On the osteology and myology of the cephalic region and pectoral girdle of *Nematogenys inermis* (Ghichenot, 1848), with comments on the autapomorphies and phylogenetic relationships of the Nematogenyidae (Teleostei : Siluriformes)

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ABSTRACT. The cephalic and pectoral girdle structures of *Nematogenys inermis* are described and compared to those of other catfishes, as the foundation for a discussion on the autapomorphies and phylogenetic relationships of the Nematogenyidae. Our observations and comparisons indicate that nematogenyids are defined, at least, by two unique, autapomorphic characters, namely : 1) anterior margin of prevomer markedly extended anteriorly, at about the same level of anterior margin of mesethmoid; 2) anterior ceratohyal with prominent, posteriorly pointed, posterodorsal projection bordering a significant part of the dorsal margin of the posterior ceratohyal. With respect to the phylogenetic relationships of the Nematogenyidae, this study supports Mo's 1991 and de Pinna's 1992 phylogenetic hypotheses according to which the nematogenyids and the trichomycterids are sister-groups.

KEY WORDS : catfish, cephalic region, Loricarioidea, morphology, myology, Nematogenyidae, osteology, pectoral girdle, phylogeny, Siluriformes.

INTRODUCTION

The Siluriformes are one of the most 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 & DE PINNA, 1999), the Nematogenyidae, a small family of Chilean catfishes including a single species, *Nematogenys inermis* (Ghichenot, 1848), is surely one of the less studied, with "little being known about the anatomy" of these fishes (DE PINNA, 1998 : 295). 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., 1984; ARRATIA, 1990; MO, 1991; DIOGO & CHARDON, 2000ab; DIOGO et al., 2000, 2001ab; etc.), the only papers describing the morphology of nematogenyids with some detail are those of ARRATIA & CHANG (1975), ARRATIA (1990), ARRATIA & HUAQUIN (1995) and AZPELICUETA & RUBILAR (1998). Moreover, as these descriptions are almost exclusively restricted to the osteology and external anatomy of the nematogenyids, important aspects of the morphology of these fishes are poorly known, such as the configuration of their pectoral girdle, the structures associated with their mandibular barbels, or the muscles and ligaments of their cephalic region and their pectoral girdle. The lack of studies concerning the morphology of the nematogenyids probably explains why, although these fishes are com-monly grouped in a separate family, Nematogenyidae, not even one single unique, autapomorphic character has been suggested so far to define this family (see DIOGO, 2003).

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 *Nematogenys inermis*, and to compare these structures with those of members of all other siluriform families as the foundation for a discussion on the autapomorphies and phylogenetic relationships of the Nematogenyidae. It is also hoped that this study could increase the knowledge of the anatomy and phylogeny of the 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

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National d'Histoire Naturelle of Paris (MNHN), from the National Museum of Natural History of Washington (USNM), and from the South African Institute for Aquatic Biodiversity (SAIAB) and the Albany Museum of Grahamstown (AMG). Anatomical descriptions are made after dissection of alcohol-

fixed or trypsin-cleared and alizarine-stained (following TAYLOR & VAN DYKE's 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The alcohol fixed (alc), trypsin-cleared and alizarine-stained (c&s), or simply alizarine-stained (s) condition of the studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Pimelodidae : *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 the anatomical descriptions of *N. inermis* 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 & CHARDON, 2003), with respect to the skeletal components of the suspensorium we follow DIOGO et al. (2001a). The myological nomenclature is based mainly on WINTERBOTTOM (1974), but for the different adductor mandibulae sections, DIOGO & CHARDON (2000a) is followed. In relation to the muscles associated with the mandibular barbels, which were not studied by WINTERBOTTOM (1974), DIOGO & CHARDON (2000b) is followed. Concerning the nomenclature of the pectoral girdle bones and muscles, DIOGO et al. (2001b) is followed.

Osteology

Os mesethmoideum. Unpaired bone situated on the antero-dorsal surface of the neurocranium (Figs 1, 2). Its anterior tip is forked with two slender branches. The antero-ventro-lateral margins of the bone are ligamentously connected to the premaxillae. The mesethmoid does not reach the anterior border of the anterior fontanel, which is exclusively surrounded by the frontals.

Os lateroethmoideum. The lateral-ethmoid (Fig. 1) presents a laterally directed articulatory facet for the autopalatine at its anterolateral margin. The anterolateral arms of the lateral-ethmoid extend laterally well beyond the lateral margins of the frontals (Fig. 2).

Os praevomerale. Large, unpaired T-shaped bone without a ventral tooth plate. Its anterior margin extends anteriorly, almost reaching the anterior margin of the mesethmoid (Fig. 2).

Os parasphenoideum. The unpaired parasphenoid is the longest bone of the cranium (Fig. 2), bearing a pair of ascending flanges that suture with the pterosphenoids and prootics.

Os orbitosphenoideum. Posterior to the lateral ethmoid (Figs 1, 2), with the dorsal edge of its lateral wall being sutured with the ventral surface of the frontal.

Os pterosphenoideum. Posterior to the orbitosphenoid (Fig. 2), covering, together with this bone, the gap between the frontals and the parasphenoid. Together with the prootic and the orbitosphenoid, the pterosphenoid borders the large foramen of the trigemino-facial nerve complex, with a part of the bone being situated dorsally to this

foramen and the other part being situated ventrally to it (Fig. 2).

Os frontale. The frontals (Figs 1, 2) are large rectangular bones that constitute a great part of the cranial roof. Posteriorly, they have a lateral extension, which sutures with the sphenotics. The frontals are largely separated by two median fontanels. The anterior median fontanel is exclusively surrounded by the frontals, while the posterior one is surrounded by both these bones and the parieto-supraoccipital.

Os sphenoticum. Smaller than the pterotic, constituting, together with this bone, an articulatory facet for the hyo-mandibulo-metapterygoid (Fig. 2). The sphenotic presents a prominent anterodorsolateral projection (Figs 1, 2) for the origin of the levator arcus palatini (Fig. 1).

Os peroticum. Large bone (Figs 1, 2) contacting the sphenotic anteriorly, the parieto-supraoccipital laterally, and the posttemporo-supracleithrum posteriorly. In a ventral view of the neurocranium, it contacts the sphenotic and the prootic anteriorly, the exoccipital mesially, and the posttemporo-supracleithrum posteriorly (Fig. 2).

Os prooticum. Together with the pterosphenoid and the orbitosphenoid, it borders the large foramen of the trigemino-facial nerve complex (Fig. 2).

Os epioccipitale. The epioccipitals are small bones situated on the posterodorsal surface of the cranial roof. They are in contact with the parieto-supraoccipital, the posttemporo-supracleithra, the pterotics and the exoccipitals.

Os exoccipitale. The large exoccipitals are situated laterally to the basioccipital (Fig. 2). There is a very small foramen on the posteroventral margin of each exoccipital.

Os *basioccipitale*. Unpaired bone, forming the posteriormost part of the floor of the neurocranium (Fig. 2). It presents two long, thin, posteroventrolateral projections that are ligamentously connected to the thin ventromedial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. Large, unpaired bone constituting the postero-dorso-median surface of the cranial roof (Fig. 1). It presents a thin, somewhat triangular posterior process. As stated anteriorly, together with the frontals the parieto-supraoccipital borders the posterior median fontanel of the skull.

Os angulo-articulare. This bone (Figs 1, 3, 4), together with the dentary bone, the coronomeckelian bone, and the Meckel's cartilage, constitute the mandible. Postero-dorsally, the angulo-articular has an articulatory facet for the quadrato-symplectic. Postero-ventrally, it is ligamentously connected to both the interopercle and the posterior ceratohyal (Fig. 5).

Os dentale. The toothed dentary bone (Fig. 1) forms a great part of the lateral surface of the mandible. The postero-dorsal margin of this bone forms, together with the antero-dorsal margin of the angulo-articular, a broad dorsal process (processus coronoideus) (Figs 3, 4), the dorsal tip of which is curved medially and projects mesially somewhat beyond the main body of the mandible (Fig. 4).

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

Os praemaxillare. The large premaxillae (Fig. 1) bear ventrally a tooth-plate with numerous large teeth having their tips slightly turned backward.

Os maxillare. The maxillary bone is connected to the coronoid process of the mandible by a strong, massive ligament (primordial ligament) (Fig. 1). As in most catfishes, the maxillary barbels are supported by the maxillary bones.

Os autopalatinum. The autopalatine (Figs 1, 2) is a large, somewhat flat bone with its posterior end capped by a small cartilage and its anterior end tipped by a large cartilage with two antero-lateral concavities that accept the two proximal heads of the maxilla. Dorsomedially, the autopalatine articulates, by means of a large, dorsomedially directed, articulatory surface, with the lateral ethmoid.

Os hyomandibulo-metapterygoideum. The homology, and, thus, the correct denomination, of this bone, as well as of the other suspensorium elements of catfish, has been the subject of endless controversies (McMurrich, 1884; De Beer, 1937; Hoedeman, 1960; Gosline, 1975; Howes, 1983ab, 1985; Arratia, 1990, 1992; Diogo el al., 2001a; Diogo & Chardon, 2003; etc.). As referred above, for the several reasons explained in detail in our recent papers (Diogo et al., 2001a; Diogo & Chardon, 2003), the nomenclature used here to describe these elements will follows strictly that presented by Diogo et al. (2001a). The hyomandibulo-metapterygoid (Figs 1, 2) is a large bone articulating dorsally with both the pterotic and the sphenotic and posteriorly with the opercular bone. Posteriorly to its cartilaginous articulation with the neurocranium, it presents a large posterodorsal extension, which is strongly connected, by means of connective tissue, with the ventrolateral margin of the pterotic, and from which originates a great part of the fibres of the levator operculi (Fig. 1).

Os sesamoideum 1. Small bone (Fig. 2) attached by means of a short but strong ligament to the anteromesial margin of the ento-ectopterygoid posteriorly and by means of a long and thick ligament to the ventrolateral margin of the prevomer anteriorly. The sesamoid bones 2 and 3 (see Diogo et al., 2001a) are absent.

Os entopterygoideo-ectopterygoideum. Large bone, its anteromesial and its anterolateral surfaces being connected to the sesamoid bone 1 of the suspensorium and to the autopalatine, respectively (Fig. 2). Posteriorly, the entopterygoideo-ectopterygoid is firmly associated with both the hyomandibulo-metapterygoid and the quadrato-symplectic.

Os quadrato-symplecticum. The quadrato-symplectic (Fig. 2) contacts the entopterygoideo-ectopterygoid anterodorsally, the hyomandibulo-metapterygoid posterodorsally, and the preopercle posteroventrally. It presents a large, anterior articulatory surface to articulate with the postero-dorsal surface of the angulo-articular.

Os praeoperculare. Long and thin bone (Fig. 1) firmly sutured to both the hyomandibulo-metapterygoid and the quadrato-symplectic. As is most other catfishes, the preopercle encloses a sensory canal, which exits the neurocranium and passes, via the preopercle, into the mandible.

Os operculare. The opercle (Figs 1, 2) is a large, roughly triangular bone attached ventrally, by means of connective tissue, to the interopercle. It presents a large, anterior articulatory surface for the hyomandibulo-metapterygoid. Anterodorsally, it presents a prominent, dorsally directed, roughly triangular process.

Os interoperculare. Its anterior surface is ligamentously connected to the postero-ventral margin of the mandible (Figs 1, 5). Medially, the interopercle is ligamentously connected to the lateral surface of the posterior ceratohyal.

Os ceratohyale anterior. Elongated bone that supports, together with the posterior ceratohyal, the eleven branchiostegal rays present on each side of the fish (Fig. 5). The anterior head of the branchiostegal ray 10 lies at the level of the cartilage situated between the anterior and the posterior ceratohyal, with the anterior head of the branchiostegal ray 11 being exclusively supported by the posterior ceratohyal and the remaining nine branchiostegal rays being exclusively supported by the anterior ceratohyal. The anterior ceratohyal presents a prominent posterodorsolateral projection, which borders, but is not sutured to, a significant part of the dorsolateral margin of the posterior ceratohyal (Fig. 5).

Os ceratohyale posterior. Somewhat triangular bone (Fig. 5) ligamentously connected to the postero-ventral edge of the mandible and to the medial surface of the interopercle. The interhyals are missing.

Os hypohyale ventrale. The ventral hypohyals (Fig. 5) 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 hypoyals.

Os parurohyale. The parurohyal (Fig. 5) is a somewhat triangular, 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.

Os posttemporo-supracleithrum. Large bone (Figs 1, 2), its dorso-medial limb being firmly associated to the epioccipital and the pterotic. Its ventro-medial limb is thin and ligamentously connected, by means of a thin and short ligament, to the basioccipital. The posteromesial surface of the posttemporo-supracleithrum is attached, by means of connective tissue, to the parapophyses of the complex centrum, which encapsulate the reduced swimbladder.

Os cleithrum. The cleithra (Figs 6, 7) are large, well-ossified stout structures forming the greatest part of the pectoral girdle and the posterior boundary of the branchial chamber. They are attached in the antero-medial line via connective tissue. Each cleithrum bears a crescentic, medially faced groove that accommodates the proximal portion of the pectoral spine, which presents a somewhat rectangular dorsomedian process (Fig. 8 : pec-sp-dmp) for the insertion of the abductor profundus.

Os scapulo-coracoideum. Large bone (Fig. 7), it does not contact its counterpart in the anteromedial line. Postero-laterally, the scapulo-coracoid bears two condyles, which articulate, respectively, with the pectoral spine and
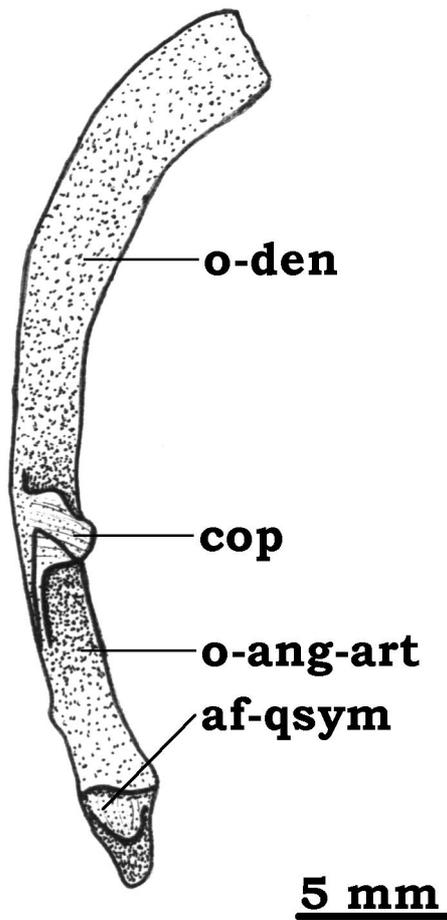
the complex radial (see Mo, 1991). The mesocoracoid arch is present (Fig. 7).

Fig. 1. – Lateral view of the cephalic musculature of *Nematogenys inermis*. *l-pri*, ligamentum primordium; *m-A1-ost, m-A2, m-A3''*, sections of musculus adductor mandibulae; *m-ad-ap*, musculus adductor arcus palatini; m-ab-sup-1, section 1 of musculus abductor superficialis; m-ad-sup-1, section 1 of musculus adductor superficialis; *m-arr-d*, musculus arrector dorsalis; *m-arr-v*, musculus arrector ventralis; *m-dil-op*, musculus dilatator operculi; *m-ep*, musculus epaxialis; *m-hyp*, musculus hypaxialis; *m-l-ap*, musculus levator arcus palatini; *m-l-op*, musculus levator operculi; *mx-b*, maxillary barbel; *o-ang-art*, os angulo-articulare; *o-apal*, os autopalatinum; *o-cl*, os cleithrum; *o-den*, os dentale; *o-fr*, os frontale; *o-hm-mp*, os hyomandibulo-metapterygoideum; *o-iop*, os interoperculare; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-mx*, os maxillare; *o-op*, os operculare; *o-osph*, os orbitosphenoideum; *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-sph*, os sphenoticum; *pec-ra*, pectoral rays; *pec-sp*, pectoral spine.

Fig. 2. – Ventral view of the neurocranium of *Nematogenys inermis*. On the right side the suspensorium, as well as the autopalatine, maxilla, adductor arcus palatini, extensor tentaculi, adductor operculi and protractor pectoralis, are also illustrated. Premaxillary teeth were removed. *cc*, complex centrum; *for-V-VII*, trigemino-facialis foramen; *m-ad-ap*, musculus adductor arcus palatini; *m-ad-op*, musculus adductor operculi; *m-ex-t*, musculus extensor tentaculi; *m-pr-pec*, musculus protractor pectoralis; *o-apal*, os autopalatinum; *o-boc*, os basioccipitale; *o-ent-ect*, os entopterygoideo-ectopterygoideum; *o-exoc*, os exoccipitale; *o-fr*, os frontale; *o-hm-mp*, os hyomandibulo-metapterygoideum; *o-iop*, os interoperculare; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-mx*, os maxillare; *o-op,* os operculare; *o-osph*, os orbitosphenoideum; *o-para*, os parasphenoideum; *o-pop,* os praeoperculare; *o-post-scl*, os post-temporo-supracleithrum; *o-prmx*, os praemaxillare; *o-prot*, os prooticum; *o-psph*, os pterosphenoideum; *o-pt*, os pteroticum; *o-pvm*, os praevomerale; *o-q-sym*, os quadrato-symplecticum; *o-ses-1*, sesamoid bone 1 of the suspensorium; *o-sph*, os sphenoticum; *pp4*, parapophysis 4.

Fig. 3. – Medial view of the left mandible of *Nematogenys inermis*, with mandibular teeth removed. *af-qsym*, articulatory facet for os quadrato-symplecticum; *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.

o-den

cop

o-ang-art
af-qsym

5 mm

Fig. 4. – Dorsal view of the left mandible of *Nematogenys inermis*, with mandibular teeth removed. *af-qsym*, articulatory facet for os quadrato-symplecticum; *cop,* coronoid process of mandible; *o-ang-art*, os angulo-articulare; *o-den*, os dentale.
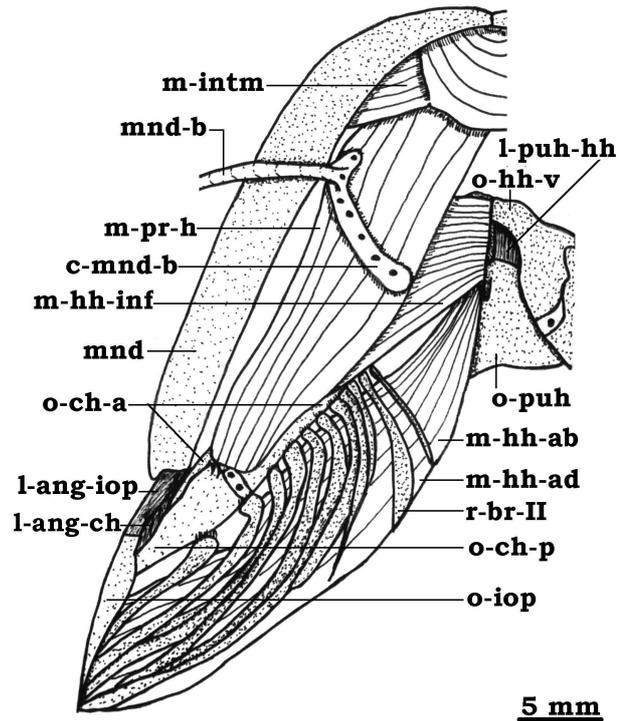

m-intm
mnd-b
l-puh-hh
o-hh-v
m-pr-h
c-mnd-b
m-hh-inf
mnd
o-ch-a
o-puh
m-hh-ab
m-hh-ad
l-ang-iop
r-br-II
l-ang-ch
o-ch-p
o-iop

5 mm

Fig. 5. – Ventral view of the cephalic musculature of *Nematogenys inermis*. On the right side, all the muscles, as well as the mandibular barbels and their associated cartilages, were removed. *c-mnd-b*, cartilago mandibularis tentaculi; *l-ang-ch,* ligamentum angulo-ceratohyale; *l-ang-iop,* ligamentum angulo-interoperculare; *l-puh-hh,* ligamentum parurohyalo-hypohyale; *mnd-b,* mandibular barbel; *m-hh-ab,* musculus hyohyoideus abductor; *m-hh-ad,* musculus hyohyoideus adductor; *m-hh-inf,* musculus hyohyoideus inferior; *m-intm,* musculus intermandibularis; *mnd,* mandible; *m-pr-h,* musculus protactor hyoideus; *o-ch-a,* os ceratohyale anterior; *o-ch-p,* os ceratohyale posterior; *o-hh-v,* os hypohyale ventrale; *o-iop,* os interoperculare; *o-puh,* os parurohyale; *r-br-II,* radius branchiostegus II.

o-cl
m-arr-v
m-ab-pro
m-arr-d
m-ab-sup-1
pec-sp
pec-ra

5 mm
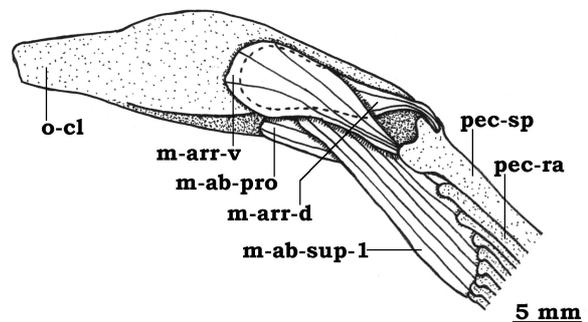
Fig. 6. – Ventral view of the pectoral girdle musculature of *Nematogenys inermis*. *m-ab-pro,* musculus abductor profundus; *m-ab-sup-1,* section 1 of musculus abductor superficialis; *m-arr-d,* musculus arrector dorsalis; *m-arr-v,* musculus arrector ventralis; *o-cl,* os cleithrum; *pec-ra,* pectoral rays; *pec-sp,* pectoral spine.
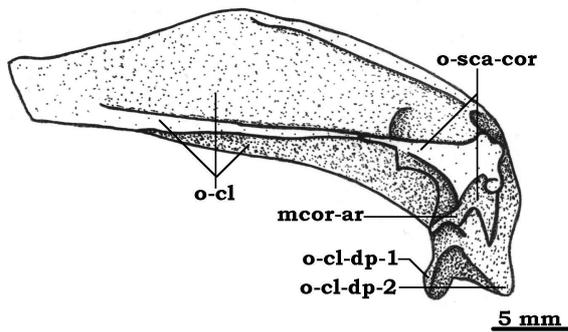
Fig. 7. – Ventral view of the pectoral girdle of *Nematogenys inermis*. The pectoral spine and pectoral rays, as well as the muscles associated with these structures, were removed. *mcor-ar*, mesocoracoid arch; *o-cl*, os cleithrum; *o-cl-dp-1, o-cl-dp-2*, dorsal process 1 and 2 of os cleithrum; *o-sca-cor*, os scapulo-coracoide.
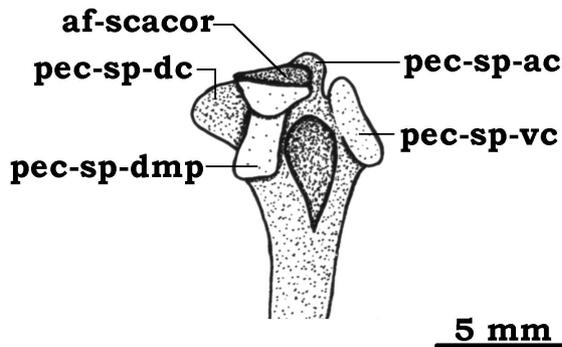

Fig. 8. – Medial view of the proximal portion of the left pectoral spine of *Nematogenys inermis*. *af-scacor*, articulatory facet for os scapulo-coracoid; *pec-sp-ac*, anterior condyle of pectoral spine; *pec-sp-dc*, dorsal condyle of pectoral spine; *pec-sp-dmp*, dorsomedial process of pectoral spine; *pec-sp-vc*, ventral condyle of pectoral spine.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost originates on the preopercle and the quadrato-symplectic and inserts on both the dorsolateral and the lateral surfaces of the angulo-articular and the dentary bone (Fig. 1). The A2 (Fig. 1), which lies dorso-mesially to the A1-ost, runs from the preopercle and hyomandibulo-metapterygoid to the medial surface of the dentary bone. The adductor mandibulae A3' is divided into a dorsal and a ventral part. The dorsal one (A3'-d), originates on the hyomandibulo-metapterygoid and inserts tendinously on the coronomeckelian bone, while the ventral one (A3'-v) originates on the quadrato-symplectic and inserts on the medial surface of the angulo-articular. The adductor mandibulae A3'' (Fig. 1), situated mesially to the A3' and to the levator arcus palatini, runs from the hyomandibulo-metapterygoid, sphenotic and entopterygoideo-ectopterygoid to the mesial surface of both the angulo-articular and the coronomeckelian bone. There is no adductor mandibulae Aω.

Musculus levator arcus palatini. The levator arcus palatini (Fig. 1) is situated medial to the adductor mandibu-

lae A3'. It originates on the sphenotic and inserts on the lateral face of the hyomandibulo-metapterygoid.

Musculus adductor arcus palatini. This muscle (Figs 1, 2) runs from the parasphenoid, pterosphenoid, orbitosphenoid and lateral ethmoid to the hyomandibulo-metapterygoid, quadrate-symplectic and the ento-ectopterygoid.

Musculus levator operculi. It originates on both the ventro-lateral margin of the pterotic and the posterodorsal surface of the hyomandibulo-metapterygoid and inserts on a great part of the lateral surface of the opercle (Fig. 1).

Musculus adductor operculi. Situated medially to the levator operculi, it runs from the ventral surface of the pterotic to the dorso-medial surface of the opercle (Fig. 2). There is no adductor hyomandibularis (sensu DIOGO et al., 2002; DIOGO & VANDEWALLE, 2003).

Musculus dilatator operculi. The dilatator operculi (Fig. 1) is a large muscle originating on the pterotic, frontal and hyomandibulo-metapterygoid, passing laterally to the adductor mandibulae A2, and inserting on the antero-dorsal margin of the opercle.

Musculus extensor tentaculi. The extensor tentaculi 1 (Fig. 2) runs from the lateral ethmoid to the posteromedian surface of the autopalatine. Some fibres of this muscle, as well as some fibres of the adductor arcus palatini, are also associated with the sesamoid bone 1 of the suspensorium and its associated ligaments. There is no retractor tentaculi.

Musculus protractor hyoidei. This muscle (Fig. 5) is constituted by a single, voluminous mass of fibres, in which are lodged the cartilages associated with the mandibular barbels. It originates on the anterior ceratohyal and inserts anteriorly on the anteromesial surface of the dentary bone. There are no small, additional muscles (see DIOGO & CHARDON, 2000b) associated with the mandibular barbels.

Musculus intermandibularis. Large muscle joining the two mandibles (Fig. 5). It should be noted that the intermandibularis can somewhat be subdivided into three parts : in the mesial part, its fibers run rather rostrally, while in the parts situated laterally to this mesial part the fibers run rather laterally until they attach to the mesial surface of each mandible.

Musculus hyohyoideus inferior. Thick muscle (Fig. 5) 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 (Fig. 5) runs from the first (medial) branchiostegal ray to a median aponeurosis, which is anteriorly associated with two long, strong tendons attached to the two ventral hypohyals.

Musculus hyohyoideus adductor. Each hyohyoideus adductor (Fig. 5) interconnects the branchiostegal rays of the respective side, with the most lateral fibers of this muscle also attaching on the mesial surface of the opercular bone.

Musculus sternohyoideus. Large, roughly triangular muscle. It runs from the posterior portion of the paruro-hyal to the anterior portion of the cleithrum. The poster-

oventral fibers of the sternohyoideus cover ventrally the anterior portion of the hypoaxialis.

Musculus arrector ventralis. The arrector ventralis runs from the ventral surface of the cleithrum to the ventral condyle of the pectoral spine (Fig. 6).

Musculus arrector dorsalis. This muscle (Fig. 6), dorsal to the arrector ventralis, originates on the ventral surface of the cleithrum and inserts on the antero-lateral edge of the pectoral spine.

Musculus abductor superficialis. This muscle is differentiated into two sections. The larger section (Fig. 6 : m-ab-sup-1) runs from the ventral margin of both the scapulo-coracoid and the cleithrum to the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section (m-ab-sup-2), situated dorsally to the larger one, runs from the lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of pectoral fin rays.

Musculus abductor profundus. This small muscle originates on the posterior surface of the scapulo-coracoid and inserts on the prominent, somewhat rectangular, dorsomedial process of the pectoral spine (Fig. 8 : pec-sp-dmp).

Musculus adductor superficialis. Situated on the posterior margin of the pectoral girdle and divided into two sections. The larger section (Fig. 1 : m-ad-sup-1) originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section (m-ad-sup-2) runs from both the postero-ventrolateral edge of the scapulo-coracoid and the dorsal surface of the proximal radials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus protractor pectoralis. Thick muscle (Fig. 2) running from the ventral surface of the pterotic to the antero-dorsal surface of the cleithrum.

DISCUSSION

As referred to in the Introduction, although the nematogenyids are commonly grouped in a separate family, the Nematogenyidae, no unique, autapomorphic characters have been published previously to characterise these fishes and to distinguish them from the other siluriforms. In fact, as stressed by DE PINNA (1998 : 297), the most conspicuous and distinctive character of nematogenyids usually mentioned in the literature is the broad insertion of the levator operculi on the lateral surface of the opercle, but even this feature is present in other catfishes, namely in some pimelodids (e.g. DIOGO, 2005).

This lack of unique characters to distinguish the nematogenyids from other catfishes is probably due to their somewhat plesiomorphic general aspect (see ARRATIA & CHANG, 1975; ARRATIA & HUAQUIN, 1995), but also to the fact that, as stressed by DE PINNA (1998) and referred in the Introduction, their morphology was poorly studied so far. In fact, although our observations and comparisons confirmed the somewhat plesiomorphic condition of the nematogenyids, they have pointed out that these fishes are characterised by at least two unique, autapomorphic characters, which are described below.

Anterior ceratohyal with a prominent, posterodorsolateral projection bordering a significant part of the dorsolateral margin of the posterior ceratohyal. Plesiomorphically catfishes lack major posterior processes on the anterior ceratohyal (see, e.g., REGAN, 1911; EIGENMAN, 1925; ALEXANDER, 1965; HOWES, 1983a, 1985; MO, 1991; DE PINNA, 1996). In all specimens of *N. inermis* studied, and in no other catfish studied by us or described in the literature, there is a prominent posterodorsolateral projection of the anterior ceratohyal bordering, but not being sutured/interdigitated with, a great part of the dorsolateral margin of the posterior ceratohyal (see, e.g., Fig. 5).

Anterior portion of prevomer markedly extended anteriorly, with anterior tip of this bone being situated at about the same level as the anterior margin of the mesethmoid. Plesiomorphically in catfishes the anterior margin of the prevomer lies significantly posterior to the anterior margin of the mesethmoid (see, e.g., REGAN, 1911; EIGENMANN, 1925; DE BEER, 1937; ALEXANDER, 1965; GOSLINE, 1975; HOWES, 1983a, 1985; GHIOT et al., 1984; MO, 1991; DE PINNA, 1996; etc.). In all specimens of *N. inermis* examined the anterior portion of the prevomer is markedly extended anteriorly, with its anterior tip and the anterior margin of the mesethmoid being situated at about the same level (see, e.g., Fig. 2). The only catfishes examined where a somewhat similar condition is found are the trichomycterids, which are very likely the sister-group of the nematogenyids (see below), with this similarity thus constituting, eventually, an additional character to support this sister-group relationship. However, in the trichomycterids examined the anterior portion of the prevomer, although situated further anteriorly than in most siluriforms, does not extend at about the same level as the anterior margin of the mesethmoid, as is the case in nematogenyids. The condition found in these latter fishes constitutes, thus, a unique, autapomorphic feature within catfishes.

The exclusive presence of these two autapomorphic, unique features in the genus *Nematogenys* thus justifies, in our opinion, the placement of this genus in its own family, Nematogenyidae (see above). With respect to the phylogenetic relationships of the Nematogenyidae, our observations and comparisons pointed out two new, additional synapomorphies to support MO's (1991) and DE PINNA's (1992) studies, according to which this family and the Trichomycteridae form a monophyletic clade that is, in turn, the sister group of the clade Callichthyidae+(Scoloplacidae+(Astroblepidae+Loricariidae)). The two additional synapomorphies supporting the sister-group relationship between the nematogenyids and the trichomycterids are described below (for an overview of the other synapomorphies supporting this sister-group relationship, see DE PINNA, 1998; DIOGO, 2005).

Proximal portion of pectoral spine with prominent, somewhat rectangular, dorsomedian process for insertion of muscle abductor profundus. Plesiomorphically in catfishes the abductor profundus inserts on the medial surface of the dorsal condyle of the pectoral girdle, which lacks major processes on its medial surface for muscular insertion (see, e.g., ALEXANDER, 1965; DIOGO et al., 2001b). In all the nematogenyids and trichomycterids

examined, however, there is a prominent, somewhat rectangular, dorsomedian process on the proximal portion of the pectoral spine (see, e.g., Fig. 8 : pec-sp-dmp) for the insertion of the muscle abductor profundus. Such a dorsomedian process of the pectoral spine is also found, within the catfishes examined, in the cetopsids. As the Trichomycteridae and the Nematogenyidae do not seem to be closely related to the Cetopsidae (see, e.g., Mo, 1991; DE PINNA, 1998; DIOGO, 2003), this feature seems to constitute a synapomorphy of the clade formed by the two former families, with its presence in the Cetopsidae being due to an independent acquisition. In fact, it should be noted that this hypothesis was strongly supported by a 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 extant catfish families (DIOGO, 2005).

Dorsal tip of coronoid process markedly curved mesially. Contrary to other catfishes, in the nematogenyids and the trichomycterids the coronoid process of the mandible is markedly curved medially, with its dorsal tip projecting medially beyond the main body of the mandible (see, e.g., Fig. 4). This feature is only found, within the catfishes studied by us or described in the literature, in the nematogenyids and the trichomycterids.

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