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Osteology and Myology of the Cephalic Region and Pectoral Girdle of the Chinese Catfish *Cranoglanis bouderius,* With a Discussion on the Autapomorphies and Phylogenetic Relationships of the Cranoglanididae (Teleostei: Siluriformes)

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ABSTRACT   The cephalic and pectoral girdle structures of the Chinese catfish *Cranoglanis bouderius* are described and compared with those of other catfishes as the foundation for an analysis on the Cranoglanididae autapomorphies and also for a discussion on the phylogenetic relationships between the cranoglanidids and the other catfishes. Our observations and comparisons indicate that cranoglanidids are defined, at least, by four autapomorphies, namely: 1) the cartilages associated with the mandibular barbels are broad, somewhat circular; 2) epioccipital with a well-developed posterodorsal process, which presents a large, deep, circular posterior concavity; 3) a well-defined, deep, anteroposteriorly elongated concavity formed by both the frontal and the lateral ethmoid to receive the anteromedial surface of the metapterygoid; 4) the adductor mandibulae A3″ is dorsally divided into two bundles and partially inserted on the posterior portion of the primordial ligament. With respect to the phylogenetic relationships of the Cranoglanididae, this study strongly suggests that these fishes are probably closely related to the Ariidae and the Claroteidae. J. Morphol. 253:229–242, 2002.   © 2002 Wiley-Liss, Inc.

KEY WORDS: autapomorphies; catfish; Cranoglanididae; myology; osteology; phylogeny; Siluriformes

The Siluriformes, or catfishes, with approximately 416 genera and over 2,500 species, represent about 32% of all freshwater fishes (Teugels, 1996). They are "one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade" (Teugels, 1996:10).

Among the 35 siluriform families (Ferraris and de Pinna, 1999), the Cranoglanididae, a small family of Chinese catfishes including a single species, *Cranoglanis bouderius* (see Burgess, 1989), is surely one of the less studied. In fact, despite the large number of works concerning catfish anatomy

(Regan, 1911; Alexander, 1965; Chardon, 1968; Gosline, 1975; Lundberg, 1975, 1982; Howes, 1983a,b, 1985; Arratia, 1987, 1990, 1992; Mo, 1991; Bornbusch, 1995; Diogo et al., 1999, 2000a,b; Diogo and Chardon, 2000a,b,c), the only article describing the morphology of cranoglanidids is that of Jayaram (1956), with this description being very incomplete and, very likely, even inaccurate in some points (see Chardon, 1968). The lack of studies concerning the morphology of the cranoglanidids probably explains why, although it is commonly accepted that these fishes should be grouped in a separate family (Cranoglanididae), not even one autapomorphy has been suggested so far to define this family (see Teugels, 1996). Furthermore, the phylogenetic relationships between the cranoglanidis and the other catfishes are still problematical (see, e.g., Teugels, 1996; de Pinna, 1998).

The aim of this work is, thus, to study in detail the osteological and myological structures of the cephalic region (branchial apparatus excluded) and pectoral girdle of *Cranoglanis bouderius* and to compare these structures with those of noncranoglanidid siluriforms (either studied and/or described in the literature) as the foundation for an analysis on the Cranoglanididae autapomorphies, and also for a discussion of the phylogenetic relationships between the cranoglanidids and the other catfishes. 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, ecomorphology, and particularly the phylogeny of these fishes.

MATERIALS 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), and from the National Museum of Natural History of Washington (USNM). Anatomical descriptions were made after dissection of alcohol-fixed or trypsin-cleared and alizarine-stained (following Taylor and Van Dyke's 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsin-cleared and alizarine-stained (cs) 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.

Amphilius brevis (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (cs). *Amphilius jacknosi* (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* (Doumeidae): MNHN 1961-0600, 1 (alc); *Arius hertzbergii* (Ariidae): LFEM, 1 (alc). *Arius heudelotii* (Ariidae): LFEM, 4 (alc). *Aspredo aspredo* (Aspredinidae): LFEM, 1 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Austroglanis sclateri* (Austroglanididae): LFEM, 1 (alc). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (cs). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (cs). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); MRAC 86-07-P-516, 1 (cs). *Belonoglanis tenuis* (Doumeinae): MRAC P.60494, 1 (alc); *Bunocephalus knerii* (Aspredinidae): LFEM, 1 (alc). *Cetopsis coecutiens* (Cetopsidae): LFEM, 1 (alc). *Chrysichthys cranchii* (Claroteidae): LFEM, 1 (alc); LFEM, 1 (cs). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 2 (cs). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 2 (cs). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Cranoglanis bouderius* (Cranoglanididae): LFEM, 2 (alc). *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Doras maculatus* (Doradidae): LFEM, 1 (alc). *Doumea typica* (Doumeidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152, 1 (alc). *Erethistes conta* (Erethistidae): LFEM, 1 (alc). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Glyptosternon reticulatum* (Sisoridae): LFEM, 1 (alc). *Glyptothorax fokiensis* (Sisoridae): LFEM, 1 (alc). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); LFEM, 1 (cs). *Heterobranchus longifilis* (Clariidae): LFEM, 2 (alc). *Heteropneustes fossilis* (Heteropneustidae): LFEM, 1 (alc). *Ictalurus punctatus* (Ictaluridae): LFEM, 5 (alc). *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Nematogenys inermis* (Nematogenyidae): LFEM, 1 (alc). *Nothoglanidium thomasi* (Claroteidae): LFEM, 2 (alc). *Paramphilius trichomycteroides* (Amphiliidae): LFEM, 2 (alc). *Paraplotosus albilabris* (Plotosidae): USNM 173554, 2 (alc). *Phractura brevicauda* (Doumeidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (cs). *Phractura intermedia* (Doumeidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias* (Pimelodidae): LFEM, 2 (alc), LFEM, 2 (cs). *Plotosus lineatus* (Plotosidae): USNM 200226), 2 (alc). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (cs). *Schilbe intermedius* (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc).

RESULTS

In this section we describe the osteology and myology of the cephalic region and pectoral girdle of *Cranoglanis bouderius*. The visual information given in the figures has preponderance over the tex-

tual one and, thus, this latter will be brief. In the anatomical descriptions the nomenclature for the osteological structures basically follows that of Arratia (1997). The nomenclature of the cephalic muscles is mainly based on Winterbottom (1974). However, for the different adductor mandibulae sections we follow Diogo and Chardon (2000b), since recent works have pointed out that, with respect to these sections, Winterbottom's (1974) nomenclature presents serious limitations (see Gosline, 1989; Diogo and Chardon, 2000b). In relation to the muscles associated with the mandibular barbels—which were not studied by Winterbottom (1974)—we follow Diogo and Chardon (2000c). With respect to the nomenclature of the pectoral girdle muscles, we follow Diogo et al. (2001).

Osteology

Os mesethmoideum. It is situated on the anterodorsal surface of the neurocranium (Figs. 1–5). Each of its anterolateral arms is ligamentously connected to the premaxillary.

Os lateroethmoideum. It exhibits a laterally directed articulatory facet for the palatine (Fig. 5: af-apal), which is visible in a dorsal view of the neurocranium (Fig. 3). There is a deep dorsal concavity between the dorsomedial surface of each lateral ethmoid and the anterodorsolateral margin of the frontals (Fig. 3). Laterally, the paired lateral ethmoids extend as two wings, which are highly expanded laterally (Figs. 3, 5) and ventrally (Figs. 1, 4).

Os vomerale. This bone is T-shaped, lacking a ventral tooth-plate (Fig. 5).

Os orbitosphenoideum. It lies posterior to the lateral ethmoid (Figs. 1, 2, 4). The dorsal edge of its lateral wall sutures with the ventral surface of the frontal (Fig. 4).

Os pterosphenoideum. It is posterior to the orbitosphenoid (Figs. 4, 5), covering, together with this bone, the gap between the frontals and the parasphenoid (Fig. 4).

Os parasphenoideum. This is the longest bone of the cranium (Figs. 4, 5). It bears a pair of ascending flanges, which suture with the pterosphenoids and prootics.

Os frontale. The frontals are large bones (Figs. 1, 3, 4) that are largely separated by both the anterior and the posterior fontanels (Fig. 3). The anterolateral margin of the frontal, together with the posterolateral surface of the lateral-ethmoid, form a deep ventral concavity (Fig. 5: cv-mp) to receive the anteromedial surface of the metapterygoid (Fig. 4).

Os sphenoticum. It bears, together with the pterotic, an articulatory facet for the hyomandibula (Figs. 4, 6).

Os pteroticum. In dorsal view it is somewhat triangular and is smaller than the sphenotic in size (Fig. 3).
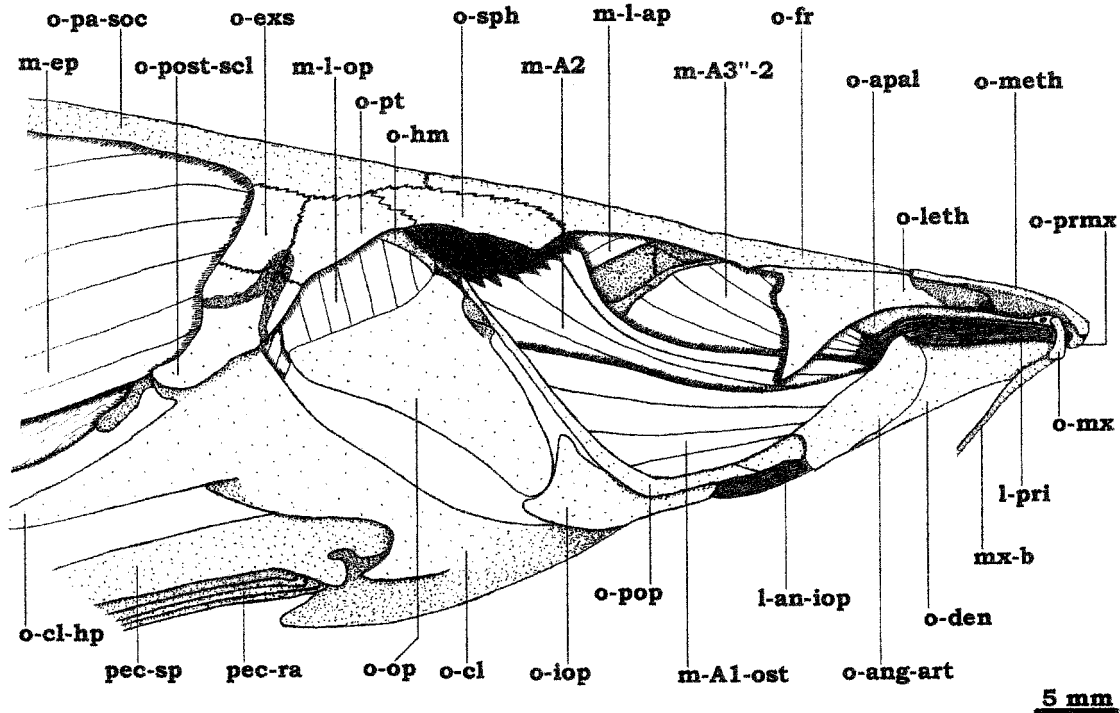
Fig. 1. Right, lateral view of the cephalic musculature of *Cranoglanis bouderius.* All the muscles are exposed. l-an-iop, ligamentum angulo-interoperculare; l-pri, ligamentum primordium; m-A1-ost, m-A2, m-A3″-2, sections of the musculus adductor mandibulae; m-ep, musculus epaxialis; m-l-ap, musculus levator arcus palatini; m-l-op, musculus levator operculi; mx-b, maxillary barbel; o-ang-art, os anguloarticulare; o-apal, os autopalatinum; o-cl, os cleithrum; o-cl-hp, humeral process of os cleithrum; o-den, os dentale; o-exs, os extrascapulare; o-fr, os frontale; o-hm, os hyomandibulare; o-iop, os interoperculare; o-leth, os lateroethmoideum; o-meth, os mesethmoideum; o-mx, os maxillare; o-op, os operculare; o-pa-soc, os parietosupraoccipitale; 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.

Os prooticum. Together with the pterosphenoid, it borders the well-developed foramen of the trigemino-facial nerve complex (Fig. 6).

Os epioccipitale. It situates on the posterodorsal surface of the neurocranium. It has a well-developed posterodorsal process (Figs. 2, 3: o-epoc-pdp) that presents a large, deep, circular posterior concavity, from which originate (Figs. 2, 3) a great part of the fibers of the muscle protractor of the anteroventral process of the fourth parapophysys (see below).

Os exoccipitale. The exoccipital is a small bone situated laterally to the basioccipital (Fig. 6).

Os basioccipitale. A well-developed, unpaired bone, which forms the posteriomost part of the floor of the neurocranium (Fig. 6). Its ventrolateral surfaces are sutured to the ventro-medial limbs of the posttemporo-supracleithra (Fig. 6).

Os parieto-supraoccipitale. It is a large bone with a well-developed, posteriorly directed posterodorsal process (Fig. 3).

Os extrascapulare. Its dorsal surface, together with the dorsal surfaces of both the pterotic and the posttemporo-supracleithrum, form a well-defined, λ-shaped dorsal concavity of the posterodorsolateral surface of the cranial roof (Figs. 1, 3).

Os angulo-articulare. This bone (Figs. 1, 2, 7, 8), together with the dentary, coronomeckelian, and Meckel's cartilage, constitute the mandible (Fig. 7C). Its anterodorsal surface, together with the posterodorsal surface of the dentary, form a prominent dorsal process (processus coronoideus), which is linked to the maxillary by means of a massive, long ligament (Figs. 1, 2, 7A: li.pri). Posterodorsally, the anguloarticular has an articulatory surface for the quadrate. Posteroventrally, it presents a well-developed, posteriorly directed posteromedial process (Fig. 7C), which situates medially to the anterior portion of the angulointeropercular ligament (1-an-iop) and thus, is not visible in a lateral view of the cranium (see Figs. 1, 2).

Os dentale. The dentaries (Figs. 1, 2, 7, 8) are firmly connected, near to their symphysis, to the supporting parts of the broad, somewhat circular cartilages (Fig. 9) associated with the mandibular barbels by means of a large number of short and thin fibers. Anterodorsally, each dentary bears numerous slightly curved teeth (Fig. 7C).

Os coronomeckelium. This is a small bone lodged in the medial surface of the mandible. Posterodorsally it bears a crest for attachment of the adductor mandibulae A3′-d (Fig. 7C).

Os praemaxillare. The premaxillary (Figs. 1, 3, 4, 5) are a pair of large triangular plates lying underneath and attaching to the mesethmoidal cornua
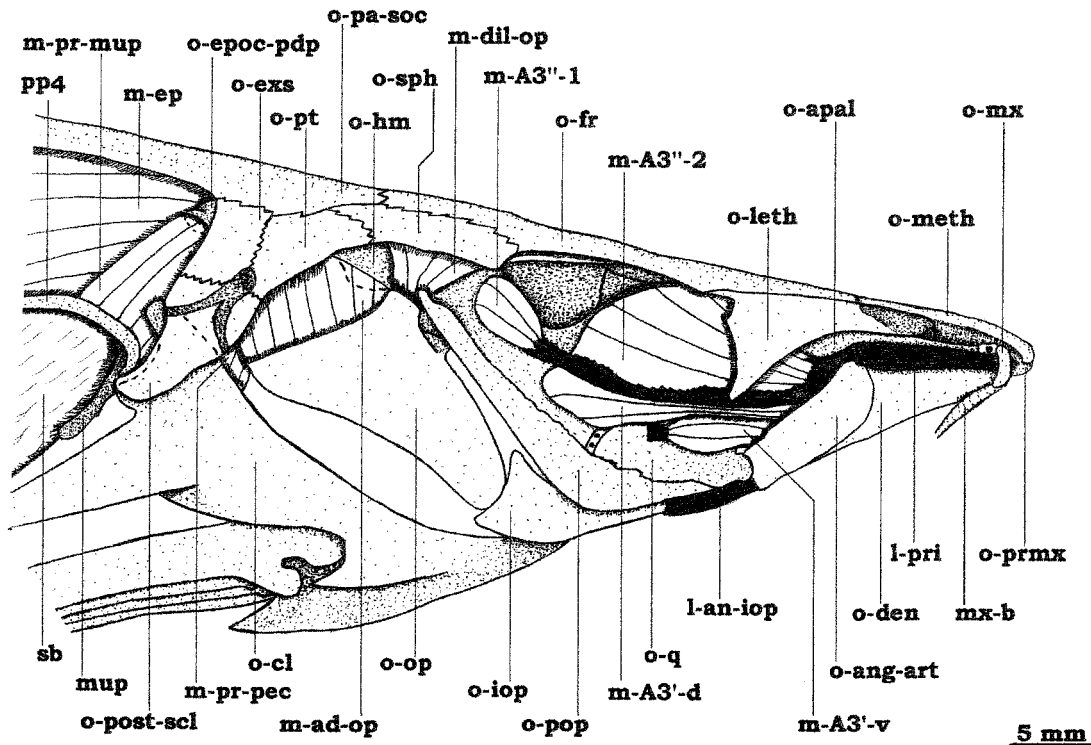
Fig. 2. Right, lateral view of the cephalic musculature of *Cranoglanis bouderius*. Levator operculi, A1-ost, A2, levator arcus palatini, and anterolateral fibers of epaxialis removed. l-an-iop, ligamentum angulointeroperculare; l-pri, ligamentum primordium; m-A3′-d, m-A3′-v, m-A3″-1, m-A3″-2, sections of the musculus adductor mandibulae; m-ad-op, musculus adductor operculi; m-dil-op, musculus dilatator operculi; m-ep, musculus epaxialis; m-pr-mup, musculus protractor of müllerian process; m-pr-pec, musculus protractor pectoralis; mup, müllerian process; mx-b, maxillary barbel; o-ang-art, os anguloarticulare; o-apal, os autopalatinum; o-cl, os cleithrum; o-den, os dentale; o-epoc-pdp, posterodorsal process of os epioccipital; o-exs, os extrascapulare; o-fr, os frontale; o-hm, os hyomandibulare; o-iop, os interoperculare; o-leth, os lateroethmoideum; o-meth, os mesethmoideum; o-mx, os maxillare; o-op, os operculare; o-pa-soc, os parietosupraoccipitale; o-pop, os praeoperculare; o-post-scl, os posttemporo-supracleithrum; o-prmx, os praemaxillare; o-pt, os pteroticum; o-sph, os sphenoticum; pp4, parapophysis 4; sb, swim-bladder.

via ligamentous tissue. Ventrally, each premaxillary bears numerous small teeth (Fig. 5) having their tips slightly turned backward.

Os maxillare. The maxillary (Figs. 1–5), is connected to the premaxillary by means of a strong, short ligament. As in most catfishes, the maxillary barbels are supported by the maxillaries (Figs. 1, 2, 5).

Os autopalatinum. This is a rod-like bone (Figs. 3–5) whose anterior end is tipped by a large cartilage with two anterolateral concavities, which accept the two proximal heads of the maxillary; its posterior tip is capped by a small cartilage. Medially, the autopalatine articulates with the lateral ethmoid (Fig. 5).

Os hyomandibulare. The homology and, thus, the correct denomination of this bone, as well as of the other suspensorium components of catfish, has been the subject of endless controversies (McMurrich, 1884; Gosline, 1975; Arratia and Menumarque, 1981; Howes, 1983a,b, 1985; Arratia, 1987, 1990, 1992). However, for the time being we will describe the suspensorial bones by their most often used names (see Arratia, 1992). The hyomandibula articulates dorsally with both the pterotic and the sphen-

otic (Figs. 4, 6). Posteriorly, the hyomandibula presents a well-developed articulatory facet for the opercular (Fig. 4).

Os entopterygoideum. Well-developed, its medial margin is connected by means of two thin, long ligaments to the vomer and to the metapterygoid (Fig. 5). Its dorsolateral surface is firmly attached, via connective tissue, to the posteroventral surface of the autopalatinum. The ectopterygoids are absent.

Os metapterygoideum. It is a large bone, which is posteriorly sutured with the hyomandibula and ventrolaterally connected, by a small cartilaginous band and by bony sutures, to the quadrate (Fig. 4). The anteromedial surface of the metapterygoid is firmly attached (see Fig. 4) to the lateral surface of the neurocranium (frontal, lateral ethmoid, and orbitosphenoid) by means of connective tissue.

Os quadratum. Its posterodorsal surface is separated from the hyomandibula by means of well-developed cartilaginous band (Fig. 4).

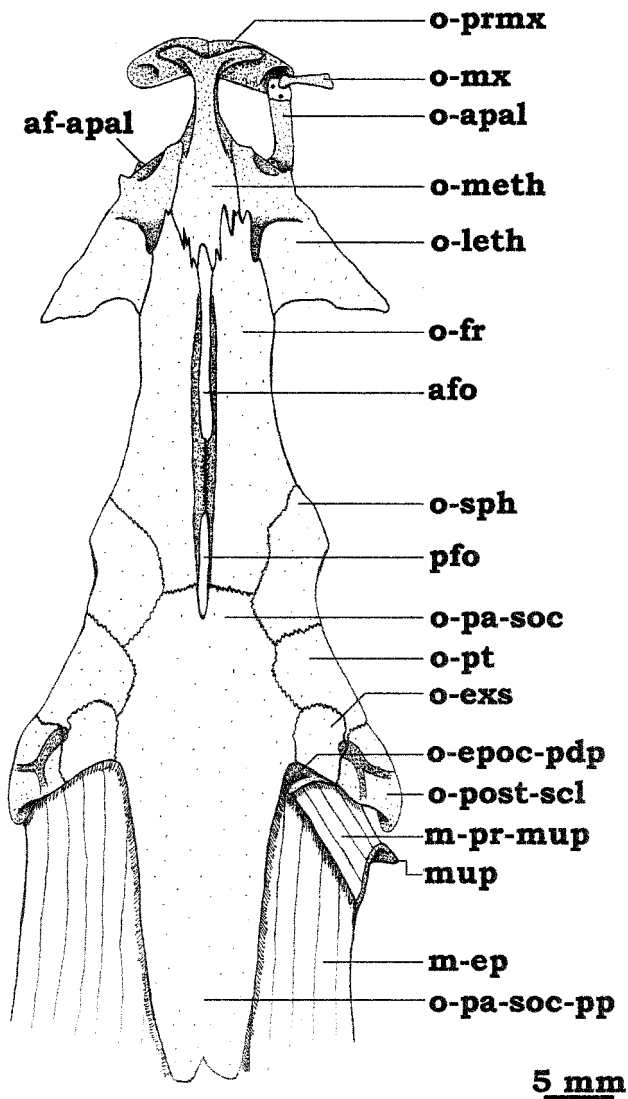**Os praeoperculare.** This is a long and thin bone firmly sutured to the hyomandibula and to the quadrate (Fig. 4).

Fig. 3. Dorsal view of the neurocranium and palatine-maxillary system of *Cranoglanis bouderius*. On the left side, palatine-maxillary system removed; on the right side, anterodorsal fibers of epaxialis removed. af-apal, articulatory facet for autopalatinum; afo, anterior fontanel; m-ep, musculus epaxialis; m-pr-mup, musculus protractor of müllerian process; mup, müllerian process; o-apal, os autopalatinum; o-epoc-pdp, posterodorsal process of os epioccipital; o-exs, os extrascapulare; o-fr, os frontale; o-leth, os lateroethmoideum; o-meth, os mesethmoideum; o-mx, os maxillare; os-pa-soc, os parietosupraoccipitale; os-pa-soc-pp, posterior process of os parietosupraoccipitale; o-post-scl, os posttemporo-supracleithrum; o-prmx, os praemaxillare; o-pt, os pteroticum; o-sph, os sphenoticum; pfo, posterior fontanel.

Os operculare. It is a triangular bone anterodorsally articulated with the hyomandibula (Fig. 2).

Os interoperculare. Its anterior and anteromedial surfaces are linked by means of thick ligamentous tissue to the angulo-articular (Figs. 1, 2, 8) and to the posterior ceratohyal (Fig. 8), respectively.

Os interhyale. The interhyal is a small bone attached, by means of ligaments, to both the poste-

rior ceratohyal and the quadratohyomandibular cartilage.

Os ceratohyale posterior. This triangular bone (Fig. 8) is linked by ligaments to the anguloarticular, interhyal, and interopercular.

Os ceratohyale anterior. Paired. Together with the posterior ceratohyal, it supports the branchiostegal rays (Fig. 8).

Os hypohyale ventrale. Each ventral hypohyal contains a ventral concavity to receive one of the anterolateral edges of the parurohyal (Fig. 8).

Os hypohyale dorsale. It is a small bone situated dorsally to the ventral hypohyal.

Os parurohyale. The parurohyal (see Arratia and Schultze, 1990) is somewhat triangular, lying medially behind the ventromedial surfaces of the ventral hypohyals and being connected to these bones by means of two strong, thick ligaments (Fig. 8).

Os posttemporo-supracleithrum. The dorsomedial limb of this well-developed bone (Figs. 1–3, 6) is sutured with the pterotic and the extrascapular (Fig. 3). Its stout ventromedial limb is firmly sutured to the basioccipital (Fig. 6). Its ventrolateral limb is deeply forked (Fig. 6), forming an articulating groove for the upper edge of the cleithrum (see Fig. 2). The posteroventral surface of the posttemporo-supracleithrum is firmly attached, by means of massive connective tissue, to the anteroventral process of the fourth parapophysis (= Müllerian process) (Figs. 2, 6: mup), which is well-developed and presents a highly mobile, circular (in posterior view) ventrolateral tip.

Os cleithrum. The cleithrum (Fig. 10) is a large, well-ossified stout structure forming the major 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 (see Fig. 11: pec-sp-dc) of the pectoral spine. The two cleithra are attached in the anteromedial line via massive connective tissue (Fig. 10). The humeral process (Fig. 1: o-cl-hp) is well developed.

Os scapulo-coracoideum. This is an elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge (Fig. 10). Mesially it joins its counterpart in an interdigitation of several strong serrations. Anterolaterally, it presents a large anteriorly directed process, usually called the coracoid bridge, which extends ventrally to the ventrolateral surface of the cleithrum, fusing with an anteroventral ridge of this bone (Fig. 10). The posterolateral end of the scapulo-coracoid bears two condyles, which articulate, respectively, with the pectoral spine and the complex radial (see Mo, 1991). Medially to these two condyles there is a ventral groove (Fig. 10: o-sca-cor-vlg), which accommodates the ventral condyle of the pectoral spine when this spine is erected. Posteriorly, the scapulocoracoid presents a well-developed foramen, which
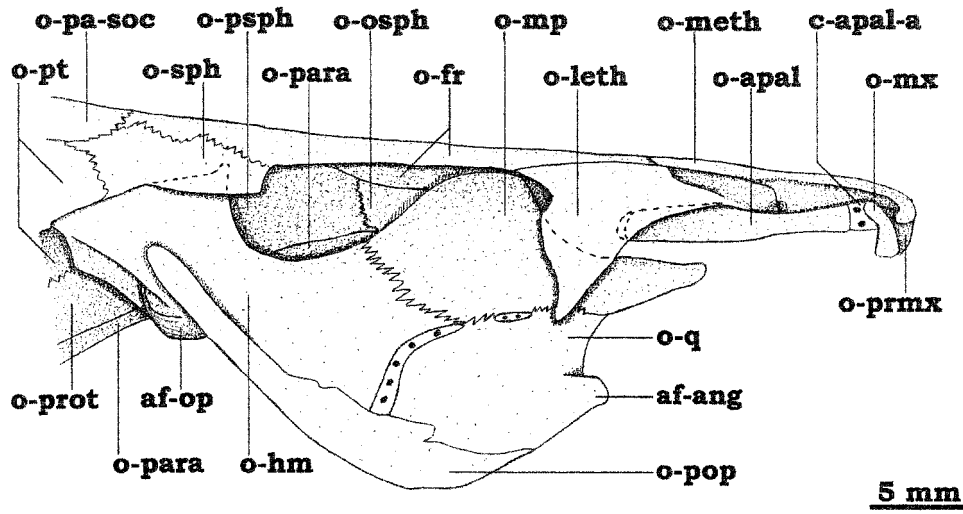
Fig. 4. Right, lateral view of the suspensorium and its attachement on the neurocranium in *Cranoglanis bouderius*. af-ang, articulatory facet for anguloarticulare; af-op, articulatory facet for operculare; c-apal-a, cartilago autopalatinus anterior; o-apal, os autopalatinum; o-fr, os frontale; o-hm, os hyomandibulare; o-leth, os latero-ethmoideum; o-meth, os mesethmoideum; o-mp, os metapterygoideum; o-mx, os maxillare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-pa-soc, os parietosupraoccipitale; o-pop, os praeoperculare; o-prmx, os praemaxillare; o-prot, os prooticum; o-psph, os pterosphenoideum; o-pt, os pteroticum; o-q, os quadratum; o-sph, os sphenoticum.

accepts the anterior condyle of the pectoral spine when this latter is abducted. There is a well-developed mesocoracoid arch (Fig. 10: mcor-ar).

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost originates on the preopercular and quadrate and inserts on the laterodorsal surface of the anguloarticular (Fig. 1). The A2, which lies dorsomesially to the A1-ost, attaches posteriorly on the lateral surface of both the preopercular and the hyomandibula and, via a well-developed tendon, on the dorsolateral surfaces of both the frontal, the sphenotic, and the pterotic (Fig. 1). Anteriorly, it
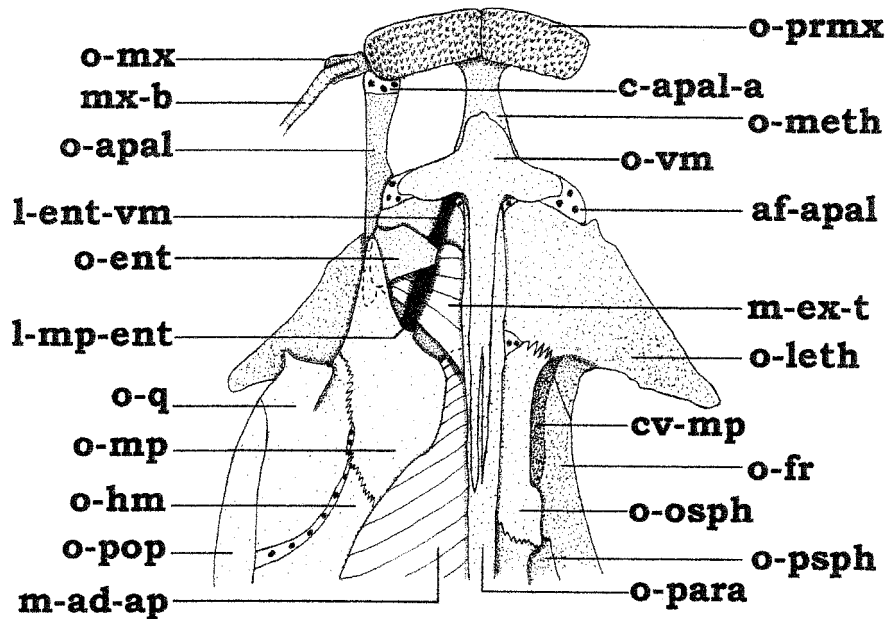

Fig. 5. Ventral view of the anterior region of the neurocranium of *Cranoglanis bouderius*. On the left side the suspensorium and palatine-maxillary system, as well as the muscles and ligaments associated with these structures, are illustrated. af-apal, articulatory facet for autopalatinum; c-apal-a, cartilago autopalatinus anterior; cv-mp, concavity for metapterygoideum; l-ent-vm, ligamentum entopterygoideo-vomerale; l-mp-ent, ligamentum metapterygoideo-entopterygoideum; m-ad-ap, musculus adductor arcus palatini; m-ex-t, musculus extensor tentaculi; mx-b, maxillary barbel; o-apal, os autopalatinum; o-ent, os entopterygoideum; o-fr, os frontale; o-hm, os hyomandibulare; o-leth, os latero-ethmoideum; o-meth, os mesethmoideum; o-mp, os metapterygoideum; o-mx, os maxillare; o-osph, os orbitosphenoideum; o-para, os parasphenoideum; o-pop, os praeoperculare; o-prmx, os praemaxillare; o-psph, os pterosphenoideum; o-q, os quadratum; o-vm, os vomerale.

Fig. 6. Ventral view of the posterior region of the neurocranium and suspensorium of *Cranoglanis bouderius*. On the left side, opercular, adductor hyomandibularis, adductor operculi, and protractor pectoralis removed. cc, complex centrum; for-V-VII, trigemino-facialis foramen; m-ad-ap, musculus arcus palatini; m-ad-hm, musculus adductor hyomandibularis; m-ad-op, musculus adductor operculi; m-pr-mup, musculus protractor of müllerian process; m-pr-pec, musculus protractor pectoralis; mup, Müllerian process; o-boc, os basioccipitale; o-exoc, os exoccipitale; o-hm, os hyomandibulare; o-op, os operculare; o-pop, os praeoperculare; o-post-scl, os posttemporo-supracleithrum; o-prot, os prooticum; o-pt, os pteroticum; o-sph, os sphenoticum; o-tri, os tripus.
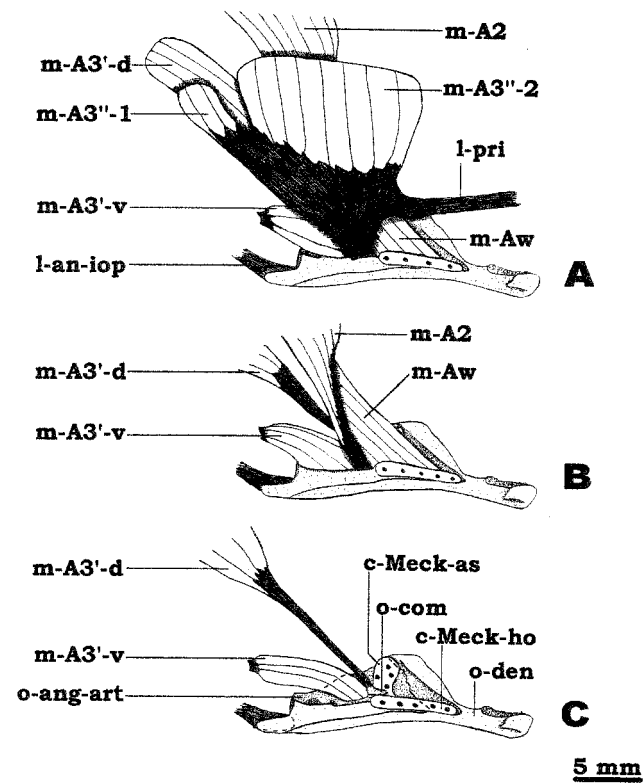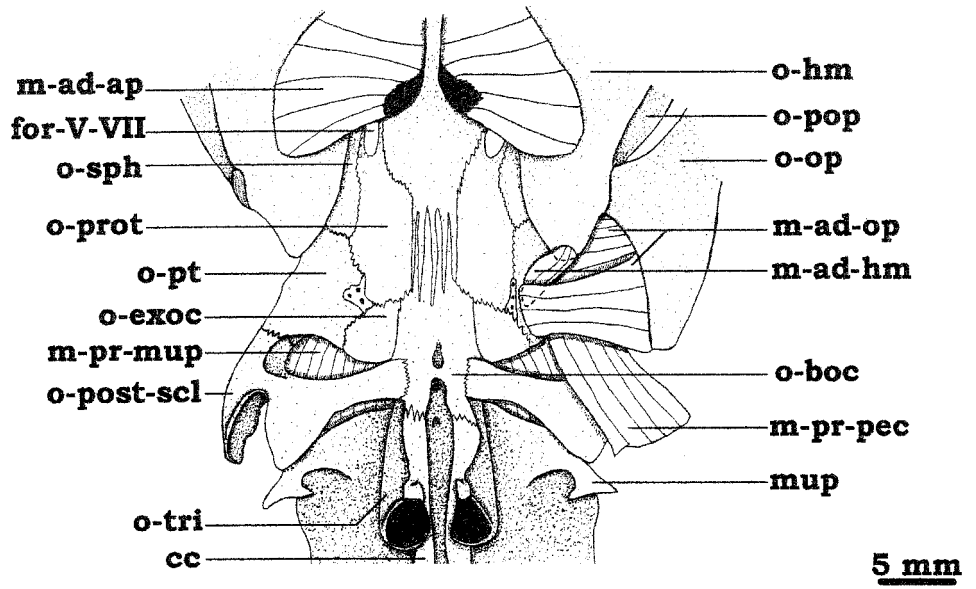

attaches tendinously on the medial crest of the anguloarticular (Fig. 7B). The adductor mandibulae A3′ is divided in a dorsal and a ventral part. The dorsal one (A3′-d) originates on the hyomandibula and metapterygoid (Fig. 2), and inserts tendinously

Fig. 7. Medial view of the left lower jaw of *Cranoglanis bouderius*. **A:** Adductor mandibulae complex, except A1-ost, completely exposed. **B:** A3″-1 and A3″-2 removed. **C:** Aω and A2 removed. c-Meck-as, c-Meck-ho, ascending and horizontal portions of cartilago Meckeli; l-an-iop, ligamentum angulointeroperculare; l-pri, ligamentum primordium; m-A2, m-A3′-d, m-A3′-v, m-A3″-1, m-A3″-2, m-Aω, sections of the musculus adductor mandibulae; o-ang-art, os anguloarticulare; o-com, os coronomeckelium; o-den, os dentale.
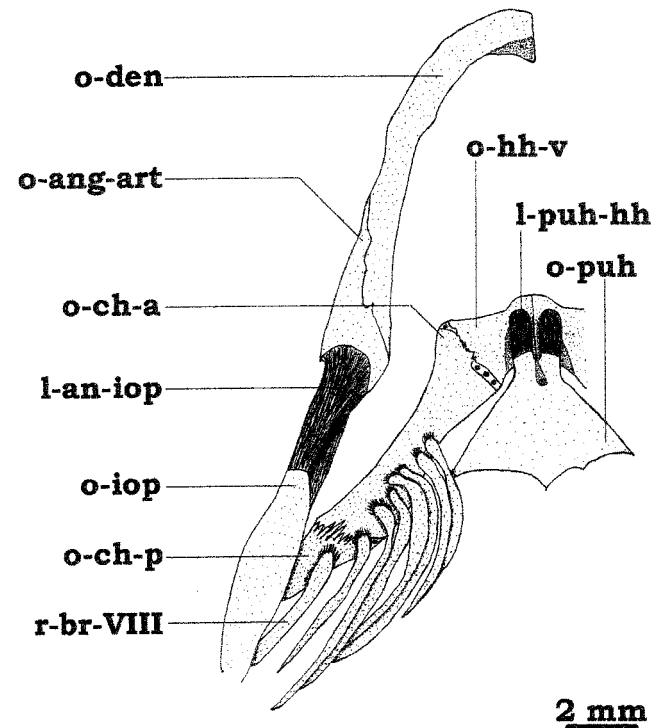

Fig. 8. Ventral view of the splanchnocranium of *Cranoglanis bouderius*. l-an-iop, ligamentum angulointeroperculare; l-puh-hh, ligamentum parurohyalohypohyale; o-ang-art, os anguloarticulare; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-den, os dentale; o-hh-v, os hypohyale ventrale; o-iop, os interoperculare; o-puh, os parurohyale; r-br-VIII, branchiostegal ray VIII.
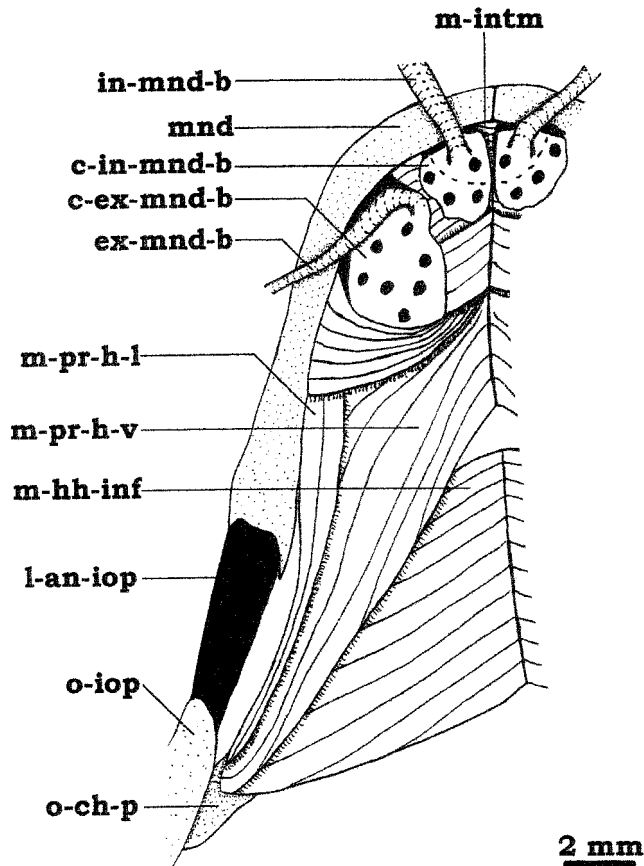
Fig. 9. Ventral view of the cephalic musculature of *Cranoglanis bouderius*. c-ex-mnd-b, cartilago externus mandibularis tentaculi; c-in-mnd-b, cartilago internus mandibularis tentaculi; ex-mnd-b, in-mnd-b, external and internal mandibular barbels; l-an-iop, ligamentum angulointeroperculare; m-hh-inf, musculus hyohyoideus inferiorm-int, musculus intermandibularis; m-pr-h-l, m-pr-h-v, pars lateralis and ventralis of musculus protractor hyoideus; o-ch-p, os ceratohyale posterior; o-iop, os interoperculare.

on the coronomeckelian bone (Fig. 7C). The ventral one (A3′-v) originates, by means of a small tendon, on the quadrate (Fig. 2) and inserts on the medial surface of the anguloarticular (Fig. 7C). The deeper bundle of the adductor mandibulae, the A3″, is posterodorsally divided (Figs. 2, 7) in a posterior, smaller bundle (A3″-1) and in an anterior, larger one (A3″-2). These two bundles are, however, anteroventrally associated in a single, massive tendon (Fig. 7A), the anterodorsal and the anteroventral portion of which are associated with the posterior portion of the primordial ligament and with the medial surface of the anguloarticular, respectively (Fig. 7A). Lastly, the Aω, which is well-developed, attaches anteroventrally on the medial surface of both the dentary and the anguloarticular and posterodorsally on the tendon of the adductor mandibulae A2 (Fig. 7B).

Musculus levator arcus palatini. It originates on the ventrolateral surface of the sphenotic, as well as on the lateral surface of the frontal (see Fig. 1), and inserts on the lateral face of the hyomandibula.

Musculus adductor arcus palatini. It extends from the lateral sides of the parasphenoid, pterosphenoid, and orbitosphenoid to the medial sides of the hyomandibula and metapterygoid (Figs. 5, 6).

Musculus adductor hyomandibularis. This small muscle (see Discussion), situated between the two bundles of the adductor operculi (Fig. 6), originates on the ventral surface of the pterotic and inserts on the posterodorsomedial surface of the hyomandibula (Fig. 6).

Musculus adductor operculi. It is somewhat differentiated into two bundles (Fig. 6). The outer one, situated lateral to the adductor hyomandibularis (Fig. 6) but mesial to the levator operculi, originates on the ventral surface of the pterotic (Fig. 6) and on the posterodorsolateral surface of the hyomandibula (Fig. 2) and inserts on the posteromedial surface of the opercular (Figs. 2, 6). The inner one, situated medial to the adductor hyomandibularis, originates on the ventral surface of the pterotic and inserts on the dorsomedial surface of the opercular (Fig. 6).

Musculus dilatator operculi. This thick muscle situates medially to the levator arcus palatini. It runs from the dorsolateral margin of the sphenotic, as well as from the ventrolateral surface of the frontal, to the anterodorsal edge of the opercular (medial to the preopercular but lateral to the articulatory facet of the opercular for the hyomandibula) (Fig. 2).

Musculus levator operculi. It originates on the ventrolateral margins of both the pterotic and the posttemporo-supracleithrum, as well as on the posterodorsolateral surface of the hyomandibula, and inserts on the dorsal edge of the opercular (Fig. 1).

Musculus extensor tentaculi. It runs from the ventromedial surface of both the lateral ethmoid and the orbitosphenoid (Fig. 5) to the ventral surface of the entopterygoid and to the posteromedial margin of the autopalatine.

Musculus protractor hyoidei. This muscle has three parts. The pars ventralis (Fig. 9: m-pr-h-v), in which are lodged the cartilages associated with the mandibular barbels, originates on both the anterior and the posterior ceratohyals and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis. The pars lateralis (Fig. 9: m-pr-h-l) originates on the posterior ceratohyal, inserting, by means of a thick tendon, on the ventromedial face of the dentary. The pars dorsalis originates tendinously on the anterior ceratohyal and inserts tendinously on the dentary, meeting its counterpart anteromedially in a medial aponeurosis.

Muscle intermandibularis. This well-developed muscle joins the two mandibles (Fig. 9).

Musculus retractor externi mandibularis tentaculi. This small muscle runs from the moving part of the cartilage associated with the outer mandibular barbel to the dentary.
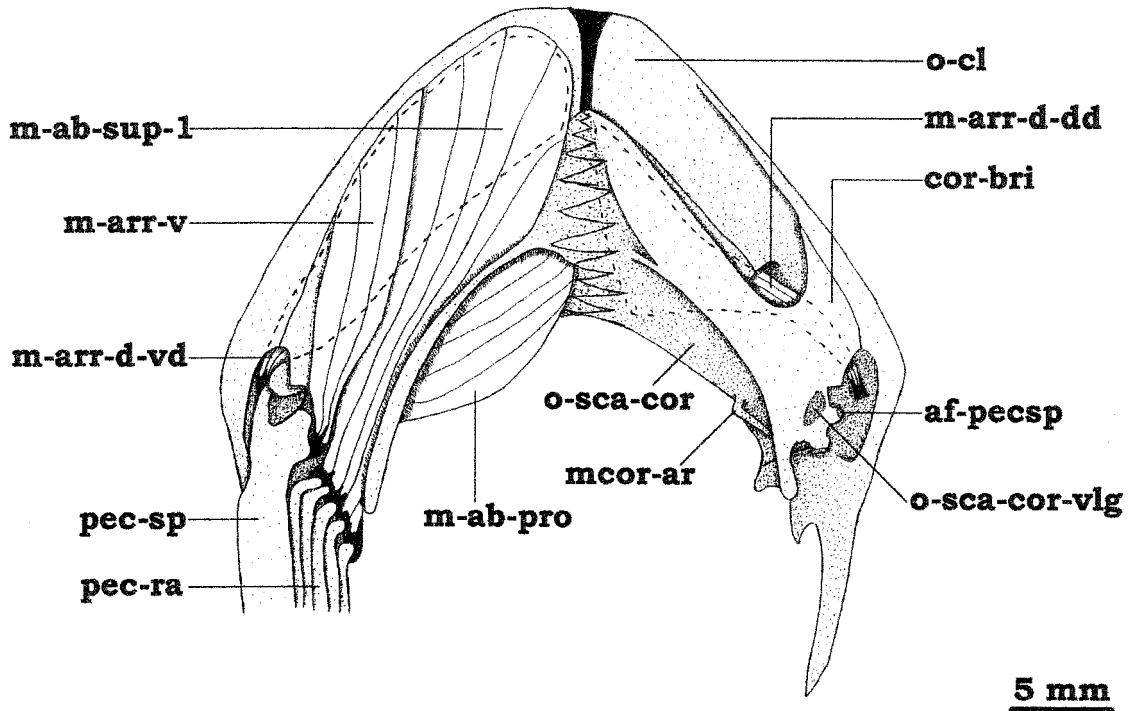
Fig. 10. Ventral view of the pectoral girdle of *Cranoglanis bouderius.* On the left side all muscles are exposed; on the right side the arrector ventralis, abductor superficialis, abductor profundus, and dorsal division of arrector dorsalis were removed. af-pecsp, articulatory facet for pectoral spine; cor-bri, coracoid bridge; m-ab-pro, musculus abductor profundus; m-ab-sup-l, musculus abductor superficialis; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor, ventro-lateral groove of os scapulo-coracoide; pec-ra, pectoral rays; pec-sp, pectoral spine.

Musculus retractor interni mandibularis tentaculi. This small muscle originates on the moving part of the cartilage associated with the internal mandibular barbel and inserts on the dentary.

Musculus hyohyoideus inferior. This thick muscle (Fig. 9) attaches medially on a median aponeurosis and laterally on the ventral surfaces of the ventral hypohyal, anterior ceratohyal, and 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.

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

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 ventrolateral surface of the cleithrum (Fig. 10) to the ventral condyle of the pectoral spine (Fig. 11).

Musculus arrector dorsalis. This muscle is differentiated into two well-developed divisions. The ventral division, situated on the ventral surface of the pectoral girdle (Fig. 10: m-arr-d-vd), originates on the ventral margin of the cleithrum and inserts

on the anterolateral edge of the pectoral spine (Fig. 11). The dorsal division, situated on the dorsal surface of the pectoral girdle (Fig. 10: m-arr-d-dd), originates on the dorsomedial edge of the scapulocoracoid and inserts on the anterior edge of the dorsal condyle of the pectoral spine (Fig. 11).

Musculus abductor profundus. It originates on the posteromedial edge of the coracoid (Fig. 10), 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 (Fig. 11).

Musculus adductor superficialis. It is differentiated in two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulocoracoid, as well as on the dorsolateral edge of the mesocoracoid arch and inserts on the anterodorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from the ventrolateral edge of the mesocoracoid arch and the dorsal surface of the proximal radials to the anteroventral 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. 10: m-ab-sup-1) attaches anteriorly on the ventral face of both the cleithrum and the scapulocoracoid and posteriorly on the anteroventral mar-
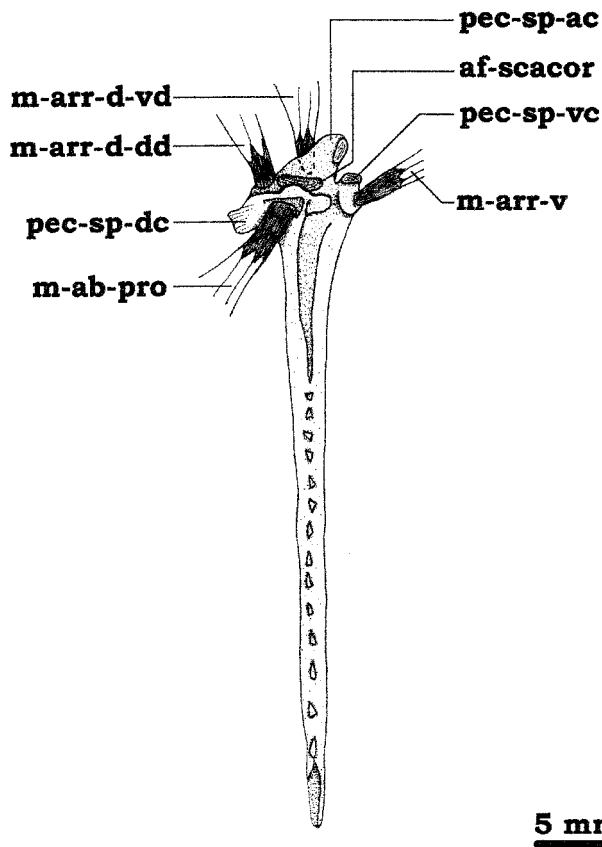
Fig. 11. Medial view of the right pectoral spine of *Cranoglanis bouderius,* showing the insertions of the muscles responsible for its movement. af-scacor, articulatory facet for scapulo-coracoide; m-ab-pro, musculus abductor profondus; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine.

gin of the ventral part of the pectoral fin rays. The smaller section runs from the posterolateral edge of the scapulocoracoid to the anterodorsal margin of the ventral part of the pectoral fin rays.

Musculus protractor pectoralis. This well-developed muscle (Figs. 2, 6) runs from the ventral surfaces of both the pterotic and the posttemporo-supracleithrum to the anterodorsal surfaces of both the cleithrum and the scapulo-coracoid.

Musculus epaxialis. Although this muscle (Figs. 1–3) is not included, by definition, in the musculature of the cephalic region nor of the pectoral girdle (see Winterbottom, 1974), it is noteworthy here, since its anteriormost fibers are differentiated (see below) in a separate muscle, the protractor of the Müllerian process, which runs from the exoccipital, epioccipital, extrascapular, pterotic, and posttemporo-supracleithrum to the Müllerian process (Figs. 2, 3, 6). In fact, the protractor of the Müllerian process, which, like other similar "protactors" (see Mo, 1991: 198), clearly seems to be the result of the differentiation of the epaxialis muscle, and clearly represents an independent muscle, which, as stated by its name, protracts the well-developed, highly mobile Müllerian process (see Discussion).

DISCUSSION

As noted in the Introduction, the aim of this work is to give, for the first time, a detailed description of the osteological and myological structures of the cephalic region and pectoral girdle of the cranoglanidids and also to compare these structures with those of noncranoglanidid siluriforms (studied by us and/or described in the literature) as the foundation for an analysis of the Cranoglanididae autapomorphies and also for a discussion of the phylogenetic relationships of the cranoglanidids. Our observations and comparisons point out that, although the cranoglanidids are "generalized" catfishes (for a definition of "generalized" catfishes see, e.g., Diogo et al., 2001); that is, although they lack a large number of derived morphological features, there are four derived characters that are exclusively found in these fishes and that, thus, represent Cranoglanididae autapomorphies, which are described below.

The cartilages associated with the mandibular barbels are broad and somewhat circular. Almost all the nondiplomystid catfishes present mandibular barbels, which are basally associated with cartilages (see Diogo and Chardon, 2000c). These cartilages could present different sizes and different shapes in different catfish taxa. For example, they could be well-developed and somewhat rectangular (e.g., erethistids, ariids, cetopsids, claroteids, heteropneustids, plotosids, and clariids), well-developed but with an irregular shape (e.g., sisorids), or significantly long and thin (e.g., nematogenyids, bagrids, amphiliids) (this study; also Takahasi, 1925; Munshi, 1960; Alexander, 1965; Singh, 1967; Singh and Munshi, 1968; Howes, 1983a; Ghiot et al., 1984; Mo, 1991; Bornbusch, 1995; Diogo et al., 1999, 2000a; Diogo and Chardon, 2000a,c). However, only in the Cranoglanididae the cartilages associated with the mandibular barbels are significantly broad, with a somewhat circular shape (see Fig. 9).

Epioccipital with a well-developed postero-dorsal process, which presents a large, deep, circular posterior concavity. Although there are some differences concerning the configuration of the epioccipital within different groups of catfishes (this study; also Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg, 1975; Arratia, 1987; Bornbusch, 1995; Mo, 1991; de Pinna, 1993), the presence of a well-developed posterodorsal process with a large, deep, circular posterior concavity, is a derived feature exclusively present in the cranoglanidids (see Figs. 2, 3). This character seems to be associated with the presence (contrary to what was supposed before this study) of an "elastic-spring-apparatus" in the Cranoglanididae. The "elastic-spring-apparatus" (Bridge and Haddon, 1984; Alexander, 1965; Chardon, 1968) is formed by the modified Müllerian pro-

cess, which is highly flexible, distantly separated from the posttemporo-supracleithrum, and posteroventrally attached to the swim-bladder, and by a "protractor" muscle inserted on the Müllerian process, the contraction and relaxation of which promotes the vibration of the swimbladder and, consequently, the production of sound. So far (see de Pinna, 1998: 306), an "elastic-spring-apparatus" had only been reported in the doradids, auchenopterids, mockokids, malapterurids, ariids, and pangasids (although bagrids present a somewhat similar mechanism to that of an "elastic-spring-apparatus" [Diogo et al., 1999], this mechanism could not be considered a true "elastic-spring-apparatus," since the protractor muscle of bagrids does not insert directly on the Müllerian process, but on the posttemporo-supracleithrum). However, the configuration of both the Müllerian process and its protractor muscle in *Cranoglanis bouderius* (see Fig. 2) clearly corresponds to that of an "elastic-spring-apparatus" (see above). It should be noted that, although some authors (e.g., Curran, 1989) hypothesize that the catfish taxa with an "elastic-spring-apparatus" form a monophyletic group, it is usually commonly accepted that the "elastic spring apparatus" is, in fact, a homoplastic feature (see Chardon, 1968; Mo, 1998; de Pinna, 1998; Chardon et al., in prep.), which is supported by our recent studies on catfish phylogeny (see below).

Well-defined, deep, anteroposteriorly elongated concavity formed by both the frontal and the lateral ethmoid to receive the anteromedial surface of the metapterygoid. In most catfishes the metapterygoid is not firmly attached to the neurocranium (this study, and also Regan, 1911; Alexander, 1965; Arratia, 1987, 1990, 1992; Bornbusch, 1995; Mo, 1991; Diogo et al., 1999; etc.). However, in some catfishes, such as, e.g., the plotosids and cetopsins examined, there is a firm attachment between the anteromedial surface of the metapterygoid and both the orbitosphenoid and the lateral ethmoid and, in some others, such as loricariids, the metapterygoid is even "sutured to the lateral ethmoid" (Arratia, 1990: 208). However, the configuration found in the cranoglanidids is clearly autapomorphic, not only since in these fishes, contrary to plotosids, cetopsins, and loricariids, there is a well-defined, deep, anteroposteriorly elongated concavity formed by both the frontal and the lateral ethmoid to receive the anteromedial surface of the metapterygoid (see Fig. 5), but also since in cranoglanidids the attachment between the metapterygoid and the neurocranium lies further dorsally (almost at the level of the cranial roof: see Fig. 4) than in the catfishes cited above.

Adductor mandibulae A3″ is dorsally divided into two bundles and partially inserted on the posterior portion of the primordial ligament. In most catfishes with an adductor mandibulae A3″ the tendon of this bundle only attaches on the medial surface of the mandible (Diogo and Chardon, 2000b). However, in some catfishes, such as the bagrids *Mystus* and *Bagrus* and the pimelodids *Megalonema* and *Pseudopimelodus,* the tendon of the A3″ is not only attached on the mandible, but is also associated with the fore end of the primordial ligament, thus attaching to the maxillary bone (such a configuration of the A3″ thus supporting the hypothesis that the retractor tentaculi of some catfishes is the result of a differentiation of the A3″) (see Diogo and Chardon, 2000b). However, the configuration found in cranoglanidids is unique since in these fishes, contrary to the bagrids and pimelodids cited above, the A3″ is dorsally divided into two bundles, and also since in cranoglanidids the tendon of the A3″ is associated with the posterior portion, and not with the fore end, of the primordial ligament (see Fig. 7).

The phylogenetic relationships between cranoglanidid and noncranoglanidid catfishes have long been problematical. The first author dealing with this problem was Jayaram (1956). That author suggested that the Cranoglanididae could be closely related to the Pangasidae, Ictaluridae, and/or Bagridae. However, as stated by some authors, such as Chardon (1968) or Burgess (1989), the arguments given by Jayaram (1956) to support his hypotheses are not convincing. Chardon (1968), based on characters of the Weberian apparatus, suggested, also without giving convincing arguments (that is, without giving a list of derived features simultaneously present in both taxa, thus supporting a close relationship between them), that the Cranoglanididae are probably closely related to the Bagridae. Lundberg and Baskin (1969: 37), after an analysis of the caudal skeleton of numerous catfishes, concluded that "the caudal skeleton yields no information on the systematic position of the monotypic Cranoglanididae." In the first explicit phylogenetic account on the interfamilial relationships of siluriforms, Mo (1991) proposed two cladograms. In the first one the relationships of the Cranoglanididae were unresolved. In the second one the Cranoglanididae were grouped with the Austroglanididae. But, once again, the author did not give any convincing argument for this latter hypothesis (the grouping of the two families in the cladogram II is based on a synapomorphy [synapomorphy number 49], which is not described subsequently by the author). The recent, detailed phylogenetic studies carried out by de Pinna also did not completely succeed in solving the phylogenetic position of the Cranoglanididae, with the latter being included in a "large pentatomy" that comprises several catfish taxa (de Pinna, 1998: 290).

The difficulty of solving the phylogenetic position of the cranoglanidids is probably related to the fact that these fishes are "generalized" siluriforms (see above), that is, that they do not present a large number of derived morphological features that could be compared with those of other catfishes as a foundation for a discussion of their phylogenetic relationships. But part of this problem seems to be solved with the inclusion of certain characters, which are

not usually included in the study on catfish phylogeny, such as those concerning the musculature, the ligaments, and/or the configuration of the structures associated with the mandibular barbels in the phylogenetic comparison between the cranoglanidids and the other catfishes. Such a comparison suggests that the Cranoglanididae are probably closely related to the Ariidae and the Claroteidae. This hypothesis is supported by the following four derived characters, which, according with our own observations and the data available in the literature, are only found in these three groups.

1. Extensor tentaculi associated with the ventral surface of the entopterygoid. In most catfishes the extensor tentaculi inserts exclusively on the autopalatine (this study; also Alexander, 1965; Gosline, 1975; Howes, 1983a,b, 1985; Mo, 1991; Arratia, 1992; Bornbusch, 1995; Diogo et al., 1999, 2000a,b; Diogo and Chardon, 2000b, 2001). However, in *Cranoglanis bouderius,* as well as in all the ariids and claroteids examined, this muscle is not only inserted on the autopalatine but also on the ventral surface of the entopterygoid.

2. Presence of a separate adductor hyomandibularis. In most nonsiluriform ostariophysans, the adductor operculi attaches exclusively on the opercular bone (Monod, 1963; Alexander, 1964; de la Hoz, 1974; Gijsen, 1974; Gijsen and Chardon, 1976; Winterbottom, 1974; Vandewalle, 1975; de la Hoz and Chardon, 1984; Mo, 1991; Bornbusch, 1995). However, our recent studies on catfish myology (this study; Diogo et al., 1999; Diogo, in prep.) have pointed that in numerous catfishes (e.g., bagrids, amphiliins, diplomystids, cetopsids, plotosids) the adductor operculi is not only inserted on the opercular, but also on the posterodorsal surface of the hyomandibula (see, e.g., Diogo et al., 1999: fig. 3). In some of these catfishes, as, e.g., the cetopsids examined, the adductor operculi is markedly bifurcated ventrolaterally, thus forming two bundles which insert on the opercular and on the hyomandibula, respectively. However, a complete differentiation of the adductor operculi in a separate muscle, named here adductor hyomandibularis, running from the pterotic to the hyomandibula is only present in the cranoglanidids, ariids, and claroteids examined.

3. Posteromedial portion of the extensor tentaculi lies ventral to the adductor arcus palatini. In most catfishes (this study; also Ghiot et al., 1984; Mo, 1991; Diogo et al., 1999, 2000a,b; Diogo and Chardon, 2000b, 2001) the posteromedial portion of the extensor tentaculi lies dorsal to the adductor arcus palatini (see, e.g., Diogo et al., 1999: fig. 3). However, in *Cranoglanis bouderius,* as well as in all the ariids and claroteins (but not in the auchenoglanins, which, together with the claroteins constitute the family Claroteidae) examined, the posteromedial portion of the extensor tentaculi lies ventral to the adductor arcus palatini (see Fig. 5).

4. Adductor mandibulae Aω obliquely oriented, with its posterodorsal fibers significantly dorsal to the upper edge of the coronoid process. In most catfishes examined in this study, as well as in most other siluriforms in which the adductor mandibulae has been studied in detail (McMurrich, 1884; Takahasi, 1925; Munshi, 1960; Singh and Munshi, 1968; Taverne and Aloulou-Triki, 1974; Winterbottom, 1974; Ghiot et al., 1984; Diogo et al., 1999, 2000a; Diogo and Chardon, 2000a,b) the adductor mandibulae Aω, if present, is a small, anteroposteriorly oriented bundle lodged in the medial surface of the mandible (see, e.g., Diogo and Chardon, 2000a: fig. 7B). However, in *Cranoglanis bouderius,* as well as in all the ariids and auchenoglanidins (but not in the claroteins) examined, the adductor mandibulae Aω is a well-developed, obliquely oriented bundle, with its posterodorsal fibers being significantly dorsal to the upper edge of the coronoid process (see Fig. 7B).

An overall phylogenetic analysis of the four derived morphological characters discussed above thus strongly suggests that the Cranoglanididae are closely related to the Ariidae and to the Claroteidae (it is, however, difficult to specify which two of these three taxa would be more closely related), and that, consequently, the absence of characters 3 and 4 in the auchenoglanidins and claroteins, respectively, is probably due to secondary loss (this hypothesis is strongly supported by a phylogenetic comparison, which is still in progress, of more than 400 morphological characters, concerning the bones, muscles, cartilages and ligaments of both the cephalic region and the pectoral girdle, in about 80 catfish genera [Oliveira et al., in prep.]).

CONCLUSIONS

Our observations and comparisons indicate that, although the cranoglanidids are "generalized" catfishes, there are four derived characters that are exclusively found in these fishes and that, thus, represent Cranoglanididae autapomorphies, namely: 1) the cartilages associated with the mandibular barbels are broad and somewhat circular; 2) the epioccipital exhibits a well-developed posterodorsal process, which presents a large, deep, circular posterior concavity; 3) a well-defined, deep, anteroposteriorly elongated concavity is formed by both the frontal and the lateral ethmoid to receive the anteromedial surface of the metapterygoid; 4) the adductor mandibulae A3″ is dorsally divided into two bundles and partially inserted on the posterior portion of the primordial ligament. Our observations and comparisons also reveal that the cranoglanidids are probably closely related to the Ariidae and the Claroteidae. Furthermore, as other studies recently published by the authors (Diogo et al., 1999, 2000a,b; Diogo and Chardon, 2000b,c), the present work also stresses that the analysis of certain characters that are not usually included in the study on

catfish phylogeny, such as, e.g., those concerning the musculature, the ligaments, and/or the configuration of the structures associated with the mandibular barbels could reveal useful data to infer the phylogenetic relationships between different catfish groups.

ACKNOWLEDGMENTS

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