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OSTEOLOGY AND MYOLOGY OF THE CEPHALIC REGION AND PECTORAL GIRDLE OF *BUNOCEPHALUS KNERII*, AND A DISCUSSION ON THE PHYLOGENETIC RELATIONSHIPS OF THE ASPREDINIDAE (TELEOSTEI: SILURIFORMES)

by

RUI DIOGO, MICHEL CHARDON and PIERRE VANDEWALLE

(*Laboratory of Functional and Evolutionary Morphology, Institut de Chimie, Bat. B6, Université de Liège, B-4000 Sart-Tilman (Liège), Belgique*)

ABSTRACT

The cephalic and pectoral girdle structures of the aspredinid *Bunocephalus knerii* (Bunocephalinae) are described and compared with those of representatives of the two other aspredinid subfamilies, *Aspredo aspredo* (Aspredininae) and *Xyliphius magdalenae* (Hoplomyzontinae), as well as with other catfishes. This comparison serves as the foundation for a discussion on the phylogenetic position and autapomorphies of the Aspredinidae. Our observations and comparisons support DE PINNA'S (1996) phylogenetic hypothesis, according to which the Sisoridae of previous authors is a paraphyletic assemblage, with a subunit of it (subsequently named Erethistidae) being more closely related to the Aspredinidae than to the remaining taxa previously allocated to the Sisoridae. In addition, our observations and comparisons pointed out 5 derived characters that are exclusively present in the aspredinid catfishes, and constitute Aspredinidae autapomorphies, namely: 1) origin of retractor tentaculi shifted posteriorly, lying medially to the levator arcus palatini; 2) preopercular with a lateral, well-developed, antero-laterally directed expansion of laminar bone extending anteriorly well beyond the remainder of this bone; 3) medial aponeurosis of hyohyoideus abductor firmly attached to the ventral surface of pectoral girdle; 4) pterotic with highly developed, broad postero-dorso-lateral shelf-like expansion of laminar bone extending laterally well beyond the remainder of the profile of the skull; 5) dilatator operculi originated on both the dorso-lateral surface of the neurocranium and the posterior surface of the hyomandibula.

KEY WORDS: Aspredinidae, autapomorphies, *Bunocephalus*, catfish, cephalic region, pectoral girdle, phylogenetic relationships, Siluriformes.

INTRODUCTION

The Siluriformes, or catfishes, with approximately 416 genera and over 2500 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

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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 & DE PINNA, 1999), the neotropical Aspredinidae, with 3 subfamilies (Aspredininae, Bunocephalinae and Hoplomyzontinae), 12 genera and about 34 species (FRIEL, 1994; DE PINNA, 1998), is surely one of the most complex families, not only from a morphological point of view, but also with respect to their phylogenetic relationships with other catfishes (see DE PINNA, 1998: 317-319). In fact, despite the large number of studies dealing with the relationships of these fishes, there is no consensus regarding their phylogenetic position within the siluriforms. The first study dealing, with some detail, with this subject was that of GÜNTHER (1864), who placed the aspredinids together with the loricarioids and the sisorids in his "sixth subfamily Siluridae Proteropodes". CHARDON (1967, 1968) also suggested a close relationship between the loricarioids and the aspredinids based on characters of the Weberian apparatus. However, subsequent studies (BASKIN, 1973; HOWES, 1983b) showed that CHARDON'S (1967, 1968) arguments were not convincing, that is, they were not supported by any putative derived synapomorphy. FERRARIS (1989) suggested, for the first time, that aspredinids were probably related to Asian taxa, namely to the Akysidae. MO (1991), in the first explicitly phylogenetic analysis of all siluriform families, placed the aspredinids as either basal to or in a polytomy with a clade containing clariids, heteropneustids, amblycipitids, akysids, sisorids, amphiliids and loricarioids. Somewhat similar hypotheses were suggested subsequently by DE PINNA (1993), who placed the Aspredinidae in a polytomy also including the Amblycipitidae, Akysidae, Sisoridae, Amphiliidae and Loricarioidea, and by CHEN (1994), who placed the Aspredinidae as the sister group of a clade composed of Amblycipitidae, Sisoridae and Akysidae. However, these hypotheses were challenged by the work of FRIEL (1994), which was principally dedicated to the interrelationships of the aspredinidids, but also to the relationships between these fishes and other Siluriformes. FRIEL (1994) proposed doradoids (see, *e.g.*, DE PINNA, 1998) as the closest relatives of aspredinidids. This hypothesis was challenged by DE PINNA (1996), who considered the Sisoridae of previous authors as a paraphyletic assemblage, with a subunit of it (which he subsequently named Erethistidae) being more closely related to the Aspredinidae than to the remaining taxa previously allocated to the Sisoridae. The relationships of the Aspredinidae have, thus, long been problematical as it was pointed out in a recent, detailed overview concerning the phylogenetic relationships of Neotropical catfishes (DE PINNA, 1998), in which the author concluded that "clearly, the position of aspredinids within siluriforms is a complex issue, plagued by some striking morphological homoplasies" (DE PINNA, 1998: 319).

It is surprising to notice that, despite the anatomical complexity of the Aspredinidae, the large number of studies concerning catfish morphology (*e.g.*, MCMURRICH, 1884; REGAN, 1911; NAWAR, 1955; JAYARAM, 1956; MUNSHI, 1960; ALEXANDER, 1965; CHARDON, 1968; TAVERNE & ALOULOU-TRIKI, 1974; GOSLINE, 1975; LUNDBERG, 1975, 1982; ARRATIA & MENUMARQUE, 1981; HOWES, 1983a, b, 1985; ARRATIA, 1987, 1990, 1992; MO, 1991; BORNBUSCH, 1995; DIOGO *et al.*, 1999a, 2000a, b; DIOGO & CHARDON, 2000a, b, c; etc.), and the large number of works dealing with the phylogenetic position of aspredinids (see above), only few, detailed morphological descriptions of the these fishes have been published so far (CHARDON, 1967, 1968; GAINER, 1967; FRIEL, 1995; FRIEL & LUNDBERG, 1996; DE PINNA, 1996). Moreover, as these descriptions are almost exclusively restricted to the osteology and external anatomy of the aspredinids, some morphological aspects of these fishes, such as the configuration of their muscles and/or ligaments, are practically unknown.

The aim of this work is to describe in detail the bones, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of the aspredinid *Bunocephalus knerii* Steindachner, 1882 (Bunocephalinae), and to compare these structures with those of representatives of the two other aspredinid subfamilies, namely *Aspredo aspredo* Linnaeus, 1758 (Aspredininae) and *Xyliphius magdalenae* Eigenmann, 1912 (Hoplomyzontinae), as well as with other catfishes. This comparison serves as the foundation for a discussion on the autapomorphies and phylogenetic position of the Aspredinidae. It is also hoped that this study will increase the knowledge of the anatomy and phylogeny of the catfishes in general, as well as pave the way for future works concerning the comparative anatomy, evolution, functional morphology, palaeontology, eco-morphology and particularly the phylogeny of the Siluriformes.

MATERIAL AND METHODS

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National d'Histoire Naturelle of Paris (MNHN) and from the National Museum of Natural History of Washington (USNM). Anatomical descriptions are made after dissection of alcohol fixed or trypsin-cleared and alizarine-stained (following TAYLOR & VAN DYKE'S 1985 method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsine-cleared and alizarine-stained (c&s) or alcohol fixed (alc) condition of the

studied fishes is given in parentheses following the number of specimens dissected. A list of the specimens dissected is given below.

Amphilius brevis (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c&s). *Amphilius jacksoni* (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): USNM 226072, 1 (alc). *Auchenipterus nigripinnis* (Auchenipteridae): LFEM, 1 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Austroglanis sclateri* (Austroglanididae): LFEM, 1 (alc). *Bagarius* sp. (Sisoridae): USNM 348830, 1 (alc); LFEM, 1 (c&s). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (c&s). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (c&s). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); MRAC 86-07-P-516, 1 (c&s). *Belonoglanis tenuis* (Doumeinae): MRAC P.60494, 1 (alc). *Bunocephalus knerii* (Aspredinidae): USNM 177206, 2 (alc). *Cetopsis coecutiens* (Cetopsidae): USNM 265628, 2 (alc). *Chrysichthys cranchii* (Claroteidae): LFEM, 1 (alc); LFEM, 1 (c&s). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 2 (c&s). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 2 (c&s). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc), LFEM, 2 (alc). *Conta conta* (Erethistidae): LFEM, 1 (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): USNM 044759, 1 (alc). *Gagata cenia* (Sisoridae): USNM 109610, 1 (alc). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Glyptosternon reticulatum* (Sisoridae): USNM 165114, 1 (alc). *Glyptothorax fokiensis* (Sisoridae): USNM 087613, 2 (alc). *Glyptothorax lampris* (Sisoridae): USNM 109607, 1 (alc). *Hara filamentosa* (Erethistidae): USNM 288437, 1 (alc). *Helogenes marmoratus* (Cetopsidae): USNM 264030, 1 (alc). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); *Hemicetopsis candiru* (Cetopsidae): USNM 167854, 1 (alc). *Heterobranchus longifilis* (Clariidae): LFEM, 2 (alc). *Heteropneustes fossilis* (Heteropneustidae): USNM 343564, 1 (alc); USNM 274063, 1 (alc). *Ictalurus punctatus* (Ictaluridae): LFEM, 5 (alc). *Loricaria cataphracta* (Loricariidae): LFEM, 1 (alc). *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *Nematogenys inermis* (Nematogenyidae): USNM 084346, 1 (alc). *Nothoglanidium thomasi* (Claroteidae): LFEM, 2 (alc). *Parakysis verrucosa* (Akysidae): LFEM, 1 (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 (c&s). *Phractura intermedia* (Doumeidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias (*Pimelodidae): LFEM, 2 (alc), LFEM, 2 (c&s). *Plotosus lineatus* (Plotosidae): USNM 200226), 2 (alc). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc), LFEM, 1 (c&s). *Schilbe intermedius* (Schilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc). *Trichomycterus taenia* (Trichomycteridae): LFEM, 2 (alc). *Xyliphius magdalenae* (Aspredinidae): USNM 120224, 1 (alc).

RESULTS

In this section we will describe the cephalic and pectoral girdle structures of the aspredinid *Bunocephalus knerii* (Bunocephalinae) and com-

pare these structures with those of representatives of the two other aspredinid subfamilies, namely *Aspredo aspredo* (Aspredininae) and *Xyliphius magdalenae* (Hoplomyzontinae). The information on the morphology is given by the figures and the text 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 & 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 & CHARDON, 2000b). With respect to the nomenclature of the pectoral girdle muscles, we follow DIOGO *et al.* (in press).

Osteology

Os mesethmoideum. Situated on the antero-dorsal surface of the neurocranium (figs 1, 2). Each of its antero-ventro-lateral margins is ligamentously connected to the premaxillary.

Os lateroethmoideum. With a well developed, laterally directed articulatory facet for the palatine (fig. 1: af-apal). The vomer, usually associated with the lateral ethmoids, is absent.

Os orbitosphenoideum. Posterior to the lateral ethmoid (fig. 2). The dorsal edge of its lateral wall sutures with the ventral surface of the frontal.

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

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

Os frontale. The frontals are large bones that constitute a great part of the cranial roof (fig. 1). They are largely separated by both the anterior and the posterior fontanels.

Os sphenoticum. This bone presents a long, narrow antero-lateral extension running lateral to the frontals (figs 1, 2) and constitutes, together with the pterotic, an articulatory facet for the hyomandibula (fig. 2: af-hm).

Os pteroticum. This bone has a dorso-lateral, large shelf-like expansion of laminar bone, which extends laterally well beyond the margin of the cranial roof (figs 1, 2). There is a well-defined, deep dorsal fossa ("supratemporal fossa": see DE PINNA, 1996) between the dorso-medial surface of

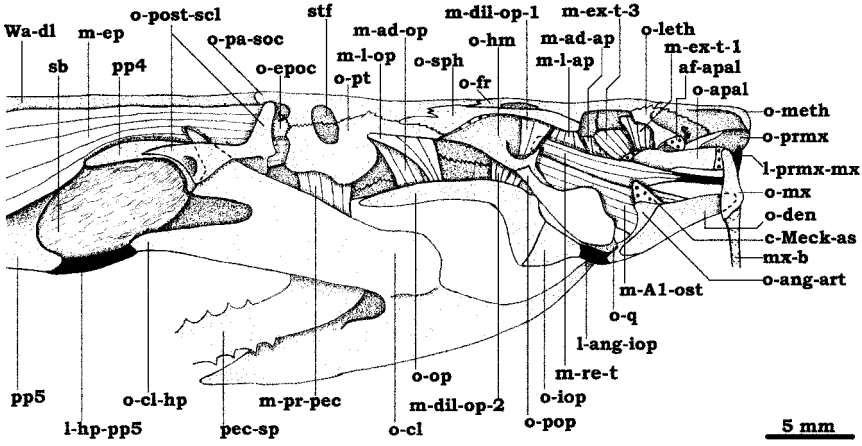

Fig. 1. Right, lateral view of the cephalic musculature of *Bunocephalus knerii*. All the muscles are exposed; dentary teeth were removed. *af-apal* articulatory facet for autopalatinum, *c-Meck-as* ascending portion of cartilago Meckeli, *l-ang-iop* ligamentum angulo-interoperculare, *l-hp-pp5* ligamentum humero-vertebrale, *l-prmx-mx* ligamentum praemaxillo-maxillare, *m-A1-ost* musculus adductor mandibulae A1-ost, *sb* swimbladder, *m-ad-ap* musculus adductor arcus palatini, *m-ad-op* musculus adductor operculi, *m-dil-op-1, m-dil-op-2* sections of musculus dilatator operculi; *m-ep* musculus epaxialis, *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, *m-pr-pec* musculus protractor pectoralis, *m-re-t* musculus retractor tentaculi, *mx-b* maxillary barbel, *o-ang-art* os angulo-articulare, *o-apal* os autopalatinum, *o-cl* os cleithrum, *o-cl-hp* humeral process of os cleithrum, *o-den* os dentale, *o-epoc* os epioccipitale, *o-fr* os frontale, *o-hm* os hyomandibulare, *o-iop* os interoperculare, *o-leth* os latero-ethmoideum, *o-meth* os mesethmoideum, *o-mx* os maxillare, *o-op* os operculare, *o-pa-soc* os parieto-supraoccipitale, *o-pop* os praeoperculare, *o-post-scl* os posttemporo-supracleithrum, *o-prmx* os praemaxillare, *o-pt* os pteroticum, *o-q* os quadratum, *o-sph* os sphenoticum, *pec-sp* pectoral spine, *pp4 pp5* parapophysis 4 and 5, *stf* supratemporal fossa, *Wa-dl* dorsal lamina of Weberian apparatus.

the pterotic and the dorso-lateral surface of the parieto-suppraoccipital (fig. 1: stf).

Os prooticum. Together with the pterosphenoid and the parasphenoid, it borders the well-developed foramen of the trigemino-facial nerve complex (fig. 2).

Os epioccipitale. Situated on the posterior surface of the neurocranium (figs 1, 2). There is a well-defined fossa between the dorso-medial surface of this bone, the postero-dorso-lateral surface of the parieto-supraoccipital and the antero-dorso-medial margin of the posttemporo-supracleithrum, which is significantly smaller than the supratemporal fossa (fig. 1). The extrascapular is missing.

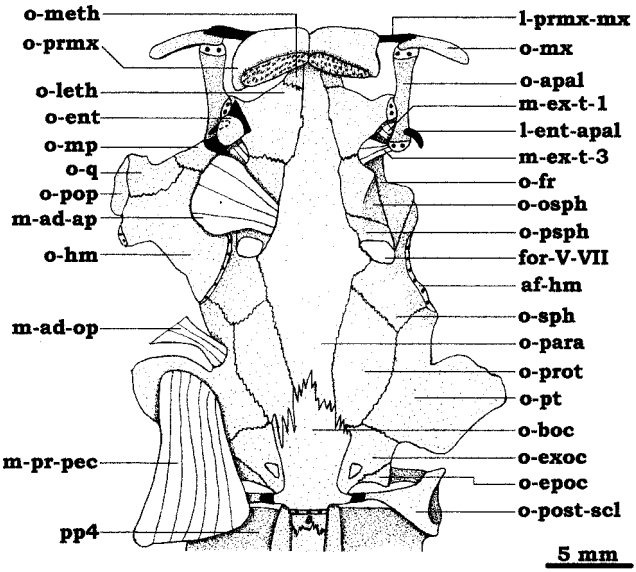

Fig. 2. Ventral view of the neurocranium and palatine-maxillary system of *Bunocephalus knerii*. On the left side the suspensorium, as well as the adductor arcus palatini, adductor operculi and protractor pectoralis, are also illustrated. *af-hm* articulatory facet for hyomandibulare, *for-V-VII* foramen trigemino-facialis, *l-ent-apal* ligamentum entopterygoideo-autopalatinum, *l-prmx-mx* ligamentum praemaxillo-maxillare, *m-ad-ap* musculus adductor arcus palatini, *m-ad-op* musculus adductor operculi; *m-ex-t-1 m-ex-t-3* sections of musculus extensor tentaculi, *m-pr-pec* musculus protractor pectoralis, *o-apal* os autopalatinum, *o-boc* os basioccipitale, *o-ent* os entopterygoideum, *o-epoc* os epioccipitale, *o-exoc* os exoccipitale, *o-fr* os frontale, *o-hm* os hyomandibulare, *o-leth* os lateroethmoideum, *o-meth* os mesethmoideum, *o-mp* os metapterygoideum, *o-mx* os maxillare, *o-osph* os orbitosphenoideum, *o-para* os parasphenoideum, *o-post-scl* os posttemporo-supracleithrum, *o-prmx* os praemaxillare, *o-prot* os prooticum, *o-psph* os pterosphenoideum, *o-pt* os pteroticum, *o-q* os quadratum, *o-sph* os sphenoticum, *pp4* parapophysis 4.

Os exoccipitale. Small, situated laterally to the basioccipital (fig. 2).

Os basioccipitale. Well-developed, unpaired bone, forming the posteriormost part of the floor of the neurocranium (fig. 6). Its well-developed ventro-lateral arms are ligamentously connected to the ventro-medial limbs of the posttemporo-supracleithra (fig. 2).

Os parieto-supraoccipitale. Large bone constituting the postero-dorso-median surface of the cranial roof, which is associated postero-medially with a well-developed dorsal lamina of the Weberian apparatus (fig. 1). There is no posterior process of the parieto-suppraoccipital (fig. 1).

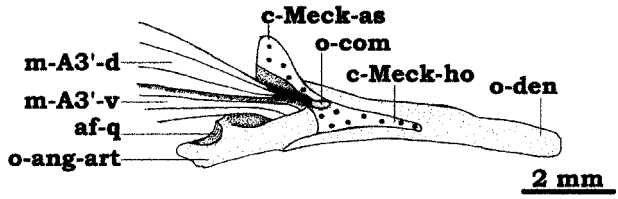

Fig. 3. Medial view of the left lower jaw and adductor mandibulae A3′ of *Bunocephalus knerii*. Dentary teeth were removed. *af-q* articulatory facet for quadratum, *c-Meck-as* c-*Meck-ho* ascending and horizontal portions of cartilago Meckeli, *m-A3′-d m-A3′-v* sections of musculus adductor mandibulae A3′, *o-ang-art* os angulo-articulare, *o-com* os coronomeckelium, *o-den* os dentale.

Os angulo-articulare. This bone (figs 1, 3), together with the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible (fig. 3). Postero-dorsally, the angulo-articular has an articulatory facet for the quadrate (fig. 3: af-q). Postero-ventrally, it is ligamentously connected by means of a thick ligament (fig. 1: l-ang-iop) to the interopercular (fig. 1).

Os dentale. The postero-dorsal surface of the toothed dentary, together with the antero-dorsal surface of the angulo-articular, form a dorsal process (processus coronoideus), the dorsal margin of which is significantly ventral (figs 1, 3) to the dorsal margin of the highly developed ascending portion of Meckel's cartilage (the latter being visible in a lateral view of the mandible: see fig. 1).

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

Os praemaxillare. The premaxillaries (figs 1, 2) are a pair of large rectangular plates lying underneath and attaching to the antero-ventro-lateral surfaces of the mesethmoid via ligamentous tissue. Postero-ventrally, each premaxillary bears numerous small teeth (fig. 2) with their tips slightly turned backward.

Os maxillare. The maxillary (figs 1, 2), is connected to the premaxillary by means of a strong, thick ligament (figs 1, 2: l-prmx-mx). As in most catfishes, the maxillary barbels are supported by the maxillaries (fig. 1).

Os autopalatinum. Rod-like bone (figs 1, 2), with a dorso-ventrally expanded posterior part. Its anterior end is tipped by a large cartilage with two antero-lateral concavities, which accept the two proximal heads of the maxillary; its posterior tip is capped by a cartilage, which, as the posterior portion of the bony autopalatine, is also dorso-ventrally expanded. Medially, the autopalatine articulates with the lateral ethmoid (figs 1, 2).

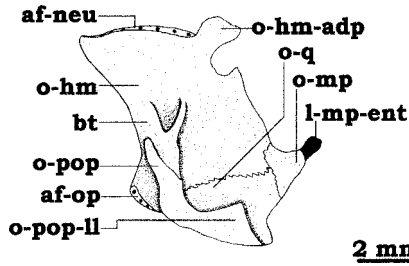

Fig. 4. Lateral view of right suspensorium of *Bunocephalus knerii*. *af-neu* articulatory facet for neurocranium, *af-op* articulatory facet for operculare, *bt* bony tunnel, *l-mp-ent* ligamentum metapterygoideo-entopterygoideum, *o-hm* os hyomandibulare, *o-hm-adp* antero-dorsal process of os hyomandibulare, *o-mp* os metapterygoideum, *o-pop* os praeoperculare, *o-pop-ll* lateral lamina of os praeoperculare, *o-q* os quadratum.

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 & MENUMARQUE, 1981; HOWES, 1983a, b, 1985; ARRATIA, 1987, 1990, 1992; etc.). However, for the time being, we will describe the suspensorial bones by their most often used names (see ARRATIA, 1992). The hyomandibula is a large bone presenting a highly developed antero-dorsal process (fig. 4: o-hm-adp). It articulates dorsally with both the pterotic and the sphenotic (figs 1, 2). Postero-ventrally, the hyomandibula presents a well-developed articulatory facet for the opercular (fig. 4: af-op). Postero-laterally, it presents a bony tunnel (fig. 4: bt) that encloses the branch of the latero-sensorial canal system between the preopercular and the pterotic (an independent, distinguishable suprapreopercular is missing).

Os entopterygoideum. Small bone attached, to the lateral ethmoid and to the metapterygoid by means of two thick ligaments (fig. 2). Its dorso-lateral surface is connected, via a thin, somewhat long ligament (fig. 2: l-ent-apal), to the postero-ventral surface of the autopalatinum. The ectopterygoids are absent.

Os metapterygoideum. Small bone postero-dorsally sutured with the hyomandibula and postero-ventrally sutured with the quadrate (fig. 4).

Os quadratum. Large bone dorsally sutured with the ventral surface of the hyomandibula (fig. 4).

Os praeoperculare. Laterally, this bone has a well developed, anterolaterally directed expansion of laminar bone (fig. 4: o-pop-ll) extending anteriorly well beyond the remainder of this bone, which encloses laterally a great part of the adductor mandibulae muscle (see fig. 1).

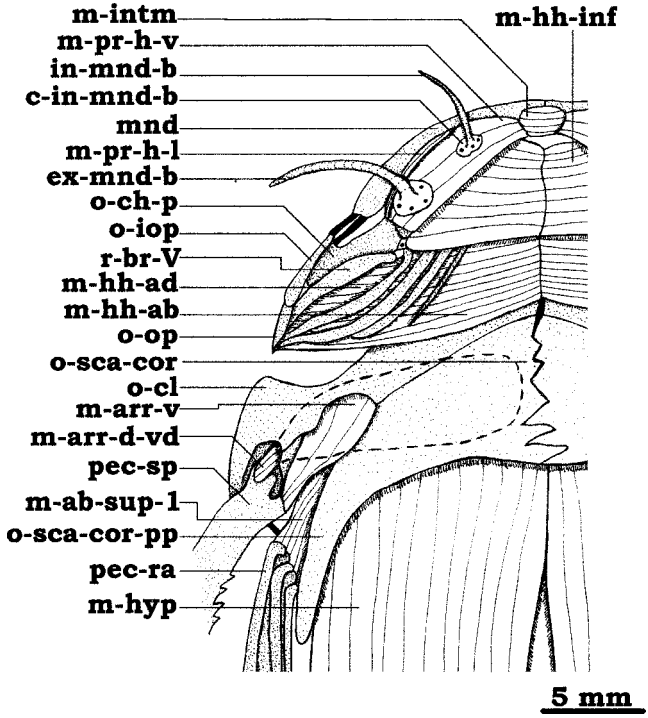

Fig. 5. Ventral view of the cephalic region and pectoral girdle of *Bunocephalus knerii*. All the muscles are exposed. *c-in-mnd-b* cartilago internus mandibularis tentaculi, *ex-mnd-b in-mnd-b* external and internal mandibular barbels, *m-ab-sup-1* section 1 of musculus abductor superficialis, *m-arr-d-vd* ventral division of musculus arrector dorsalis, *m-arr-v* musculus arrector ventralis, *m-hh-ab* musculus hyohyoideus abductor, *m-hh-add* musculus hyohyoideus adductor, *m-hh-inf* musculus hyohyoideus inferior; *m-hyp* musculus hypoaxialis, *m-intm* musculus intermandibularis, *mnd* mandible, *m-pr-h-l m-pr-h-v* pars lateralis and ventralis of musculus protactor hyoideus, *o-ch-p* os ceratohyale posterior, *o-cl* os cleithrum, *o-iop* os interoperculare, *o-op* os operculare, *o-sca-cor* os scapulo-coracoide, *o-sca-cor-pp* posterior process of os scapulo-coracoide, *pec-ra* pectoral rays, *pec-sp* pectoral spine, *r-br-V* radius branchiostegus V.

Os operculare. L-shaped bone, ventrally attached, by means of connective tissue, to the interopercular (fig. 1).

Os interoperculare. Its anterior surface is connected to the postero-ventral margin of the mandible via a strong, long ligament (figs 1, 5, 6). Medially, the interopercular is firmly attached (figs 5, 6), by connective tissue, to the lateral surface of the posterior ceratohyal.

Os ceratohyale posterior. Well-developed (figs 5, 6), connected, by means of two long ligaments, to the postero-ventral edge of the mandible

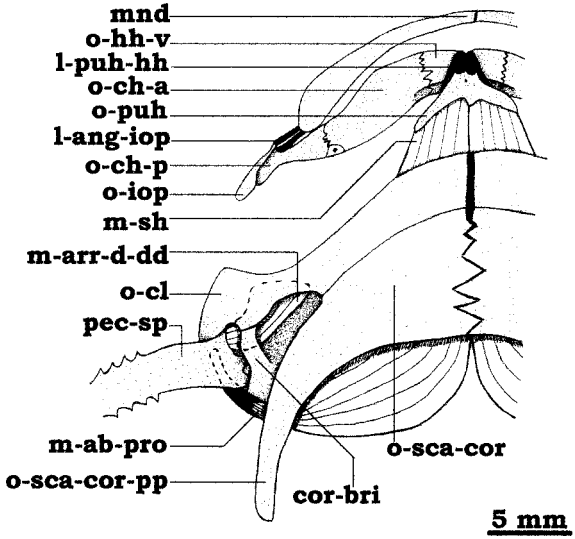

Fig. 6. Ventral view of the cephalic region and pectoral girdle of *Bunocephalus knerii*. The mandibular barbels, opercular, branchiostegal rays, pectoral rays, protractor hyoidei, intermandibularis, hyohyoideus inferior, hyohyoideus adductor, hyohyoideus abductor, arrector ventralis, abductor superioris, hypoaxialis and ventral division of arrector dorsalis were removed (see fig. 5). *cor-bri* coracoid bridge, *l-ang-iop* ligamentum angulointeroperculare, *l-puh-hh* ligamentum parurohyalo-hypohyale, *m-ab-pro* musculus abductor profundus, *m-arr-d-dd* dorsal division of musculus arrector dorsalis, *mnd* mandible, *m-sh* musculus sternohyoideus, *o-ch-a* os ceratohyale anterior, *o-ch-p* os ceratohyale posterior, *o-cl* os cleithrum, *o-hh-v* os hypohyale ventrale, *o-iop* os interoperculare, *o-puh* os parurohyale, *o-sca-cor* os scapulo-coracoide, *o-sca-cor-pp* posterior process of os scapulo-coracoide, *pec-sp* pectoral spine.

(figs 5, 6) and to the medial surface of the suspensorium (the interhyal is missing), respectively.

Os ceratohyale anterior. Together with the posterior ceratohyal, it supports the five branchiostegal rays (fig. 6).

Os hypohyale ventrale. The ventral hypohyals are ligamentously connected to the antero-lateral edges of the parurohyal (fig. 6). The dorsal hypohyals are missing.

Os parurohyale. The parurohyal (see ARRATIA & SCHULTZE, 1990) is a somewhat triangular bone with two well-developed postero-lateral arms and a small postero-medial process (fig. 6).

Os posttemporo-supracleithrum . This bone (figs 1, 2), together with the cleithrum and the scapulo-coracoid, constitute the pectoral girdle. Its thin dorso-medial limb situated dorsally to the postero-dorsal surfaces of

both the epioccipital and the parieto-supraoccipital (fig. 1), to which it is loosely attached by means of connective tissue. Its thin ventro-medial limb is also loosely attached, *via* a small, thin ligament to the basiocccipital (fig. 2). Its postero-lateral margin is deeply forked, forming an articulating groove for the upper edge of the cleithrum (see fig. 1). Postero-dorsally, the posttemporo-supracleithru m has a large, posteriorly directed process, which is firmly ankylosed with the fourth parapophysis (fig. 1).

Os cleithrum. The cleithrum (fig. 10) is a large, well-ossified stout structure forming a large 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, which presents prominent serrations not only on its posterior margin, but also on its anterior surface (see figs 1, 6). The two cleithra are attached in the antero-medial line via massive connective tissue (fig. 10). The well-developed humeral process of the cleithrum (fig. 1: o-cl-hp) is connected, by means of a thick, long ligament (fig. 1: l-hp-pp5) to the stout, strongly flattened parapophysis of the fifth vertebra, which is highly expanded laterally (fig. 1).

Os scapulo-coracoide. Elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge (fig. 6). Medially it joins its counterpart in an interdigitation of several strong serrations. Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge (fig. 6: cor-bri), which extends ventrally to the ventro-lateral surface of the cleithrum, fusing with an antero-ventral ridge of this bone (fig. 6). Postero-laterally, the scapulo-coracoid has a prominent, posteriorly directed posterior process (figs 5, 6: o-sca-cor-pp). The mesocoracoid arch is missing.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost originates on the hyomandibula, preopercular and quadrate and inserts on the dorsal surface of both the angulo-articular and the dentary (fig. 1). The A2, which lies dorso-mesially to the A1 but is deeply mixed with this latter, attaches posteriorly on the lateral surface of both the preopercular and the hyomandibula and anteriorly on the dorso-medial surface of both the dentary and the angulo-articular. The adductor mandibulae A3′ is divided in a dorsal and a ventral part. The dorsal one (A3′-d) originates on the hyomandibula and quadrate and inserts tendinously on the coronomeckelian bone (fig. 3). The ventral one (A3′-v), the fibers of which are deeply mixed with those of the A3′-d, originates on the quadrate and inserts on the medial surface of the angulo-articular (fig. 3). There is no A3″ nor Aω.

Musculus levator arcus palatini. It originates on the dorso-lateral surface of the sphenotic (fig. 1) and inserts on the lateral face of the hyomandibula.

Musculus adductor arcus palatini. This muscle (figs 1, 2) runs from the lateral sides of the parasphenoid, pterosphenoid and orbitosphenoid to the medial sides of both the hyomandibula and the metapterygoid (fig. 2).

Musculus levator operculi. The thin, little developed levator operculi originates on the lateral margin of the pterotic and inserts on the dorsal surface of the opercular (fig. 1).

Musculus adductor operculi. Situated medially to the levator operculi (fig. 1). It originates on the ventral surface of the pterotic (figs 1, 2) and inserts on the dorso-medial surface of the opercular (fig. 1).

Musculus dilatator operculi. It is somewhat divided into two bundles, which are fused ventrally. The anterior one (fig. 1: m-dil-op-1) originates on the sphenotic, passes medially to the bony tunnel of the hyomandibula (see fig. 4: bt) and inserts on the opercular (fig. 1). The posterior one (fig. 1: m-dil-op-2) runs from the posterior surface of the hyomandibula to the opercular (fig. 1).

Musculus extensor tentaculi. This muscle is divided into three bundles. The extensor tentaculi 1 (figs 1, 2: m-ex-t-1) runs from the lateral ethmoid to the postero-dorsal surface of the autopalatine (figs 1, 2). The extensor tentaculi 2 originates on the lateral ethmoid and inserts on the postero-medial surface of the autopalatine. Lastly, the extensor tentaculi 3 (figs 1, 2: m-ex-t-3) runs from both the lateral ethmoid and the orbitosphenoid to the postero-ventral margin of the autopalatine (figs 1, 2).

Musculus retractor tentaculi. Well-developed muscle, the posterior portion of which is medial to the anterior bundle of the dilator operculi (fig. 1). It originates on the hyomandibula and inserts, by means of a thick, long tendon, on the maxillary (fig. 1).

Musculus protractor hyoidei. This muscle has 3 parts. The pars ventralis (fig. 5: m-pr-h-v), in which are lodged the small cartilages associated with the internal and external mandibular barbels, originates on the anterior ceratohyal and inserts on the dentary (fig. 5). The pars lateralis (fig. 5: m-pr-h-l) originates on both the anterior and posterior ceratohyals, inserting on the ventro-medial face of the dentary (fig. 5). The pars dorsalis runs from the anterior ceratohyal to the dentary. There are no independent muscles for the movement of the mandibular barbels.

Muscle intermandibularis. Small muscle joining the two mandibles, the lateral fibers of which are mixed with the antero-medial fibers of the pars ventralis of the protractor hyoidei (fig. 5).

Musculus hyohyoideus inferior. Thick muscle (fig. 5) attaching medially on a median aponeurosis and laterally on the ventral surfaces of both the ventral hypohyal and the anterior ceratohyal.

Musculus hyohyoideus abductor. This muscle runs from the first (medial) branchiostegal ray to a median aponeurosis, which is firmly attached to the ventral surface of the pectoral girdle (see fig. 5).

Musculus hyohyoideus adductor. Each hyohyoideus adductor connects the branchiostegal rays of the respective side (fig. 5).

Musculus sternohyoideus. Originates on the anterior portion of the cleithrum and inserts on the posterior portion of the parurohyal (fig. 6).

Musculus arrector ventralis. This muscle runs from both the postero-ventro-lateral surface of the cleithrum and the antero-ventro-lateral surface of the scapulo-coracoid to the ventral condyle of the pectoral spine (fig. 5).

Musculus arrector dorsalis. This muscle is differentiated into two well-developed divisions. The ventral division (fig. 5: m-arr-d-vd), situated dorsally to the muscle arrector ventralis, originates on the dorsal margin of both the cleithrum and the scapulo-coracoid and inserts on the antero-lateral edge of the pectoral spine (fig. 5). The dorsal division (fig. 6: m-arr-d-dd), which is significantly smaller than the ventral one, runs from the ventral surface of the antero-dorso-lateral margin of the cleithrum (fig. 6) to the anterior edge of the dorsal condyle of the pectoral spine.

Musculus abductor profundus. This highly developed muscle occupies almost all of the posterior margin of the pectoral girdle (see fig. 6), and is situated dorsally to the anterior portion of the hypoaxialis muscle (see figs 5, 6). It originates on the postero-medial surface of the coracoid (fig. 6) and inserts on the medial surface of the dorsal condyle of the pectoral spine.

Musculus abductor superficialis. This muscle is differentiated in two sections. The larger section (fig. 5: m-ab-sup-1) attaches anteriorly on the ventro-lateral margin of the scapulo-coracoid and posteriorly on the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section runs from the postero-ventro-lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus adductor superficialis. This muscle is situated on the posterior margin of the pectoral girdle and divided into two sections. The muscle is little developed, due to the very large muscle abductor profundus. The

larger section of the adductor superficialis originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section runs from both the postero-ventro-lateral edge of the scapulo-coracoid and the dorsal surface of the proximal radials to the antero-ventral margin of the dorsal part of the pectoral fin rays.

Musculus protractor pectoralis. Well-developed muscle, running from the ventral surface of the pterotic (figs 1, 2) to the antero-dorsal surface of the cleithrum (fig. 1).

Aspredo aspredo

The configuration of the structures of the cephalic region and pectoral girdle of *Aspredo aspredo* resembles that of *Bunocephalus knerii*. Therefore, only the principal differences between the two species will be mentioned. These are: 1) the interopercular, as well as the angulo-interopercular ligament between this bone and the mandible, are absent; 2) the maxillary is highly developed proximo-distally; 3) the ascending portion of Meckel's cartilage is not as dorsally expanded as in *B. knerii*; 4) the L-shaped opercular bone is even less developed than that of *B. knerii*; 5) although present, the antero-laterally directed lamina of the preopercular is not as developed as in *B. knerii*; 6) on each side of the body, there is an "additional maxillary barbel", the proximal end of which is associated with a small cartilaginous structure firmly attached to the external surface of the maxillary, and not (as is the proximal end of the true maxillary barbels) firmly incrusted in the hollow distal end of this latter bone; 7) the posterior process of the scapulo-coracoid, as well as the humeral process of the cleithrum, are even more developed than those of *B. knerii*; 8) the antero-dorsal process of the hyomandibula is missing; 9) the metapterygoid is absent; 10) the premaxillary is highly expanded antero-posteriorly; 11) the parurohyal is not a large, triangular bone with two prominent postero-lateral arms, but instead a small, rectangular bone without any prominent posterior process.

Xyliphius magdalenae

The principal differences between the cephalic and pectoral girdle structures of *X. magdalenae* and those of *Bunocephalus knerii* are: 1) the premaxillary teeth are absent; 2) the muscle arrector ventralis is ventrally enclosed by a prominent ventro-antero-lateral laminar expansion of the scapulo-coracoid and, thus, is not visible in a ventral view of the pectoral girdle; 3) the interopercular, although present, is highly reduced in size; 4) an independent, distinguishable suprapreopercular is present in

each side of the body; 5) each cleithrum has a prominent, semi-circular antero-medial process, which meets its counterpart medially, thus forming a prominent, circular antero-medial expansion of the pectoral girdle; 6) only the posterior margin of the pectoral spine presents well-developed serrations; 7) although present, the antero-laterally directed lamina of the preopercular is not as developed as in *B. knerii*.

DISCUSSION

The aim of this work was to describe in detail the bones, muscles and ligaments of the cephalic region and pectoral girdle of the aspredinidid *Bunocephalus knerii* (Bunocephalinae), and to compare these structures with those of representatives of the two other aspredinid subfamilies, *Aspredo aspredo* (Aspredininae) and *Xyliphius magdalenae* (Hoplomyzontinae), as well as with other catfishes studied by us or described in the literature. With respect to the problematic phylogenetic position of aspredinidids our observations and comparisons support DE PINNA'S (1996) phylogenetic hypothesis, according to which the Sisoridae of previous authors is a paraphyletic assemblage. A subunit of the Sisoridae, the Erethistidae, is more closely related to the Aspredinidae than to the remaining taxa previously allocated in the Sisoridae. This hypothesis is also supported by a phylogenetic comparison of more than 400 morphological characters concerning the configuration of the cephalic and pectoral girdle bones, muscles and ligaments of about 80 catfish genera (OLIVEIRA *et al.*, in prep.).

DE PINNA'S (1996) grouping of the Erethistidae, Aspredinidae and Sisoridae in a monophyletic clade was based on 10 synapomorphies (see DE PINNA, 1996: 61), of which 5 concern the configuration of structures examined in this work, namely: *I)* "posterior portion of supracleithrum (posttemporo-supracleithrum) ankylosed to margin of Weberian lamina — state 1" (see fig. 1); *II)* "parapophysis of fifth vertebra strongly flattened and expanded" (see fig. 1); *III)* "parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall" (see fig. 1); *IV)* "humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament — state 3" (see fig. 1); *V)* "coracoid with ventral anterior (posterior) process" (see fig. 6). Our observations and comparisons not only confirmed these 5 synapomorphies, but also pointed out an additional synapomorphy to support the clade formed by sisorids, aspredinids and erethistids.

This additional synapomorphy is a well-defined, long ligament attaching on the antero-dorso-lateral margin of the entopterygoid and running posteriorly to attach on the postero-ventral margin of the autopalatine.

In catfishes, the autopalatine can be ligamentously connected in several different ways to one or more elements of the pterygoid series (to the ectopterygoid in, *e.g.*, ariids, claroteids and some pimelodids; to the metapterygoid in, *e.g.*, diplomystids and nematogenyids; to the entopterygoid in, *e.g.*, clariids, cranoglanidids, aspredinidids, erethistidids, sisorids, some ictalurids and some schilbeids; to both the metapterygoid and the ectopterygoid in, *e.g.*, bagrids) (this study, see also REGAN, 1911; ALEXANDER, 1965; GOSLINE, 1975; GHIOT *et al.*, 1984; ARRATIA, 1987, 1990, 1992; MO, 1991; DIOGO *et al.*, 1999, 2000b; DIOGO & CHARDON, 2000a, in press; etc.). However, a well-defined, long ligament attaching on the antero-dorso-lateral margin of the entopterygoid and running posteriorly to attach on the postero-ventral margin of the autopalatine is exclusively present in the aspredinids (see fig. 2), sisorids and erethistids.

DE PINNA'S (1996) proposal of a sister-group relationship between the Erethistidae and the Aspredinidae was based on 5 synapomorphies (DE PINNA, 1996: 64), of which 3 concern the configuration of structures examined in this work, namely: *I)* "anterior margin of pectoral spine with serrations" (see, *e.g.*, figs 1, 6); *II)* "internal support for pectoral fin rays small in size"; *III)* "anterior portion of lateral line running closely in parallel to lateral margin of Weberian lamina". Our observations and comparisons confirmed these 3 synapomorphies, but failed to show additional synapomorphic characters to support the clade formed by aspredinids and erethistids. However, our observations showed a single derived feature present in both the erethistids and sisorids but absent in aspredinids. The coronoid process of the mandible is exclusively formed by the dorsal margin of the dentary, and not, as in most catfishes, by the dorsal surfaces of both this bone and the angulo-articular). We were unable to show a single derived feature present in both the sisorids and aspredinids but absent in erethistids. Therefore, this study supports a sister-group relationship between the Erethistidae and the Aspredinidae, and shows that the Sisoridae of previous authors is a paraphyletic group (see above).

Several characters have been proposed to define the Aspredinidae. COPE (1871) defined the aspredinids as catfishes without an opercle. GILL (1872) proposed the following 4 characters to define the aspredinids: 1) neural spines of Weberian complex coalesced to form a continuos ridge from occiput to dorsal fin; 2) gill openings restricted to small slits in front of the pectoral-fin bases; 3) adipose fin absent; 4) caudal vertebrae compressed with neural spines expanded (see FRIEL, 1994: 14). Regan (1911) provided 3 additional features to diagnose the aspredinids, namely: 1) mesocoracoid absent; 2) pre-caudal vertebrae without parapophyses; 3) horizontal processes on centra. FRIEL (1994), in an extensive and detailed, but unfortunately unpublished work concerning the phylogeny and

systematics of aspredinids, proposed the 25 following characters to diagnose these fishes: 1) ethmoid cartilage on midline discontinuous with cartilage on lateral condyle; 2) laminar processes of pterotic are pointed and directed laterally; 3) vomer absent; 4) mandibular lateralis canal does not enter lower jaw; 5) opercle "L" shaped resembles branchiostegal rays; 6) opercular apertures reduced to ventral slits; 7) 5 of fewer branchiostegal rays; 8) second hypobranchial completely cartilaginous; 9) lower pharyngeal tooth plates with teeth restricted to medial edge; 10) dorsal lamina of Weberian complex contacts dorsal surface of body; 11) origin of parapophysis of fifth vertebra shifted ventrally; 12) parapophysis of fifth vertebra extends past parapophysis of fourth vertebra; 13) hemal canal forms de novo without a transformation series of rib parapophyses; 14) abdominal vertebrae with peg and socket articulations; 15) parapophyses for ribs reduced or absent; 16) anterior nuchal plate absent; 17) modal # of anal rays or fewer; 18) modal # of caudal rays 5+5; 19) expanded bases on caudal rays present; 20) anterior margin of coracoid moderately concave; 21) basipterygia anterior arms absent; 22) basiopterygia posterior cartilage reduced; 23) mental barbels bases reduced; 24) rows of unculiferous tubercles present on body; 25) alarm cells & fright reaction absent. Lastly, in 1996, DE PINNA (1996) considered that the aspredinids could be defined by the 11 following characters: 1) condyle for opercle on hyomandibula directed ventrally; 2) pterotic with lateral shelf-like expansion; 3) lateral cartilage of first hypobranchial enlarged; 4) vertebrae with transverse process; 5) first lateral line ossicle enlarged, overlapping with posterior portion of supracleithrum, 6) nasal elongated anteriorly to level of anterior margin of mesethmoid cornua; 7) lacrimal with dorsal shelf-like portion directed mesially; 8) hyomandibula with bony tunnel enclosing branch of the laterosensory canal between preopercle and pterotic; 9) reversal of basipterygium with ventral longitudinal keel, extending anteriorly alongside internal arm; 10) cartilage on posterior process of basipterygium reduced or absent; 11) anterior arms of basipterygium undifferentiated from main part of bone.

The apparent abundance of characters to define the Aspredinidae is misleading. In fact, many of the characters mentioned above can not be considered, in a strictly cladistic classificatory scheme, as valid to define the aspredinids. This is due not only to certain anatomical misinterpretations, (*e.g.*, the proposal of the character "absence of opercle" to define the aspredinids, which is due to a confusion about the highly modified, L-shaped opercle of aspredinidids and a branchiostegal ray), but also to the procedure followed by some taxonomists. Often a certain taxon is defined with homoplastic characters that are also present in other taxa. The use of such a procedure raises serious important theoretical, as well as practical, objections (see, *e.g.*, DIOGO *et al.*, 1999). One of the practical objections is

exemplified with the analysis of some of the characters provided by FRIEL (1994) to define the Aspredinidae. For example, FRIEL (1994: 74) used the character "origin of parapophysis of fifth vertebra shifted ventrally" to diagnose the aspredinids, although he was conscious that this character was also present in the Asiatic "Amblycipitidae, Sisoridae and Akysidae" (FRIEL, 1994: 42). Later studies (DE PINNA, 1996, in prep.; this study; Oliveira *et al.*, in prep.) have subsequently pointed out that these Asiatic groups probably constitute, together with the Aspredinidae, a monophyletic clade (superfamily Sisoroidea), which is supported, among others features, by a ventral positioning of the parapophysis of the fifth vertebra (see DE PINNA, 1996: 59). Therefore, this character can not be considered as valid to define the family Aspredinidae. This is also the case for other characters used by FRIEL (1994) to define the aspredinids, namely the "parapophysis of fifth vertebrae extends past parapophysis of fourth vertebra", which very likely constitutes a synapomorphy of the clade formed by the aspredinids, the sisorids and the erethistids (see above). Several other characters proposed by FRIEL (1994) and/or by other authors to define this group may prove not valid, and future studies may reveal more parsimonious hypotheses concerning the phylogenetic position of aspredinids.

Here we prefer to adopt the procedure of restricting the characters defining the Aspredinidae to those autapomorphic, non-homoplastic, well defined characters that are *exclusively* found in members of this taxon. Therefore, among the characters concerning the configuration of the structures examined in this work, we propose the 5 following autapomorphies to define the family Aspredinidae.

1. Origin of retractor tentaculi shifted posteriorly, lying medially to the levator arcus palatini. The presence of a retractor tentaculi muscle is clearly a derived feature within catfishes, which is only present in some catfish groups (see, *e.g.*, DIOGO & CHARDON 2000b; DIOGO *et al.*, 2000b). Among the catfishes with a retractor tentaculi, several, somewhat different muscle configurations are found (this study, and also TAKAHASI, 1925; NAWAR, 1955; MUNSHI, 1960; ALEXANDER, 1965; SINGH & MUNSHI, 1968; GOSLINE, 1975; HOWES, 1983a, b, 1985; MO, 1991; DIOGO & CHARDON, 2000b; DIOGO *et al.*, 2000a, b in press). However, an origin of the retractor tentaculi on the dorso-lateral surface of the hyomandibula, at the level of, and medial to, the levator arcus palatini (see fig. 1), is only found in the aspredinid catfishes.

2. Preopercular with a lateral well developed, antero-laterally directed expansion of laminar bone extending anteriorly well beyond the margin of this bone. The preopercular of catfishes is typically a somewhat

elongated bone without any prominent antero-lateral process or lamina (this study, and also ALEXANDER, 1965; ARRATIA, 1987, 1990, 1992; MO, 1991; DE PINNA, 1993; DIOGO *et al.*, 1999, 2000a). However, in the aspredinid catfishes, the preopercular presents laterally a well-developed, antero-laterally directed expansion of laminar bone (which is more developed in the bunocephalin *Bunocephalus knerii* than in both the aspredinin *Aspredo aspredo* and the hoplomyzontin *Xyliphius magdalenae*) extending anteriorly well beyond the bone and enclosing laterally a significant part of the adductor mandibulae muscle (see, fig. 1).

3. Medial aponeurosis of hyohyoideus abductor firmly attached to the ventral surface of pectoral girdle. The hyohyoideus abductor of catfishes runs from a medial aponeurosis to the first branchiostegal ray, with the medial aponeurosis usually firmly attached to the postero-ventral surface of the parurohyal bone and/or to the medial aponeurosis of the hyohyoideus inferior (this study, and also TAKAHASI, 1925; NAWAR, 1955; MUNSHI, 1960; SINGH, 1967; SINGH & MUNSHI, 1968; TAVERNE & ALOULOU-TRIKI, 1974; WINTERBOTTOM, 1974; HOWES, 1983a, b, 1985; GHIOT *et al.*, 1984; MO, 1991). However, in the aspredinid catfishes the medial aponeurosis of the hyohyoideus abductor is firmly attached to the ventral surface of the well-developed pectoral girdle (see fig. 5).

4. Pterotic with highly developed, broad postero-dorso-lateral shelf-like expansion of laminar bone extending laterally well beyond the margin the skull. This character was already reported by both FRIEL (1994) and DE PINNA (1996). The plesiomorphic siluriform condition of the pterotic is that the dorso-lateral surface of this bone does not extend significantly beyond the cranial roof (this study, see also CHARDON, 1968; MO, 1991; DE PINNA, 1993, 1996; FRIEL, 1994). However, in the aspredinids, the pterotic presents a highly developed, broad postero-dorso-lateral shelf-like lamina extending laterally well beyond the remainder of the skull (see fig. 2). Although a somewhat similar configuration also occurs in scoloplacids and bagrids, the situation found in aspredinids is unique, since in scoloplacids the dorso-lateral extension of the cranial roof is essentially realised by an antero-dorso-lateral expansion of the pterotic-posttemporo-supracleithrum (SCHAEFER, 1990), and not by a postero-dorso-lateral expansion of the pterotic bone. In bagrids the postero-dorso-lateral expansion of the pterotic is by far more slender and more reduced (MO, 1991; DIOGO *et al.*, 1999) than the highly developed, broad expansion found in aspredinids.

5. Dilatator operculi originated on both the dorso-lateral surface of the neurocranium and the posterior surface of the hyomandibula. The dilatator operculi of catfishes is typically a well developed muscle originated on

the dorso-lateral surface of the neurocranium and inserted on the antero-dorsal margin of the opercular bone (this study, and also TAKAHASI, 1925; NAWAR, 1955; MUNSHI, 1960; SINGH & MUNSHI, 1968; TAVERNE & ALOULOU-TRIKI, 1974; WINTERBOTTOM, 1974; GHIOT *et al.*, 1984; DIOGO *et al.*, 1999, 2000a; DIOGO & CHARDON, 2000a). However, in the aspredinid catfishes, this muscle is somewhat divided dorsally into two bundles, which originate on the dorso-lateral surface of the neurocranium and on the posterior surface of the hyomandibula, respectively. The two bundles are fused at the level of their insertion on the opercular bone (fig. 1).

GENERAL CONCLUSIONS

In conclusion, our observations and comparisons support DE PINNA'S (1996) phylogenetic hypothesis, according to which the Sisoridae of previous authors are a paraphyletic assemblage, with the actual Erethistidae being more closely related to the Aspredinidae than to the remaining taxa previously allocated to the Sisoridae. In addition, our observations and comparisons pointed out 5 derived characters exclusively present in the aspredinid catfishes, namely: 1) origin of retractor tentaculi shifted posteriorly, lying medially to the levator arcus palatini; 2) preopercular with a lateral, well-developed, antero-laterally directed expansion of laminar bone extending anteriorly well beyond the remainder of this bone; 3) medial aponeurosis of hyohyoideus abductor firmly attached to the ventral surface of pectoral girdle; 4) pterotic with highly developed, broad postero-dorso-lateral shelf-like expansion of laminar bone extending laterally well beyond the margin skull; 5) dilatator operculi originates on both the dorso-lateral surface of the neurocranium and the posterior surface of the hyomandibula. As other studies recently published by the authors (DIOGO *et al.*, 1999, 2000a, b; DIOGO & CHARDON, 2000b, c), the present work stresses that the analysis of certain characters that are not usually included in the study of catfish phylogeny, such as those concerning the configuration of the muscles and/or ligaments of the cephalic region and pectoral girdle, could reveal useful data to infer the phylogenetic position and/or autapomorphies of catfish taxa.

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