

## **On the osteology and myology of the cephalic region and pectoral girdle of *Chaca bankanensis* Bleeker 1852, with comments on the autapomorphies and phylogenetic relationships of the Chacidae (Teleostei: Siluriformes)**

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**Abstract**—The cephalic and pectoral girdle structures of *Chaca bankanensis* are described and compared to those of other catfishes, as the foundation for a discussion on the autapomorphies and phylogenetic relationships of the Chacidae. Our observations and comparisons pointed out six new chacid autapomorphies, namely: (1) absence of abductor superficialis; (2) ethmoid cartilage with long, thin, anterolateral projections situated ventrally to the anterolateral arms of mesethmoid; (3) interopercular with well-developed, deep concavity to articulate with posterior surface of preopercular; (4) dorsal process 2 of the cleithrum highly developed and markedly extended posteriorly. In addition, our observations and comparisons support a close relationship between the chacids, the plotosids and the clariids.

**Keywords:** catfish; cephalic region; Chacidae; morphology; myology; osteology; pectoral girdle; phylogeny; Siluriformes.

### **INTRODUCTION**

The Siluriformes are one of the economically important groups of fresh and brackish water fishes in the world and, in many countries, form a significant part of inland fisheries (Teugels, 1996). Among the 35 siluriform families (Ferraris and de Pinna, 1999), the Chacidae, a small family of Asian catfishes including a single genus, *Chaca*, and three species, is surely one of the less studied. In fact, despite the large number of works concerning catfish anatomy (e.g., McMurrich, 1884; Regan, 1911; de Beer, 1937; Alexander, 1965; Gosline, 1975; Ghiot, 1978; Ghiot et al.,

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1984; Arratia, 1990; Mo, 1991; Diogo and Chardon, 2000a, b; Diogo et al., 2000, 2001a, b), the only papers describing the morphology of chacids with some detail are those of Chardon (1968), Gauba (1970), Tilak (1971) and Brown and Ferraris (1988). Moreover, as these descriptions are almost exclusively restricted to the osteology or external anatomy of the cephalic region of chacids, important aspects of the morphology of these fishes are poorly known (e.g., the configuration of their pectoral girdle) or even practically unknown (e.g., the configuration of their musculature, and of the structures associated with their mandibular barbels).

The aim of this work is, thus, to study the osteological and myological structures of the cephalic region (branchial apparatus excluded) and pectoral girdle of *Chaca bankanensis* Bleeker 1852, and to compare these structures with those of other chacid and non-chacid siluriforms as the foundation for a discussion on the autapomorphies and phylogenetic relationships of the Chacidae. It is also hoped that this study could increase the knowledge on the anatomy and phylogeny of catfishes in general, as well as pave the way for future works concerning the comparative anatomy, evolution, functional morphology, palaeontology, eco-morphology and particularly the phylogeny of these fishes.

## MATERIAL AND METHODS

In the anatomical descriptions of *Chaca bankanensis* the nomenclature for the osteological structures of the cephalic region follows basically that of Arratia (1997). However, for the several reasons explained in detail in our recent papers (Diogo et al., 2001a; Diogo 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 mandibular sections, Diogo and Chardon (2000a) are followed. In relation to the muscles associated with the mandibular barbels, which were not studied by Winterbottom (1974), Diogo and Chardon (2000b) are followed. Concerning the nomenclature of the pectoral girdle bones and muscles, Diogo et al. (2001b) are followed.

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale de Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National D'Histoire Naturelle de 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 (1985) method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The alcohol fixed (alc), trypsin-cleared and alizarine-stained (c&s), or simply alizarine-stained (s) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

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

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

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

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

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

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

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

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

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

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

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

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

Clariidae: *Clarias anguillaris* LFEM, 2 (alc). *Clarias batrachus* LFEM, 2 (alc). *Clarias 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: *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 anguillar* LFEM, 2(alc). *Plotosus lineatus* USNM 200226, 2 (alc).

Schilbidae: *Ailia colia* USNM 165080, 1 (alc). *Laides hexanema* USNM 316734, 1 (alc). *Pseudeutropius brachyopterus* 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).

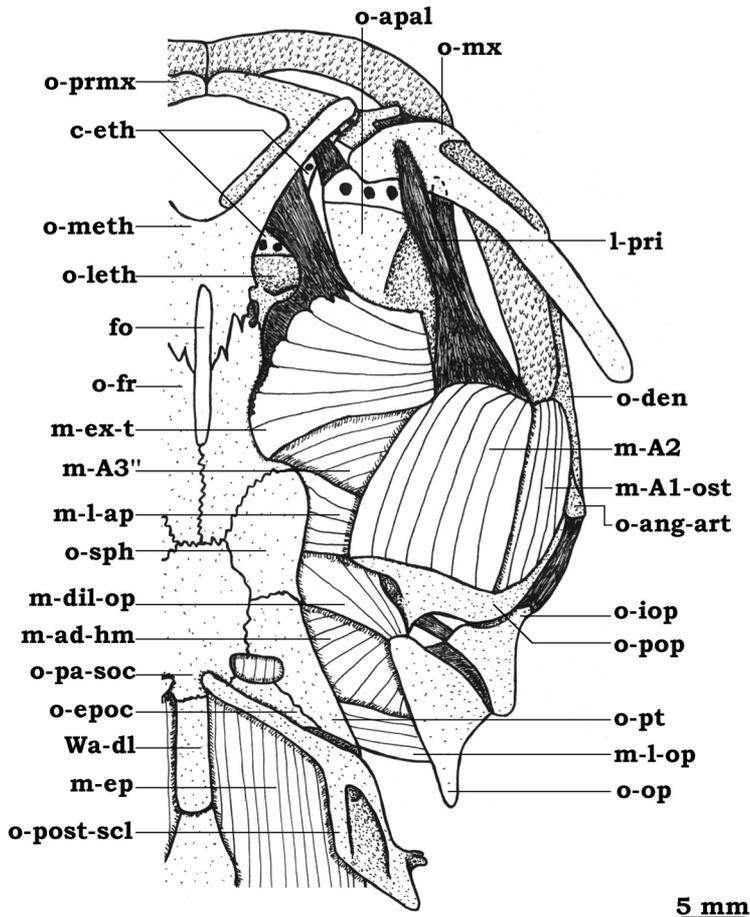
Trichomycteridae: *Hatcheria macraei* LFEM, 2 (alc). *Trichomycterus areolatus* LFEM, 2 (alc). *Trichomycterus banneaui* LFEM, 2 (alc). *Trichomycterus immaculatus* USNM 301015, 2 (alc).

## RESULTS

### *Osteology*

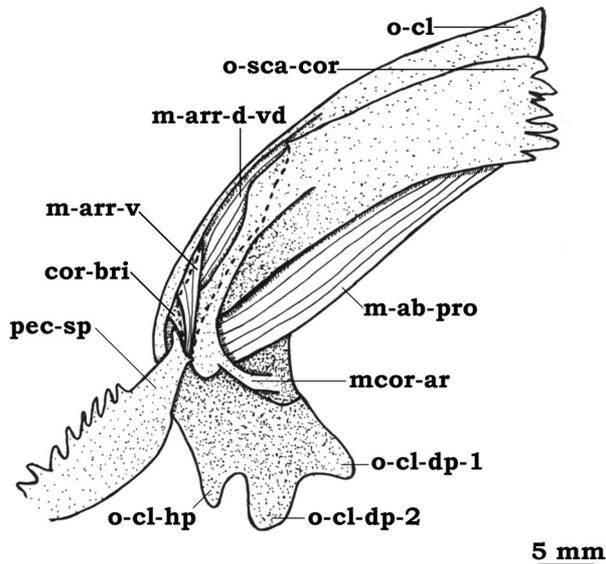
*Os mesethmoideum*. Unpaired bone situated on the anterodorsal surface of the neurocranium (fig. 1). It presents two highly-developed, thin, long anterolateral arms, ventrally to which lie the also highly-developed, long and thin anterolateral projections of the ethmoid cartilage (fig. 1).

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



**Figure 1.** Dorsal view of the musculature and skeleton structures of the cephalic region of *Chaca bankanensis* (note: bones are stippled with small black points and cartilages with large black circles). *c-eth* cartilago ethmoideus, *fo* fontanel, *l-pri* ligamentum primordium, *m-A1-ost*, *m-A2*, *m-A3''* sections of musculus adductor mandibulae, *m-ad-hm* musculus adductor hyomandibularis, *m-dil-op* musculus dilatator operculi, *m-ep* musculus epaxialis, *m-ex-t* musculus extensor tentaculi, *m-l-ap* musculus levator arcus palatini, *m-l-op* musculus levator operculi, *o-ang-art* os angulo-articulare, *o-apal* os autopalatinum, *o-den* os dentale, *o-epoc* os epioccipitale, *o-fr* os frontale, *o-iop* os interoperculare, *o-leth* os latero-ethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-op* os operculare, *o-pa-soc* os parieto-supraoccipitale, *o-pop* os praeoperculare, *o-post-scl* os posttemporo-supraacleithrum, *o-prmx* os praemaxillare, *o-pt* os pteroticum, *o-sph* os sphenoticum, *Wa-dl* dorsal lamina of Weberian apparatus.

*Os parasphenoideum.* The unpaired parasphenoid is the longest bone of the cranium, bearing a pair of ascending flanges that suture with the ptersphenoids and prootics.



**Figure 2.** Ventral view of the musculature and skeleton structures of the pectoral girdle of *Chaca bankanensis*. *cor-bri* coracoid bridge, *m-ab-pro* musculus abductor profundus, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector ventralis, *mcor-ar* mesocoracoid arch, *o-cl* os cleithrum, *o-cl-dp-1*, *o-cl-dp-2* dorsal process 1 and 2 of os cleithrum, *o-cl-hp* humeral process of os cleithrum, *o-sca-cor* os scapulo-coracoid, *pec-sp* pectoral spine.

*Os orbitosphenoideum.* Posterior to the lateral ethmoid, with the dorsal edge of its lateral wall being sutured with the ventral surface of the frontal. The ventral surfaces of the orbitosphenoids do not meet along the ventral midline.

*Os pterosphenoideum.* Poorly developed, posterior to the orbitosphenoid (fig. 2), covering, together with this bone, the gap between the frontals and the parasphenoid.

*Os frontale.* The frontals (fig. 1) are large bones that constitute a great part of the cranial roof. They are largely separated by a median fontanel.

*Os sphenoticum.* Of about the same size of the pterotic (fig. 1), it presents a well-developed, ventrolateral articulatory facet for the hyomandibulo-metapterygoid.

*Os pteroticum.* Well-developed, somewhat triangular bone situated posteriorly to the sphenotic (fig. 1) and attached, by means of connective tissue, to the anterolateral surface of the posttemporo-supracleithrum.

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

*Os epioccipitale.* Well developed, it situates on the posterodorsal surface of the cranial roof. Between the anterior surface of the epioccipital, the posterolateral surface of the parieto-supraoccipital and the lateral surface of the pterotic there is a well-developed, roughly oval, dorsal foramen.

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

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

*Os parieto-supraoccipitale*. Large, unpaired bone constituting the postero-dorso-medial surface of the cranial roof, which is associated posteromesially with a well-developed dorsal lamina of the Weberian apparatus (Fig. 1). There is no posterior process of the parieto-supraoccipital.

*Os angulo-articulare*. This bone (fig. 1), together with the dentary, the coronomeckelian and the Meckel's cartilage, 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 (fig. 1) covers a great part of the lateral surface of the mandible. The posterodorsal margin of the dentary forms, together with the anterodorsal margin of the angulo-articular, a well-developed dorsal process (processus coronoideus).

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

*Os praemaxillare*. The well-developed premaxillaries (fig. 1) bear ventrally a well-developed tooth-plate with numerous small teeth having their tips slightly turned backward. Posteriorly, each premaxilla bears a prominent, posteromesially directed process.

*Os maxillare*. The highly-developed maxillary bone (fig. 1) is connected to the coronoid process of the mandible by a strong, massive ligament (primordial ligament) that is markedly bifurcated anteriorly, its anterodorsal and anteroventral divisions attaching on the dorsal and ventral surfaces of the maxillary, respectively. As in most catfishes, the maxillary barbels are supported by the maxillaries.

*Os autopalatinum*. The autopalatine (fig. 1) is a well-developed, somewhat flat bone presenting two dorsal, oblique arms that are joined together along their lateral surfaces with a lateral projection of laminar bone. Anteriorly, the autopalatine presents a well-developed cartilage with two anterolateral concavities to accept the two proximal heads of the maxillary. Medially, the autopalatine presents a well-developed, anteromesially directed articulatory surface to articulate with the lateral ethmoid. The posterior portion of the autopalatine is markedly incurved laterally.

*Os hyomandibulo-metapterygoideum*. The homology and, thus, the correct denomination, of this bone, as well as of the other suspensorium elements of catfish, has been the subject of endless controversies (McMurrich, 1884; De Beer, 1937; Hoedeman, 1960; Gosline, 1975; Howes, 1983a, b, 1985; Arratia, 1990, 1992; Diogo et al., 2001a; Diogo and Chardon, 2003; etc.). As referred above, 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 will follow strictly that presented by Diogo et al. (2001a). The hyomandibulo-metapterygoid is

a large bone articulating dorsomesially with the sphenotic and posteriorly with the opercular.

*Os sesamoideum 1.* Small bone attached by means of a short but strong ligament to the anterior margin of the ento-ectopterygoid posteriorly and by means of a short and thin ligament to the ventral margin of the autopalatine anteriorly. The sesamoid bones 2 and 3 (see Diogo et al., 2001a) are absent.

*Os entopterygoide-ectopterygoideum.* Well-developed bone associated anteriorly with the sesamoid bone 1 of the suspensorium and posteriorly with both the hyomandibulo-metapterygoid and the quadrate-symplectic.

*Os quadrato-symplecticum.* The quadrate-symplectic presents a well-developed, anterior articular surface to articulate with the posterodorsal surface of the angulo-articular.

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

*Os operculare.* The opercular (fig. 1) is a well-developed, roughly triangular bone attached ventrally, by means of massive connective tissue, to the interopercular. Anteriorly, it presents a well-developed, anteriorly directed, articular surface for the hyomandibulo-metapterygoid.

*Os interoperculare.* Its anteroventral surface is ligamentously connected to the posteroventral margin of the mandible and its anterodorsal surface is ligamentously connected to the preopercular (fig. 1). The interopercular presents a well-developed, deep anterior concavity to articulate with the posterior surface of the preopercular.

*Os interhyal.* Well developed, its ventral surface is ligamentously connected to the dorsal surface of the posterior ceratohyal and its dorsal surface is ligamentously connected to the median surfaces of both the preopercular and the hyomandibulo-metapterygoid.

*Os ceratohyale posterior.* Well-developed, somewhat triangular bone ligamentously connected to the posteroventral edge of the mandible, to the medial surface of the interopercular, and to the well-developed interhyal.

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

*Os hypohyale ventrale.* The ventral hypohyals are well developed and ligamentously connected to the anterolateral edges of the parurohyal. Posteriorly, each ventral hypohyal presents a prominent, posteroventral process to receive part of the fibres of the hypertrophied sternohyoideus. The dorsal hypohyals are missing.

*Os parurohyale.* The parurohyal is an unpaired bone lying medially behind the ventromedial surfaces of the ventral hypohyals and being connected to these bones by means of two strong, thick ligaments. It presents two well-developed posterolateral arms and a poorly developed posteromedian process.

*Os posttemporo-supraclithrum.* The thin dorso-mesial limb of this bone (fig. 1) situates dorsally to the posterodorsal surfaces of both the epioccipital and the parieto-supraoccipital, to which it is loosely attached by means of connective tissue. Its thin ventromesial limb is also loosely attached, via a small, thin ligament, to the

basioccipital. Its posterolateral surface presents a well-developed, laterally directed process.

*Os cleithrum.* The cleithra (fig. 2) are large, well-ossified stout structures forming a significant part of the pectoral girdle and the posterior boundary of the branchial chamber. They are attached in the anteromedial line via connective tissue. Each cleithrum bears a crescentic, medially-faced groove that accommodates the proximal portion of the pectoral spine, which is a highly-developed, markedly enlarged structure (fig. 2). Posterodorsally, the cleithrum presents two prominent dorsal processes to articulate with the posttemporo-supracleithrum (fig. 2: o-cl-dp-1, o-cl-dp-2), the most ventral of which (o-cl-dp-2) being particularly developed and markedly extended posteriorly. The humeral process of the cleithrum is well developed.

*Os scapulo-coracoideum.* The scapulo-coracoid (fig. 2) is an elongated bony plate suturing with the cleithrum along its anterolateral edge. Anterolaterally, it presents a large anteriorly directed process, usually called the coracoid bridge (fig. 2: cor-bri), which extends ventrally to the ventrolateral surface of the cleithrum, fusing with an anteroventral ridge of this bone. There is a well-developed mesocoracoid arch (fig. 2: mcor-ar).

### Myology

*Musculus adductor mandibulae.* The adductor mandibulae A1-ost (fig. 1) (see Diogo and Chardon, 2000a) originates on the preopercular and the quadrate-symplectic and inserts on the dorsolateral surface of the angulo-articular. The A2 (fig. 1), which lies dorsomesially to the A1-ost, runs from the preopercular and hyomandibulo-metapterygoid to the medial surface of the angulo-articular. The adductor mandibulae A3' is divided into a dorsal and a ventral part. The dorsal one (A3'-d) originates on the hyomandibulo-metapterygoid and preopercular and inserts tendinously on the coronomeckelian bone, while the ventral one (A3'-v) originates on both the quadrate-symplectic and the preopercular and inserts on the medial surface of the angulo-articular. The adductor mandibulae A3'' (fig. 1), situated mesially to the A3' and to the levator arcus palatini, runs from the hyomandibulo-metapterygoid and the sphenotic to the mesial surface of the angulo-articular and the coronomeckelian. It should be noted that, with respect to the insertion on the mandible, the most medial insertion on the mandible is that of the A3', with that of the A3'' being mesial to that of the A2, and with this latter being, in turn, medial to that of the A1-ost. The adductor mandibulae A $\omega$  is missing.

*Musculus levator arcus palatini.* The levator arcus palatini (fig. 1) originates on the sphenotic and inserts on the lateral face of the hyomandibulo-metapterygoid.

*Musculus adductor arcus palatini.* Highly developed, it runs from the lateral surfaces of the parasphenoid, pterosphenoid and orbitosphenoid, as well as from the dorsolateral surfaces of the frontal and lateral ethmoid, to both the hyomandibulo-metapterygoid, the ento-ectopterygoid, and the sesamoid bone 1 of the suspensorium.

*Musculus levator operculi.* Poorly developed (fig. 1), it originates on the pterotic and inserts on the dorsal margin of the opercular.

*Musculus adductor hyomandibularis.* The adductor hyomandibularis (sensu Diogo et al., 2002; Diogo and Vandewalle, 2003) is highly developed (fig. 1), lying medially to the levator operculi and laterally to the adductor operculi. It runs from the ventral surface of the pterotic to the posterodorsal surface of the hyomandibulo-metapterygoid.

*Musculus adductor operculi.* It originates on the ventral surface of the pterotic and inserts on the dorso-medial surface of the opercular.

*Musculus dilatator operculi.* The dilatator operculi (fig. 1) is a well-developed muscle originating on the pterosphenoid, sphenotic, frontal and hyomandibulo-metapterygoid and inserting on the anterodorsal margin of the opercular.

*Musculus extensor tentaculi.* The extensor tentaculi (fig. 1) is somewhat divided into two parts, with the dorsal one running from the mesethmoid, lateral ethmoid and frontal to the posterolateral surface of the autopalatine and the ventral one running from the frontal and lateral ethmoid to the posteromesial surfaces of the autopalatine. There is no retractor tentaculi.

*Musculus protractor hyoidei.* This muscle (fig. 3) has three parts. The pars ventralis, in which are lodged the small, widely separated cartilages associated with the internal and external mandibular barbels, originates on the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis. The pars lateralis runs from the anterior ceratohyal to the ventro-medial face of the dentary (fig. 3). The pars dorsalis runs from the anterior ceratohyal to the dentary. There are no small, additional muscles (Diogo and Chardon, 2000b) associated with the mandibular barbels.

*Musculus intermandibularis.* Well developed, it joins 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 and the anterior ceratohyal.

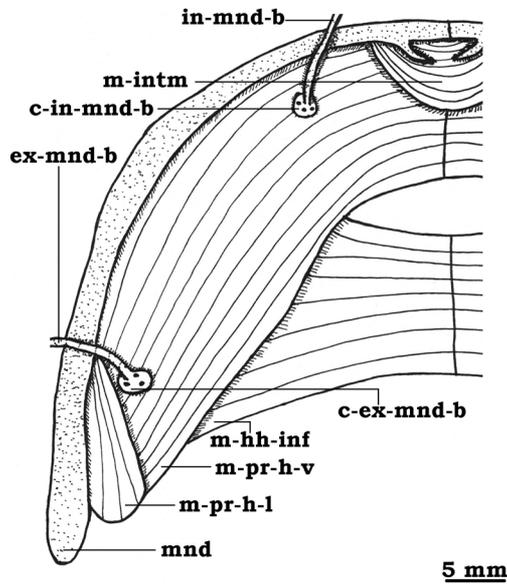
*Musculus hyohyoideus abductor.* The hyohyoideus abductor runs from the first (medial) branchiostegal ray to a median aponeurosis, which is associated with two long, strong tendons, attached, respectively, to the two ventral hypohyals.

*Musculus hyohyoideus adductor.* Each hyohyoideus adductor connects the branchiostegal rays of the respective side, with their most lateral fibres also attaching to the mesial surface of the opercular.

*Musculus sternohyoideus.* The hypertrophied sternohyoideus runs from the posteroventral processes of the ventral hypohyals and from both the ventral and posterior surfaces of the parurohyal to the anterior portion of the cleithrum.

*Musculus arrector ventralis.* The arrector ventralis is a small muscle running from the ventral surface of the cleithrum to the ventral condyle of the pectoral spine (fig. 2).

*Musculus arrector dorsalis.* This muscle (fig. 2) is differentiated into a well-developed ventral division and a well-developed dorsal division. The ventral divi-



**Figure 3.** Ventral view of the musculature and skeleton structures of the cephalic region of *Chaca bankanensis* (note: bones are stippled with small black points and cartilages with large black circles). *c-ex-mnd-b*, *c-in-mnd-b* cartilages of external and internal mandibular barbels, *ex-mnd-b*, *in-mnd-b* external and internal mandibular barbels, *m-hh-inf* musculus hyohyoideus inferior, *m-intm* musculus intermandibularis, *m-hh-inf* musculus hyohyoideus inferior, *mnd* mandible, *m-pr-h-l*, *m-pr-h-v* pars lateralis and ventralis of musculus protractor hyoideus.

sion (fig. 2: *m-arr-d-vd*) originates on both the cleithrum and the scapulo-coracoid and inserts on the anterolateral margin of the pectoral spine, with its lateral fibres lying on the ventral surface of the pectoral girdle and its median fibres lying on the dorsal surface of this girdle. With respect to the dorsal division of the arrector dorsalis, it situates on the dorsal surface of the pectoral girdle and runs from the dorsal margin of the scapulo-coracoid to the anterior edge of the dorsal condyle of the pectoral spine.

*Musculus abductor profundus*. This well-developed muscle (fig. 2) originates on the posterior surface of the scapulo-coracoid and inserts on the dorsal condyle of the pectoral spine. The muscle abductor superficialis (sensu Diogo et al., 2001b) is missing.

*Musculus adductor superficialis*. Situated on the posterior margin of the pectoral girdle and divided into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the anterodorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from both the postero-ventrolateral edge of the scapulo-coracoid and the dorsal surface of the proximal radials to the anteroventral margin of the dorsal part of the pectoral fin rays.

*Musculus protractor pectoralis*. Highly developed, it originates on the pterotic and inserts on the lateral surface of the cleithrum.

## DISCUSSION

Brown and Ferraris (1988: 13-14) listed the following seven autapomorphic characters to define the Chacidae, namely: (1) anterior ray of the pelvic fin branched; (2) two obliquely oriented arms of the autopalatine joined together along their lateral surfaces with a lamina of bone ventrally; (3) orbitosphenoid a paired element, not meeting along the ventral midline; (4) mesethmoid with two large, anterolaterally expanded cornua; (5) first three basibranchial elements greatly reduced in size; (6) premaxilla with posteromesially directed process; (7) autopalatine with a lateral flexure posteriorly, behind the articular facet. Our observations and comparisons indicate that the chacids could be defined, in addition to the characters listed above, by some other unique features. However, before describing these features, it is important to notice that, of the seven characters of Brown and Ferraris (1988) listed above, only the first six represent, in fact, unique, autapomorphic characters within the Siluriformes. In fact, in the trichomycterids, the nematogenyids, and the specimens examined of the genus *Parakysis*, the autopalatine also presents a marked lateral flexure behind the articular facet, with the situation in *Parakysis* being particularly similar to that found in *Chaca*. Attending to the phylogenetic hypotheses of Mo (1991), De Pinna (1998), and Diogo (in press), it can be argued that this character could, nevertheless, constitute a valid synapomorphy to define the chacids. However, as it is not exclusively present in this latter group of catfishes, it does not represent an unique, autapomorphic character within catfishes, and, thus, it cannot be seen as a Chacidae autapomorphy.

In addition to the six chacid autapomorphies of Brown and Ferraris (1988) (see above), our observations and comparisons pointed out the following ones:

*Absence of abductor superficialis.* Plesiomorphically catfishes present a well-developed muscle abductor superficialis running from the ventral surface of the pectoral girdle to the proximal surface of the pectoral rays (Alexander, 1965; Diogo et al., 2001b). In all the chacids examined this muscle is missing.

*Ethmoid cartilage with long, thin, anterolateral projections situated ventrally to the anterolateral arms of mesethmoid.* In catfishes the ethmoid cartilage is usually a broad structure with a somewhat circular or rectangular shape lying in the ethmoid region (Regan, 1911; Eigenmann, 1925; De Beer, 1937; Alexander, 1965; Gosline, 1975; Howes, 1983a, 1985; Ghiot et al., 1984; Mo, 1991; De Pinna, 1996). In all the chacids examined, this cartilage is a Y-shaped structure, presenting two long, thin anterolateral projections situated ventrally to the also long and thin anterolateral arms of the mesethmoid (fig. 1). Such a configuration of the ethmoid cartilage is not found elsewhere in the siluriforms.

*Interopercular with well-developed, deep concavity to articulate with posterior surface of preopercular.* Plesiomorphically in catfishes the interopercular does not present major anterior concavities and/or articulatory surfaces (Regan, 1911; Eigenmann, 1925; De Beer, 1937; Alexander, 1965; Howes, 1983a, 1985; Mo, 1991; De Pinna, 1996). Exclusively in the chacid catfishes examined, the interopercular

presents a well-developed, deep anterior concavity to receive the posterior surface of the preopercular (fig. 1).

*Dorsal process 2 of the cleithrum highly developed and markedly extended posteriorly.* Catfishes usually present two well-developed dorsal processes of the cleithrum to articulate with the posttemporo-supracleithrum (Alexander, 1965; Diogo et al., 2001b), but in chacids the most ventral of these processes (dorsal process 2, sensu Diogo et al., 2001b) is extremely developed and extended posteriorly (fig. 2).

With respect to the phylogenetic relationships of the Chacidae, our observations and comparisons pointed out two derived characters to support the close relationship suggested by authors such as Tilak (1971), Brown and Ferraris (1988) or De Pinna (1998) between this family and the Plotosidae, as well as between these two families and the Clariidae. These two characters are described below. It is important to notice here that the phylogenetic considerations made in the present work were corroborated by an explicit phylogenetic comparison of 440 morphological characters, concerning the bones, muscles, cartilages and ligaments of both the cephalic region and the pectoral girdle, in 87 genera representing all the extend catfish families (Diogo, in press).

*Articulatory facet of autopalatine for lateral ethmoid anteromesially directed.* In the great majority of the catfishes the articulatory facet of the autopalatine for the lateral ethmoid is directed medially, posteromesially or dorsomesially (Alexander, 1965; Gosline, 1975; Howes, 1983a, 1985; Ghiot et al., 1984; Arratia, 1990, 1992; De Pinna, 1996; Diogo et al., 2000, 2001a). However, in the chacids, plotosids and clariids, and exclusively in these three catfish groups, the articulatory facet of the autopalatine for the lateral ethmoid is markedly directed anteromesially (Diogo et al., 2000: fig. 6B).

*Adductor arcus palatini inserts on sesamoid bone 1 of suspensorium.* Plesiomorphically in catfishes the adductor arcus palatini inserts on the hyomandibulo-metapterygoid, ento-ectopterygoid and/or quadrate-symplectic (Diogo and Vandewalle, 2003). However, in the chacids, clariids and plotosids this muscle also inserts on the sesamoid bone 1 of the suspensorium (Diogo et al., 2001a: fig. 9). Such an insertion of the adductor arcus palatini on this latter bone is rare among catfishes, only occurring, apart from in the chacids, clariids and plotosids, in some sisoroids (Diogo and Vandewalle, 2003).

In addition to these two characters, there are two other characters studied, unique within the Siluriformes, that support a close relationship between the Chacidae and the Clariidae, and between the Chacidae and the Plotosidae, respectively.

The character uniting the Chacidae and the Clariidae is the hypertrophy of the muscle protractor pectoralis and its broad insertion on the lateral, and not the anterodorsal or dorsolateral surface of the cleithrum (Diogo et al., 2001b: fig. 8). Such a hypertrophy and lateral insertion of the protractor pectoralis is only found,

apart from in the chacids examined, in the catfishes of the family Clariidae (Diogo et al., 2001b).

The character uniting the Chacidae and the Plotosidae is the markedly anterior origin of the muscle extensor tentaculi on the neurocranium, a feature supposedly only found in the plotosid catfishes (Oliveira et al., 2001) but that, in fact, is also present in all the chacids examined (fig. 1).

Therefore, although the present study does support a close relationship between the Chacidae, the Plotosidae and the Clariidae, it is difficult to hypothesise, in view of the data available at the moment, which two families could be more closely related within these three catfish groups.

## GENERAL CONCLUSIONS

In conclusion, our observations and comparisons pointed out four additional, unique features characterising the chacid catfishes, namely: (1) absence of abductor superficialis; (2) ethmoid cartilage with long, thin, anterolateral projections situated ventrally to the anterolateral arms of mesethmoid; (3) interopercular with well-developed, deep concavity to articulate with posterior surface of preopercular; (4) dorsal process 2 of the cleithrum highly developed and markedly extended posteriorly. In addition, our observations and comparisons support a close relationship between the chacids, the plotosids and the clariids. As other studies recently published by the authors (e.g. *DIOGO et al.*, 2001b, 2002; *DIOGO & CHARDON*, 2000a, b; *DIOGO & VANDEWALLE*, 2003), 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, could reveal useful data to infer the phylogenetic position and/or autapomorphies of certain catfish taxa.

## ACKNOWLEDGEMENTS

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

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