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On the osteology and myology of the cephalic region and pectoral girdle of *Franciscodoras marmoratus* (Lütken 1874), comparison with other doradids, and comments on the synapomorphies and phylogenetic relationships of the Doradidae (Teleostei: Siluriformes)

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Abstract—The cephalic and pectoral girdle structures of *Franciscodoras marmoratus* are described and compared to those of representatives of the three main doradid groups, namely *Anadoras weddellii* (Astrodoradinae), *Acanthodoras cataphractus* (Platydoradinae) and *Doras punctatus* (Doradinae), as well as members of the other siluriform families, as the foundation for a discussion on the phylogenetic relationships of the Doradidae. Our observations and comparisons support the idea that the Doradidae is closely related to the Auchenipteridae. In addition, our observations and comparisons pointed out a potentially new doradid synapomorphy, namely, the presence of a well-developed, deep, oval fossa between the dorsomedian surface of the pterotic and the dorsolateral surface of the parieto-supraoccipital.

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

INTRODUCTION

The Siluriformes are “one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade” (Teugels, 1996). Among the 35 catfish families (Ferraris

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and de Pinna, 1999), the family Doradidae, with 30 genera and approximately 80 species, constitutes a conspicuous Neotropical catfish group (De Pinna, 1998). The phylogeny and systematics of the Doradidae were recently revised by De Pinna (1998), who referred to an unpublished thesis by Higuchi, 1992. According to the cladogram provided on De Pinna's (1998) figure 14, the doradid genera *Wertheimeria* and *Franciscodoras* are the sister-groups of a clade containing the three main doradid groups, the Platydoradinae, Astrodoradinae and Doradinae, with these three groups and the former two genera being associated by the presence of the following three doradid synapomorphies: delimitation of a tympanic area bordered by the supracleithrum anteriorly, the postoccipital process dorsally, the infranuchal scute posteriorly and the humeral process ventrally; presence of at least two ossified lateral scutes in the postcranial region, one of which articulating with posterior nuchal plate and first pleural rib; reduction or absence of the middle posterodorsal process of cleithrum, between the articular and humeral processes.

It is worth noting that, despite the relatively large number of studies concerning siluriform morphology (e.g., McMurrich, 1884; Regan, 1911; de Beer, 1937; Gauba, 1962, 1966, 1968, 1969; Mahajan, 1963, 1966a, b, 1967a, b; Alexander, 1965; Gosline, 1975; Ghiot, 1978; Ghiot et al., 1984; Arratia, 1992; Mo, 1991; Diogo et al., 1999, 2000, 2001a, b, c, 2002a, b; Oliveira et al., 2001, 2002; etc.) the only few, somewhat detailed, morphological descriptions of the doradid catfishes published so far are those of Eigenmann (1925), Alexander (1965), Chardon (1968) and Ladich (2001). Moreover, as these descriptions are almost exclusively restricted to the osteology and external anatomy of the doradids, important aspects of the morphology of these fishes, such as, for example, the configuration of their pectoral girdle, the structures associated with their mandibular barbels, or both the muscles and the ligaments of their cephalic region and their pectoral girdle, are poorly known. This not only complicates the study of the functional morphology of the doradids, but also restricts considerably the data available to infer the synapomorphies and the phylogenetic relationships of these catfishes.

The aim of this work is to describe the bones, cartilages, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of the plesiomorphic doradid *Franciscodoras marmoratus* (Lütken, 1874), and to compare these structures with those of representatives of the three main doradid groups, namely, *Anadoras weddellii* (Castelnau, 1855) (Astrodoradinae), *Acanthodoras cataphractus* (Linnaeus, 1758) (Platydoradinae) and *Doras punctatus* Kner, 1855 (Doradinae), as well as of members of the other siluriform families, as the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Doradidae.

MATERIAL AND METHODS

In the anatomical descriptions, 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 mandibulae sections, Diogo and Chardon (2000a) are followed since recent works have pointed out that, with respect to these sections, the nomenclature of Winterbottom (1974) presents serious limitations (see e.g., Gosline, 1989; Diogo and Chardon, 2000a). 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).

Astroblepididae: *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 boudierus* 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 cotoides* 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 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

Franciscodoras marmoratus

Osteology

Os mesethmoideum. Unpaired bone situated on the anterodorsal surface of the neurocranium (fig. 1), with each of its antero-ventrolateral margins ligamentously connected to the premaxillary.

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

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

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

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

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

Os frontale. The frontals (fig. 1) are large bones that constitute a great part of the cranial roof. They are largely separated by two median fontanels. There is a well-developed, deep, roughly oval fossa between the postero-dorsolateral margin of the frontal and the anterodorsolateral surface of the parieto-supraoccipital (fig. 1).

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

Os pteroticum. Well-developed, irregularly-shaped bone situated posteriorly to the sphenotic (fig. 1). There is an oval, deep fossa ('supratemporal fossa': see below) between the dorsolateral surface of the pterotic and the dorsomedian surface of the parieto-supraoccipital (fig. 1).

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

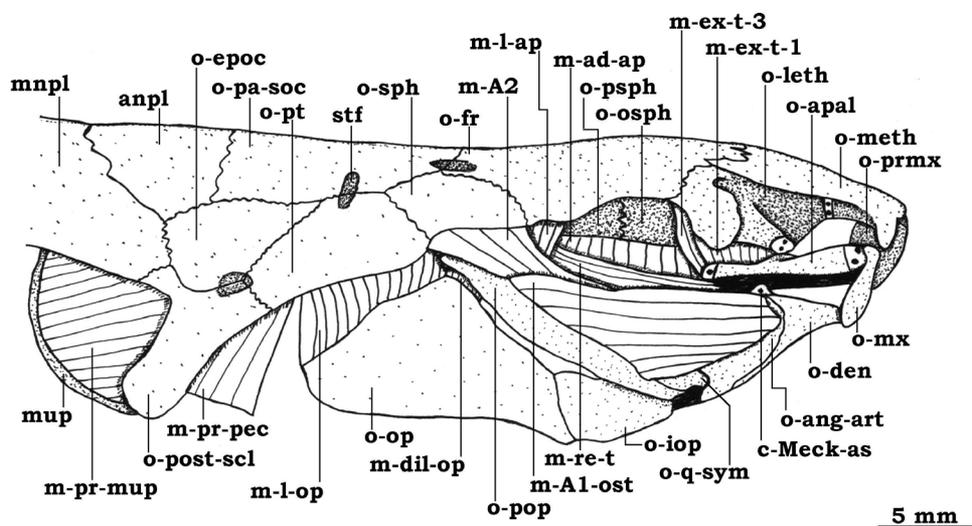


Figure 1. Lateral view of the musculature and skeleton structures of the cephalic region *Francisodoras marmoratus* (note: bones are stippled with small black points and cartilages with large black circles). *anpl* anterior nuchal plate, *c-Meck-as* ascending portion of cartilago Meckeli, *m-A1-ost*, *m-A2* sections of musculus adductor mandibulae, *m-ad-ap* musculus adductor arcus palatini, *m-dil-op* musculus dilatator operculi, *m-ex-t-1*, *m-ex-t-3* sections of musculus extensor tentaculi, *m-l-ap* musculus levator arcus palatini, *m-l-op* musculus levator operculi, *mnpl* median nuchal plate, *m-pr-mup* musculus protractor of the müllerian process, *m-pr-pec* musculus protractor pectoralis, *m-re-t* musculus retractor tentaculi, *mup* müllerian process, *o-ang-art* os angulo-articulare, *o-apal* os autopalatini, *o-den* os dentale, *o-epoc* os epioccipitale, *o-fr* os frontale, *o-iop* os interoperculare, *o-leth* os lateroethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-op* os operculare, *o-osph* os orbitosphenoidium, *o-pa-soc* os parieto-supraoccipitale, *o-pop* os praeoperculare, *o-post-scl* os posttemporo-supracleithrum, *o-prmx* os praemaxillare, *o-psph* os pterosphenoidium, *o-pt* os pteroticum, *o-q-sym* os quadrato-symplecticum, *o-sph* os sphenoticum, *stf* supratemporal fossa.

Os epioccipitale. Well-developed bone situated on the posterodorsal surface of the cranial roof (fig. 1). There is a well-developed fossa between the anterodorsolateral margin of the epioccipital, the posterodorsal margin of the pterotic and the dorso-medial margin of the posttemporo-supracleithrum (fig. 1). The extrascapulars are missing.

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 ventrolateral surfaces are firmly sutured to the ventromedial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. Large, unpaired bone constituting the postero-dorso-medial surface of the cranial roof (fig. 1). It is truncated posteriorly, contacting a well-developed, roughly triangular, unpaired anterior nuchal plate, which is enclosed by the parieto-supraoccipital anteriorly, by a even larger, unpaired median

nuchal plate posteriorly and posterolaterally, and by the well-developed epioccipitals anterolaterally (fig. 1).

Os angulo-articulare. This bone (fig. 1), together with the dentary, the coronomeckelian and the highly-developed Meckel's cartilage (fig. 1), constitute the mandible. Posterodorsally, the angulo-articular has an articulatory facet for the quadrate-symplectic. Posteroventrally, it is ligamentously connected to both the interopercular and the posterior ceratohyal.

Os dentale. The toothed dentary 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 somewhat developed dorsal process (processus coronoideus) (fig. 1).

Os coronomeckelium. Well developed, lodged in the medial surface of the mandible. Posterodorsally it bears a crest for attachment of the adductor mandibulae A3'-d.

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

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

Os autopalatinum. The autopalatine (fig. 1) is a rod-like, antero-posteriorly elongated bone with its posterior end capped by a small cartilage and its anterior end tipped by a well-developed cartilage with two anterolateral concavities that accept the two proximal heads of the maxillary. Medially, the autopalatine articulates, by means of a small, circular articulatory surface, with the lateral ethmoid.

Os hyomandibulo-metapterygoideum. The homology and, thus, the correct denomination, of this bone, as well as of the other suspensorium elements of catfish, has been the subject of endless controversies (McMurrich, 1884; De Beer, 1937; Hoedeman, 1960; Gosline, 1975; Howes, 1983, 1985; Arratia, 1990, 1992; Diogo et al., 2001a; Diogo and Chardon, 2003; etc.). The hyomandibulo-metapterygoideum is a large bone presenting a markedly broad anterodorsal spine. It articulates dorsally with both the pterotic and the sphenotic and posteriorly with the opercular.

Os sesamoideum 1. Well-developed bone attached by means of a short but strong ligament to the ento-ectopterygoideum posteriorly and by means of a long and thick ligament to both the prevomer and the lateral ethmoid anteriorly. The sesamoid bones 2 and 3 (see Diogo et al., 2001a) are absent.

Os entopterygoide-ectopterygoideum. Poorly-developed, with its posterior surface being sutured with both the hyomandibulo-metapterygoideum and the quadrate-symplectic.

Os quadrato-symplecticum. The quadrate-symplectic (fig. 1) presents a well-developed, anterior articulatory 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 connective tissue, to the interopercular. It presents a well-developed, anterodorsal articulatory surface for the hyomandibulo-metapterygoid.

Os interoperculare. Its anterior surface is ligamentously connected to the posteroventral margin of the mandible. Medially, the interopercular articulates with the lateral surface of the posterior ceratohyal.

Os interhyale. Small bone ligamentously connects to both the posterodorsal surface of the posterior ceratohyal and the median surface of the hyomandibulo-metapterygoid.

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

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

Os hypohyale ventrale. The ventral hypohyals are ligamentously connected to the anterolateral edges of the parurohyal.

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

Os parurohyale. The parurohyal is an irregular, unpaired, T-shaped bone with its posterior portion being a somewhat rectangular, markedly narrow structure.

Os posttemporo-supracleithrum. The dorso-medial limb of this bone (fig. 1) is firmly sutured to the median nuchal plate, the epioccipital and the pterotic. Its ventromedial limb is firmly sutured with the basioccipital. Its posterolateral margin is deeply forked, forming an articulating groove for the upper edge of the cleithrum. The posteroventral surface of the posttemporo-supracleithrum is weakly attached, by means of connective tissue, to the anteroventral process of the fourth parapophysis (= Müllerian process) (fig. 1: mup), which is well developed and highly mobile. This highly mobile Müllerian process, together with a well-developed, separate muscle, the protractor of the Müllerian process (fig. 1: m-pr-mup), running from its anterior surface to the posterior surface of the cranium, form an "elastic-spring-apparatus" (see, e.g., Bridge and Haddon, 1894; Alexander, 1965; Chardon, 1968).

Os cleithrum. The cleithrum (fig. 2) is a large, well-ossified stout structure forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially faced groove that accommodates the dorsal condyle of the well-developed pectoral spine. The two cleithra are attached in the anteromedial line *via* connective tissue. The humeral process is well developed.

Os scapulo-coracoideum. This is an elongated bony plate suturing with the cleithrum along its anterolateral edge (fig. 2). Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge (see Diogo et al.,

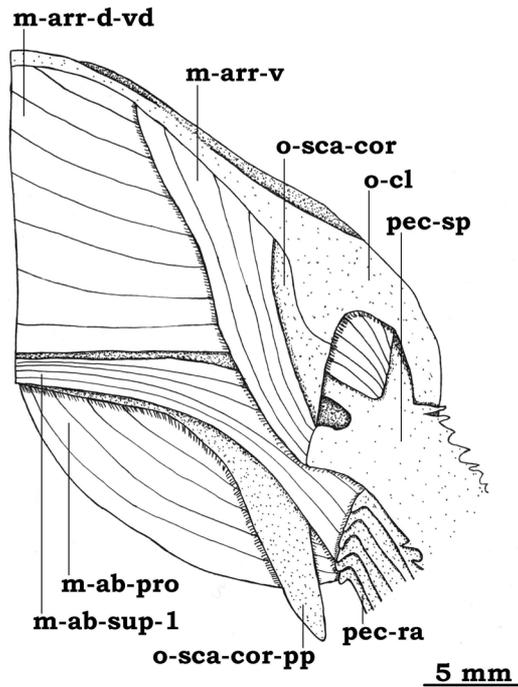


Figure 2. Ventral view of the musculature and skeleton structures of the pectoral girdle of *Franciscodoras marmoratus*. *m-ab-pro* musculus abductor profundus, *m-ab-sup-1* section 1 of musculus abductor superficialis, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector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

2001b), which extends ventrally to the ventrolateral surface of the cleithrum, fusing with an anteroventral ridge of this bone. Mesially, the scapulo-coracoid joins its counterpart in an interdigitation of several strong serrations. Posterolaterally, it bears two condyles, which articulate, respectively, with the pectoral spine and the complex radial (Mo, 1991), and it presents a prominent, triangular, posteriorly directed posterior process (fig. 2: *o-sca-cor-pp*). The main scapulo-coracoid articular surface for the pectoral spine (see Diogo et al., 2001b) is a markedly narrow, dorsoventrally elongated structure. The mesocoracoid arch is undifferentiated.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (Diogo and Chardon, 2000a) originates on the preopercular and the quadrate-symplectic and inserts on both the dorsolateral and the lateral surfaces of the angulo-articular (fig. 1). The A2 (fig. 1), which lies dorso-mesially to the A1-ost, runs from the preopercular, pterotic, sphenotic and hyomandibulo-metapterygoid to the medial surfaces of both the dentary and the coronomeckelian. The adductor mandibulae

A3' is divided into a dorsal and a ventral part. The dorsal one (A3'-d), originates on the hyomandibulo-metapterygoid, quadrato-symplectic and ento-ectopterygoid 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'', situated mesially to the A3', runs from the hyomandibulo-metapterygoid to the mesial surface of the angulo-articular. There is no adductor mandibulae A ω .

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

Musculus adductor arcus palatini. This muscle (fig. 1) runs from the parasphenoid, pterosphenoid and orbitosphenoid to the hyomandibulo-metapterygoid and the ento-ectopterygoid.

Musculus levator operculi. It originates on the ventrolateral margin of the pterotic and inserts on the dorsal surface of the opercular (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 opercular. There is no adductor hyomandibularis (sensu Diogo and Vandewalle, 2003).

Musculus dilatator operculi. The dilatator operculi (fig. 1) originates on the pterosphenoid, frontal and hyomandibulo-metapterygoid and inserts on the anterodorsal margin of the opercular.

Musculus extensor tentaculi. This muscle is divided into three bundles. The extensor tentaculi 1 (fig. 1) runs from both the lateral ethmoid and the orbitosphenoid to the posterodorsal surface of the autopalatine. The extensor tentaculi 2 originates on the lateral ethmoid and the orbitosphenoid and inserts on the posteromedian surface of the autopalatine. Lastly, the extensor tentaculi 3 (fig. 1) runs from the lateral ethmoid and the orbitosphenoid to the posteroventral margin of the autopalatine.

Musculus retractor tentaculi. Well-developed muscle (fig. 1) originating on the lateral surface of the hyomandibulo-metapterygoid and inserting, by means of a thick and long tendon, on the maxilla. Some of its fibres are mixed with those of the adductor mandibulae A3''.

Musculus protractor hyoidei. This muscle (fig. 3) has three parts. The pars ventralis, in which are lodged the cartilages associated with the internal and external mandibular barbels (fig. 3: c-in-mnd-t; c-ex-mnd-t), originates on the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis. The pars lateralis (fig. 3) runs from both the posterior and the anterior ceratohyals to the ventromedial face of the dentary. The pars dorsalis runs from the anterior ceratohyal to the anterodorsal surface of the dentary.

Musculus retractor externi mandibularis tentaculi. Small muscles running from the anterodorsal surface of the moving part of the cartilages associated with the outer mandibular barbels to the dentary (for the nomenclature of the small muscles and cartilages associated with the mandibular barbels, see Diogo and Chardon, 2000b).

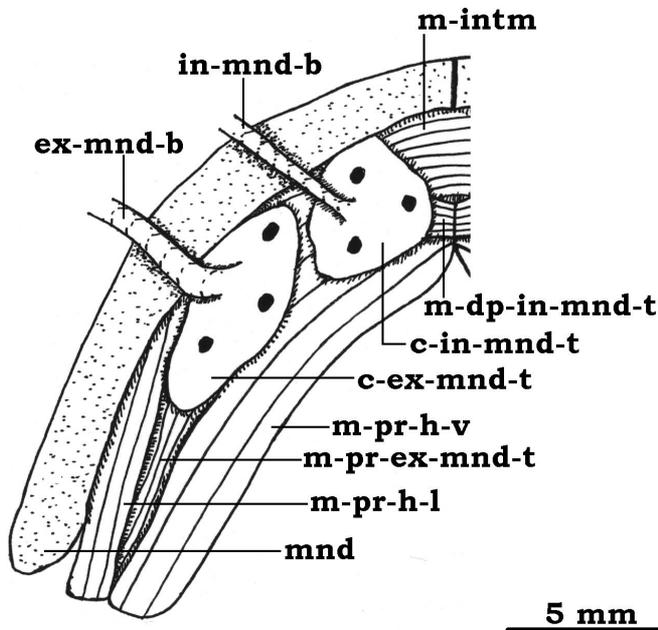


Figure 3. Ventral view of the musculature and the skeleton structures of the cephalic region of *Franciscodoras marmoratus* (note: bones are stippled with small black points and cartilages with large black circles). *c-ex-mnd-t*, *c-in-mnd-t* cartilages of external and internal mandibular barbels, *ex-mnd-b*, *in-mnd-b* external and internal mandibular barbels, *m-dp-in-mnd-t*, musculus depressor interni mandibularis tentaculi, *m-intm* musculus intermandibularis, *mnd* mandible, *m-pr-ex-mnd-t* musculus protractor externi mandibularis tentaculi, *m-pr-h-l*, *m-pr-h-v* pars lateralis and ventralis of musculus protractor hyoideus.

Musculus retractor interni mandibularis tentaculi. Small muscles connecting the dentaries to the anterodorsal surface of the moving part of the cartilages associated with the internal mandibular barbels.

Musculus depressor interni mandibularis tentaculi. Small muscles (fig. 3) running from a median aponeurosis to the median surfaces of the cartilages associated with the internal mandibular barbels.

Musculus protractor externi mandibularis tentaculi. Narrow, elongated muscles (fig. 3) originating on the anterior ceratohyals and inserting on the anterodorsal surface of the moving part of the cartilages associated with the outer mandibular barbels.

Muscle intermandibularis. Well-developed muscle joining the two mandibles (fig. 3).

Musculus hyohyoideus inferior. Thick muscle attaching medially on a median aponeurosis and laterally on the ventral surfaces of the ventral hypohyal, the anterior ceratohyal and the posterior ceratohyal.

Musculus hyohyoideus abductor. It runs from the first (medial) branchiostegal ray to a median aponeurosis, which is associated with two long, strong tendons,

attached, respectively, to the two ventral hypohyals. Some of the posteromedian fibres of the hyohyoideus abductor are firmly connected to the anteroventral surface of the pectoral girdle.

Musculus hyohyoideus adductor. Each hyohyoideus adductor connects the branchiostegal rays of the respective side, with their most lateral fibres being also attached on the mesial surface of the opercular bone.

Musculus sternohyoideus. It runs from the posterior portion of the parurohyal to the anterior portion of the cleithrum.

Musculus arrector ventralis. It runs from the cleithrum to the ventral condyle of the pectoral spine (fig. 2).

Musculus arrector dorsalis. This muscle, dorsal to the arrector ventralis and the abductor superficialis, is differentiated into two well-developed divisions. The ventral division (fig. 2: m-arr-d-vd) is situated on the ventral surface of the pectoral girdle and runs from the ventral margin of the cleithrum to the anterolateral edge of the pectoral spine. The dorsal division of the arrector dorsalis is subdivided, in turn, into two sections, with the dorsal one being situated on the dorsal surface of the pectoral girdle and, thus, being originated on the dorsal surface of the scapulo-coracoid, and the ventral one being situated on the ventral surface of the pectoral girdle and, thus, being originated on the ventral surface of this bone. Both these sections of the dorsal division of the arrector dorsalis insert on the anterior edge of the dorsal condyle of the pectoral spine.

Musculus abductor superficialis. This muscle is differentiated into two sections. The larger section (fig. 2: m-ab-sup-1) runs from the ventral margin of the scapulo-coracoid to the anteroventral 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 anterodorsal margin of the ventral part of the pectoral fin rays.

Musculus abductor profundus. This highly-developed muscle (fig. 2) originates on the posterior surface of the scapulo-coracoid and inserts on the medial surface of the dorsal condyle of the pectoral spine.

Musculus adductor superficialis. This muscle situates on the posterior margin of the pectoral girdle and is divided into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the 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. Well-developed muscle (fig. 1) running from the ventral surfaces the pterotic to the anterodorsal surface of the cleithrum.

Anadoras weddellii

The principal differences between the structures of the cephalic region and pectoral girdle of this species and those of *Franciscodoras marmoratus* are that in *Anadoras*

weddellii: (1) the cartilages associated with the mandibular barbels are considerably narrower than in *F. marmoratus*; (2) the cartilages associated with the inner mandibular barbels are in connected with those associated with the outer mandibular barbels; (3) the posterior process of the scapulo-coracoid is still more developed than in *F. marmoratus*; (4) the second dorsal process of the cleithrum (sensu Diogo et al., 2001b) is missing; (5) the muscle retractor tentaculi is absent; (6) the adductor mandibulae A2 does not reach the neurocranium, originating exclusively on the lateral surface of the suspensorium; (7) the sesamoid bone 1 of the suspensorium is ligamentously connected anteriorly to the lateral ethmoid, and not to both this bone and the prevomer; (8) the coronomeckelian is not as developed as in *F. marmoratus*.

Acanthodoras cataphractus

The most significant differences between the structures of the cephalic region and pectoral girdle of *Acanthoras cataphractus* and those of *Franciscodoras marmoratus* are: in the former species (1) the sesamoid bone 1 of the suspensorium is considerably smaller than that of *F. marmoratus*; (2) the second dorsal process of the cleithrum is missing; (3) the cartilages associated with the mandibular barbels are considerably narrower than in *F. marmoratus*; (4) the retractor tentaculi is absent; (5) the muscle extensor tentaculi inserts not only on the autopalatine, but on both this bone and the sesamoid bone 1 of the suspensorium; (6) the adductor mandibulae does not contact the neurocranium, originating exclusively on the suspensorium; (7) the sesamoid bone 1 of the suspensorium is ligamentously connected anteriorly with the lateral ethmoid, and not to this bone and the prevomer; (8) the epioccipital presents a prominent posterior extension that is ligamentously connected to the Weberian complex and nuchal plates; (9) the coronomeckelian is smaller than that of *F. marmoratus*.

Doras punctatus

The principal differences between the structures of the cephalic region and pectoral girdle of *Franciscodoras marmoratus* and *Doras punctatus* are: in this latter species (1) the anterodorsal process of the hyomandibulo-metapterygoid is markedly less developed than in *F. marmoratus*, being almost vestigial; (2) the cartilages associated with the mandibular barbels are considerably narrower than in *F. marmoratus*; (3) the ento-ectopterygoid is poorly-developed and significantly smaller than the sesamoid bone 1 of the suspensorium; (4) the posterior process of the scapulo-coracoid is still more developed than in *F. marmoratus*; (5) the hyomandibulo-metapterygoid and the ento-ectopterygoid are largely separated by a well-developed quadrate-symplectic; (6) the second dorsal process of the cleithrum is missing; (7) the anterolateral arms of the T-shaped prevomer are considerably less developed than in *F. marmoratus*; (8) the muscle retractor tentaculi is absent; (9) the premaxillaries are markedly compressed transversally and the anterolateral arms of the mesethmoid are poorly developed; (10) the adductor mandibulae A2 does

not reach the neurocranium, originating exclusively on the lateral surface of the suspensorium; (11) the sesamoid bone 1 of the suspensorium is ligamentously connected anteriorly to the lateral ethmoid, and not to both this bone and the prevomer; (12) the coronomeckelian is not as developed as in *F. marmoratus*; (13) the epioccipital presents a prominent posterior extension that is ligamentously connected to the nuchal plates.

DISCUSSION

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

Before describing these three synapomorphies, it is important to notice here that the phylogenetic considerations made in the present work were corroborated by an explicit cladistic 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).

Meckel's cartilage highly developed, with its ascending portion extending dorsally to the dorsal surface of the coronoid process of the mandible and, thus, with a significant part of this ascending portion being visible in a lateral view of the cranium. Plesiomorphically in catfishes the Meckel's cartilage does not extend dorsally to the dorsal surface of the coronoid process of the mandible (Mo, 1991; Diogo and Chardon, 2000a, c). However, in all doradids and auchenipterids examined the ascending portion of the Meckel's cartilage extends far beyond the dorsal surface of the coronoid process, with a considerable part of this ascending portion being, thus, visible in a lateral view of the skull (fig. 1). Such a peculiar feature is only also found in the aspredinid catfishes (Diogo et al., 2001c: fig. 1). However, since the aspredinids are seemingly more related to other siluriform

families (Erethistidae, Sisoridae, Akysidae, Amblycipitidae) than to the doradids and auchenipterids (De Pinna, 1996, 1998; Diogo et al., 2001c, 2002b; Diogo, 2003), this character seems to constitute a synapomorphy to support the clade constituted by the Auchenipteridae and the Doradidae.

Epioccipital constituting a significant part of the dorsal surface of the cranial roof. This character was proposed by Lundberg (1993) as a synapomorphy of a clade formed by the Doradidae, Auchenipteridae and the African Mochokidae (see below). However, as noted by Curran (1989) and Mo (1991), and corroborated by the present study (this character is absent in all mochokids studied), an epioccipital forming a significant part of the dorsal surface of the cranial roof (fig. 1) constitutes, in fact, a synapomorphy of the clade formed by the former two Neotropical families, and not by these two families and the African Mochokidae.

Posterolateral surface of the scapulo-coracoid presenting a prominent, triangular posterior process. Plesiomorphically in catfishes the scapulo-coracoid lacks major posterior processes (Mo, 1991; De Pinna, 1996; Diogo et al., 2001b). However, in all doradids and auchenipterids examined, with exception to the peculiar genus *Ageneiosus*, the scapulo-coracoid presents a prominent, triangular posterior process (fig. 2). Such a feature is only found, apart from the doradids and auchenipterids, in some few catfishes such as some bagrids (Diogo et al., 2001b: fig. 5) or the catfishes of the sisoroid clade including sisorids, auchenipterids and erethistids (Diogo et al., 2002b: fig. 5). As these latter catfishes are seemingly more closely related to other siluriforms than to doradids and auchenipterids (e.g., Mo, 1991; De Pinna, 1996, 1998; Diogo et al., 2001c, 2002b; Diogo, 2003), and due to the highly derived position occupied by the genus *Ageneiosus* among the Auchenipteridae (De Pinna, 1998), this feature seems to constitute an additional synapomorphy to support the clade formed by the doradids and auchenipterids, being secondarily lost in the peculiar genus *Ageneiosus*.

With respect to the doradid synapomorphies, three characters were listed by De Pinna (1998: fig. 14), namely: (1) “delimitation of a tympanic area bordered by the supracleithrum anteriorly, the postoccipital process dorsally, the infranuchal scute posteriorly and the humeral process ventrally”; (2) “presence of at least two ossified lateral scutes in the postcranial region, one of which articulating with posterior nuchal plate and first pleural rib”; (3) “reduction or absence of the middle posterodorsal process of cleithrum, between the articular and humeral processes”.

Our observations and comparisons corroborated the first two of these three synapomorphies. However, we would like to note that we do not agree with the third synapomorphy of De Pinna (1998) figure 14, which, as mentioned above, was based on an unpublished thesis by Higuchi (1992). Although we did find this derived character in the representatives of the three main doradid groups, that is, in *Acanthodoras* (Platydoradinae), *Anadoras* (Astrodoradinae) and *Doras* (Doradinae), the plesiomorphic doradid genus *Franciscodoras* presents the plesiomorphic catfish condition in which there are two well-developed dorsal processes of the cleithrum (Diogo et al., 2001b). This seems also to be the case

in the even more plesiomorphic doradid genus *Wertheimeria*, which is seemingly the most basal doradid genus (see Introduction). In fact, in the illustrations of *Wertheimeria* provided by Higuchi (1992), contrary to what is referred to in the textual descriptions given by this author, two well-developed, totally normal dorsal processes of the cleithrum are figured (Higuchi, 1992: fig. 17A) compared to Diogo et al. (2001b: fig. 2A). Therefore, this third character listed by Higuchi (1992) (and, consequently listed in De Pinna, 1998; fig. 14) does not seem to constitute, under the cladistic paradigm, a valid synapomorphy of the family Doradidae. However, our observations and comparisons point out that, apart from the two other synapomorphies listed by Higuchi (1992) (and De Pinna, 1998, fig. 14), doradid catfishes could, very likely, be diagnosed by an additional synapomorphy. This is described below:

Presence of a well-developed, roughly oval, deep fossa between the dorsal surfaces of the parieto-supraoccipital and the pterotic. The well-developed, roughly oval, deep fossa situated between the dorsal surfaces of the pterotic and the parieto-supraoccipital present in all the doradids examined (fig. 1) seems to correspond to the 'supratemporal fossa' described by De Pinna (1996) to diagnose the clade formed by the akysid, sisorid, aspredinid and erethistid sisoroid catfishes (De Pinna, 1996: fig. 10). Since (1) this fossa is present in the plesiomorphic doradid genus *Franciscodoras* and in representatives of all the three main doradid groups, namely *Anadoras* (Astrodoradinae), *Acanthodoras* (Platydoradinae) and *Doras* (Doradinae) (see Introduction); (2) the akysids, sisorids, aspredinids and erethistids are seemingly more related to sisoroid amblycipitids than to doradids (see above); and (3) these doradid catfishes clearly appear to be more closely related to auchenipterids than to sisoroids (see above), this feature could probably constitute a new Doradidae synapomorphy.

GENERAL CONCLUSIONS

In conclusion, our observations and comparisons pointed out one new, potential synapomorphy to characterise the doradid catfishes, namely the presence of a well-developed, roughly oval, deep fossa between the dorsal surfaces of the parieto-supraoccipital and the pterotic. Our study also pointed out three additional synapomorphies supporting the view of authors such as Regan (1911), Chardon (1968), Curran (1989), Mo (1991), Lundberg (1993) or De Pinna (1998), according to which the doradids are closely related to the auchenipterid catfishes. These are: (1) Meckel's cartilage highly developed, with its ascending portion extending dorsally to the dorsal surface of the coronoid process of the mandible and, thus, with a significant part of this ascending portion being visible in a lateral view of the cranium; (2) epioccipital constituting a significant part of the dorsal surface of the cranial roof; (3) posterolateral surface of the scapulo-coracoid presenting a prominent, triangular posterior process.

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