fibres + tendon).

Musculus retractor externi mandibularis tentaculi. Small muscles running from the antero-dorsal surface of the moving part (Diogo and Chardon, 2000b) of the cartilages associated with the outer mandibular barbels (fibres) to the dentary (fibres).

Musculus retractor interni mandibularis tentaculi. Small muscles connecting the dentaries (tendon + fibres) to the antero-dorsal surface of the moving part of the cartilages associated with the internal mandibular barbels (fibres).

Musculus protractor externi mandibularis tentaculi. Narrow, elongated muscles (fig. 3: *m-pr-ex-mnd-t*) originating on the anterior ceratohyals (fibres) and inserting on the antero-dorsal surface of the moving part of the cartilages associated with the outer mandibular barbels (fibres).

Muscle intermandibularis. Small muscle joining the two mandibles (fibres) (fig. 3: m-intm).

Musculus hyohyoieus inferior. Thick muscle (fig. 3: m-hh-inf) attaching medially on a median aponeurosis (fibres) and laterally on the ventral surfaces of the ventral hypohyal, the anterior ceratohyal and the posterior ceratohyal (fibres).

Musculus hyohyoideus abductor. It runs from the first (medial) branchiostegal ray (fibres) to a median aponeurosis, which is associated with two long, strong tendons, attached, respectively, to the two ventral hypohyals. Some of the posteromedian fibres of the hyohyoideus abductor are firmly connected to the antero-ventral surface of the pectoral girdle.

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

Musculus sternohyoideus. It runs from the posterior portion of the parurohyal (tendon + fibres) to the anterior portion of the cleithrum (fibres).

Musculus arrector ventralis. It runs from the cleithrum (fibres) to the ventral condyle of the pectoral spine (fibres) (fig. 2: m-arr-v).

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) is situated on the ventral surface of the pectoral girdle and runs from the ventral margin of the cleithrum (fibres) to the antero-lateral edge of the pectoral spine (fibres). The dorsal division of the arrector dorsalis is subdivided, in turn, into two sections, with the dorsal one situated on the dorsal surface of the pectoral girdle, and therefore originating on the dorsal surface of the scapulo-coracoid (fibres), and the ventral one situated on the ventral surface of the pectoral girdle and therefore originating on the ventral surface of this bone (fibres). Both these sections of the dorsal division of the arrector dorsalis insert on the anterior edge of the dorsal condyle of the pectoral spine (fibres).

Musculus abductor superficialis. This muscle is differentiated into two sections. The dorsal section (fig. 2: m-ab-sup-1) runs from the ventral margin of the scapulo-coracoid (fibres) to the antero-ventral margin of the ventral part of the pectoral fin rays (fibres). The ventral section (m-ab-sup-2), situated dorsally to the ventral one, is highly developed and runs from both the lateral and the posterior surfaces of the scapulo-coracoid (fibres) to the antero-dorsal margin of the ventral part of the pectoral fin rays (fibres).

Musculus abductor profundus. Well-developed muscle originating on the posterior surface of the scapulo-coracoid (fibres) and inserting on the medial surface of the dorsal condyle of the pectoral spine (tendon).

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

coracoid and the dorsal surface of the proximal radials (fibres) to the antero-ventral margin of the dorsal part of the pectoral fin rays (fibres).

Musculus protractor pectoralis. Well-developed muscle running from the ventral surfaces the pterotic (fibres) to the antero-dorsal surface of the cleithrum (fibres).

Ageneiosus vittatus

The principal differences between the structures of the cephalic region and pectoral girdle of this species and those of *Centromochlus heckelii* are that in *Ageneiosus vittatus*: 1) the mandibular barbels are absent; 2) the parurohyal is a T-shaped bone with a somewhat rectangular, markedly narrow posterior portion; 3) the coracoid bridge is significantly narrower than in *C. heckelii*; 4) there is no posterior process of the scapulo-coracoid; 5) the humeral process of the cleithrum is undifferentiated; 6) the abductor superficialis 2 is considerably less developed than in *C. heckelii*; 7) the anterior nuchal plate is absent; 8) the levator operculi originates exclusively on the pterotic, and not on both this bone and the posttemporo-supracleithrum; 9) the premaxillae are bifurcated laterally; 10) there is no muscle retractor tentaculi; 11) the autopalatine presents a well-developed, deep fossa on its dorsal surface; 12) the extensor tentaculi is highly-developed, originating not only on the ethmoideal region, but also on the frontal and even on the sphenotic; 13) there is a prominent, deep concavity between the dorsal surfaces of the frontal and the lateral ethmoid; 14) the mesethmoid is markedly bifurcated anteriorly; 15) the sesamoid bone 1 of the suspensorium is considerably larger than that of *C. heckelii*; 15) there is only one fontanel, and not two, on the dorsomedian surface of the cranial roof; 16) the anterolateral arms of the T-shaped prevomer are short and poorly-developed; and 17) the antero-ventral surface of the quadrate-symplectic is pierced by a well-developed, circular foramen.

Auchenipterus dentatus

The principal differences between the configuration of the structures of the cephalic region and pectoral girdle of *Auchenipterus dentatus* and those of *Centromochlus heckelii* are that in the former species: 1) the parurohyal is a T-shaped bone with a somewhat rectangular, markedly narrow posterior portion; 2) the abductor superficialis 1 does not originate on the ventral surface of the scapulo-coracoid only, but on the ventral surfaces of this bone and also of the cleithrum; 3) the abductor superficialis 2 is considerably less developed than in *C. heckelii*; 4) there is no muscle retractor tentaculi; 5) the extensor tentaculi is highly-developed, originating not only on the ethmoideal region, but also on the frontal and the sphenotic; 6) the sesamoid bone 1 is ligamentously connected to the prevomer, and not to the lateral ethmoid; 7) the dorsal margins of the pterotic and the frontal are in contact; 8) the ento-ectopterygoid is bifurcated anteriorly; 9) the sesamoid bone 1 of the suspensorium is considerably larger than that of *C. heckelii*; and 10)

the hyomandibulo-metapterygoid and the ento-ectopterygoid are sutured, and not largely separated by the dorsal portion of the quadrato-symplectic.

DISCUSSION

According to most authors (e.g., Regan, 1911; Chardon, 1968; Curran, 1989; Mo, 1991; Lundberg, 1993; de Pinna, 1998) the Auchenipteridae and the Doradidae are closely related, constituting a monophyletic, natural clade. De Pinna (1998; pp. 305-306), in a detailed, recent overview of the phylogenetic relationships of Neotropical catfishes, revised the evidence given by different authors to support this sister-group relationship, defining the clade formed by the Doradidae and the Auchenipteridae “on the basis of the following six synapomorphies: 1) an expanded transformator process of the tripus; 2) the exoccipitals sutured to ossifications of the neural arch of the complex centrum; 3) the depressor muscle with at least some fibres wrapping around the ventral process of the second dorsal-fin spine; 4) the basiptyrgial cartilage expanded anterolaterally; 5) the os suspensorium reduced to an independent nodule, free from the parapophysis of the complex centrum; and 6) the nuchal shield composed of expanded pterygiophores sutured to the posterior margin of the neurocranium”. Our observations and comparisons not only confirmed these synapomorphies, but also pointed out four other synapomorphies to support the clade formed by the Doradidae and the Auchenipteridae:

1. *Meckel's cartilage highly-developed, with its ascending portion extending dorsally to the dorsal surface of the coronoid process of the mandible and, thus, with a significant part of this ascending portion being visible in a lateral view of the cranium.* Plesiomorphically in catfishes the Meckel's cartilage does not extend dorsally to the dorsal surface of the coronoid process of the mandible (Mo, 1991; Diogo and Chardon, 2000a, c). However, in all doradids and auchenipterids examined, the ascending portion of the Meckel's cartilage extends far beyond the dorsal surface of the coronoid process, with a considerable part of this ascending portion, therefore, visible in a lateral view of the skull (fig. 1). Since such a peculiar feature is also found only in the aspredinid catfishes (Diogo et al., 2001c: fig. 1), and since the aspredinids are seemingly more related to a series of other siluriform families (Erethistidae, Sisoridae, Akysidae, Amblycipitidae) than to the doradids and auchenipterids (de Pinna, 1996, 1998; Diogo et al., 2001c, 2002b; Diogo, in press), this character seems to constitute a synapomorphy to support the clade constituted by the Auchenipteridae and the Doradidae.

2. *Epioccipital constituting a significant part of the dorsal surface of the cranial roof.* This character was proposed by Lundberg (1993) as a synapomorphy of a clade formed by the Doradidae, Auchenipteridae and the African Mochokidae (see below). However, as noted by Curran (1989) and Mo (1991), and as corroborated by the present study (this character is absent in all mochokids studied), an epioccipital forming a significant part of the dorsal surface of the cranial roof (fig. 1) constitutes,

in fact, a synapomorphy of the clade formed by the former two Neotropical families, and not by these two families and the African Mochokidae.

3. *Posterolateral surface of the scapulo-coracoid presenting a prominent, triangular, posteriorly pointed posterior process.* Plesiomorphically in catfishes the scapulo-coracoid lacks major posterior processes (Mo, 1991; de Pinna, 1996; Diogo et al., 2001b). However, in all doradids and auchenipterids examined, with exception to the peculiar genus *Ageneiosus*, the scapulo-coracoid presents a prominent, triangular, posteriorly pointed posterior process (fig. 2). Such a feature is only found, apart the doradids and auchenipterids, in some few catfishes such as some bagrids (Diogo et al., 2001b: fig. 5) or the catfishes of the sisoroid clade including sisorids, auchenipterids and erethistids (see, e.g., Diogo et al., 2002b: fig. 5). Due to the fact that the catfishes referred above are seemingly more closely related to other catfishes than to the doradids and the auchenipterids (Mo, 1991; de Pinna, 1996, 1998; Diogo et al., 2001c, 2002b; Diogo, in press-a; this study), and due to the highly derived position occupied by the genus *Ageneiosus* among the Auchenipteridae (de Pinna, 1998: fig. 15), this feature seems to constitute an additional synapomorphy to support the clade formed by the doradids and auchenipterids, which was secondarily lost in the peculiar genus *Ageneiosus*.

4. *Articulatory surface of the scapulo-coracoid for the pectoral spine markedly narrow and dorsoventrally elongated.* Plesiomorphically in catfishes (Diogo et al., 2001b) the scapulo-coracoid presents a well-developed, somewhat cylindrical articulatory surface (Diogo et al., 2001b: fig. 5, af-pecp) to articulate with a also well-developed, deep concavity present on the proximal region of the pectoral spine (Diogo et al., 2001b: fig. 3, af-scacor). However, in all doradids and auchenipterids examined, the articulatory surface of the scapulo-coracoid for the pectoral spine is considerably more developed than in the other catfishes, being highly-developed and remarkably elongated dorsoventrally. Since such an extreme development of the articulatory surface of the scapulo-coracoid for the pectoral spine is present in all the doradids and auchenipterids examined, and in no other catfish examined by us or described in the literature, this feature clearly seems to constitute an autapomorphy to support the sister-group relationship between these two groups of catfishes.

Although not as consensual as the sister-group relationship between the doradids and auchenipterids (de Pinna, 1998; Diogo, in press-a), some authors have proposed a close relationship between the African Mochokidae and the clade formed by the Neotropical Auchenipteridae and Doradidae (Chardon, 1968; Mo, 1991; Lundberg, 1993; de Pinna, 1998). The main characters proposed to support this sister-group relationship were revised by Lundberg (1993: fig. 8.9) who listed seven synapomorphies to support the clade formed by the Mochokidae, the Doradidae and the Auchenipteridae. These were: 1) distal end of elastic spring expanded to form a disc; 2) depressor dorsalis muscle of second dorsal-fin lepidotrich, or spine, inserts on base of first lepidotrich, or spinelet; 3) first dorsal-fin lepidotrich with greatly elongated and recurved limbs; 4) first and second dorsal-fin basals tightly bound or

sutured to fourth, fifth, and sometimes sixth, neural spines; 5) tripus with a recurved transformer process that enters the peritoneal tunic of swim bladder; 6) compound of Weberian complex strongly sutured to exoccipitals; 7) epioccipital with a large superficial dermal component in the skull roof. Our observations and comparisons strongly support such a sister-group relationship between the mochokids and the clade formed by both the doradids and the auchenipterids, identifying two new, additional synapomorphies to support this sister-group relationship. However, before describing these two synapomorphies, we would like to draw attention to the fact that, as explained above, one of the characters listed by Lundberg (1993), namely the “epioccipital with a large superficial dermal component in the skull roof”, constitutes, in fact, a synapomorphy of the clade constituted by the Doradidae and Auchenipteridae, and not by these two families and the Mochokidae (see above).

The two new, additional synapomorphies to support the sister-group relationship between the mochokids and both the doradids and the auchenipterids are:

1. *Dorsal division of arrector dorsalis differentiated into two sections originated, which originate, respectively, on the dorsal and ventral surfaces of the pectoral girdle.* Plesiomorphically in catfishes the dorsal division of the muscle arrector dorsalis is constituted by a single mass of fibres, which originates on the dorsal surface of the pectoral girdle (Diogo et al., 2001b). However, in all the doradids, auchenipterids and mochokids examined, the dorsal division of the arrector dorsalis is subdivided into two sections, with one of these sections originating on the dorsal surface of the pectoral girdle and the other section originating on the ventral surface of this girdle. Such a feature is highly peculiar and rare among catfishes, being also found only in some derived amphiliids such as *Zaireichthys*, *Leptoglanis* or *Doumea* (see Diogo, in press-b). Therefore, it is likely that this character constitutes an additional, conspicuous synapomorphy to support the clade constituted by the Auchenipteridae, the Doradidae and the Mochokidae.

2. *Some of the medial fibres of hyohyoideus abductor contacting the ventral surface of pectoral girdle.* The hyohyoideus abductor of catfishes runs from a medial aponeurosis to the first branchiostegal ray, with the medial aponeurosis usually firmly attached to the postero-ventral surface of the parurohyal bone and/or to the medial aponeurosis of the hyohyoideus inferior and, therefore, not contacting the pectoral girdle (Diogo and Vandewalle, in press). However, in all doradids, auchenipterids and mochokids examined, some of the posteromedian fibres of the hyohyoideus abductor do attach onto the antero-ventral surface of the pectoral girdle. A somewhat similar configuration is among the Siluriformes only found in the aspredinid catfishes, but in these catfishes there is a much tighter contact between the hyohyoideus abductor and the pectoral girdle, with a great part of this muscle originating inclusively on the ventral surface of the pectoral girdle (Diogo et al., 2001c: fig. 5), with this character constituting an Aspredinidae autapomorphy (Diogo et al., 2001c). As the configurations found in the aspredinids and in the mochokids, doradids and auchenipterids are, thus, somewhat different and,

principally, since the Aspredinidae are seemingly more closely related, as explained above, to the other four sisoroid groups than to the Mochokidae, Doradidae and Auchenipteridae, this character probably constitutes an additional synapomorphy to support the clade constituted by these three latter families.

With respect to the auchenipterid synapomorphies, three characters were listed by de Pinna (1998: fig. 15), namely: 1) “anterior rays of anal fin enlarged and thickened in adult males”; 2) “maxillary barbel, when adducted, fits in a groove in the cheek integument, just ventral to eye”; 3) “abducted maxillary barbel directed laterally and dorsally”. Our observations and comparisons strongly support the monophyly of the auchenipterids, and identify an additional, potential auchenipterid synapomorphy, which is described below:

1. Maxilla markedly elongated proximo-distally. In the great majority of the catfishes the maxilla is a small, relatively short structure (Alexander, 1965; Gosline, 1975; Arratia, 1990, 1992; Mo, 1991; Diogo et al., 2000a). However, in all auchenipterids examined, the maxilla is markedly elongated proximodistally (fig. 1). As this feature is only present, apart from the auchenipterid catfishes, in a few, specific catfish taxa such as the amphiliid genera *Leptoglanis* and *Zaireichthys*, the sisorid genera *Bagarius*, *Gagata* and *Glyptosternon*, or the silurid genus *Wallago*, and since this feature is absent in the auchenipterids and the mochokids (see above), it seems probable that this constitutes an auchenipterid synapomorphy.

GENERAL CONCLUSIONS

In conclusion, our observations and comparisons support a sister-group relationship between the Neotropical Auchenipteridae and Doradidae, as well as a sister-group relationship between the clade constituted by these two families and the African Mochokidae. In addition, our observations and comparisons identified one additional, potential auchenipterid synapomorphy, namely a markedly proximodistally elongated maxilla. As in other studies recently published by the authors (Diogo et al., 1999, 2000a, b; Diogo and Chardon, 2001b, c, 2002a, b; Diogo, in press-b; Diogo and Vandewalle, in press), the present work also stresses that the analysis of certain characters that are not usually included in the study of catfish phylogeny, such as those concerning the configuration of the muscles, ligaments and cartilages of the cephalic region and pectoral girdle, can reveal useful data to infer the phylogenetic position and/or autapomorphies of certain catfish taxa.

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