

Osteology and myology of the cephalic region and pectoral girdle of *Erethistes pusillus*, comparison with other erethistids, and comments on the synapomorphies and phylogenetic relationships of the Erethistidae (Teleostei: Siluriformes)

R. DIOGO*, M. CHARDON AND P. VANDEWALLE

Laboratory of Functional and Evolutionary Morphology, Bat. B6, University of Liège, B-4000 Sart-Tilman (Liège), Belgium

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The cephalic and pectoral girdle structures of the erethistid *Erethistes pusillus* (Erethistinae) are described and compared with those of another species of the subfamily Erethistinae, namely *Hara filamentosa*, and of the single species of the subfamily Continae, *Conta conta*, as well as of several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic position of the Erethistidae. The observations and comparisons support de Pinna's phylogenetic hypothesis, according to which the Erethistidae is the sister-group of the Aspredinidae, with the clade formed by these two families being the sister-group of the Sisoridae *sensu stricto*. In addition, the observations and comparisons pointed out a new, additional character to diagnose the family Erethistidae, namely: mesocoracoid arch deeply bifurcated dorsally.

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Key words: catfishes; *Erethistes*; Erethistidae synapomorphies; myology; osteology; phylogeny; Siluriformes.

INTRODUCTION

The Siluriformes, with *c.* 416 genera and >2500 species, represent *c.* 32% of all freshwater fishes and are one of the economically important groups of fresh- and brackish water fishes in the world (Teugels, 1996). Among the 35 siluriform families (Ferraris & de Pinna, 1999), the Asiatic family Erethistidae, with six genera and *c.* 13 species (de Pinna, 1996), is surely one of the least studied. In fact, this family, as currently defined, was only established in 1996 (de Pinna, 1996). Until de Pinna's (1996) work the six erethistid genera, *Conta*, *Erethistes*, *Erethistoides*, *Hara*, *Laguvia* and *Pseudolaguvia*, were included in the family Sisoridae. de Pinna (1996), however, based on a detailed phylogenetic analysis including not only the Asiatic families Sisoridae, Amblycipitidae and Akysidae,

*Author to whom correspondence should be addressed. Tel.: +32 4 3665024; fax: +32 4 3663715; email: R.Diogo@student.ulg.ac.be

but also the Neotropical family Aspredinidae, concluded that these six genera were more closely related to the neotropical aspredinids than to the remaining sisorids. Therefore, these 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*, that is, the family constituted by the remaining genera previously allocated in the family Sisoridae. According to the phylogenetic results of de Pinna (1996), the family Erethistidae is divided into two subfamilies, namely the Erethistinae, which includes the genera *Erethistes*, *Erethistoides*, *Hara*, *Laguvia* and *Pseudolaguvia*, and the Continae, which included the single genus *Conta*, with this genus being the sister-group of the other five erethistid genera. Probably due to the previous allocation of the erethistid genera in the family Sisoridae, the anatomy of the erethistids was rarely studied in detail, with much more attention being given to the remaining sisorids (Bathia, 1950; Gauba, 1962, 1966, 1968, 1969; Tilak, 1963; Mithel, 1964; Mahajan, 1963, 1966a, b, 1967a, b; Lal *et al.*, 1966; Chardon, 1968; Shrestha, 1969; He, 1996, 1967). In fact, the only papers in which the morphology of the erethistids is described with some detail are those of Gauba (1967, 1970a, b), Saxena & Chandy (1966) and de Pinna (1996), with the configuration of their cephalic and pectoral girdle musculature, for example, being practically unknown.

The aim of this work is, thus, to describe in detail the bones, muscles and ligaments of the cephalic region (branchial apparatus excluded) and pectoral girdle of a species belonging to the type genus of the Erethistidae, *Erethistes pusillus* Müller & Troschel (Erethistinae), and to compare these structures with those of another species of the subfamily Erethistinae, namely *Hara filamentosa* Blyth, and of the single species of the subfamily Continae, *Conta conta* (Hamilton), as well as of several other catfishes, as the foundation for a discussion on the synapomorphies and phylogenetic position of the Erethistidae.

MATERIALS AND METHODS

The fishes studied are from the private collection of the Laboratory of Functional and Evolutionary Morphology (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 specimens (Taylor & Van Dyke, 1985). Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsin-cleared and alizarine-stained (t&a) 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* (Doumeidae): 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* 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, 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 boudierus* (Cranoglanididae): LFEM, 2 (alc). *Diplomystes chilensis* (Diplomystidae): LFEM, 2 (alc). *Doumea typica* (Doumeidae): 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, 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 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* (Mochoidae): 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* (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc). *Trachyglanis inae* (Amphiliidae): MRAC P.125552-125553, 2 (alc). *Xylophius magdalenae* (Aspredinidae): USNM 120224, 1 (alc). *Zaireichthys zonatus* (Amphiliidae): MRAC 89-043-P-2243–2245, 3 (alc).

RESULTS

In this section the cephalic and pectoral girdle structures of the erethistin *E. pusillus* (Erethistinae) are described and compared and with those of another erethistin species, *H. filamentosa*, as well as of the single species of the subfamily Continae, *C. conta*. 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). For the different adductor mandibulae sections, however, Diogo & Chardon (2000a) is followed since recent works have pointed out that, with respect to these sections, Winterbottom's (1974) nomenclature presents serious limitations (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 muscles, Diogo *et al.* (2001a) is followed.

ERETHISTES PUSILLUS

Osteology

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

Os lateroethmoideum. With a well-developed, laterally directed articular facet for the autopalatine (Fig. 1). The vomer, usually associated with the lateral ethmoids, is absent.

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

Os orbitosphenoideum. Posterior to the lateral ethmoid (Fig. 1). 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. 1).

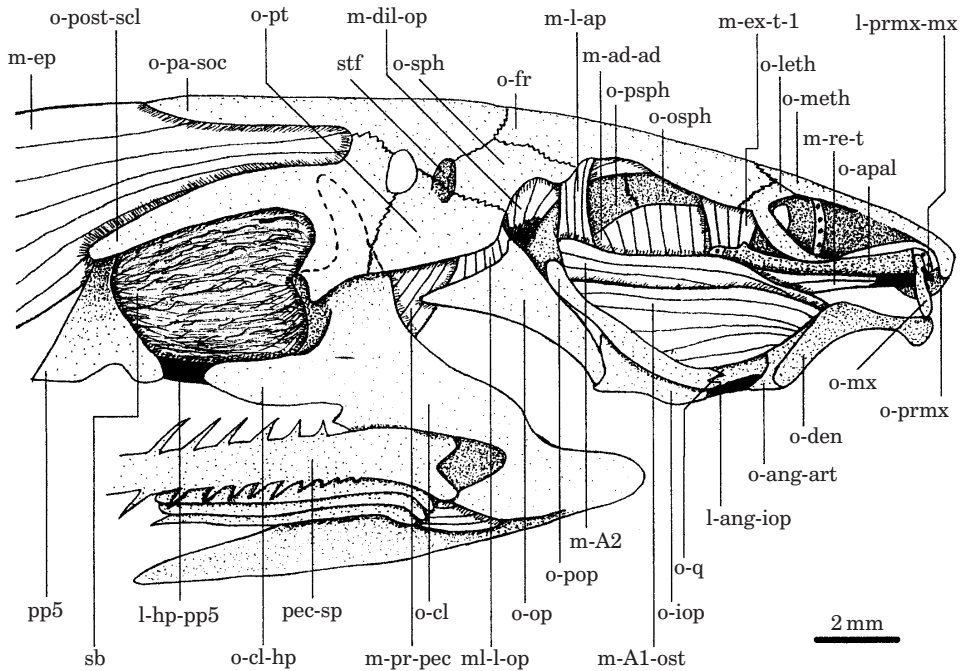


FIG. 1. Lateral view of the cephalic musculature of *Erethistes pusillus*. The dentary and premaxillary teeth were removed. l-ang-iop, ligamentum angulo-interoperculare; l-hp-pp5, ligamentum humero-vertebrale; l-prmx-mx, ligamentum praemaxillo-maxillare; m-A1-ost, m-A2, sections of musculus adductor mandibulae; m-ad-ap, musculus adductor arcus palatini; m-dil-op, musculus dilatator operculi; m-ep, musculus epaxialis; m-ex-t-1, section 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; o-ang-art, os angulo-articulare; o-apal, os autopalatini; 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-osph, os orbitosphenoideum; o-pa-soc, os parieto-supraoccipitale; o-pop, os praeoperculare; o-post-scl, os posttemporo-supracleithrum; o-prmx, os praemaxillare; o-pt, os pteroticum; o-psph, os pterosphenoideum; o-q, os quadratum; o-sph, os sphenoticum; pec-sp, pectoral spine; pp5, parapophysis 5; sb, swimbladder; stf, supratemporal fossa.

Os parasphenoideum. The longest bone of the cranium. 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 a well-developed anterior fontanel.

Os sphenoticum. It presents a somewhat long, narrow anterior extension running lateral to the frontals (Fig. 1) and constitutes, together with the pterotic, an articulatory facet for the hyomandibula.

Os pteroticum. It is somewhat wider than the sphenotic (Fig. 1). There is a well-defined, deep dorsal fossa ('supratemporal fossa'; de Pinna, 1996) between the dorso-medial surface of the pterotic and the dorso-lateral surface of both the sphenotic and the parieto-supraoccipital (Fig. 1: stf). Posteriorly to this fossa, there is also a well-developed, somewhat circular foramen between the postero-medial surface of the pterotic, the antero-medial surface of the posttemporo-supracleithrum and the lateral margin of the parieto-supraoccipital (Fig. 1).

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

Os epioccipitale. Situated on the posterior surface of the neurocranium. The extrascapular is missing.

Os exoccipitale. Small, situated laterally to the basioccipital.

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

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

Os angulo-articulare. This bone [Figs 1 and 2(a)], together with the dentary, coronomeckelian and Meckel's cartilage, constitute the mandible [Fig. 2(a)]. Postero-dorsally, the angulo-articulare has an articulatory facet for the quadrate. Postero-ventrally, it is ligamentously connected, by means of a thick ligament, to the interopercular (Fig. 1).

Os dentale. The postero-dorsal surface of the toothed dentary forms a dorsal process (processus conoideus), the postero-dorsal margin of which is markedly pointed posteriorly [Fig. 2(a)].

Os coronomeckelium. Small bone lodged in the medial surface of the mandible [Fig. 2(a)]. Postero-dorsally it bears a crest for attachment of the adductor mandibulae A3'-d.

Os praemaxillare. The premaxillaries (Fig. 1) 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 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, antero-posteriorly elongated bone [Figs 1 and 2(b)], with its posterior portion being somewhat dorso-ventrally expanded

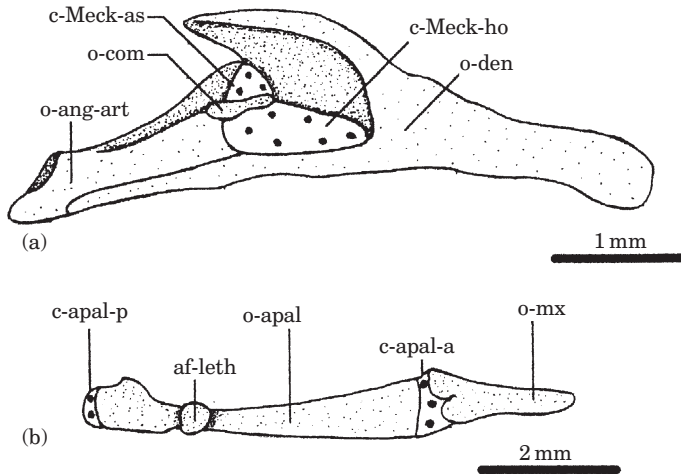


FIG. 2. *Erethistes pusillus*. (a) Medial view of the left mandible, the mandibular teeth were removed. (b) Medial view of the left autopalatine and maxillary. af-leth, articular facet for lateral ethmoid; c-apal-a, c-apal-p, anterior and posterior cartilages of os autopalatinum; c-Meck-as, c-Meck-ho, ascending and horizontal portions of cartilago Meckeli; o-ang-art, os angulo-articulare; o-apal, os autopalatinum; o-com, os coronomeckelium; o-den, os dentale; o-mx, os maxillare.

[Fig. 2(b)]. Its anterior end is tipped by a well-developed cartilage with two antero-lateral concavities, which accept the two proximal heads of the maxillary, and its posterior end is capped by a small cartilage [Fig. 2(b)]. Medially, the autopalatine articulates with the lateral ethmoid [Figs 1 and 2(b)].

Os hyomandibulare. The homology, and, thus, the correct denomination, of this bone, as well as of the other suspensorium components of catfishes, has been the subject of endless controversies (McMurrich, 1884; Gosline, 1975; Arratia & Menuemarque, 1981; Howes, 1983*a, b*, 1985; Arratia, 1987, 1990, 1992). For the time being, the suspensorial bones are described by their most often used names (Arratia, 1992). The hyomandibula is a large bone presenting a poorly developed antero-dorsal process (Fig. 3). Dorsally it articulates with both the pterotic and the sphenotic, and postero-ventrally it articulates with the opercular (Fig. 1).

Os entopterygoideum. Well-developed bone attached, by means of two thick ligaments, to the metapterygoid (Fig. 3) and to the vomer, respectively. Its antero-dorsal surface is connected, *via* a thin, somewhat long ligament (Fig. 3: l-ent-apal), to the postero-ventral surface of the autopalatinum. The ectopterygoideum is absent.

Os metapterygoidium. Poorly developed, posteriorly sutured with the hyomandibula and ventrally sutured with the quadrate (Fig. 3).

Os quadratum. Large bone ventral to both the hyomandibula and the metapterygoid (Fig. 3).

Os praeoperculare. Long and thin bone sutured firmly to the hyomandibula and to the quadrate (Fig. 3).

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

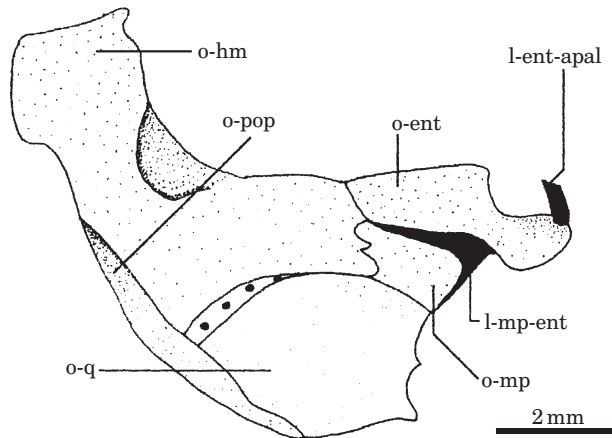


FIG.3. Medial view of the left suspensorium of *Erethistes pusillus*. l-ent-apal, ligamentum entopterygoideo-autopalatinum; l-mp-ent, ligamentum metapterygoideo-entopterygoideum; o-ent, os entopterygoideum; o-hm, os hyomandibulare; o-mp, os metapterygoideum; o-pop, os praeperculare; o-q, os quadratum.

Os interoperculare. Its anterior surface is connected, *via* a strong, long ligament, to the postero-ventral margin of the mandible (Figs 1, 4 and 5). Medially, the interopercular is firmly attached (Figs 4 and 5), by connective tissue, to the lateral surface of the posterior ceratohyal.

Os ceratohyale posterior. Well-developed, somewhat triangular bone (Figs 4 and 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, which presents a well-developed postero-dorsal lamina, supports, together with the posterior ceratohyal, the seven branchiostegal rays (Fig. 5).

Os hypohyale ventrale. The ventral hypohyals are ligamentously connected to the antero-lateral edges of the parurohyal (Fig. 5). The dorsal hypohyals are missing.

Os parurohyale. The parurohyal (Arratia & Schultze, 1990) is a somewhat triangular bone with two poorly developed postero-lateral arms and a well-developed postero-medial process (Fig. 5).

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 thin ventro-medial limb is loosely attached, *via* a small, thin ligament to the basioccipital. Its postero-lateral margin is deeply forked, forming an articulating groove for the upper edge of the cleithrum (Fig. 1). Posterodorsally, 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 6 and 7) is a large, well-ossified stout structure forming a great part of the pectoral girdle and the posterior boundary

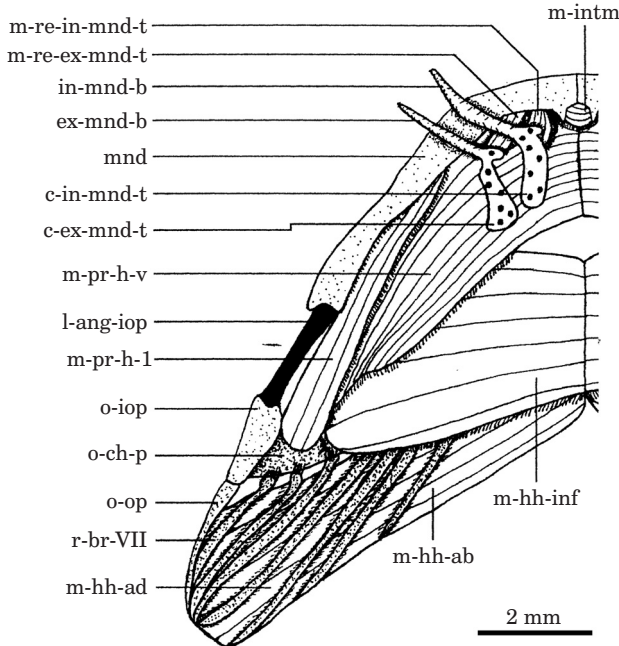


FIG.4. Ventral view of the cephalic musculature of *Erethistes pusillus*. c-ex-mnd-b, cartilago externus mandibularis tentaculi; c-in-mnd-b, cartilago internus mandibularis tentaculi; ex-mnd-b, in-mnd-b, external and internal mandibular barbels; l-ang-iop, ligamentum angulo-interoperculare; m-hh-ab, musculus hyohyoideus abductor; m-hh-ad, musculus hyohyoideus adductor; m-hh-inf, musculus hyohyoideus inferior; m-intm, musculus intermandibularis; m-pr-h-l, m-pr-h-v, pars lateralis and ventralis of musculus protractor hyoideus; m-re-ex-mnd-t, musculus retractor externi mandibularis tentaculi; m-re-in-mnd-t, musculus retractor interni mandibularis tentaculi; mnd, mandible; o-ch-p, os ceratohyale posterior; o-iop, os interoperculare; o-op, os operculare; r-br-VII, radius branchiostegus VII.

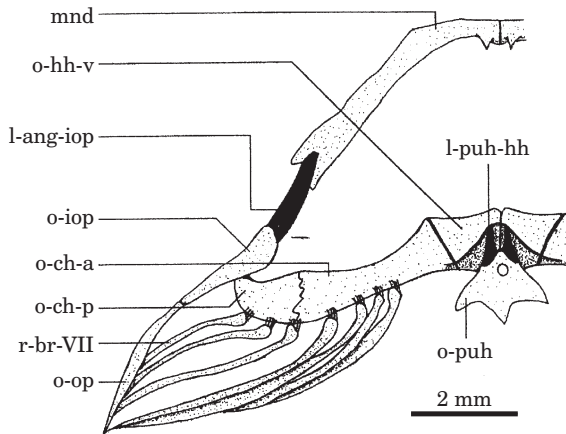


FIG.5. Ventral view of the splanchnocranium of *Erethistes pusillus*. l-ang-iop, ligamentum angulo-interoperculare; l-puh-hh, ligamentum parurohyalo-hypohyale; mnd, mandible; o-ch-a, os ceratohyale anterior; o-ch-p, os ceratohyale posterior; o-hh-v, os hypohyale ventrale; o-iop, os interoperculare; o-op, os operculare; o-puh, os parurohyale; r-br-VII, radius branchiostegus VII.

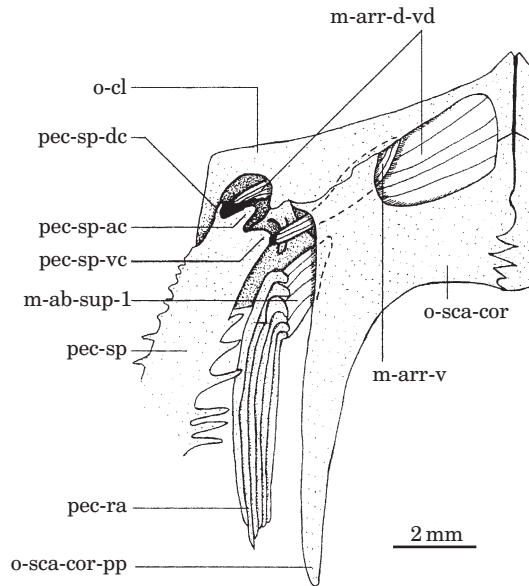


FIG. 6. Ventral view of the pectoral girdle of *Bunocephalus knerii*. m-ab-sup-1, section of musculus abductor superficialis; m-arr-d-vd, ventral division of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-pp, posterior process of os scapulo-coracoide; pec-ra, pectoral rays; pec-sp, pectoral spine; pec-sp-ac, pec-sp-dc, anterior, dorsal and ventral condyles of pectoral spine.

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 Fig. 6). The two cleithra are attached in the antero-medial line *via* massive connective tissue (Fig. 6). The well-developed humeral process

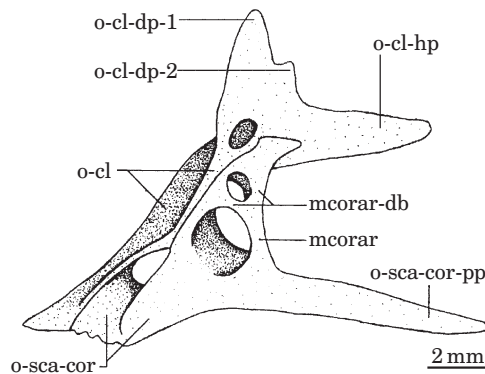


FIG. 7. Medial view of right pectoral girdle of *Erethistes pusillus*. mcorar, mesocoracoid arch; mcorar-db, dorsal bifurcation of mesocoracoid arch; o-cl, os cleithrum; o-cl-dp-1, o-cl-dp-2, dorsal processes of os cleithrum; o-cl-hp, humeral process of os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-pp, posterior process of os scapulo-coracoide.

of the cleithrum 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 and bifurcated distally (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 (Fig. 6). Antero-laterally, it presents a large anteriorly directed process, usually called the coracoid bridge, 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 6 and 7: o-sca-cor-pp). There is a well-developed mesocoracoid arch, which is deeply bifurcated dorsally, with its dorsomedial and dorsolateral arms being separated by a well-developed, circular foramen (Fig. 7).

Myology

Musculus adductor mandibulae. The adductor mandibulae A1-ost (Diogo & Chardon, 2000a) 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 (Fig. 1), 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' originates on the hyomandibula, preopercular and quadrate and inserts tendinously on the coronomeckelian bone. There is no A3' nor A ω .

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

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

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. It originates on the ventral surface of the pterotic and inserts on the dorso-medial surface of the opercular.

Musculus dilatator operculi. Highly developed, originating on the pterosphenoid, frontal, sphenotic and pterotic 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 (Fig. 1) runs from both the orbitosphenoid and the lateral ethmoid to the postero-dorsal surface of the autopalatine. The extensor tentaculi 2 originates on the lateral ethmoid and inserts on the postero-medial surface of the autopalatine. The extensor tentaculi 3 runs from both the lateral ethmoid and the orbitosphenoid 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, long 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 the anterior ceratohyal and inserts on the dentary, meeting its counterpart in a well-developed median aponeurosis (Fig. 4). The pars lateralis originates on both the anterior and posterior ceratohyals, inserting on the ventro-medial face of the dentary (Fig. 4). The pars dorsalis runs from both the anterior and posterior ceratohyals to the dentary.

Musculus retractor externi mandibularis tentaculi. Small muscle running from the dentary to the cartilage associated with the outer mandibular barbel (Fig. 4).

Musculus retractor interni mandibularis tentaculi. Small muscle attached posteriorly to the cartilage associated with the internal mandibular barbel and anteriorly to the dentary (Fig. 4).

Muscle intermandibularis. Small muscle joining the two mandibles (Fig. 4).

Musculus hyohyoideus inferior. Thick muscle (Fig. 4) 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 (Fig. 4) 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. 4).

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

Musculus arrector ventralis. Thin muscle running from the cleithrum to the ventral condyle of the pectoral spine (Fig. 6).

Musculus arrector dorsalis. This muscle is differentiated into two well-developed divisions. The ventral division (Fig. 6), 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 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 (Fig. 6: 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 situates on the posterior margin of the pectoral girdle and is divided into two sections. The larger section originates on the posterior surfaces of both the cleithrum and the scapulo-coracoid and inserts on the 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 (Fig. 1) running from the ventral surfaces of both the pterotic and the posttemporo-supracleithrum to the antero-dorsal surface of the cleithrum.

HARA FILAMENTOSA

The configuration of the structures described above for *E. pusillus* is remarkably similar to that of the structures of *H. filamentosa*, with the only significant difference being that in *H. filamentosa*, in contrast to *E. pusillus*, there is no well-developed foramen between the dorsal surfaces of the pterotic, posttemporo-supracleithrum and parieto-supraoccipital (Fig. 1), but just a small dorsal fossa in the same region.

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In a general way, the configuration of the cephalic and pectoral girdle structures of this species resembles that of *E. pusillus*, with the only significant differences between these species concerning these structures being: 1) the posterior process of the posttemporo-supracleithrum is not as developed in *C. conta* as it is in *E. pusillus*; 2) in *C. conta* the lateral margin of the parapophysis of the fifth vertebra is not bifurcated; 3) as in *H. filamentosa*, in *C. conta* there is no well-developed foramen between the dorsal surfaces of the pterotic, posttemporo-supracleithrum and parieto-supraoccipital, but just a small dorsal fossa in the same region.

DISCUSSION

The phylogenetic position of aspredinidids from the present observations and comparisons support de Pinna's (1996) phylogenetic hypothesis, according to which the Erethistidae 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* de Pinna (1996) [this hypothesis is also supported by a phylogenetic comparison, which is still in progress, of more than 400 morphological characters concerning the configuration of the cephalic and pectoral girdle bones, muscles and ligaments of about 80 catfish genera (Diogo, in press.)].

De Pinna's (1996) grouping of the Erethistidae, Aspredinidae and Sisoridae in a monophyletic clade was based on 10 synapomorphies (de Pinna, 1996), of which five concern the configuration of structures examined in this work, namely: 1) 'posterior portion of supraclithrum (posttemporo-supracleithrum) ankylosed to margin of Weberian lamina – state 1' (Fig. 1); 2) 'parapophysis of fifth vertebra strongly flattened and expanded' (Fig. 1); 3) 'parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall' (Fig. 1); 4) 'humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament – state 3' (Fig. 1); 5) 'coracoid with ventral anterior (posterior) process' (Figs 6 and 7). The present observations and comparisons not only confirmed these two synapomorphies, but also pointed out an additional synapomorphy to support the clade formed by sisorids, aspredinids and erethistids, which is described below.

'Well-defined, long ligament attaching on the antero-dorsal 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, cranoglanidids, aspredinidids, erethistidids, sisorids, some ictalurids and some shilbeids; to both the metapterygoid and the ectopterygoid in, *e.g.* bagrids) (Regan, 1911; Alexander, 1965; Gosline, 1975; Arratia, 1987, 1990, 1992; Mo, 1991; Diogo *et al.*, 1999, 2000, 2001*b*; Diogo & Chardon, 2000*c*, 2003; this study). A well-defined, long ligament attaching on the antero-dorsal margin of the entopterygoid (Fig. 3) and running posteriorly to attach on the postero-ventral margin of the autopalatine, however, 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), of which three concern the configuration of structures examined in this work, namely: 1) 'anterior margin of pectoral spine with serrations' (Fig. 6); 2) 'internal support for pectoral fin rays small in size'; 3) 'anterior portion of lateral line running closely in parallel to lateral margin of Weberian lamina'. The present observations and comparisons confirmed these three synapomorphies, but failed to point out additional synapomorphic characters to support the clade formed by aspredinids and erethistids. As the present observations only pointed out a single derived feature present in both the erethistids and sisorids but absent in aspredinids (namely, 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), and did not even point out a single derived feature present in both the sisorids and aspredinids but absent in erethistids. This study supports a sister-group relationship between the Erethistidae and the Aspredinidae, and, consequently, de Pinna's (1996) statement that the Sisoridae of previous authors was, in fact, a paraphyletic group.

De Pinna's (1996) listed six characters to support the monophyly of the Erethistidae, of which only one concerns the configuration of structures examined in this work, namely: 1) 'posterior margin of anterior ceratohyal with laminar expansion forming process directed laterally'. The present observations and comparisons not only confirmed this synapomorphy, but also pointed out a character that is found in the three erethistid species examined, that is, in members of the two subfamilies of the family Erethistidae, and in no other catfishes examined or described in the literature, which, thus, constitutes very likely an additional character to diagnose this family. This character is described below.

'Mesocoracoid arch deeply bifurcated dorsally'. The plesiomorphic condition for catfishes is that in which the mesocoracoid arch is a thin, simple tubular structure (Diogo *et al.*, 2001*a*). In the erethistids examined, however, the mesocoracoid arch is deeply bifurcated dorsally, with its dorso-lateral and dorso-medial arms being separated by a well-developed, circular foramen (Fig. 7).

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