Osteology and myology of the cephalic region and pectoral girdle of *Schilbe mystus* and comparison with other schilbids, with comments on the monophyly and phylogenetic relationships of the Schilbidae (Teleostei: Siluriformes)

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Abstract—The cephalic and pectoral girdle structures of *Schilbe mystus* are described and compared with those of other schilbids, as well as several other non-schilbid catfishes, as the foundation for a discussion on the monophyly and the phylogenetic relationships of the Schilbidae. Our observations and comparisons suggest that the family Schilbidae is a monophyletic group, defined, at least, by three autapomorphies, namely: 1) the adductor mandibulae A2 is lateral to the A1-Ost; 2) the posterior margin of the horizontal portion of Meckel's cartilage is situated further beyond the coronoid process; 3) the adductor mandibulae Aω is visible in a lateral view of the cephalic region. With respect to the phylogenetic relationships of the Schilbidae, our observations and comparisons support a close relationship between this family and the Pangasiidae.

Keywords: autapomorphies; catfish; comparative morphology; myology; osteology; phylogeny; Schilbidae; Siluriformes.

INTRODUCTION

The Siluriformes, or catfishes, with approximately 416 genera and over 2500 species, represent about 32% of all freshwater fishes. They are one of the world's economically important groups of fresh and brackish water fishes, and numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade (Teugels, 1996). Among the 33 extant siluriform families (Ferraris and de Pinna, 1999), the Schilbidae, an Afro-Asian family

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with five African (*Schilbe*, *Parailia*, *Siluranodon*, *Irvinea*, *Pareutropius*) and eight Asian (*Ailia*, *Ailiichthys*, *Clupisoma*, *Eutropiichthys*, *Laides*, *Platytropius*, *Proeutropiichthys*, *Pseudeutropius*) genera, is surely one of the least studied from a phylogenetic point of view. In fact, as noted by Diogo (in press-a) in a recent overview concerning the phylogeny of the Siluriformes, to date there is not a single cladistic study published which deals with the phylogenetic relationships, or even the monophyly, of the Schilbidae. Several authors (Howes, 1985; Mo, 1991; Teugels, 1996) have questioned if this family is, indeed, a monophyletic assemblage. Moreover, despite some detailed descriptions concerning schilbid morphology (e.g., Tilak, 1961, 1964; Rastogi, 1963, 1964; Chardon, 1968; de Vos, 1995), some aspects of the anatomy of these fishes, such as the configuration of their cranial muscles and of the structures associated with their mandibular barbels, are little known, and others, e.g., the configuration of the pectoral girdle musculature, are all practically unknown (Diogo and Vandewalle, in press).

The aim of this work is, therefore, to study in detail the osteological and myological structures of the cephalic region and pectoral girdle of *Schilbe mystus*, and to compare these structures with those of other schilbids, providing a detailed account on some little known aspects of schilbid anatomy such as the configuration of musculature or of the structures associated with their mandibular barbels. In addition, the present study provides some comments on the phylogenetic status and relationships of the Schilbidae. It is also hoped that this study could increase knowledge of the anatomy and phylogeny of the siluriforms in general, as well as pave the way for future works on the comparative anatomy, evolution, functional morphology, paleontology, 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 de Paris (MNHN), from the National Museum of Natural History of Washington (USNM), from the American Museum of Natural History of New York (AMNH), from the South African Institute for Aquatic Biodiversity (SAIAB) and from the Albany Museum of Grahamstown (AMG). The specimens examined include representatives of all 33 catfish families. The five schilbid genera embrace and, at the same time represent, all the different schilbid divisions considered by both Regan (1911) (who first divided the family into three subfamilies: Schilbinae, Siluranodontinae, Ailiinae), Mo (1991) (*Schilbe* group, *Pseudeutropius* group, *Ailia* group) and de Pinna (1993) (*Laides*, *Ailia* group and *Schilbe* group). Thus the genus *Schilbe* is the representative of both the Schilbinae of Regan (1911) and the *Schilbe* groups of Mo (1991) and de Pinna (1993). *Siluranodon* represents the subfamily Siluranodontinae of Regan (1911). *Ailia* represents both the Ailiinae of Regan (1911) and the *Ailia* groups

of Mo (1991) and de Pinna (1993). *Pseudeutropius* represents the *Pseudeutropius* group of Mo (1991). Lastly, *Laides* represents the *Laides* group of de Pinna (1993).

The 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 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). *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).

Anchariidae: *Ancharius fuscus* AMNH 93702, 1 (alc).

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

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

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

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

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

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

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

Cetopsidae: *Cetopsis coecutiens* USNM 265628, 2 (alc). *Helogenes marmuratus* USNM 264030, 1 (alc). *Hemicetopsis candiru* USNM 167854, 1 (alc).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

RESULTS

In this section, we will describe the cephalic and pectoral girdle structures of the schilbid *Schilbe mystus* (Linnaeus, 1758) and compare these structures with those of representatives of the four other schilbid groups mentioned above; respectively, *Siluranodon auritus* (Geoffroy Saint-Hilaire, 1809), *Ailia coila* (Hamilton, 1822), *Pseudeutropius brachypopterus* (Bleeker, 1858) and *Laides hexanema* (Bleeker, 1852). In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region follows basically that of Arratia (1997). However, for several 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 is based mainly on Winterbottom (1974) but, for reasons explained in Diogo and Chardon (2000a), the names for the different adductor mandibulae sections follow those of this last paper. 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.

Schilbe mystus

Osteology

Os mesethmoideum. It is situated on the antero-dorsal surface of the neurocranium (fig. 1). Each of its well-developed antero-lateral arms is ligamentously connected to the premaxillary.

Os lateroethmoideum. Well-developed, irregular bone (fig. 1), which exhibits a laterally directed articulatory facet for the autopalatine. There is a well-developed, roughly oval foramen between the postero-dorso-mesial surface of the lateral ethmoid and the antero-dorsal surface of the frontal.

Os praeovomerale. T-shaped bony plate (fig. 2) lying underneath the ethmoideal region and presenting two well-developed, posterolaterally directed antero-lateral arms. Each of these antero-lateral arms bears, ventrally, a well-developed tooth-plate.

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

Os pterosphenoideum. Posterior to the orbitosphenoid, covering, together with this bone, the gap between the frontals and the parasphenoid.
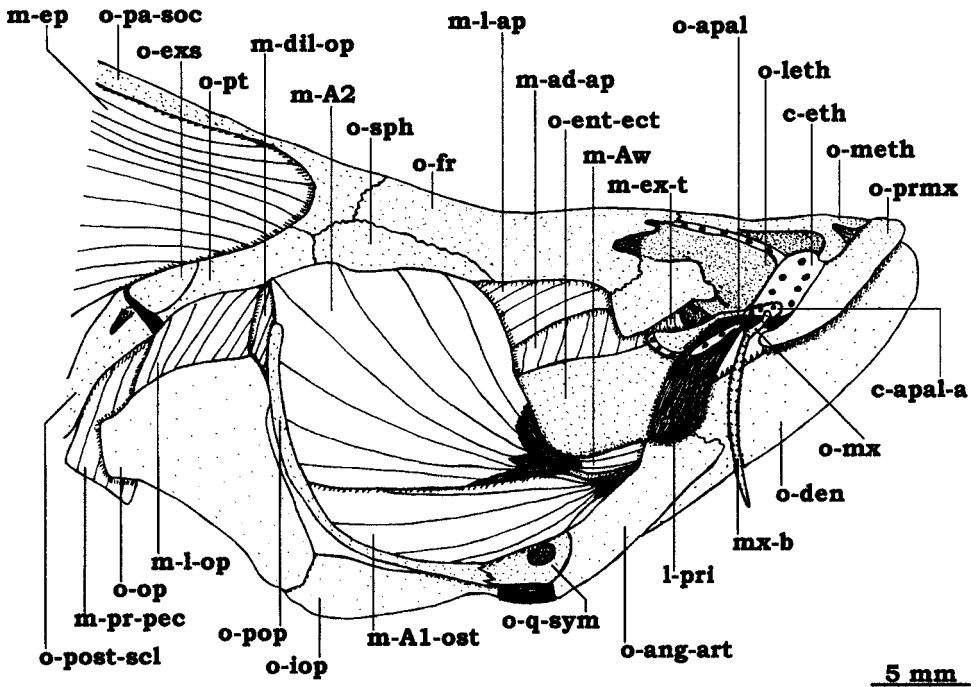
Figure 1. Right lateral view of the cephalic musculature of *Schilbe mystus.* All the muscles are exposed. *c-apal-a* cartilago autopalatinus anterior, *c-eth* cartilago ethmoideus, *l-pri* ligamentum primordium, *m-A1-ost*, *m-A2*, *m-Aω* sections of the musculus adductor mandibulae, *m-ad-ap* musculus adductor arcus palatini, *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, *m-pr-pec* musculus protractor pectoralis, *mx-b* maxillary barbel, *o-ang-art* os angulo-articulare, *o-apal* os autopalatinum, *o-den* os dentale, *o-ent-ect* os ento-ectopterygoideum, *o-exs* os extrascapulare, *o-fr* os frontale, *o-iop* os interoperculare, *o-leth* os latero-ethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-op* os operculare, *o-pa-soc* os parieto-supraoccipitale, *o-pop* os praeoperculare, *o-post-scl* os posttemporo-supracleithrum, *o-prmx* os praemaxillare, *o-pt* os pteroticum, *o-q-sym* os quadrato-symplecticum, *o-sph* os sphenoticum.

Os parasphenoideum. The parasphenoid (fig. 2) is the longest bone of the cranium. It bears a pair of salient ascending flanges, which suture with the pterosphenoids and prootics.

Os frontale. The frontals (fig. 1) are large, roughly rectangular bones that are largely separated by both the anterior and the posterior fontanels.

Os sphenoticum. This bone (fig. 1) bears, together with the pterotic, an well-developed, elongated articulatory facet for the hyomandibulo-metapterygoid.

Os pteroticum. In dorsal view it is somewhat triangular. Its size is somewhat similar to that of the sphenotic.

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

Os epioccipitale. A small bone situated on the postero-dorsal surface of the neurocranium.

Os exoccipitale. A small bone situated laterally to the basioccipital and ventrally to the epioccipitale.

Os basioccipitale. A well-developed, unpaired bone, which forms the posterior-most part of the floor of the neurocranium. Its ventro-lateral surfaces are firmly connected, by strong ligamentous tissue, to the ventro-medial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. The parieto-supraoccipital (fig. 1) is a large, un-paired bone with a well-developed, posteriorly directed postero-dorsal process.

Os extrascapulare. A small, roughly oval bone (fig. 1) situated on the postero-dorso-lateral surface of the neurocranium, between the pterotic an the posttemporo-supracleithrum.

Os angulo-articulare. This bone (figs 1, 3), together with the dentary, coro-nomeckelian and Meckel's cartilage constitute the mandible (fig. 3). Its antero-dorsal surface, together with the postero-dorsal surface of the dentary, form a small dorsal process (processus coronoideus), which is linked to the maxillary by means of a massive, long ligament (fig. 1: l-pri) that bears a small, narrow cartilage. Postero-dorsally, the angulo-articular has an articulatory surface for the quadrato-symplectic. Postero-ventrally, it presents a well-developed, posteriorly di-rected postero-medial process that is ligamentously connected to the interopercular (fig. 1).

Os dentale. The dentaries (Figs 1, 3) are large bones firmly connected antero-mesially by strong connective tissue. Dorsally, they bear numerous small, roughly conical teeth (fig. 1).

Os coronomeckelium. This is a small bone lodged in the medial surface of the mandible (fig. 3). Postero-dorsally it bears a crest for attachment of the adductor mandibulae A3′-d.

Os praemaxillare. The premaxillaries (figs 1, 2) are a pair of large rectangular plates lying underneath and attaching to the mesethmoidal cornua via ligamentous tissue. Ventrally, each premaxillary bears numerous small teeth (fig. 2) with their tips slightly turned backward.

Os maxillare. The maxillaries (fig. 1) are small, narrow bones connected to the premaxillary by means of a short but strong ligament. As in most catfishes, the maxillary barbels are supported by the maxillaries (fig. 1).

Os autopalatinum. A rod-like bone (figs 1, 2) with the anterior end tipped by a cartilage with two antero-lateral concavities which accept the two proximal heads of the maxillary, and the posterior tip capped by a small cartilage. Medially, the autopalatine articulates with the lateral ethmoid. Anteriorly the autopalatine presents a small antero-ventro-lateral projection.

Os hyomandibulo-metapterygoideum. The homology and, thus, the correct de-nomination of this bone, as well as of the other suspensorium elements of the cat-fishes, has been the subject of endless controversies (McMurrich, 1884; Gosline,
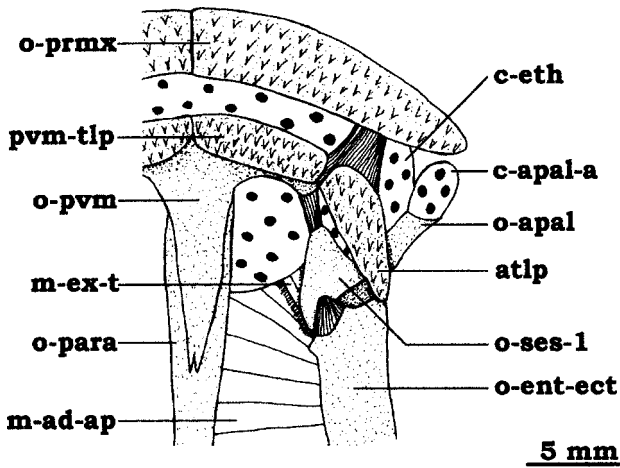
Figure 2. Ventral view of the anterior region of the neurocranium of *Schilbe mystus*. The suspensorium and the autopalatine as well as the muscles and ligaments associated with these structures are also illustrated. *atlp* additional tooth-plate, *c-apal-a* cartilago autopalatinus anterior, *c-eth* cartilago ethmoideus, *m-ad-ap* musculus adductor arcus palatini, *m-ex-t* musculus extensor tentaculi, *o-apal* os autopalatinum, *o-ent-ect* os ento-ectopterygoideum, *o-para* os parasphenoideum, *o-prmx* os praemaxillare, *o-pvm* os praeovomerale, *o-ses-1* os sesamoideum 1, *pvm-tlp* prevomeral tooth-plate.
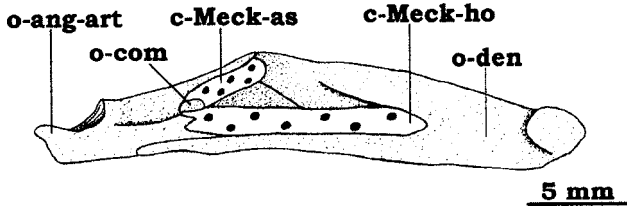

Figure 3. Medial view of the left lower jaw of *Schilbe mystus*. *c-Meck-as*, *c-Meck-ho*, ascending and horizontal portions of cartilago Meckeli, *o-ang-art* os angulo-articulare, *o-com* os coronomeckelium, *o-den* os dentale.

1975; Howes, 1983a, b; 1985; Arratia, 1992; Diogo et al., 2000, 2001a; Diogo and Chardon, 2000c; in press; etc.). As mentioned before, 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 will follow that presented by Diogo et al. (2001a). The hyomandibulo-metapterygoid is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercular.

Os sesamoideum 1. A well-developed, roughly triangular bone attached, by means of two thick ligaments, to the ento-ectopterygoid posteriorly and to the prevomer anteriorly, respectively (fig. 2). Its antero-dorso-lateral surface is weakly attached, via connective tissue, to the to the postero-ventral surface of the autopalatinum. The sesamoid bones 2 and 3 (see Diogo et al., 2001a) are absent, but there is a well-developed tooth-plate (fig. 2) situated ventrally to, and firmly embedded in, a strong

ligament connecting the antero-lateral surface of the ento-ectopterygoid, the antero-lateral surface of the prevomer and the postero-ventral margin of the premaxillary.

Os entopterygoide-ectopterygoideum. Well-developed (figs 1, 2), roughly rectangular bone situated anteriorly to the hyomandibulo-metapterygoid and antero-dorsally to the quadrato-symplectic. Its anterior surface is slightly bifurcated.

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

Os praeoperculare. A long and thin bone (fig. 1) firmly sutured to the hyomandibulo-metapterygoid and to the quadrato-symplectic.

Os operculare. A triangular bone (fig. 1) antero-dorsally articulated with the hyomandibulo-metapterygoid and antero-ventrally articulated with the interopercular.

Os interoperculare. Its anterior and antero-medial surfaces are linked, by means of thick ligamentous tissue, to the angulo-articular (fig. 1) and to the posterior ceratohyal, respectively.

Os interhyale. A small bone attached, by means of ligaments, to both the posterior ceratohyal and the hyomandibulo-metapterygoid.

Os ceratohyale posterior. A triangular bone linked by ligaments to the angulo-articular, interhyal and interopercular.

Os ceratohyale anterior. Situated between the hypohyal ventral and the posterior ceratohyal, it supports, together with this latter bone, the branchiostegal rays.

Os hypohyale ventrale. Each ventral hypohyal contains a ventral concavity to receive one of the antero-lateral edges of the parurohyal.

Os hypohyale dorsale. A small bone situated dorsally to the ventral hypohyal.

Os parurohyale. A well-developed bone with two small postero-lateral arms and a large postero-mesial process. It lies medially behind the ventro-medial surfaces of the ventral hypohyals and is connected to these latter bones by means of two strong, thick ligaments.

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 (fig. 1). Its stout ventro-medial limb is connective, by a short but strong ligament, to the basioccipital. Its ventro-lateral limb is deeply forked, forming an articulating groove for the upper edge of the cleithrum.

Os cleithrum. The cleithrum (fig. 4) is a large, well-ossified stout structure forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially faced groove, with rough surfaces, which accommodates the thick crescentic dorsal condyle of the pectoral spine. The two cleithra are firmly attached in the antero-medial line via connective tissue. The humeral process is well-developed.

Os scapulo-coracoideum. An elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge (fig. 1). Antero-laterally, it presents a large
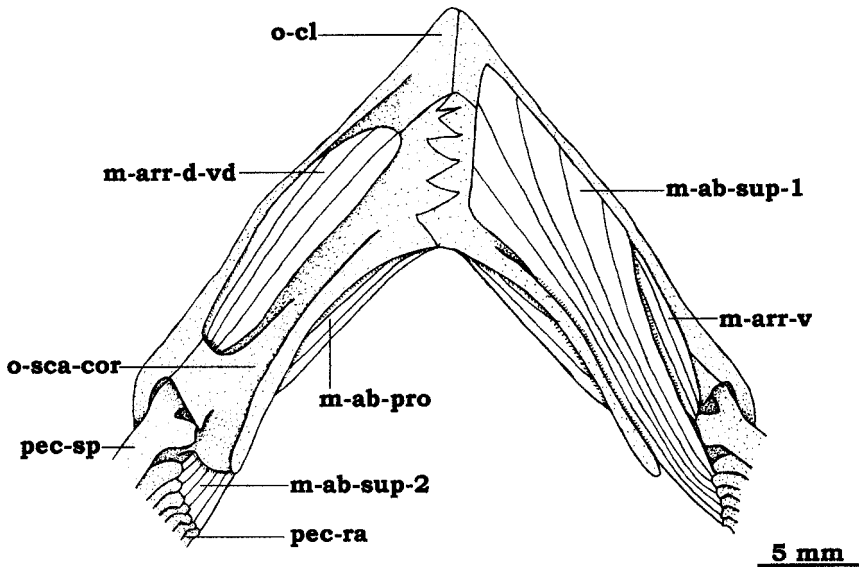
Figure 4. Ventral view of the pectoral girdle of *Schilbe mystus*. On the left side all the musculature is exposed on the right side both the abductor superficialis 1 and the arrector ventralis were removed. *m-ab-pro* musculus abductor profundus, *m-ab-sup-1, m-ab-sup-2,* sections of musculus abductor superficialis, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector ventralis, *o-cl* os cleithrum, *o-sca-cor* os scapulo-coracoide, *pec-ra* pectoral rays, *pec-sp* pectoral spine.

anteriorly directed process, usually called the coracoid bridge, 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). Its posterior surface is pierced by a well-developed foramen, which accepts the anterior condyle of the pectoral spine when this latter is abducted. There is a well-developed mesocoracoid arch.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost originates on the preopercular, quadrato-symplectic and hyomandibulo-metapterygoid and inserts on the latero-dorsal surface of the angulo-articular (fig. 1). The A2, which lies dorso-laterally to the A1-ost, attaches posteriorly on the lateral surface of both the preopercular, hyomandibulo-metapterygoid, pterotic and sphenotic (fig. 1). Anteriorly, it presents a well-developed tendon that is associated with the posterior part of the adductor mandibulae $A\omega$ (fig. 1), which is a well-developed bundle attaching anteriorly on the medial surface of both the dentary and the angulo-articular. The adductor mandibulae A3′ is divided in a dorsal and a ventral part. The dorsal one (A3′-d) originates on the hyomandibulo-metapterygoid and quadrato-

symplectic and inserts tendinously on the coronomeckelian bone, while the ventral one (A3$'$-v) originates on the quadrato-symplectic and inserts on the medial surface of the angulo-articular. Lastly, the deeper bundle of the adductor mandibulae, the A3$''$, attaches posteriorly on both the hyomandibulo-metapterygoid and the ento-ectopterygoid and anteriorly on the mesial surface of the angulo-articular.

Musculus levator arcus palatini. The levator arcus palatini (fig. 1) originates on the lateral ethmoid, orbitosphenoid, pleurosphenoid, frontal and sphenotic and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. Well-developed (figs 1, 2), extending from the lateral sides of the parasphenoid, pterosphenoid and orbitosphenoid to the medial sides of the hyomandibulo-metapterygoid and ento-ectopterygoid.

Musculus levator operculi. It originates on the ventro-lateral margin of the pterotic, as well as on the postero-dorso-lateral surface of the hyomandibulo-metapterygoid, and inserts on the dorsal edge of the opercular (fig. 1).

Musculus adductor hyomandibularis. Small muscle situated mesially to the levator operculi and laterally to the adductor operculi. It originates on the ventral surface of the pterotic and inserts on the postero-dorso-medial surface of the hyomandibulo-metapterygoid.

Musculus adductor operculi. Well-developed muscle running from the ventral surface of the pterotic to the dorsomesial surface of the opercular.

Musculus dilatator operculi. Situates medially to the levator arcus palatini (fig. 2), it runs from the pterotic, sphenotic and frontal to the antero-dorsal edge of the opercular (medial to the preopercular but lateral to the articulatory facet of the opercular for the hyomandibulo-metapterygoid).

Musculus extensor tentaculi. Small muscle (figs 1, 2) originating on the lateral ethmoid and inserting on both the ventral surface of the sesamoid bone 1 of the suspensorium (fig. 2: o-ses-1) and the postero-medial margin of the autopalatine.

Musculus protractor hyoidei. This muscle has three parts (fig. 5). The pars lateralis (fig. 5: m-pr-h-l) originates on both the anterior and the posterior ceratohyal and inserts on the ventro-medial face of the dentary. The pars ventralis (fig. 5: m-pr-h-v), in which are lodged the cartilages associated with the mandibular barbels, originates on the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis. Lastly, the pars dorsalis (fig. 5: m-pr-h-d) runs from the anterior ceratohyal to the anterio-mesial surface of the dentary.

Muscle intermandibularis. Well-developed muscle joining the two mandibles (fig. 5).

Musculus protractor externi mandibularis tentaculi. Well-developed, elongated muscle (fig. 5) running from the anterior ceratohyal to the moving part of the cartilage associated with the external mandibular barbel.

Musculus retractor externi mandibularis tentaculi. This small muscle (fig. 5) runs from the moving part of the cartilage associated with the outer mandibular barbel to the dentary.
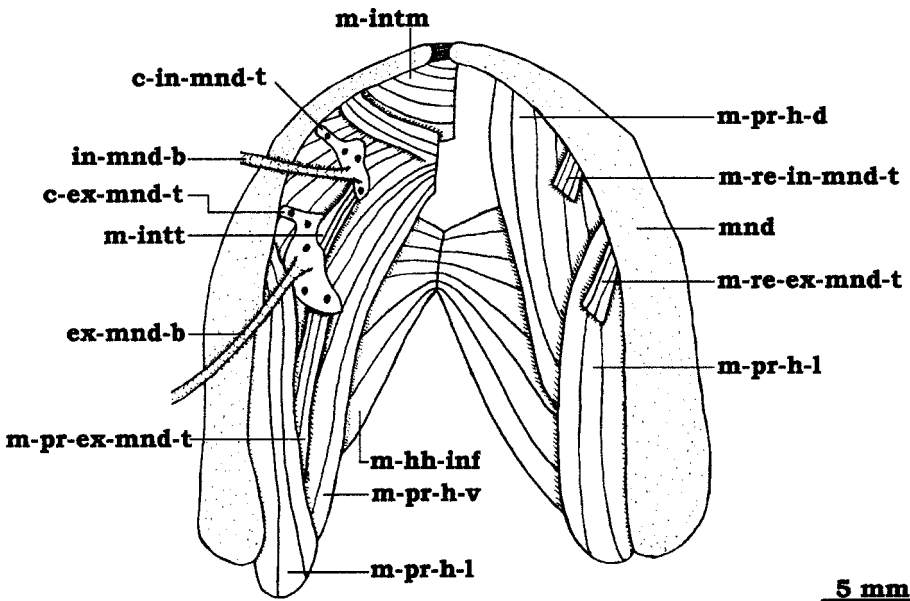
Figure 5. Ventral view of the cephalic musculature of *Schilbe mystus.* On the left side all the muscu-
lature is exposed on the right side the intermandibularis the protractor hyoideus ventral the interten-
tacularis and the protractor externi mandibularis tentaculi as well as the mandibular barbels and their
respective cartilages were removed. *c-ex-mnd-t* cartilago externus mandibularis tentaculi, *c-in-mnd-t*
cartilago internus mandibularis tentaculi, *ex-mnd-b, in-mnd-b* external and internal mandibular bar-
bels, *m-hh-inf* musculus hyohyoideus inferior, *m-intm* musculus intermandibularis, *m-intt* musculus
intertentacularis, *mnd* mandible, *m-pr-ex-mnd-t* musculus protractor externi mandibularis tentaculi,
m-pr-h-d, m-pr-h-l, m-pr-h-v pars dorsalis lateralis and ventralis of musculus protactor hyoideus, *m-re-
ex-mnd-t* musculus retractor externi mandibularis tentaculi, *m-re-in-mnd-t* musculus retractor interni
mandibularis tentaculi.

Musculus retractor interni mandibularis tentaculi. Small muscle (fig. 5) origi-
nating on the moving part of the cartilage associated with the internal mandibular
barbel and inserting on the dentary.

Musculus intertentacularis. Small muscle (fig. 5) connecting the moving parts of
the cartilages associated with the mandibular barbels of the same side of the fish.

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 bran-
chiostegal rays of the respective side.

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

Musculus sternohyoideus. It originates on the anterior region of the cleithrum and
inserts on the posterior region of the parurohyal.

Musculus arrector ventralis. It runs from the ventral surface of the cleithrum to the ventral condyle of the pectoral spine (fig. 4).

Musculus arrector dorsalis. It is differentiated into two well-developed divisions. The ventral division, situated on the ventral surface of the pectoral girdle (fig. 4: m-arr-d-vd), originates on the ventral margin of both the cleithrum and the scapulo-coracoid 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 adductor superficialis. It is differentiated into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid, as well as on the dorso-lateral edge of the mesocoracoid arch and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from the ventro-lateral edge of the mesocoracoid arch and the dorsal surface of the proximal radials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus abductor superficialis. This muscle is also differentiated in two sections. The larger section (fig. 4: m-ab-sup-1) runs from the ventral face 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 (fig. 4: m-ab-sup-2) runs from the postero-lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus abductor profundus. It originates on the postero-medial edge of the coracoid (fig. 4), passes anteriorly to the mesocoracoid arch and to the adductor superficialis muscle and inserts on the medial surface of the dorsal condyle of the pectoral spine.

Musculus protractor pectoralis. This well-developed muscle (fig. 1) originates on the ventral surfaces of the pterotic, posttemporo-supracleithrum and exoccipital and inserts on the antero-dorsal surface of the cleithrum.

Siluranodon auritus

Osteology

In a general way, the configuration of the osteological structures of the pectoral girdle and cephalic region of this species resembles that of Sc*hilbe mystus*, with the most significant differences between these species concerning these structures being: 1) the ventral hypohyal presents a prominent, postero-lateral process; 2) the coracoid bridge is missing; 3) the pectoral spine is a narrow structure that is somewhat similar to a pectoral ray, without any distinguishable anterior condyle; 4) both the mandible and the premaxillary are edentated; 5) the quadrato-symplectic does not present an antero-ventral foramen; 6) the additional tooth-plate of the suspensorium is missing; 7) the autopalatine is truncated anteriorly, i.e., there is no antero-ventro-lateral process of this bone.

Myology

The configuration of the cephalic and pectoral girdle muscles of *S. auritus* resembles that of *S. mystus*, with the principal differences between the species concerning these muscles being: 1) the abductor superficialis of *S. auritus* is still more developed than that of *S. mystus*; 2) not only the dorsal, but also the ventral division of the arrector dorsalis, are situated on the dorsal surface of the pectoral girdle; 3) there is a muscle retractor tentaculi, running from the ento-ectopterygoid to the maxilla; 4) the extensor tentaculi does not contact both the sesamoid bone 1 of the suspensorium and the autopalatine, but only this latter bone.

Ailia Coila

Osteology

The principal differences between the configuration of the osteological structures of the cephalic region and pectoral girdle of *A. Coila* and those of *S. mystus* are: 1) the postero-mesial process of the parurohyal, the humeral process of the cleithrum and the coracoid bridge are missing; 2) the pectoral spine is a narrow structure that is somewhat similar to a pectoral ray, without any distinguishable anterior condyle; 3) the dorso-medial limb of the posttemporo-supracleithrum is firmly ankylosed to the neurocranium, and the extrascapular is missing; 4) the ventro-medial limbs of the posttemporo-supracleithrum are undifferentiated; 5) the autopalatine is truncated anteriorly; 6) the quadrato-symplectic does not present an antero-ventral foramen; 7) the additional tooth-plate of the suspensorium is missing; 8) the posterior process of the parieto-supraoccipital of *A. Coila* is significantly smaller than that of *S. mystus*.

Myology

The most significant differences between the configuration of the cephalic and pectoral girdle muscles of *A. coila* and those of *S. mystus* are: 1) both the ventral and the dorsal divisions of the arrector dorsalis are situated on the dorsal surface of the pectoral girdle; 2) the extensor tentaculi only inserts on the autopalatine, and not on both this bone and the sesamoid bone 1 of the suspensorium; 3) there is a muscle retractor tentaculi, connecting the ento-ectopterygoid to the maxilla.

Pseudeutropius brachypopterus

Osteology

The principal differences between the configuration of the osteological structures of the cephalic region and pectoral girdle of *P. brachypopterus* and those of *S. mystus* are: 1) the ventral hypohyal presents a prominent, postero-lateral process; 2) there is a well-developed, triangular process on the dorsal condyle of the pectoral spine; 3) the quadrato-symplectic does not present an antero-ventral foramen; 4)

the autopalatine presents a well-developed, dorsally pointed, triangular process anterodorsally to its articulatory surface for the neurocranium; 5) the additional tooth-plate of the suspensorium is missing.

Myology

The only significant difference between the cephalic and pectoral girdle muscles of *P. brachypopterus* and those of *S. mystus* is: 1) contrary to *S. mystus*, in *P. brachypopterus* the extensor tentaculi is differentiated into different bundles, namely into two bundles that attach, respectively, on the posterior and posteromesial surface of the autopalatine.

Laides hexanema

Osteology

The most significant differences between the configuration of the osteological structures of the cephalic region and pectoral girdle of *L. hexanema* and those of *S. mystus* are: 1) the coracoid bridge is missing; 2) the quadrato-symplectic does not present an antero-ventral foramen; 3) there is a well-developed fossa on the dorso-lateral surface of the neurocranium, between the pterotic, the extrascapular and the supraoccipital; 4) the autopalatine is truncated anteriorly; 5) the interopercular presents a broad, posteroventral laminar projection, which is of about the same size as the main body of this bone; 6) the additional tooth-plate of the suspensorium is missing.

Myology

The principal differences, concerning the configuration of the cephalic and pectoral girdle musculature, between *L. hexanema* and *S. mystus* are: 1) the abductor superficialis is hypertrophied; 2) there is a muscle retractor tentaculi running from the ento-ectopterygoid to the maxilla; 3) the arrector dorsalis originates only on the dorsal surface of the pectoral girdle and not on both the dorsal and ventral surfaces of this structure; 4) the extensor tentaculi does not contact both the sesamoid bone 1 of the suspensorium and the autopalatine, but only this latter bone.

DISCUSSION

As mentioned in the Introduction, although the 'Schilbidae' is commonly cited as a valid siluriform family, most authors agree that this family is a non-monophyletic assemblage. Mo (1991), for example, considered the Schilbidae to be a non-monophyletic assemblage, with a 'Schilbe group' representing the real schilbids, one phylogenetically distinct '*Ailia* group' being closer to the Clariidae and Heteropneustidae and one third, also phylogenetically distinct '*Pseudeutropius* group' being closer to the Bagridae or Pangasiidae.

However, Mo's (1991) view was contested 2 years later, in an unpublished thesis by de Pinna (1993). Although, unfortunately, de Pinna's (1993) results were not published, it is worth mentioning that this author included three different groups of schilbids in his analysis of the higher-level phylogeny of the Siluriformes, namely the '*Laides*', '*remaining Schilbinae*' and '*Ailiinae*' groups. He proposed that the schilbids constitute, in fact, a monophyletic group, which could be diagnosed by a peculiar, unique feature: Meckel's cartilage extending posteriorly much further beyond the limit of dentary-anguloarticular in the coronoid process (de Pinna, 1993: 151).

Since de Pinna's results were not published, Teugels (1996), in a well-structured overview of the taxonomy, phylogeny and biogeography of the catfishes, continued to state that there were no published autapomorphies to support the monophyly of the Schilbidae, and that, in fact, this family was probably a non-monophyletic assemblage.

The cladistic analysis undertaken by the authors, which includes about 450 characters and 90 terminal taxa representing all the extant catfish families, as well as the five schilbid groups examined in the present work (see above), and which is being published in the form of a book (Diogo, in press-b), corroborated de Pinna's results supporting schilbid monophyly. In fact, as explained above, these five groups of schilbids were precisely and carefully chosen to represent, at the same time, all the different schilbid divisions considered by Regan (1911), Mo (1991) and de Pinna (1993) (see Material and Methods), and hence to address the question of schilbid monophyly. Furthermore, according to the results of that analysis, these five schilbid groups appear, as suggested in de Pinna's (1993) study, to precisely form a monophyletic, well-defined Schilbidae, which is diagnosed by three autapomorphic features found in the representatives of all these five schilbid groups and in no other catfish examined. These three features are described below.

Adductor mandibulae A2 is lateral to the adductor mandibulae A1-ost. Plesiomorphically in catfishes the A1-ost is the most superficial section of the adductor mandibulae complex. However, in all the schilbids studied, and exclusively in these catfishes, the A2 is the most superficial adductor mandibulae section, being lateral to the A1-ost (fig. 1).

Posterior margin of the horizontal portion of Meckel's cartilage is markedly posterior to the anguloarticular/dentary suture on the coronoid process. This character was first proposed in de Pinna's (1993) unpublished thesis (see above). In non-schilbid catfishes, the posterior limit of the horizontal portion of Meckel's cartilage situates approximately at the level of the suture between the angulo-articular and the dentary on the coronoid process. However, in all the schilbid examined, the horizontal portion of Meckel's cartilage extends further posteriorly, with its posterior margin being markedly posterior to the anguloarticular/dentary suture of the coronoid process (fig. 3).

Adductor mandibulae Aω is clearly visible in a lateral view of the cephalic region. Plesiomorphically in catfishes the adductor mandibulae $A\omega$ is completely covered

laterally by the remaining adductor mandibulae sections (Diogo and Vandewalle, in press). However, in all the schilbids analysed, and exclusively in these catfishes, the configuration of the adductor mandibulae is such that the *Aω* is clearly visible in a lateral view of the cephalic musculature, without needing to remove any of the other sections of the adductor mandibulae or any other muscle (fig. 1).

It is stressed here that, as noted by de Pinna (1998) and Diogo (in press-ab), the presence of unique, distinct, non-homoplastic characters in such a vast, diverse and complex group as the order Siluriformes is particularly rare and, thus, clearly constitutes a very strong argument to support the monophyly of that group. Therefore, as pointed out by Diogo (in press-b), the presence, not of one, but of three of these type of characters in the Schilbidae, constitutes a very strong argument in favour of the monophyletic status of this family.

With respect to the phylogenetic relationships of the Schilbidae, this is also a somewhat controversial subject. In fact, although a large number of authors consider that the Pangasiidae are the sister-group of the Schilbidae (Teugels, 1996; de Pinna, 1998), many others have a different opinion. The Bagridae (Regan, 1911; Rastogi, 1963, 1964; Chardon, 1968), Siluridae (Rastogi, 1963, 1964; Howes, 1985) or even the Plotosidae (Mo, 1991), for example, have already been proposed as potential sister-groups of the Schilbidae.

In this regard, the cladistic analysis undertaken by the authors including a large number of specimens representing all the extant catfish families (see above) strongly corroborated the sister-group relationship between the Schilbidae and the Pangasiidae. Two peculiar, synapomorphic features support this sister-group relationship:

Anterior margin of the cartilages associated with the mandibular barbels somewhat bifurcated, presenting two anterolateral arms. Usually in catfishes the cartilages associated with the mandibular barbels, when present, are not bifurcated anteriorly or do not present antero-lateral arms. However, in the schilbid and pangasiid catfishes examined, these cartilages are somewhat bifurcated anteriorly, presenting two more or less distinguished antero-lateral arms (fig. 5: c-in-mnd-t). Among all the siluriforms studied by us or described in the literature, this feature is only found in these two groups of catfishes.

Presence of a true foramen between the dorsal surfaces of the frontal and the lateral ethmoid. In some catfishes, such as the silurids, cranoglanidids, ictalurids and doradids examined, as well as in part of the mochokids (*Synodontis*) and auchenipterids (*Ageneiosus*) analysed, there is a groove, or a fossa, between the dorsal surfaces of the frontal and the lateral ethmoid. However, a complete perforation of the dorsal surface of the neurocranium by a true foramen between the frontal and the lateral ethmoid is a feature only found in the pangasiid, schilbid and ariid catfishes examined. As the Ariidae are very likely phylogenetically closer to other catfish groups (namely the Claroteinae, Auchenoglanidinae and the Cranoglanididae: Diogo et al., 2002; Oliveira et al., 2002a; Diogo, in press-b) than to the Schilbidae and the Pangasiidae, this feature was probably acquired

independently in the Ariidae and hence probably constitutes a valid synapomorphy to support the sister-group relationship between the Schilbidae and the Pangasiidae.

GENERAL CONCLUSIONS

Three peculiar, distinct derived characters are exclusively found in the schilbids, thus supporting the monophyly of the family Schilbidae: 1) the adductor mandibulae A2 is the most superficial section of the adductor mandibulae complex; 2) the posterior margin of the horizontal portion of Meckel's cartilage extends posteriorly further beyond the anguloarticular/dentary suture on the coronoid process; 3) the adductor mandibulae $A\omega$ is visible in a lateral view of the cephalic region. According to our observations and phylogenetic comparisons, the schilbids are closely related to the pangasiid catfishes, with this close relationship supported by two peculiar, synapomorphic features, of which the first one is inclusively uniquely present in these two groups: 1) the anterior margin of the cartilages associated with the mandibular barbels is somewhat bifurcated, presenting two anterolateral arms; 2) there is a true foramen between the dorsal surfaces of the frontal and the lateral ethmoid. As other studies recently published by the authors (Diogo et al., 1999, 2000a, b, 2001c, 2002a, b; Diogo and Chardon, 2000c; Oliveira et al., 2001), the present work also indicates, therefore, that the analysis of certain characters that are not usually included in a study of catfish phylogeny, such as those concerning the configuration of the cephalic musculature or the structures associated with the mandibular barbels, could reveal useful data to infer the phylogeny of these fishes.

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