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Osteology and myology of the cephalic region and pectoral girdle of *Glyptothorax fukiensis* (Rendahl, 1925), comparison with other sisorids, and comments on the synapomorphies of the Sisoridae (Teleostei: Siluriformes)

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ABSTRACT. The cephalic and pectoral girdle structures of the sisorid *Glyptothorax fukiensis* (tribe Glyptothoracini) are described and compared with those of representatives of the other three sisorid tribes, namely *Glyptosternon reticulatum* (tribe Glyptosternini), *Bagarius yarreli* (tribe Bagariini) and *Gagata cenia* (tribe Sisorini), as well as with those of several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Sisoridae. Our observations and comparisons support de Pinna's (1996) phylogenetic hypothesis, according to which the Asiatic Sisoridae is the sister-group of a clade formed by the Neotropical Aspredinidae and the Asiatic Erethistidae. In addition, our observations and comparisons pointed out a new, additional character to diagnose the family Sisoridae, namely: presence of a well-developed, wide, deep fossa on the neurocranial floor between the ventro-medial surface of the pterotic and the ventro-lateral surface of the exoccipital.

KEY WORDS: catfish, cephalic region, comparative morphology, *Glyptothorax*, myology, pectoral girdle, phylogeny, Sisoridae, Siluriformes.

INTRODUCTION

The Siluriformes is "one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade" (TEUGELS, 1996). Among the 35 siluriform families (FERRARIS & DE PINNA, 1999), the Sisoridae, with 14 genera and more than 97 species, is one of the largest and most diverse Asiatic families (DE PINNA, 1996). This higher-level phylogeny and systematics of the Sisoridae were recently revised by DE PINNA (1996), who concluded that six genera previously included in this family, namely *Conta* Hora, 1950, *Erethistes* Müller and Troschel, 1849, *Erethistoides* Hora, 1950, *Hara* Blyth, 1860, *Laguvia* Hora, 1921 and *Pseudolaguvia* Misra, 1976, were more closely related to the Neotropical Aspredinidae than to the remaining 14 sisorid genera. Therefore, these six genera were assigned to the family Erethistidae, which, according to DE PINNA (1996), is the sister-group of the Neotropical Aspredinidae, with the clade formed by these two families being, in turn, the sister-group of the Sisoridae sensu stricto. Still according to the phylogenetic results of DE PINNA (1996), the Sisoridae (sensu stricto) can be divided into the subfamilies Sisorinae and Glyptosterninae, with the former comprising the tribes Sisorini (including the genera *Sisor* Hamilton, 1822, *Gagata* Bleeker, 1858, *Nangra* Day, 1877) and Bagariini (*Bagarius* Bleeker, 1853), and the latter comprising the tribes Glyptothoracini (*Glyptothorax* Blyth, 1860) and Glyptosternini (*Glyptosternon* McClelland, 1842, *Glaridoglanis* Norman, 1925, *Oreoglanis* Smith, 1933, *Exostoma* Blyth, 1860, *Myersglanis* Hora & Silas, 1952, *Coraglanis* Hora & Silas, 1952, *Euchiloglanis* Regan, 1907, *Pseudexostoma* Chu, 1979, *Pseudecheneis* Blyth, 1860).

The morphology of the sisorids has been the subject of several studies, such as, e.g., BATHIA (1950), GAUBA (1962, 1966, 1968, 1969), TILAK (1963), LAL *et al.* (1966), MAHAJAN (1963, 1966ab, 1967ab), CHARDON (1968),

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SHRESTHA (1970); HE (1996, 1997). However, most of these studies are concerned exclusively with osteological structures, while some capital aspects of the morphology of this important group of catfishes, such as, for example, the configuration of both the muscles and the ligaments of their cephalic region or the configuration of the structures associated with their mandibular barbels, are practically unknown. This not only complicates the study of the functional morphology of the sisorids, but also restricts considerably the data available for inference of the phylogenetic relationships of these catfishes (see DE PINNA, 1996: 9).

The aim of this work is to describe in detail the bones, cartilages, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of the sisorid *Glyptothorax fukiensis* (Rendahl, 1925) (Glyptosterninae, Glyptothoracini), and to compare these structures with those of representatives of the other three sisorid tribes, namely *Glyptosternon reticulatum* McClelland, 1842 (Glyptosterninae, Glyptosternini), *Bagarius yarreli* (Sykes, 1839) (Sisorinae, Bagariini) and *Gagata cenia* (Hamilton, 1822) (Sisorinae, Sisorini), as well as with those of several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic relationships of the Sisoridae.

MATERIAL AND METHODS

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Muséum National D'Histoire Naturelle of Paris (MNHN), from the University of Gent (UG) 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 jacknosi* (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* (Amphiliidae): MNHN 1961-0600, 2 (alc); *Arius hertzbergii* (Ariidae): LFEM, 1 (alc). *Arius heudelotii* (Ariidae): LFEM, 4 (alc). *Aspredo aspredo* (Aspredinidae): USNM 226072, 1 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagarius yarreli* (Sisoridae): USNM 348830, 2 (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* (Amphiliidae): MRAC P.60494, 2 (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, 2 (alc). *Cranoglanis bouderius* (Cranoglanididae): LFEM, 2 (alc). *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Doumea typica* (Amphiliidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152, 1 (alc). *Erethistes pusillus* (Erethistidae): USNM 044759, 2 (alc). *Gagata cenia* (Sisoridae): USNM 109610, 2 (alc). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Glyptosternon reticulatum* (Sisoridae): USNM 165114, 1 (alc). *Glyptothorax fukiensis* (Sisoridae): USNM 087613, 2 (alc). *Hara filamentosa* (Erethistidae): USNM 288437, 1 (alc). *Helogenes marmuratus* (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). *Leptoglanis rotundiceps* (Amphiliidae): MRAC P.186591-93, 3 (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* (Amphiliidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c&s). *Phractura intermedia* (Amphiliidae): 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* (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc). *Trachyglanis ineac* (Amphiliidae): MRAC P.125552-125553, 2 (alc). *Xyliphius magdalenae* (Aspredinidae): USNM 120224, 1 (alc). *Zaireichthys zonatus* (Amphiliidae): MRAC 89-043-P-2243-2245, 3 (alc).

RESULTS

In the anatomical descriptions, the nomenclature for the osteological structures of the cephalic region follows basically that of ARRATIA (1997). The myological nomenclature is based mainly on WINTERBOTTOM (1974). However, for the different adductor mandibulae sections, DIOGO & CHARDON (2000a) is followed since recent works have pointed out that, with respect to these sections, WINTERBOTTOM's (1974) nomenclature presents serious

limitations (see, e.g., GOSLINE, 1989; DIOGO & CHARDON, 2000a). In relation to the muscles associated with the mandibular barbels, which were not studied by WINTERBOTTOM (1974), DIOGO & CHARDON (2000b) is followed. With respect to the nomenclature of the pectoral girdle bones and muscles, DIOGO *et al.* (2001a) is followed.

Glyptothorax fukiensis

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 autopalatine (Fig. 2). Posteriorly, the lateral ethmoid presents a long, narrow lateral extension directed posteriorly alongside a significant part of the lateral margin of the frontal (Fig. 1).

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

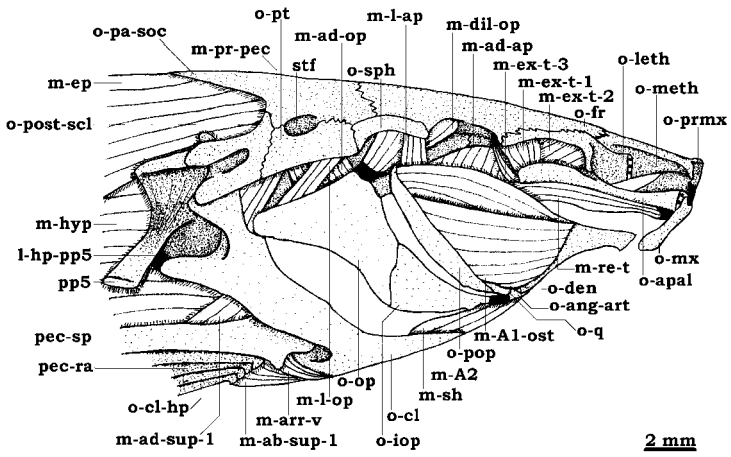

Fig. 1. – Lateral view of the cephalic musculature of *Glyptothorax fukiensis*. All the muscles are exposed; dentary and premaxillary teeth were removed. *l-hp-pp5*, ligamentum humero-vertebrale; *m-A1-ost, m-A2,* sections of musculus adductor mandibulae; *m-ab-sup-1*, musculus abductor superficialis 1; *m-ad-ap*, musculus adductor arcus palatini; *m-ad-op*, musculus adductor operculi; *m-ad-sup-1*, musculus adductor superficialis 1; *m-arr-v*, musculus arrector ventralis; *m-dil-op,* musculus dilatator operculi; *m-ep*, musculus epaxialis; *m-ex-t-1, m-ex-t-2, m-ex-t-3,* sections of musculus extensor tentaculi; *m-hyp,* musculus hypoaxialis; *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; *m-sh*, musculus sternohyoideus; *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-fr*, os frontale; *o-iop*, os interoperculare; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-mx*, os maxillare; *o-op*, os operculare; *o-pa-soc*, os parieto-supraoccipitale; *o-pop*, os praeoperculare; *o-post-scl*, os posttemporo-supracleithrum; *o-prmx*, os praemaxillare; *o-pt*, os pteroticum; *o-q*, os quadratum; *o-sph*, os sphenoticum; *pec-ra*, pectoral rays; *pec-sp*, pectoral spine; *pp5*, parapophysis 5; *stf*, supratemporal fossa.

Os orbitosphenoideum. Posterior to the lateral ethmoid (Figs 1, 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 (Figs 1, 2) are large bones that constitute a great part of the cranial roof (Fig. 1). They are largely separated by a well-developed anterior fontanel.

Os sphenoticum. Significantly smaller than the pterotic (Figs 1, 2), constituting, together with this bone, an articulatory facet for the hyomandibula (Fig. 2).

Os pteroticum. There is a well-defined, deep dorsal fossa ("supratemporal fossa": see DE PINNA, 1996) between the dorso-medial surface of the pterotic and the dorso-lateral surface of the parieto-suppraoccipital (Fig.

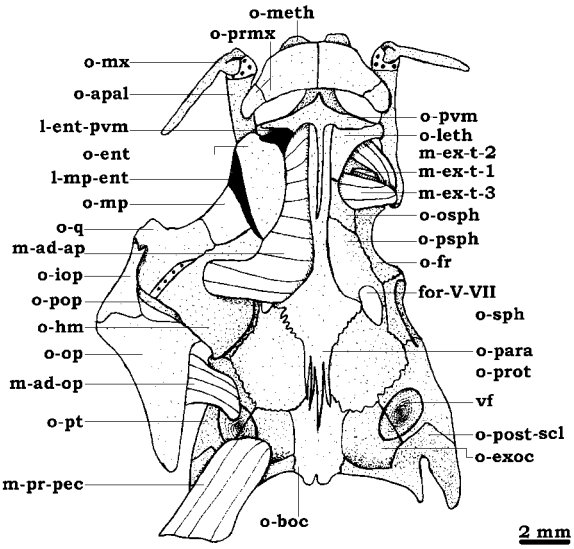

Fig. 2. – Ventral view of the neurocranium and palatine-maxillary system of *Glyptothorax fukiensis*. On the left side the suspensorium, as well as the adductor arcus palatini, adductor operculi and protractor pectoralis, are also illustrated. Premaxillary teeth were removed. *for-V-VII,* trigemino-facialis foramen; *l-ent-pvm*, ligamentum entopterygoideo-praevomerale; *l-mp-ent,* ligamentum metapterygoideo-entopterygoideum; *m-ad-ap*, musculus adductor arcus palatini; *m-ad-op*, musculus adductor operculi; *m-ex-t-1, m-ex-t-2, 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-exoc*, os exoccipitale; *o-fr*, os frontale; *o-hm*, os hyomandibulare; *o-iop,* os interoperculare; *o-leth*, os latero-ethmoideum; *o-meth*, os mesethmoideum; *o-mp*, os metapterygoideum; *o-mx*, os maxillare; *o-op,* os operculare; *o-osph*, os orbitosphenoideum; *o-para*, os parasphenoideum; *o-pop,* os praeoperculare; *o-post-scl*, os posttemporo-supracleithrum; *o-prmx*, os praemaxillare; *o-prot*, os prooticum; *o-psph*, os pterosphenoideum; *o-pt*, os pteroticum; *o-pvm*, os praevomerale; *o-q*, os quadratum; *o-sph*, os sphenoticum; *vf*, ventral fossa.

1: stf). In addition, there is a well-defined, large, deep ventral fossa between the ventro-medial surface of the pterotic and the ventro-lateral surface of the exoccipital (Fig. 2: vf).

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. The extrascapulars are missing.

Os exoccipitale. Well-developed, situated laterally to the basioccipital (Fig. 2).

Os *basioccipitale.* Well-developed, unpaired bone (Fig. 2), forming the posterior-most part of the floor of the neurocranium. Its well-developed ventro-lateral arms are firmly attached to the ventro-medial limbs of the posttemporo-supracleithra.

Os parieto-supraoccipitale. Large bone constituting the postero-dorso-median surface of the cranial roof, which bears a well-developed, anteroposteriorly elongated posterior process (Fig. 1).

Os angulo-articulare. This bone (Figs 1, 3A), together with the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible (Fig. 3A). Postero-dorsally, the angulo-articular has an articulatory facet for the quadrate. Postero-ventrally, it is ligamentously connected, by means of two thick ligaments, to both the interopercular (Fig. 1) and the posterior ceratohyal.

Os dentale. The postero-dorsal surface of the toothed dentary forms a dorsal process (processus coronoideus) (Fig. 3A).

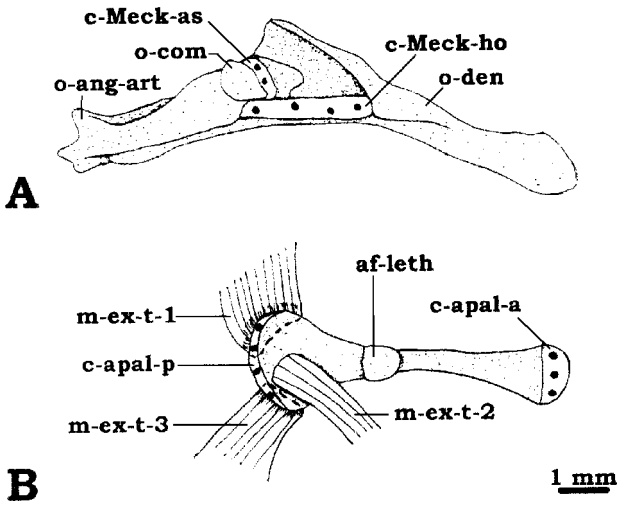

Fig. 3. – *Glyptothorax fukiensis.* (A) Medial view of the left mandible, with mandibular teeth removed. (B) Medial view of the left autopalatine and the insertions of the different sections of the extensor tentaculi on its posterior portion. *af-leth*, articulatory facet for lateral ethmoid; *c-apal-a, c-apal-p*, anterior and posterior cartilages of os autopalatinum; *c-Meck-as, c-Meck-ho*, ascending and horizontal portions of cartilago Meckeli; *m-ex-t-1, m-ex-t-2, m-ex-t-3*, sections of musculus extensor tentaculi; *o-ang-art*, os angulo-articulare; *o-com*, os coronomeckelium; *o-den*, os dentale.

Os coronomeckelium. Small bone lodged in the medial surface of the mandible. It projects to the top of the dorsal margin of the angulo-articular (Fig. 3A).

Os praemaxillare. Each premaxillary is constituted by two bony pieces (Fig. 2), which are firmly attached by connective tissue. Ventrally, the premaxillaries bear numerous small teeth (not shown in Fig. 2) having their tips slightly turned backward.

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

Os autopalatinum. Rod-like, anteroposteriorly elongated bone (Figs 1, 2, 3B), with its posterior portion being markedly expanded dorsoventrally (Fig. 3B). Its posterior end is capped by a cartilage also markedly expanded dorsoventrally (Fig. 3B). Its anterior end is tipped by a well-developed cartilage with two antero-lateral concavities, which accept the two proximal heads of the maxillary (Fig. 2). Medially, the autopalatine articulates, by means of a small, circular articulatory surface (Fig. 3B), with the lateral ethmoid (Figs 1, 2).

Os hyomandibulare. Large bone presenting a poorly-developed antero-dorsal process (Fig. 4). Dorsally it articulates with both the pterotic and the sphenotic (Fig. 2), and postero-dorsally it articulates with the opercular (Figs 2, 4).

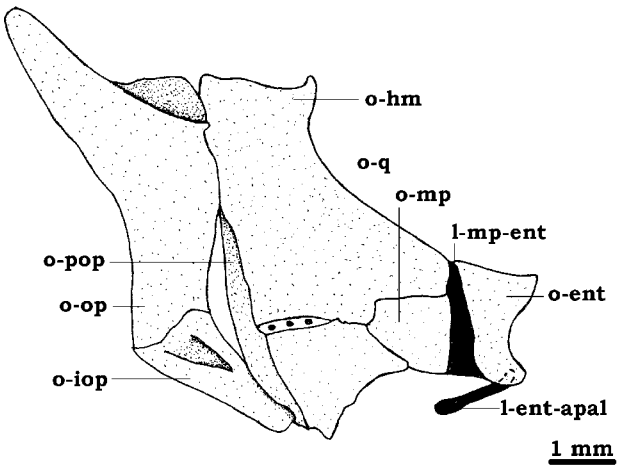

Fig. 4. – Medial view of the left suspensorium of *Glyptothorax fukiensis*. *l-ent-apal*, ligamentum entopterygoideo-autopalatinum; *l-mp-ent*, ligamentum metapterygoideo-entopterygoideum; *o-ent*, os entopterygoideum; *o-hm*, os hyomandibulare; *o-iop*, os interoperculare; *o-mp*, os metapterygoideum; *o-op*, os operculare; *o-pop*, os praeoperculare; *o-q*, os quadratum.

Os entopterygoideum. Well-developed bone attached, by means of two thick ligaments, to the metapterygoid (Figs 2, 4) and to the prevomer (Fig. 2), respectively. Its antero-dorso-lateral surface is connected, *via* a thin, somewhat long ligament (Fig. 4: l-ent-apal), to the postero-ventral surface of the autopalatinum. The ectopterygoids are absent.

Os metapterygoideum. Poorly-developed, with both its dorsal and postero-dorsal surfaces being sutured with the hyomandibular and with its postero-ventral surface being sutured with the quadrate (Fig. 4).

Os quadratum. Well-developed, triangular bone (Fig. 4). Anteriorly, it articulates with the postero-dorsal surface of the angulo-articular.

Os praeoperculare. Long and thin bone firmly sutured to both the hyomandibula and the quadrate (Fig. 4).

Os operculare. Well-developed, roughly triangular bone (Figs 1, 2, 4) ventrally attached, by means of connective tissue, to the interopercular.

Os interoperculare. Its anterior surface is ligamentously connected to the postero-ventral margin of the mandible (Figs 1, 5). Medially, the interopercular is firmly attached (Fig. 5), by connective tissue, to the lateral surface of the posterior ceratohyal.

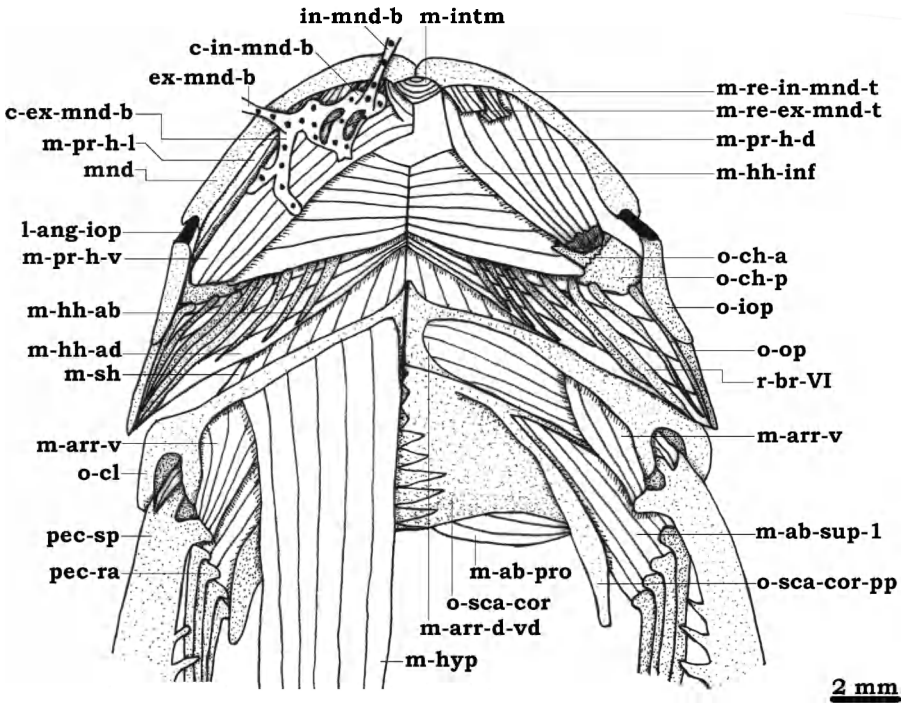

Fig. 5. – Ventral view of the cephalic region and pectoral girdle of *Glyptothorax fukiensis*. On the left side, all the muscles are exposed; on the right side, the mandibular barbels, the cartilages associated with these barbels, the hypaxialis and the ventral and lateral parts of the protractor hyoidei were removed. On both sides, the ligament between the posterior ceratohyal and the angulo-articular were removed. *c-in-mnd-b*, cartilago internus mandibularis tentaculi; *c-ex-mnd-b*, cartilago externus mandibularis tentaculi; *ex-mnd-b, in-mnd-b*; external and internal mandibular barbels; *l-ang-iop*, ligamentum angulo-interoperculare; *m-ab-pro,* musculus abductor profundus; *m-ab-sup-1*, section 1 of musculus abductor superficialis; *m-arr-d-vd*, ventral division of musculus arrector dorsalis; *m-arr-v*, musculus arrector ventralis; *m-hh-ab*, musculus hyohyoideus abductor; *m-hh-ad*, musculus hyohyoideus adductor; *m-hh-inf*, musculus hyohyoideus inferior; *m-hyp*, musculus hypoaxialis; *m-intm*, musculus intermandibularis; *mnd,* mandible; *m-pr-h-d, m-pr-h-l, m-pr-h-v*, pars dorsalis, lateralis and ventralis of musculus protactor hyoideus; *m-re-ex-mnd-t*, musculus retractor externi mandibularis tentaculi; *m-re-in-mnd-t*, musculus retractor interni mandibularis tentaculi; *m-sh*, musculus sternohyoideus; *o-ch-a*, os ceratohyale anterior; *o-ch-p*, os ceratohyale posterior; *o-cl*, os cleithrum; *o-iop*, os interoperculare; *o-op*, os operculare; *o-sca-cor*, os scapulo-coracoideum; *o-sca-cor-pp*, posterior process of os scapulo-coracoideum; *pec-ra*, pectoral rays; *pec-sp*, pectoral spine; *r-br-VI*, radius branchiostegus VI.

Os ceratohyale posterior. Well-developed, somewhat triangular bone (Fig. 5) connected, by means of two long ligaments, to the postero-ventral edge of the mandible and to the medial surface of the suspensorium (the interhyal is missing), respectively.

Os ceratohyale anterior. This bone supports, together with the posterior ceratohyal, the eight branchiostegal rays (Fig. 5).

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

Os parurohyale. The parurohyal (see ARRATIA & SCHULTZE, 1990) is an irregular bone markedly compressed anteroposteriorly, which presents two well-developed postero-lateral arms and a poorly-developed postero-median process.

Os posttemporo-supracleithrum. This bone (Fig. 1), together with the cleithrum and the scapulo-coracoid, constitute the pectoral girdle. Its dorso-medial limb is firmly sutured with both the parieto-supraoccipital and the pterotic (Fig. 1). Its ventro-medial limb is firmly attached to the basiocccipital (Fig. 2). Its postero-lateral margin is deeply forked (Fig. 2), forming an articulating groove for the upper edge of the cleithrum (Fig. 1). Postero-dorsally, the posttemporo-supracleithrum has a prominent, posteriorly directed process (Fig. 1), which is firmly ankylosed with the parapophysis of the fourth vertebra.

Os cleithrum. The cleithrum (Figs 1, 5) is a large, well-ossified stout structure forming a great part of the pectoral girdle and the posterior boundary of the branchial chamber. It bears a deep crescentic, medially-faced groove that accommodates the dorsal condyle of the well-developed pectoral spine. The two cleithra are attached in the antero-medial line *via* connective tissue (Fig. 5). The well-developed humeral process of the cleithrum is connected, by means of a thick, short 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-coracoideum. Elongated, irregular bony plate suturing with the cleithrum along its antero-lateral edge (Fig. 5). Medially it joins

its counterpart in an interdigitation of several strong serrations (Fig. 5). Postero-laterally, the scapulo-coracoid has a prominent, posteriorly-directed posterior process (Fig. 5: o-sca-cor-pp). There is a well-developed mesocoracoid arch, which is significantly enlarged transversally.

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (see DIOGO & CHARDON, 2000a) originates on the preopercular and quadrate and inserts on both the angulo-articular and the dentary (Fig. 1). The A2 (Fig. 1), which lies dorso-mesially to the A1-ost 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' originates on the hyomandibula and quadrate and inserts tendinously on the coronomeckelian bone. There is no A3'' nor Aω.

Musculus levator arcus palatini. Poorly-developed muscle situated medially to the adductor mandibulae A3'. It originates on the antero-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 the hyomandibula and entopterygoid.

Musculus levator operculi. The 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 and inserts on the dorso-medial surface of the opercular (Figs 1, 2).

Musculus dilatator operculi. Well-developed, originating on the pterosphenoid, frontal, sphenotic and also on the dorso-lateral surface of the hyomandibula and inserting on the antero-dorsal margin of the opercular (Fig. 1).

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

Musculus retractor tentaculi. Well-developed muscle situated medially to the adductor mandibulae (Fig. 1). It originates on the metapterygoid and inserts, by means of a thick tendon (Fig. 1), on the maxillary.

Musculus protractor hyoidei. This muscle (Fig. 4) has three parts. The pars ventralis, in which are lodged the cartilages associated with the internal and external mandibular barbels, originates on both the anterior and posterior ceratohyals and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis (Fig. 5). The pars lateralis runs from both the anterior and posterior ceratohyals to the ventro-medial face of the dentary (Fig. 5). The pars dorsalis runs from both the anterior ceratohyal to the dentary (Fig. 5).

Musculus retractor externi mandibularis tentaculi. Small muscle running from the dentary to the cartilage associated with the outer mandibular barbel, which is connected with the cartilage associated with the internal mandibular barbel and is markedly bifurcated posteriorly (Fig. 5).

Musculus retractor interni mandibularis tentaculi. Small muscle attached anteriorly to the dentary and posteriorly to the cartilage associated with the internal mandibular barbel, the posterior portion of which is pierced by a well-developed foramen (Fig. 5).

Muscle intermandibularis. Small muscle joining the two mandibles (Fig. 5).

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

Musculus hyohyoideus abductor. This muscle (Fig. 5) 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 (Fig. 5).

Musculus sternohyoideus. Ir runs from the posterior portion of the parurohyal to the anterior portion of the cleithrum (Fig. 5).

Musculus arrector ventralis. It runs from the cleithrum to the ventral condyle of the pectoral spine (Figs 1, 5).

Musculus arrector dorsalis. This muscle is differentiated into two well-developed divisions. The ventral division (Fig. 5), situated on the ventral surface of the pectoral girdle, originates on the ventral margin of both the cleithrum and the scapulo-coracoid and inserts on the antero-lateral edge of the pectoral spine. The dorsal division, situated on the dorsal surface of the pectoral girdle, originates on the dorso-medial edge of the scapulo-coracoid and inserts on the anterior edge of the dorsal condyle of the pectoral spine.

Musculus abductor profundus. Well-developed muscle (Fig. 5) originating on the postero-medial surface of the coracoid and inserting on the medial surface of the dorsal condyle of the pectoral spine.

Musculus abductor superficialis. This muscle is differentiated into two sections. The larger section (Figs 1, 5:

m-ab-sup-1) runs from the lateral margin of the scapulo-coracoid to the antero-ventral margin of the ventral part of the pectoral fin rays. The smaller section, situated dorsally to the larger one, runs from the lateral edge of the scapulo-coracoid to the antero-dorsal margin of the ventral part of the pectoral fin rays.

Musculus adductor superficialis. This muscle is situated on the posterior margin of the pectoral girdle and is divided into two sections. The larger section (Fig. 1: m-ad-sup-1) originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the antero-dorsal margin of the dorsal part of the pectoral fin rays. The smaller section 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 (Figs 1, 2) running from the ventral surfaces of both the pterotic, the posttemporo-supracleithrum and the exoccipital to the antero-dorsal surface of the cleithrum.

Glyptosternon reticulatum

The principal differences between the structures of the cephalic region and pectoral girdle of this species and those of *Glyptothorax fukiensis* are that in *Glyptosternon reticulatum*: 1) the parurohyal presents a well-developed postero-median process; 2) the anterior ceratohyal presents a well-developed antero-ventro-lateral process directed laterally; 3) the coracoid bridge (see DIOGO *et al.*, 2001a), the postero-lateral process of the scapulo-coracoid, the humeral process of the cleithrum and the ligamentous connection between this bone and the parapophysis of the fifth vertebra, the postero-dorsal process of the posttemporo-supracleithrum and the ventro-medial process of the posttemporo-supracleithrum are absent; 4) the hyomandibula articulates dorsally exclusively with the sphenotic; 9) the maxillary is markedly elongated proximo-distally; 5) the anterior portion of the autopalatine is significantly expanded transversally; 6) each premaxillary is constituted by a single bony piece; 7) the arrector ventralis is a highly-developed muscle essentially oriented transversally, and not obliquely.

Bagarius yarreli

The principal differences between *Glyptothorax fukiensis* and *Bagarius yarreli* are that in this latter species: 1) the cartilage associated with the inner mandibular barbel is not pierced, the cartilage associated with the outer mandibular barbel is not bifurcated posteriorly, and these two cartilages are not connected; 2) the ventral part of the muscle arrector ventralis is poorly developed, being confined to the ventro-lateral surface of the pectoral girdle; 3) although present, the postero-lateral process of the scapulo-coracoid is not as developed in *Glyptothorax fukiensis*; 4) the entopterygoid presents a prominent antero-lateral process, which is associated with the dorsal surface of the premaxillary by connective tissue; 5) the maxillary is markedly elongated proximo-distally; 6) the coronoid process of the mandible is poorly developed, that is, the mandible is markedly compressed ventrodorsally; 7) the mesocoracoid arch is not significantly enlarged transversally; 8) the adductor mandibulae A3'' is present, running from the lateral surface of both the hyomandibula and the quadrate to the medial surface of the angulo-articular; 9) the sphenotic bears a well-developed antero-dorso-lateral laminar projection, which extends markedly beyond the remainder of the cranial roof.

Gagata cenia

The principal differences between *Gagata cenia* and *Glyptothorax fukiensis* are that in the former species: 1) the cartilage associated with the external mandibular barbel is not bifurcated posteriorly and the cartilage associated with the internal mandibular barbel is not pierced; 2) the postero-lateral process of the scapulo-coracoid, the premaxillary teeth, and the postero-lateral extensions of the lateral ethmoid are missing; 3) the arrector ventralis and the abductor superficialis 1 are significantly more developed than in *Glyptothorax fukiensis*; 4) each premaxillary is constituted by a single bony piece; 5) the mesocoracoid arch is not enlarged transversally; 6) the maxillary is markedly elongated proximo-distally; 7) the parurohyal does not present two well-developed postero-lateral arms, but only a well-developed, wide, triangular posterior process; 8) the entopterygoid and metapterygoid are, respectively, significantly smaller and significantly wider than those of *Glyptothorax fukiensis*.

DISCUSSION

Our observations and comparisons support DE PINNA's (1996) phylogenetic hypothesis, according to which the Sisoridae is the sister-group of a clade formed by the Aspredinidae and the Erethistidae. 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 five 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; reversed to 0 in Glyptosternini" (see, e.g., Fig. 1); II) "parapophysis of fifth vertebra strongly flattened and expanded - reversed in Glyptosternini)" (see, e.g., Fig. 1); III) "parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall" (see, e.g., Fig. 1); IV) "humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament – state 3; reversed to 0 in Glyptosternina" (see, e.g., Fig. 1); V) "coracoid with ventral anterior (posterior) process (reversed to 0 in Glyptosternina)" (see, e.g., Fig.

5). Our observations and comparisons not only confirmed these five synapomorphies, but also pointed out an additional synapomorphy to support the clade formed by sisorids, aspredinids and erethistids:

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 could 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, plotosids, cranoglanidids, aspredinidids, erethistidids, sisorids, some ictalurids and some schilbeids; to both the metapterygoid and the ectopterygoid in, e.g., bagrids) (this study, see also e.g. REGAN, 1911; ALEXANDER, 1965; GOSLINE, 1975; GHIOT, 1978; GHIOT et al., 1984; ARRATIA, 1987, 1990, 1992; MO, 1991; DIOGO et al., 1999, 2000, 2001b; DIOGO & CHARDON, 2000c; OLIVEIRA et al., 2001; etc.). However, a well-defined, long ligament attaching on the antero-dorso-lateral margin of the entopterygoid (see, e.g., Fig. 4) and running posteriorly to attach on the postero-ventral margin of the autopalatine is exclusively found in the aspredinids, sisorids and erethistids.

DE PINNA's (1996) proposal of a sister-group relationship between the Erethistidae and the Aspredinidae was based on five synapomorphies (DE PINNA, 1996: 64), of which three concern the configuration of structures examined in this work, namely: I) "anterior margin of pectoral spine with serrations"; 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 not only confirmed these three synapomorphies, but also pointed out an additional synapomorphy to support the clade formed by the aspredinids and the erethistids:

Well-developed fossa between the antero-medial surface of the dorso-medial limb of the posttemporo-supracleithrum and the parieto-supraoccipital.

Plesiomorphically in catfishes there is no well-developed fossa on the dorsal surface of the posterior region of the cranium between the posttemporo-supracleitrum and the parieto-supraoccipital (see, e.g., CHARDON, 1968; MO, 1991). However, in all the aspredinids and erethistids examined, there is a well-developed, deep fossa between the antero-medial surface of the posttemporo-supraclethirum and the parieto-supraoccipital. As such a fossa is absent in all the non-erethistid and non-aspredinid catfishes examined, and particularly in the sisorids (see above), this character constitutes, very likely, an additional synapomorphy to support the clade Aspredinidae plus Erethistidae.

With respect to the synapomorphies of the Sisoridae, four characters were presented by DE PINNA (1996: 62), of which only one concerns the configuration of structures examined in this work, namely: I) "lateral ethmoid with narrow lateral extensions directed posteriorly alongside lateral margin of frontals (missing in tribe Sisorini)" (see, e.g., Fig. 1). Our observations and comparisons confirmed this synapomorphy, and also pointed out a clear, well-defined derived character that is found in the four sisorid species examined, that is, in members of all the four tribes of the family Sisoridae, and in no other catfish examined or described in the literature, which, thus, constitutes, very likely, an additional apomorphy of this taxon:

A well-developed, wide, deep fossa on the neurocranial floor between the ventro-medial surface of the pterotic and the ventro-lateral surface of the exoccipital (see, e.g., Fig. 2: vf).

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