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On the Osteology and Myology of Catfish Pectoral Girdle, With a Reflection on Catfish (Teleostei: Siluriformes) Plesiomorphies

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ABSTRACT The configuration of the pectoral girdle bones and muscles of numerous catfishes was studied in detail and compared with that of other siluriforms, as well as of other teleosts, described in the literature. The pectoral girdle of catfishes is composed of only three bones, which probably correspond to the posttemporo-supracleithrum (posttemporal + supracleithrum), scapulo-coracoid (scapula + coracoid), and cleithrum of other teleosts. These latter two bones constitute the place of origin of the pectoral girdle muscles. Two of these muscles are related to the movements of the pectoral fin. These two muscles correspond, very likely, to the abductor superfi-

cialis and to the adductor superficialis of other teleostean fishes. In relation to the pectoral spine (thickened first pectoral fin ray), it is usually moved by three well-developed muscles, which are probably homologous with the arrector ventralis, arrector dorsalis, and abductor profundus of nonsiluriform teleosts. The morphological diversity and the plesiomorphic configuration of these muscles, as well as of the other catfish pectoral girdle structures, are discussed. *J. Morphol.* 249:100–125, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: catfish plesiomorphies; myology; Ostariophysii; osteology; pectoral girdle; Siluriformes

The Siluriformes, or catfishes, with their 2,584 species, represent about 32% of all freshwater fishes (Teugels, 1996). They are “one of the economically important groups of fresh and brackish water fishes in the world: in many countries, they form a significant part of inland fisheries; several species have been introduced in fish culture; numerous species are of interest to the aquarium industry where they represent a substantial portion of the world trade” (Teugels, 1996:10). These fishes present a large number of morphological specializations, which make them easily recognizable, even in fossils in which only some small, disarticulated fragments are available (Regan, 1911a; Alexander, 1965; Chardon, 1968; Fink and Fink, 1981; Arratia, 1987; etc.). One of the more remarkable anatomical specializations of catfishes, of considerable value to paleontologists, is the peculiar transformation of all the pectoral girdle, and especially of the first pectoral ray (Reed, 1924; Hubbs and Hibbard, 1951; Alexander, 1965; Lundberg, 1975ab; Gosline, 1977; Brosseau, 1978; Grande, 1987; Grande and Eastman, 1987; etc.). In fact, contrary to most basal teleosts, in which the pectoral girdle is constituted by a large and variable number of bones and is highly mobile in relation to the neurocranium, in catfishes the pectoral girdle is only composed of three skeletal elements, being deeply attached to the neurocranium (see Gosline, 1977). The homologies between the three components of catfish pectoral girdle and those of most

basal teleosts has been a subject of discussion and uncertainty in the past (Regan, 1911a; Alexander, 1965; Chardon, 1968; Lundberg, 1975a; Gosline, 1977; Brosseau, 1978; Fink and Fink, 1981; Howes, 1983a, 1985; Jollie, 1986; etc.). However, it is now commonly accepted (Schaefer, 1990, 1998; Howes and Fumihito, 1991; Arratia and Gayet, 1995; Adriães, 1997; Adrianes and Verraes, 1998; Gayet and Meunier, 1998; Cabuy et al., 1999; He et al., 1999; etc.) that these bones probably correspond to the cleithrum, scapulo-coracoid (scapula+coracoid) and posttemporo-supracleithrum (posttemporal + supracleithrum) of other teleosts. The particular configuration of these bones is probably related to other peculiar catfish features, such as the ankylosis between the posterior region of the neurocranium, the pectoral girdle and the anterior vertebrae, but also the friction-locking mechanism of the thickened first pectoral ray (see Tilak, 1963; Alexander, 1965; Gainer, 1967; Chardon, 1968; Gosline, 1977; Schaefer, 1984; Fine et al., 1997). This friction-

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locking mechanism, which is well described by Alexander (1965), seems to be related principally to a protective function (Alexander, 1965), but could sometimes be associated with terrestrial locomotion (Vaillant, 1895; Donnelly, 1973; Gougnard and Vandewalle, 1980; etc.), sound production (Gainer, 1967; Fine et al., 1997; Kaatz, 1997; Ladich, 1997; Pruzsinszky and Ladich, 1998; etc.), feeding habits (see, e.g., Tilney and Hecht, 1990) or reproductive behavior (see Winemiler, 1987; Pruzsinszky and Ladich, 1998).

The pectoral spine and its friction-locking mechanism, as well as the pectoral fin rays and radials, and also the dorsal connection between the pectoral girdle and the posterodorsal region of the neurocranium have been the subject of detailed studies (e.g., Reed, 1924; Tilak, 1963; Alexander, 1965; Lundberg, 1975a; Gainer, 1967; Schaefer, 1984; Arratia and Gayet, 1995; Fine et al., 1997). However, it is surprising that the osteology, but principally the myology, of the pectoral girdle *sensu stricto* (pectoral fin rays and radials not included) of siluriforms has never been the subject of a detailed, comparative study. In fact, there are only a few descriptions of the pectoral girdle muscles of specific catfish groups (e.g., McMurrich, 1884; Jaquet, 1898; Nawar, 1955; Alexander, 1965; Dubale and Rao, 1961; Gainer, 1967; Taverne and Aloulou-Triki, 1974), and almost nothing has been done on their function, on their taxonomical distribution, and principally on their phylogenetic significance. Moreover, very little is known about the differences between these muscles and those of other ostariophysans and, consequently, about the morphological transformations that have led to such differences. The absence of detailed, comparative studies on the osteology and myology of catfish pectoral girdle is particularly problematic, not only due to the anatomical, paleontological, functional, ethological, and ecological importance of this complex structure (see above), but principally due to the lack of data available to disclose catfish phylogeny (see Mo, 1991; De Pinna, 1993, 1998).

That is why we studied in detail the osteology and myology of the pectoral girdle *sensu stricto* in numerous catfishes. The configuration of the pectoral spine, as well as the sites of insertion of the muscles responsible for its movements, was also studied. It is hoped that our descriptions and comparisons not only increase knowledge of the myology and osteology of catfish pectoral girdle but also pave the way for future works concerning the comparative anatomy, functional morphology, paleontology, eco-morphology, and particularly the phylogeny of these fishes.

MATERIALS AND METHODS

The fishes studied are from the collection of our laboratory (LFEM), from the Musée Royal de l'Afrique Centrale of Tervuren (MRAC), from the Université Nationale du Bénin (UNB), from the Mu-

séum 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 alizarin-stained (following the Taylor and Van Dike, 1985, method) specimens. Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The trypsin-cleared and stained-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.¹

RESULTS

We describe the osteology and myology of the pectoral girdle of representatives of eight catfish families, namely, *Amphilius brevis* Boulenger, 1902 (Amphiliidae), *Arius heudelotii* Valenciennes, 1840 (Ariidae), *Bagrus docmak* Forsskall, 1775 (Bagridae), *Clarias gariepinus* Burchell, 1822 (Clariidae), *Chrysichthys nigrodigitatus* Lacépède, 1803 (Claroteidae), *Diplomystes chilensis* Molina, 1782 (Diplomystidae), *Phractura brevicauda* Boulenger, 1911 (Doumeidae), and *Plotosus lineatus* Thunberg, 1787 (Plotosidae) (He, 1997; He et al., 1999; Diogo and Chardon, in preparation, have shown that the "Amphiliidae" are not a monophyletic group, and that the subfamilies "Doumeinae" and "Amphiliidae" should be raised to the family level; therefore, the Amphiliidae and Doumeidae of the present study

¹*Amphilius brevis* (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (t&a). *Amphilius jacknosi* (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* (Doumeidae): MNHN 1961-0600, 1 (alc); *Arius hertzbergii* (Ariidae): FFEM, 1 (alc). *Arius heudelotii* (Ariidae): FFEM, 4 (alc). *Auchenoglanis biscutatus* (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagre marinus* (Ariidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus bayad* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Bagrus docmak* (Bagridae): MRAC 86-07-P-512, 1 (alc); LFEM, 2 (alc); MRAC 86-07-P-516, 1 (t&a). *Belonoglanis tenuis* (Doumeinae): MRAC P.60494, 1 (alc); *Chrysichthys cranchii* (Claroteidae): LFEM, 1 (alc); LFEM, 1 (t&a). *Chrysichthys auratus* (Claroteidae): UNB, 2 (alc); UNB, 2 (t&a). *Chrysichthys nigrodigitatus* (Claroteidae): UNB, 2 (alc); UNB, 2 (t&a). *Clarias gariepinus* (Clariidae): MRAC 93-152-P-1356, 1 (alc); 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). *Genidens genidens* (Ariidae): LFEM, 2 (alc). *Hemibagrus wycki* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Heterobranchius longifilis* (Clariidae): LFEM, 2 (alc). *Ictalurus punctatus* (Ictaluridae): LFEM, 5 (alc). *Mochokus niloticus* (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Bagridae): LFEM, 1 (alc). *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 (t&a). *Phractura intermedia* (Doumeidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias* (Pimelodidae): LFEM, 2 (alc); LFEM, 2 (t&a). *Plotosus lineatus* (Plotosidae): USNM 200226, 2 (alc). *Pseudomystus bicolor* (Bagridae): LFEM, 1 (alc); LFEM, 1 (t&a). *Schilbe intermedius* (Schilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* (Siluridae): LFEM, 2 (alc). *Tandanus rendahli* (Plotosidae): USNM 173554, 2 (alc).

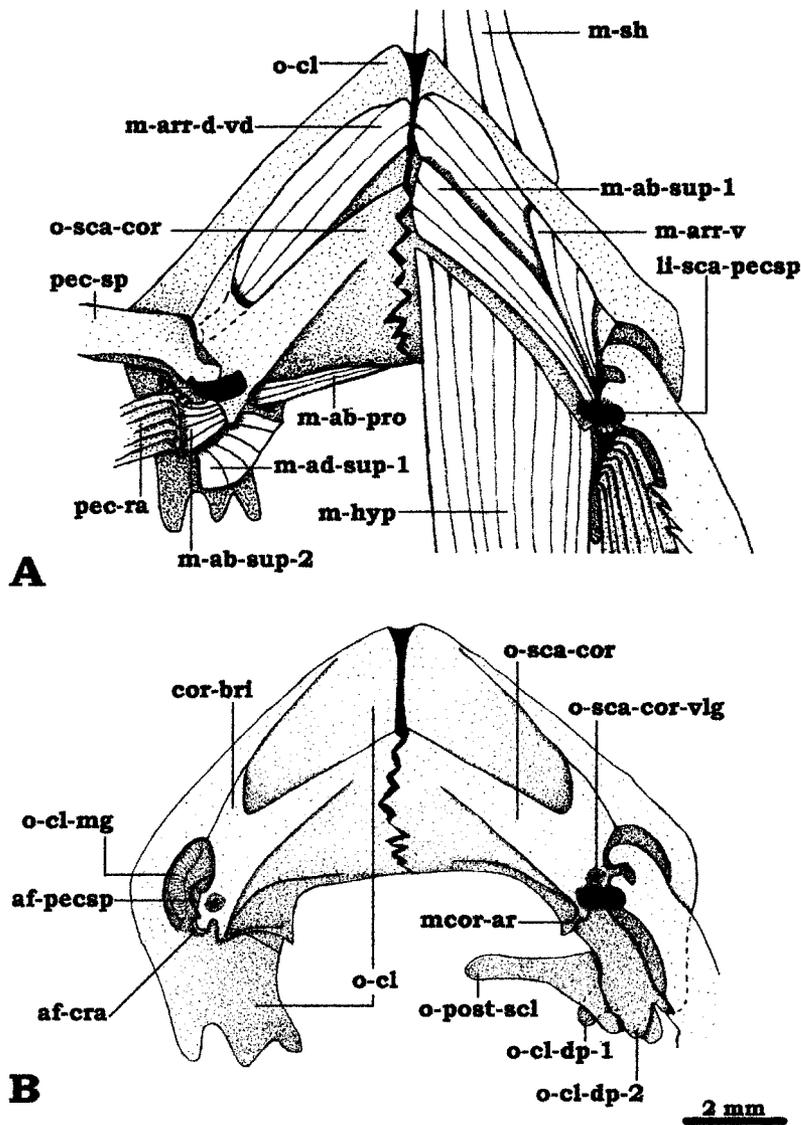


Fig. 1. Ventral view of the pectoral girdle of *Chrysichthys nigrodigitatus*. **A**: In the right side all the muscles are exposed; in the left side the arrector ventralis, section 1 of the abductor superficialis, hypoaxialis, and sternohyoideus are removed. **B**: Pectoral fins and all muscles removed. In the right side the posttemporo-supracleithrum and the pectoral spine are also removed. af-cra, articularity facet for complex radial; af-pecsp, articularity facet for pectoral spine; cor-bri, coracoid bridge; li-sca-pecsp, ligament between scapulo-coracoid and pectoral spine; m-ab-pro, musculus abductor profundus; m-ab-sup-1, m-ab-sup-2, sections of musculus abductor superficialis; m-ad-sup-1, section 1 of musculus adductor superficialis; m-arr-d-vd, ventral division of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesacoracoid arch; o-cl, os cleithrum; o-cl-mg, medial groove of cleithrum; o-cl-dp-1, o-cl-dp-2, dorsal processes of cleithrum; o-post-scl, os posttemporo-supracleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-vlg, ventro-lateral groove of scapulo-coracoide; pec-ra, pectoral rays; pec-sp, pectoral spine.

correspond, respectively, to the former “Amphiliinae” and “Doumeinae”). Significant differences between these species and other species of the same families will also be mentioned. The nomenclature used in the osteological descriptions corresponds to that most commonly accepted currently (see above). In relation to the myological descriptions, we follow Winterbottom (1974). Initially, it seems very difficult to homologize the highly transformed muscles of catfish pectoral girdle with those of other teleosts. However, this does not constitute a problem, since Winterbottom (1974:271–276) synonymized the pectoral girdle muscles of some siluriforms, described by, e.g., McMurrich (1884), Nawar (1955), or Saxena and Chandy (1966), with those of other teleostean fishes. In order to facilitate and to simplify the descriptions, first we describe the configuration of the pectoral girdle muscles and bones of *Chrysichthys nigrodigitatus* (Claroteidae), which, with very few

exceptions, probably represents the generalized condition for catfishes (see Discussion). Then we briefly summarize the main differences between the situation found in the representatives of the other seven families and that of *C. nigrodigitatus*.

Chrysichthys nigrodigitatus

The pectoral girdle of *Chrysichthys nigrodigitatus* is constituted by three paired, well-developed bones: the cleithrum, the scapulo-coracoid, and the posttemporo-supracleithrum (Figs. 1B, 2A, 3A). The most dorsal of these bones, the posttemporo-supracleithrum, is strongly attached to the neurocranium. Its dorsomedial limb is sandwiched between the extrascapular, parieto-supraoccipital, and pterotic bones (Fig. 3A), and is linked to these bones by means of extensive ligamentous tissue. Its strong median limb, usually called ossified Baudelot's liga-

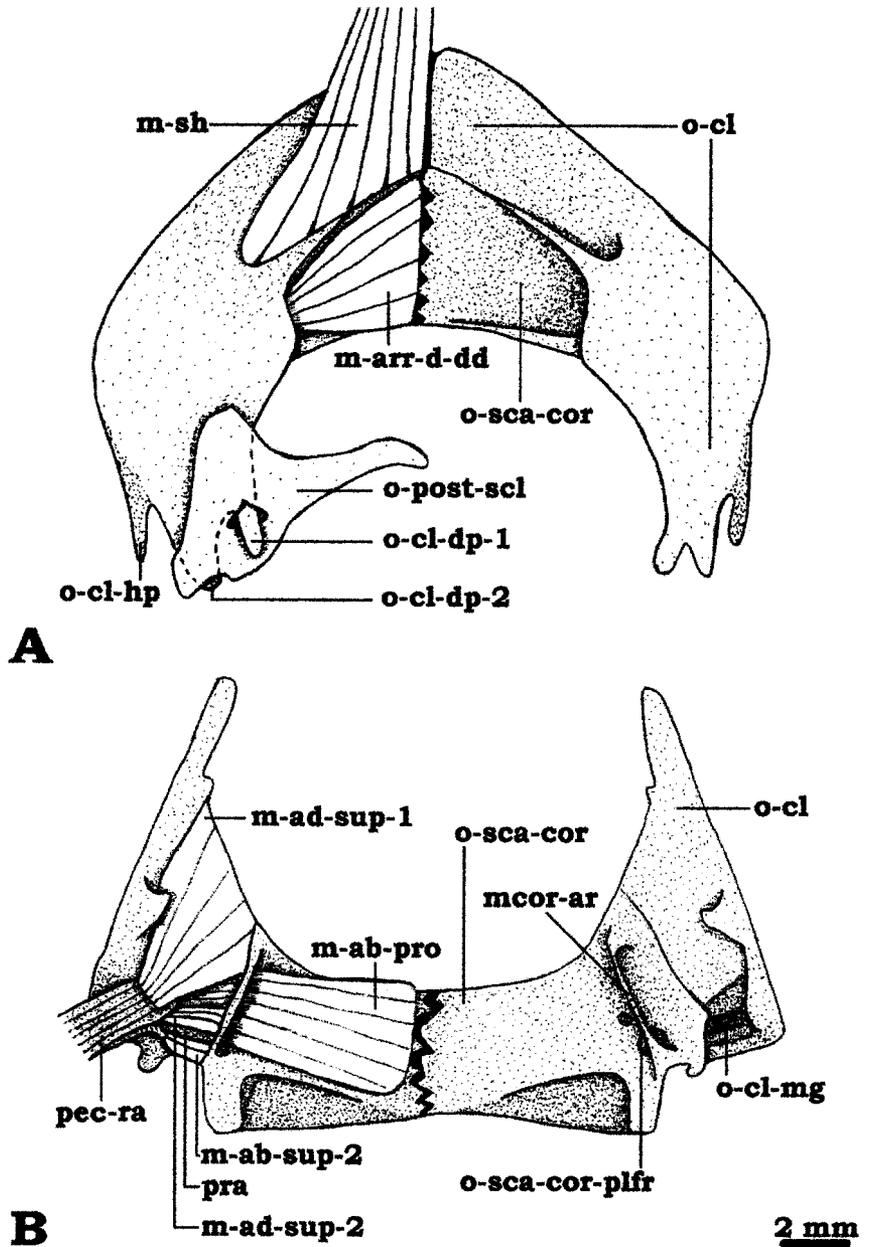


Fig. 2. Pectoral girdle of *Chrysichthys nigrodigitatus*. **A**: Dorsal view. In the right side the posttemporo-supracleithrum, as well as all muscles, are removed. **B**: Posterior view, posttemporo-supracleithrum removed. In the right side all muscles are also removed. m-ab-pro, musculus abductor profundus; m-ab-sup-2, section 2 of musculus abductor superficialis; m-ad-sup-1, m-ad-sup-2, sections of musculus adductor superficialis; m-arr-d-dd, dorsal division of musculus arrector dorsalis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-cl-mg, medial groove of cleithrum; o-cl-dp-1, o-cl-dp-2, dorsal processes of cleithrum; o-cl-hp, humeral process of cleithrum; o-post-scl, os posttemporo-supracleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-plfr, postero-lateral foramen of scapulo-coracoide; pec-ra, pectoral rays; pra, proximal radial.

ment, is firmly attached to the basioccipital via a strong, short ligament (see Diogo and Chardon, 2000a: fig. 3). The posteroventrolateral edge of the posttemporo-supracleithrum is deeply bifurcated (Fig. 1B) to receive the dorsal processes of the cleithrum (the dorsal surface of the cleithrum is also deeply bifurcated, thus presenting two well-developed processes for the articulation with the posttemporo-supracleithrum. To simplify the descriptions, we call the anterodorsal one "first dorsal process of the cleithrum" and the posteroventral one "second dorsal process of the cleithrum": see Figs. 1B, 2A, 3A). In addition, the posttemporo-supracleithrum also presents a large posterodorsal foramen into which enters the first dorsal process of

the cleithrum (Figs. 2A, 3A). This type of articulation between the posttemporo-supracleithrum and the cleithrum permits an extensive protraction or retraction of the ventral part of the solid complex formed by both the cleithrum and the scapulo-coracoide (see Diogo and Chardon, 2000a).

The cleithrum is a large, well-ossified, stout structure forming the major part of the pectoral girdle (Figs. 1B, 2A, 3A). It forms the posterior boundary of the branchial chamber. Posterolaterally, the cleithrum bears a large, posteriorly directed process, the humeral process (o-cl-hp), which is granulated on the outer surface. At this point of curvature, the cleithrum bears a deep, crescentic, medially faced groove (o-cl-mg), with rough surfaces (Figs. 1B, 2B),

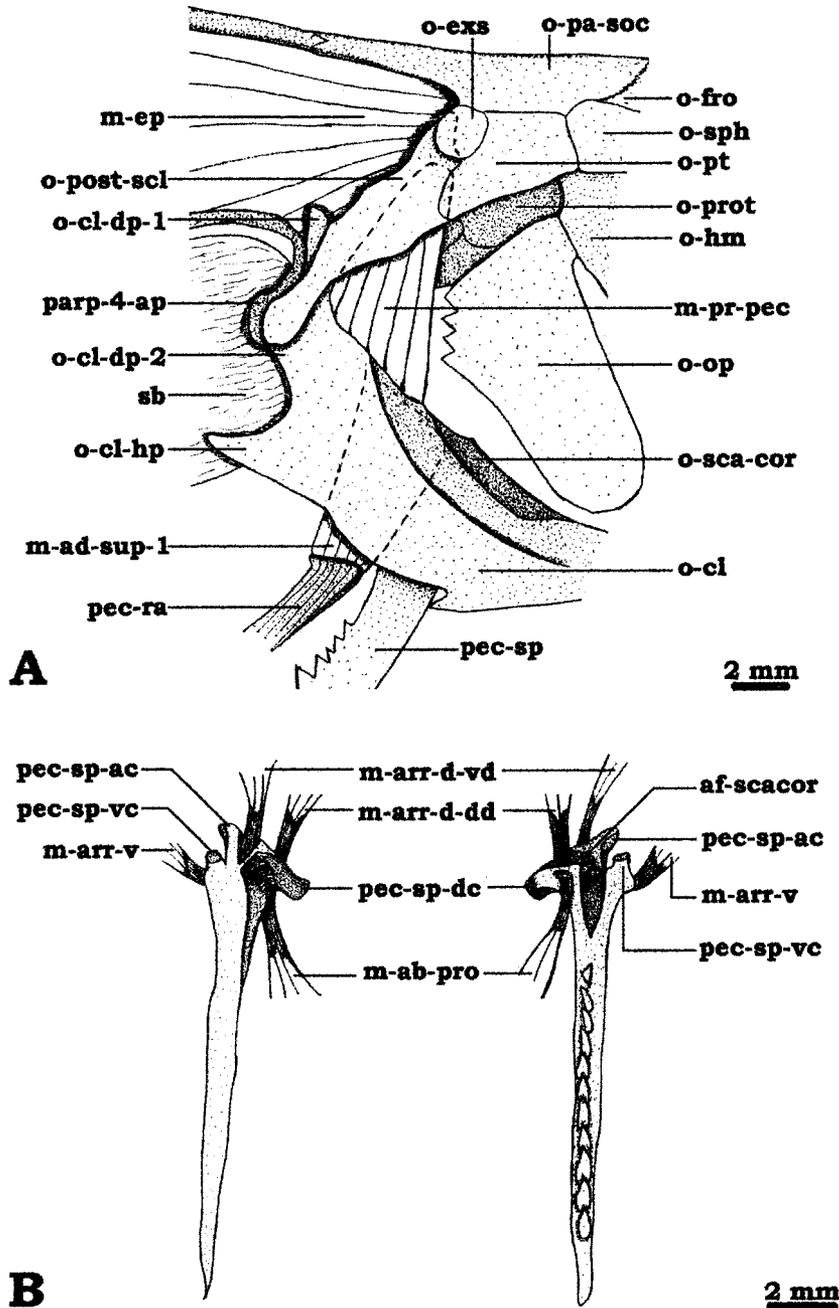


Fig. 3. *Chrysichthys nigrodigitatus*. **A**: Lateral view of the posterior region of the cranium. Opercular bone cut and opercular muscles removed. **B**: Lateral (in left) and medial (in right) view of the pectoral spine, showing the insertions of the muscles responsible for its movement. af-scacor, articular facet for scapulo-coracoide; m-ab-pro, musculus abductor profundus; m-ad-sup-1, section 1 of musculus adductor superficialis; m-arr-d-dd, m-arr-d-vc, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-ep, musculus epaxialis; m-pr-pec, musculus protractor pectoralis; o-cl, os cleithrum; o-cl-dp-1, o-cl-dp-2, dorsal processes of cleithrum; o-cl-hp, humeral process of cleithrum; o-exs, os extracapulare; o-fro, os frontale; o-hm, os hiomandibulare; o-op, os operculare; o-pa-soc, os parieto-supraoccipitale; o-post-scl, os posttemporo-supracleithrum; o-prot, os prooticum; o-pt, os pteroticum; o-sca-cor, os scapulo-coracoide; o-sph, os sphenoticum; parp-4-ap, anterior process of parapophysis 4; pec-ra, pectoral rays; pec-sp, pectoral spine; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine; sb, swim-bladder.

which accommodates (Fig. 1A,B) the thick crescentic dorsal condyle of the pectoral spine (see Fig. 3B), to form an anteroposteriorly mobile articulation (osteological base of the friction-locking mechanism). The two cleithra are attached in the anteromesial line by a strong ligament.

The scapulo-coracoide is an elongate, irregular bony plate suturing with the cleithrum along its anterolateral edge (Figs. 1B, 2A, 2B). Mesially, it joins its counterpart in an interdigitation of several strong serrations (Figs. 1B, 2A, 2B). Anterolaterally, it presents an anteriorly directed process, sometimes called coracoid bridge (cor-bri), which extends

ventrally to the ventrolateral surface of the cleithrum, fusing with an anteroventral ridge of this bone (Fig. 1B). The posterolateral end of the scapulo-coracoide bears two condyles. The dorsolateral one (Fig. 1B: af-pecsp) has a dorsolaterally elongated articular facet, which lodges in a groove of the base of the pectoral spine (see below). The small median one (Fig. 1B: af-cra) has a long stalk and articulates with a large complex radial (see below). Mesially to these two articular facets there is a ventral groove (Fig. 1B: o-sca-cor-vcg), which accommodates the ventral condyle of the pectoral spine when this spine is erected (see Fig. 1A). Near this

groove there is a slender ascending process, the mesocoracoid (mcor-ar), whose dorsal and ventral ends are fused with, respectively, the posterodorsolateral and posteroventrolateral surfaces of the scapulo-coracoid, thus forming a tunnel (Figs. 1B, 2B), here named the mesocoracoid tunnel. Anterodorsally to the ventral surface of the mesocoracoid arch there are two foramina (Fig. 1B). The dorsal, smaller one provides a passage for nerve and blood vessel. The ventral, larger one accepts the anterior condyle of the pectoral spine when this spine is erected.

There are two separate rod-like proximal radials, the proximal ends of which contact the scapulo-coracoid. Lateral to these proximal radials lies a large trapezoidal cartilage, the complex radial (Mo, 1991), which probably is the result of fusion of at least three radial elements (see Mo, 1991). This cartilage assists in the articulation of the pectoral spine, as well as of the following two pectoral fin rays. Median to the complex radial and at the distal ends of the two rod-like proximal radials lie two very small distal radials, which remain cartilaginous during growth. The pectoral spine is stout (Figs. 1, 3). Its proximal end is a complicated, multiarticulated structure (Fig. 3B) that articulates with the cleithrum and scapulo-coracoid (Fig. 1) to form a "friction-locking mechanism" (see above). It presents anterior (pec-sp-ac) and ventral (pec-sp-vc) vice-like condyles and a thick, crescentic dorsal condyle (pec-sp-dc) (*sensu* Hubbs and Hibbard, 1951) (Fig. 3B). The inner surface of the pectoral spine bears numerous, strong, irregularly spaced dentations (Fig. 3B).

The pectoral girdle is connected to the parurohyal bone (see Arratia and Schultze, 1990) by means of the massive sternohyoideus muscle (Fig. 1A), which inserts anteriorly on the posterodorsal margins of the parurohyal and posteriorly on the anterodorsal margins of the cleithrum (Figs. 1A, 2A). Apart from its osteological connection, via the posttemporo-supracleithrum bone, with the neurocranium, the complex formed by the cleithrum and the scapulo-coracoid is also connected with the posterior surface of the neurocranium by means of a well-developed muscle, the protractor pectoralis. This muscle originates on the ventral surfaces of the exoccipital, epioccipital, posttemporo-supracleithrum, and pterotic bones, and inserts on the anterodorsal margin of the cleithrum (Fig. 3B). The anterior fibers of the massive hypoaxialis muscle insert principally on the posteroventral surface of the scapulo-coracoid, but also on the posterolateral margins of both the cleithrum and the scapulo-coracoid (Fig. 1A).

There are three muscles directly associated with the movement of the pectoral spine, the arrector dorsalis, the arrector ventralis, and the abductor profundus (it should be noticed that, since the nomenclature of the pectoral girdle muscles followed here is that of Winterbottom [1974], which refers to the function of these muscles in general teleosts, and since the functioning of the pectoral girdle in general

teleosts is quite different from that in catfishes [see, e.g., Alexander, 1965; Gosline, 1977], the names used here have little to do with the real function of these muscles in catfishes). The arrector dorsalis muscle is differentiated into two well-developed, completely separated divisions. The dorsal division (m-arr-d-dd) (which promotes the abduction and/or locking of the pectoral spine: Diogo and Chardon, in preparation) originates on the dorsomesial surface of the scapulo-coracoid (Fig. 1A) and inserts tendinously on the anterior margin of the dorsal condyle of the pectoral spine (Fig. 3B). The ventral division (m-arr-d-vd) (which, like the dorsal one, also promotes the abduction and/or locking of the pectoral spine: Diogo and Chardon, in preparation) runs from the ventromesial surface of the cleithrum (Fig. 1A) to the anterolateral surface of the pectoral spine, to which it attaches tendinously (Fig. 3B). The abductor profundus muscle (which assists the adduction and/or unlocking of the pectoral spine: Diogo and Chardon, in preparation) originates on the posteromesial edge of the coracoid (Figs. 1B, 2B), passes anteriorly to the mesocoracoid arch and to the adductor superficialis muscle (Figs. 1B, 2B), and inserts tendinously on the mesial surface of the dorsal condyle of the pectoral spine (Fig. 3B). The arrector ventralis muscle (which promotes the unlocking, but not the adduction, of the pectoral spine: Diogo and Chardon, in preparation) is a small muscle, situated ventrally to the coracoid bridge. It runs from the ventrolateral surface of both the cleithrum and the coracoid (Fig. 1A) and attaches, by means of a thin tendon, on the posteroventral edge of the ventral condyle of the pectoral spine (Figs. 1A, 3B).

There are two muscles directly related with the movement of the pectoral fin, the adductor superficialis (which is associated with the raising of the distal end of the pectoral fin: Diogo and Chardon, in preparation) and the abductor superficialis (antagonist of the adductor superficialis; that is, associated with the depression of the pectoral fin: Diogo and Chardon, in preparation). Both these muscles are differentiated into two sections. The larger section (here called section 1) of the adductor superficialis muscle originates on the posterior surfaces of the cleithrum and scapulo-coracoid and also on the dorsolateral edge of the mesocoracoid arch and inserts on the anterodorsal margin of the dorsal part of the pectoral fin rays (Figs. 1A, 2B, 3A). The smaller section (here called section 2) of this muscle runs from the ventrolateral edge of the mesocoracoid arch and the dorsal surface of the proximal radials to the anteroventral margin of the dorsal part of the pectoral fin rays (Fig. 2B). The larger section (section 1) of the abductor superficialis muscle attaches medially on the ventral face of both the cleithrum and the scapulo-coracoid and attaches laterally, by means of numerous thin tendons, on the anteroventral margin of the ventral part of the pectoral fin rays (Fig. 1A). Finally, the smaller section of this muscle (sec-

tion 2) runs from the posterolateral edge of the scapulo-coracoid to the anterodorsal margin of the ventral part of the pectoral fin rays (Figs. 1A, 2B).

Arius heudelotii

In general, the configuration of the bones and muscles of the pectoral girdle of this species resembles that of *Chrysichthys nigrodigitatus*. Therefore, only the principal differences between the two species will be described. These differences are: 1) There is large fossa, the posttemporal fossa, between the dorsal surfaces of the posttemporo-supracleithrum, extrascapular, and pterotic bones. However, it should be noticed that this is not the case for all the ariids examined, since *Genidens Genidens* presents only a small posttemporal fossa and *Bagre marinus* presents no posttemporal fossa at all. 2) The posttemporo-supracleithrum does not present a dorsal foramen to receive the first dorsal process of the cleithrum. 3) The posttemporo-supracleithrum is sutured, and not only ligamentously, linked to the basioccipital ventromesially and to the extrascapular and pterotic dorsomesially. 4) There is a thin, long, ventrodorsally oriented saliency in the posterolateral surface of the scapulo-coracoid bone (Fig. 4B), which clearly corresponds to the mesocoracoid arch of *C. nigrodigitatus*. However, contrary to *C. nigrodigitatus*, in *Arius heudelotii* the mesocoracoid is completely fused anteriorly with the main body of the scapulo-coracoid (Fig. 4B) and, thus, there is no mesocoracoid tunnel. 5) In *A. heudelotii* there is only a large foramen in the posterolateral surface of the scapulo-coracoid (Fig. 4B), which provides a passage for a nerve and a blood vessel; the foramen for the anterior condyle of the pectoral spine (see above) is absent. 6) The arrector ventralis muscle and section 1 of the abductor profundus muscle are much more developed in *Arius heudelotii* (Fig. 4A) than in *C. nigrodigitatus*. 7) In *A. heudelotii* the abductor profundus muscle passes posteriorly, and not anteriorly, to the mesocoracoid arch, which is clearly associated to the absence, in this species, of a mesocoracoid tunnel (see above).

Bagrus docmak

The configuration of the muscles and bones of the pectoral girdle of this species does not differ significantly from that of *Chrysichthys nigrodigitatus*. The main differences are: 1) The posttemporo-supracleithrum of *Bagrus docmak* (see Diogo et al., 1999b) is a large, heavily ossified bone, with a prominent posterior process and a thickened dorsomedian limb, and is linked to the pterotic by a well-developed muscle, the protractor posttemporalis. 2) There is a large, posteriorly directed projection (Fig. 5A: o-sca-cor-plsp) of the posterolateral surface of the scapulo-coracoid bone. 3) The dorsal condyle of the pectoral spine bears a small anterior process

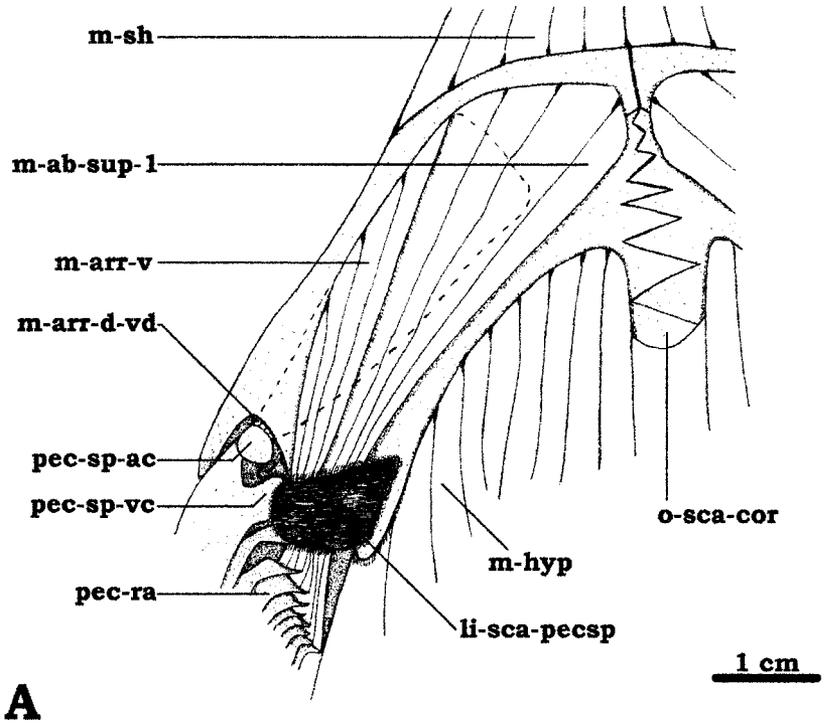
(Fig. 5B: ap-dc), in which inserts the thin tendon of the dorsal division of the arrector dorsalis muscle. 4) Only a small portion of the poorly developed ventral division of the arrector ventralis muscle (Fig. 5A) is visible in ventral view. 5) The hypaxialis muscle (Fig. 5A) invades almost all the ventral surface of both the scapulo-coracoid and the cleithrum. 6) Since there is a large foramen between the anterolateral surface of the scapulo-coracoid bone and the cleithrum (Fig. 5A), part of the dorsal division of the arrector dorsalis muscle is visible in ventral view.

Plotosus lineatus

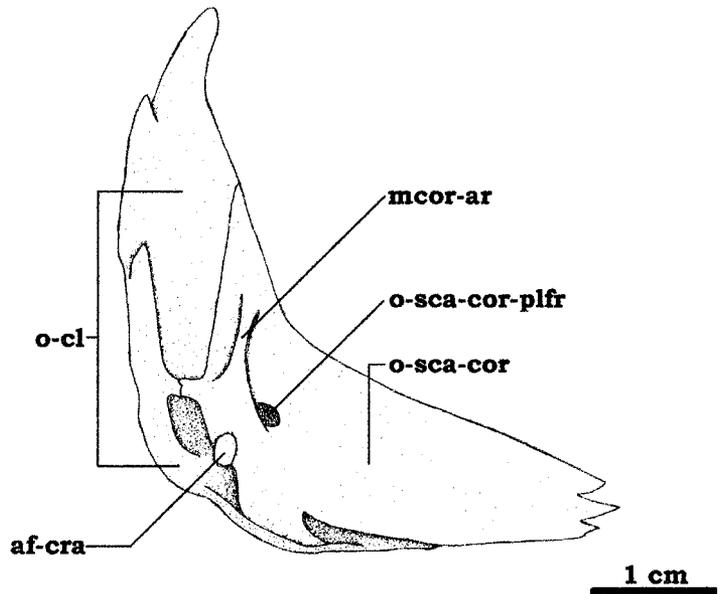
There are some significant differences between the configuration of the pectoral girdle bones and muscles of this species and that of *Chrysichthys nigrodigitatus*, namely: 1) The posttemporo-supracleithrum does not present a dorsal foramen to receive the first dorsal process of the cleithrum. 2) The median process of the posttemporo-supracleithrum is very thin. 3) The humeral process of the cleithrum is absent; however, this is not the case in the other species of Plotosidae examined, where this process, although reduced, is present. 4) Contrary to the situation in *C. nigrodigitatus*, in *Plotosus lineatus* (Fig. 6A) there is no posterolateral groove of the scapulo-coracoid to receive the ventral condyle of the pectoral spine, when this spine is erected. 5) The anterior, massive part of the hypaxialis muscle invades almost all the ventral surface of the pectoral girdle (Fig. 6A) contacting, inclusively, the posterior fibers of the sternohyoideus muscle. In the other plotosids studied the hypoxialis muscle also invades almost all the ventral surface of the pectoral girdle, but its anterior fibers do not contact the sternohyoideus. 6) There is only a division of the arrector dorsalis muscle (Fig. 6A). Although this division clearly corresponds to the dorsal division of *C. nigrodigitatus* (Fig. 6A, c.f. Figs. 1A, 2A), it does not insert on the anterior surface of the dorsal condyle of the pectoral spine, but on the anterolateral edge of this spine (Fig. 6B, c.f. Fig. 3B); that is, where the ventral division inserts in *C. nigrodigitatus*. 7) In *P. lineatus* the arrector ventralis and the abductor superficialis muscles are much smaller than those of *C. nigrodigitatus* (Fig. 6A). However, this is not the case for all plotosids since, for example, in *Tandanus tandanus* these muscles are even larger than those of *C. nigrodigitatus*. 8) Since there is a large foramen between the anterolateral surface of the scapulo-coracoid bone and the cleithrum (Fig. 6A), part of the dorsal division of the arrector dorsalis muscle is visible in ventral view.

Clarias gariepinus

There are several significant differences between the configuration of the pectoral girdle muscles and bones of *Clarias gariepinus* and that of *Chrysichthys*



A



B

Fig. 4. Pectoral girdle of *Arius heudelotii*. **A:** Ventral view, all muscles exposed. **B:** Posterior view, posttemporo-supracleithrum, as well as all muscles, removed. af-cra, articular facet for complex radial; li-sca-pecsp, ligament between scapulo-coracoid and pectoral spine; 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-hyp, musculus hypaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-plfr, postero-lateral foramen of scapulo-coracoide; pec-ra, pectoral rays; pec-sp-ac, pec-sp-vc, antero and ventral condyles of pectoral spine.

nigrodigitatus, namely: 1) There is a large foramen (Fig. 7B) between the anterolateral edge of the scapulo-coracoid and the cleithrum. 2) Both the posterolateral edge of the scapulo-coracoid and the mesocoracoid arch bear large, posteriorly directed projections, which are firmly attached to the posterolateral edge of the cleithrum (Fig. 7B), thus reinforcing the pectoral girdle. 3) The thin, small coracoid bridge is fused dorsally with the main body of the ventrolateral surface of both the cleithrum and the scapulo-coracoid bones (Fig. 7B); that is, the

tunnel usually formed by this bridge is closed. 4) There is no (Fig. 7B) posterolateral groove of the scapulo-coracoid to receive the ventral condyle of the pectoral spine when this spine is erected. 5) The cleithrum bears a small, anteriorly directed anterolateral process (Fig. 7A-C: o-cl-alp). 6) The large posttemporo-supracleithrum bone (Fig. 8) does not present the usual median process attached to the basioccipital, but presents a well-developed, posterior process (transcapular process sensu Adriaens, 1997) that attaches on the dorsolateral margin of the

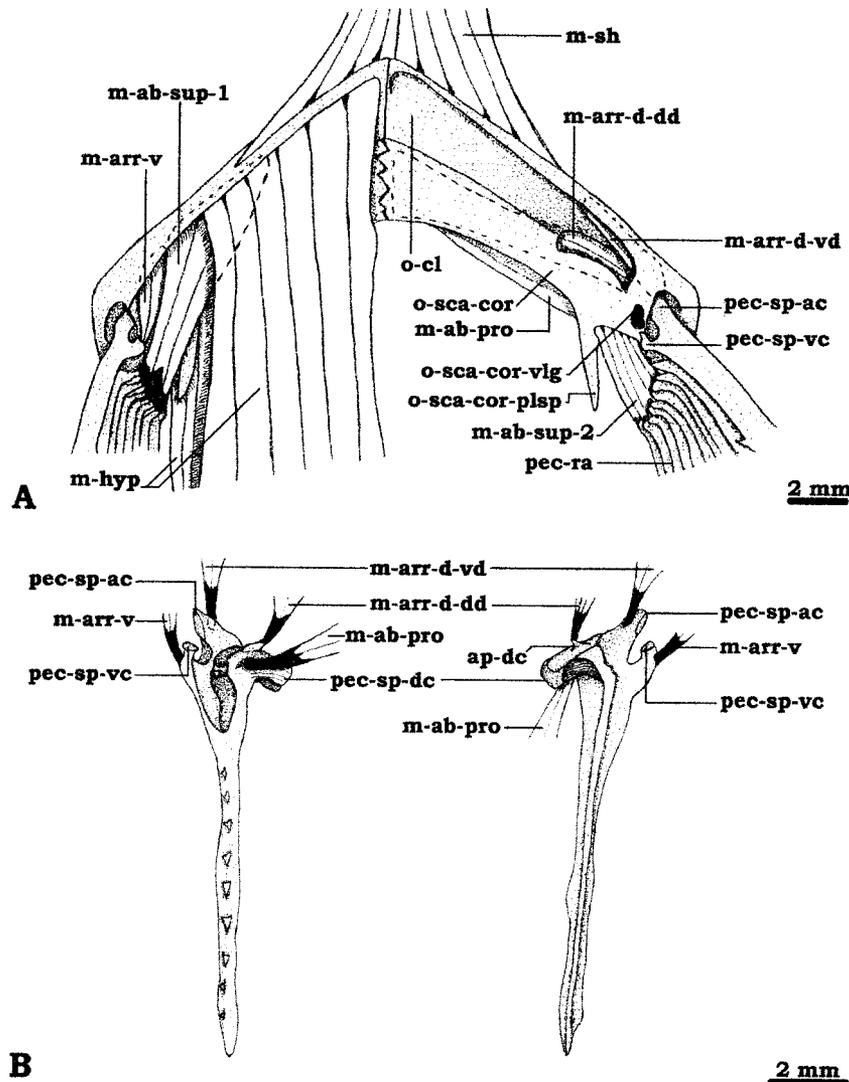


Fig. 5. *Bagrus docmak*. **A**: Ventral view of the pectoral girdle. In the left side all muscles are exposed; in the right side the hypaxialis, arrector ventralis, section 1 of the abductor superficialis and the posttemporo-supracleithrum are removed. **B**: Median (in the left side) and lateral (in the right side) view of the pectoral spine, showing the insertions of the muscles responsible for its movement. ap-dc, anterior process of dorsal condyle; m-ab-pro, musculus abductor profundus; m-ab-sup-1, m-ab-sup-2, sections of musculus abductor superficialis; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-plsp, postero-lateral spine of scapulo-coracoide; o-sca-cor-vlg, ventro-lateral groove of scapulo-coracoide; pec-ra, pectoral rays; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine.

fourth parapophysis. 7) The humeral process of the cleithrum is absent (Fig. 8). 8) The protractor pectoralis is a very large muscle (Fig. 8), running from the suprapreopercular, pterotic, and posttemporo-supracleithrum bones, to the anteroposteriorly enlarged dorsolateral surface of the cleithrum. 9) The hypoaxialis muscle invades (Fig. 7A) a large part of the ventral surface of the pectoral girdle. 10) The arrector ventralis and the abductor superficialis muscles are much smaller (Fig. 7A) than those of *C. nigrodigitatus*. 11) The massive sternohyoideus muscle (Fig. 7A) invades the anteroventral surface of the cleithrum, as well as the posteroventral surface of the parurohyal bone. 12) As in *C. nigrodigitatus*, the arrector dorsalis muscle is divided in two separate, well-developed dorsal and ventral divisions (Fig. 7C,D). However, contrary to this species, in *C. gariepinus* both these divisions are situated in the dorsal side (Figs. 7A,B, c.f. Figs. 1A, 2A) of the pectoral girdle. 13) The tendons of the muscles directly related to the movement of the pectoral spine,

particularly that of the abductor profundus muscle, are thicker (Fig. 7D, c.f. Fig. 3B) than those of *C. nigrodigitatus*.

Amphilius brevis

There are several significant differences between the configuration of the pectoral girdle muscles and bones of *Clarias gariepinus* and that of *Chrysichthys nigrodigitatus*, namely: 1) The median process of the posttemporo-supracleithrum bone is very thin and is attached to a prominent ventrolateral process of the basioccipital. 2) There is no dorsal foramen of the posttemporo-supracleithrum to receive the first dorsal process of the cleithrum. 3) The second dorsal process of the cleithrum is absent, but the first dorsal process (Figs. 9B, 10A,B: o-cl-dp-1) of this bone presents a large dorsal hook-like projection, which articulates in a deep bifurcation of the posteroventrolateral edge of the posttemporo-supracleithrum.

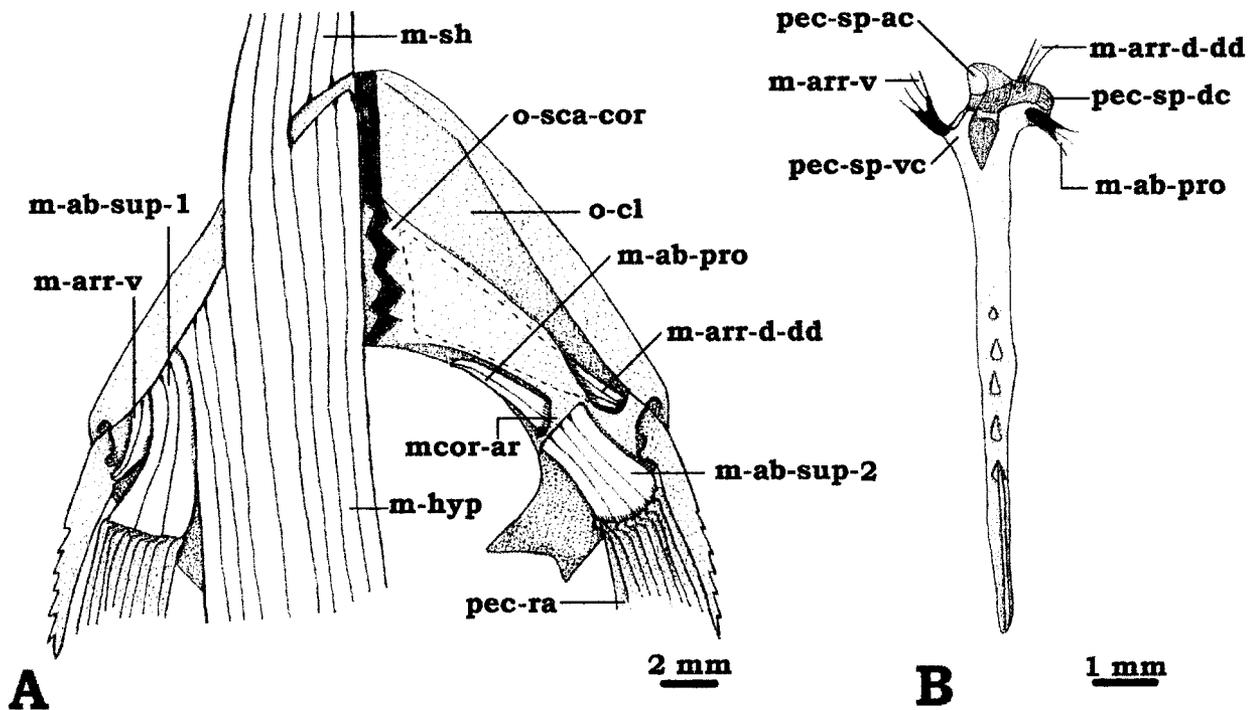


Fig. 6. *Plotosus lineatus*. **A**: Ventral view of the pectoral girdle. In the left side all muscles are exposed; in the right side the hypaxialis, sternohyoideus, arrector ventralis, section 1 of the abductor superficialis, and the posttemporo-supracleithrum are removed. **B**: Median view of the pectoral spine, showing the insertions of the muscles responsible for its movement. m-ab-pro, musculus abductor profundus; m-ab-sup-1, m-ab-sup-2, sections of musculus abductor superficialis; m-arr-d-dd, dorsal division of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; pec-ra, pectoral rays; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine.

4) The first pectoral ray of *Amphilius brevis*, which is not a true pectoral spine but a long and thick unbranched ray constituted distally of a series of segments (see Fig. 9B), presents only two, and not three, well-developed condyles (Fig. 9B). The configuration of these condyles, and principally their relations with the tendons of the arrector ventralis, arrector dorsalis, and abductor profundus muscles, seems to indicate that they correspond, respectively, to the ventral condyle and to the fusion of the anterior+dorsal condyles (Fig. 9C, c.f. Fig. 3B) of *C. nigrodigitatus*. 5) Contrary to *C. nigrodigitatus*, in *A. brevis* there is no locking mechanism of the first pectoral ray (see above). 6) Both the cleithrum and the scapulo-coracoid (Figs. 9B, 10A), and not only the latter, join their counterparts in an interdigitation of several strong serrations. 7) There is no posterolateral groove of the scapulo-coracoid to receive the ventral condyle of the first pectoral ray when this ray is erected (Fig. 9B). 8) The mesocoracoid arch (Figs. 9B, 10B) is compressed anteroposteriorly, but is broadened mesiolaterally. 9) The scapulo-coracoid of *A. brevis* presents a spherical, laterally expanded articular facet for the first pectoral ray (Fig. 9B: af-pecra1), which articulates with a deep, anterior spherical articular facet (Fig. 9C: af-sca-cor) of this ray. 10) The arrector ven-

tralis is a massive, mesially bifurcated muscle (Fig. 9A) which inserts, by means of a thick tendon (Figs. 9C), in the ventral condyle (see above) of the first pectoral ray. 11) The small dorsal division of the arrector ventralis lies on the ventral, and not on the dorsal (Figs. 9A,B, 10A, c.f. Figs. 1A, 2A), side of the pectoral girdle. 12) The abductor profundus muscle is differentiated in two well-developed sections (Fig. 10B), which insert through the same tendon (Fig. 9C) on the first pectoral ray.

Phractura brevicauda

The principal differences between the configuration of the muscles and bones of the pectoral spine of *Phractura brevicauda* and that of *Chrysichthys nigrodigitatus* are: 1) The mesial process of the posttemporo-supracleithrum bone is very thin and is attached to a prominent ventrolateral process of the basioccipital. 2) The posttemporo-supracleithrum bears a prominent, posteriorly directed posterolateral process. 3) In addition to its two dorsal articulatory processes for the posttemporo-supracleithrum, the cleithrum presents a well-developed, posterodorsal process (Fig. 11B: o-cl-pdsp). 4) The first pectoral ray of *P. brevicauda* is not a true pectoral spine, but a long and thick unbranched ray, which presents only two,

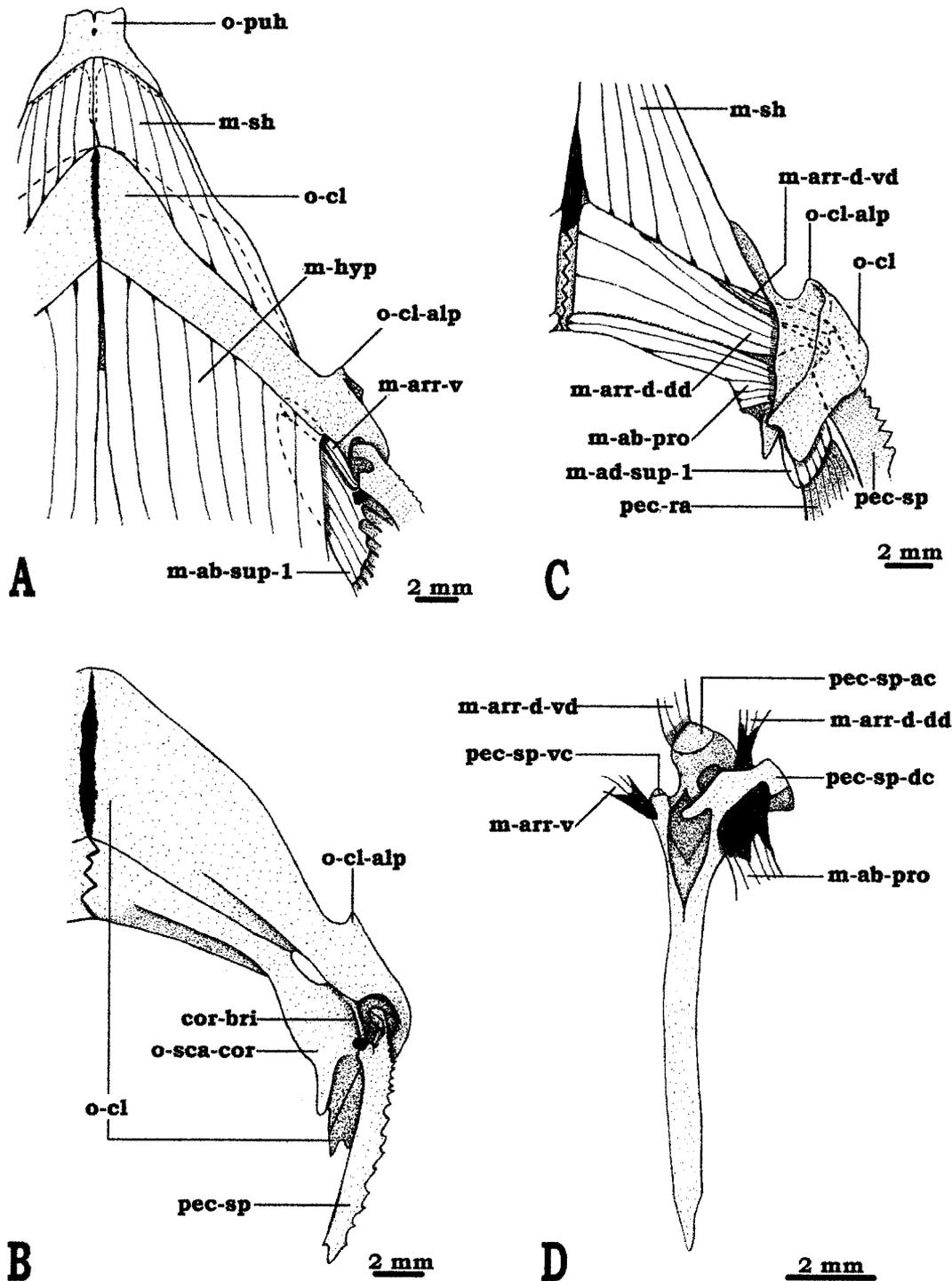


Fig. 7. *Clarias gariepinus*. **A**: Ventral view of the pectoral girdle, all muscles exposed. **B**: Ventral view of the pectoral girdle. Pectoral fins, posttemporo-supracleithrum and all muscles removed. **C**: Dorsal view of pectoral girdle. All muscles exposed; posttemporo-supracleithrum removed. **D**: Median view of the pectoral spine, showing the insertions of the muscles responsible for its movement. cor-bri, coracoid bridge; m-ab-pro, musculus abductor profundus; m-ab-sup-1, section 1 of musculus abductor superficialis; m-ad-sup-1, section 1 of musculus adductor superficialis; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; o-cl, os cleithrum; o-cl-alp, anterolateral process of cleithrum; o-puh, os parurohyale; o-sca-cor, os scapulo-coracoide; pec-ra, pectoral rays; pec-sp, pectoral spine; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal and ventral condyles of pectoral spine.

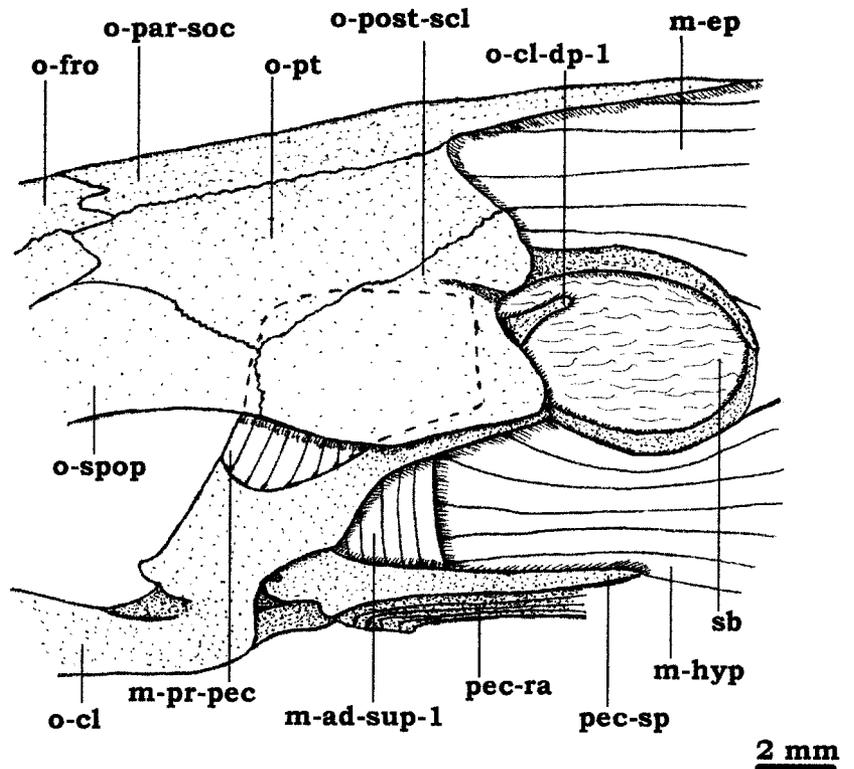


Fig. 8. Lateral view of the posterior region of the cranium of *Clarias gariepinus*. m-ad-sup-1, section 1 of musculus adductor superficialis; m-ep, musculus epaxialis; m-hyp, musculus hypoaxialis; m-pr-pec, musculus protractor pectoralis; o-cl, os cleithrum; o-cl-dp-1, dorsal process 1 of cleithrum; o-fro, os frontale; o-par-soc, os parieto-supraoccipitale; o-post-scl, os posttemporo-supracleithrum; o-pt, os pteroticum; o-spop, os supraoperculare; pec-ra, pectoral rays; pec-sp, pectoral spine; sb, swim-bladder.

and not three, well-developed condyles (Fig. 9B). The configuration of these condyles, and principally their relations with the tendons of the muscles associated with the movement of the first pectoral ray, seem to indicate that they correspond, respectively, to the ventral condyle and to the fusion of the anterior+dorsal condyles (Fig. 10C, c.f. Fig. 3B) of *C. nigrodigitatus*. 5) In *P. brevicauda* (Fig. 11B) the articulation of the scapulo-coracoid bone for the first pectoral ray is not oriented laterally, as in *C. nigrodigitatus*, but lateroventrally. 6) There is no locking mechanism of the first pectoral ray. 7) Near to the dorsal edge of the mesocoracoid arch (Fig. 11B), the scapulo-coracoid bears a small, mesially directed process. 8) Both the cleithrum and the scapulo-coracoid (Fig. 11A), and not only the latter, join their counterparts in an interdigitation of several strong serrations. 9) The mesocoracoid arch (Fig. 11B) is significantly broadened mesiolaterally. 10) There is no posterolateral groove of the scapulo-coracoid to receive the ventral condyle of the first pectoral ray when this ray is erected. 11) In *P. brevicauda* (Fig. 11A,C) there are four, and not three, muscles directly associated with the movement of the first pectoral ray, the arrector ventralis, the arrector dorsalis, the abductor profundus, and another separated, well-developed muscle. This muscle (which probably promotes the adduction of the first pectoral ray: Diogo and Chardon, in preparation), called here an "additional muscle" (Fig. 11A: addi-m), runs from the mesioventral surface of the scapulo-coracoid to

the anterior margin of the anterior condyle of the first pectoral ray. 12) The small dorsal division of the arrector ventralis lies on the ventral, and not on the dorsal (Fig. 11A, c.f. Figs. 1A, 2A), side of the pectoral girdle.

Diplomystes chilensis

There are some significant differences between the configuration of the pectoral girdle bones and muscles of this species and that of *Chrysichthys nigrodigitatus*, namely: 1) The posttemporo-supracleithrum does not bear a dorsal foramen to receive the first dorsal process of the cleithrum. 2) The scapulo-coracoid of *Diplomystes chilensis* is a very narrow bone (Figs. 12C, 13B), not visible in dorsal view (Fig. 14A), that does not meet its counterpart in a mesial interdigitation (Figs. 12C, 13B). In addition, only its anteromesial and anterolateral surfaces are firmly attached to the cleithrum (Figs. 12C, 13B), as its main body is separated from this bone. 3) In the two specimens of *D. chilensis* studied, there is a long, incomplete suture (Figs. 12C, 13B: isut) that separates the ventral portion of the mesocoracoid arch from the main body of the scapulo-coracoid. 4) The hypoaxialis muscle (Fig. 12A) invades almost all the ventral surface of the pectoral girdle. 5) The arrector ventralis is a well-developed muscle (Fig. 12A,B) situated dorsally to the also well-developed first section of the abductor superfi-

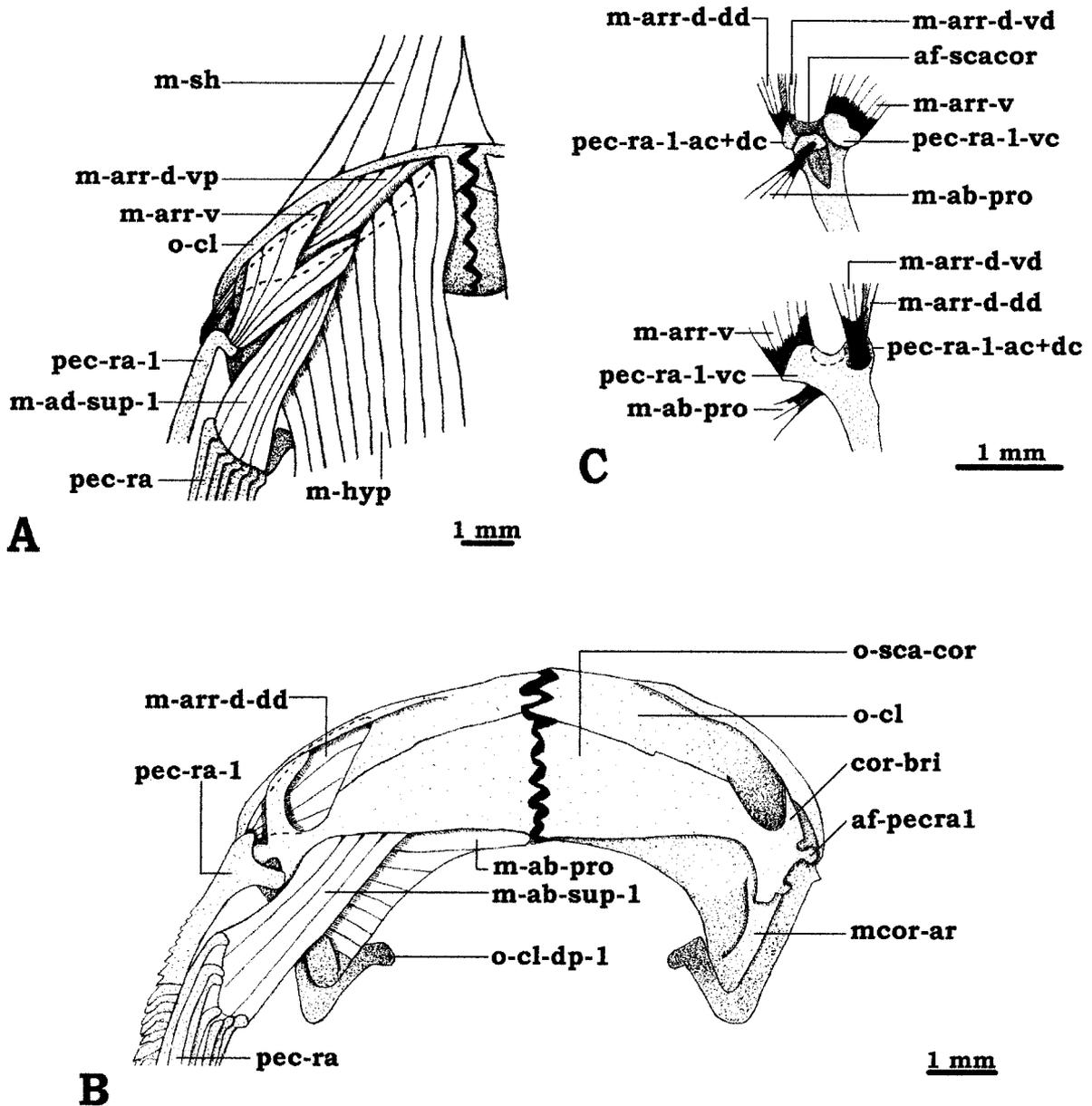


Fig. 9. *Amphilius brevis*. **A:** Ventral view of the pectoral girdle, all muscles exposed. **B:** Ventral view of pectoral girdle. On the left side the hypoaxialis, sternohyoideus, arrector ventralis, ventral division of the arrector dorsalis and the posttemporo-supracleithrum are removed; on the right side the pectoral fin, posttemporo-supracleithrum and the muscles are removed. **C:** Median (above) and ventral (below) view of the anterior region of the first pectoral ray, showing the insertions of the muscles responsible for its movement. af-pecra1, articular facet for first pectoral ray; af-scacor, articular facet for scapulo-coracoid; cor-bri, coracoid bridge; m-ab-pro, musculus abductor profundus; m-ab-sup-1, section 1 of musculus abductor superficialis; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-cl-dp-1, dorsal process 1 of cleithrum; o-sca-cor, os scapulo-coracoid; pec-ra, pectoral rays; pec-ra-1, first pectoral ray; pec-ra-1-ac+dc, pec-ra-1-vc, anterodorsal and ventral condyles of first pectoral ray.

cialis muscle. 6) Although bifurcated mesially, the arrector dorsalis muscle is constituted by a single, broad mass of fibers (Fig. 12B), which originate on both the ventral surface of the cleithrum and the dorsal surface of the scapulo-coracoid (Figs. 12B, 13A) and insert on the anterolateral edge of the pectoral spine (Fig. 14B).

DISCUSSION

In this section we will not only refer to the morphological diversity of the different osteological and myological pectoral girdle structures within the siluriforms, but will also discuss which of the different types of configuration of these structures could rep-

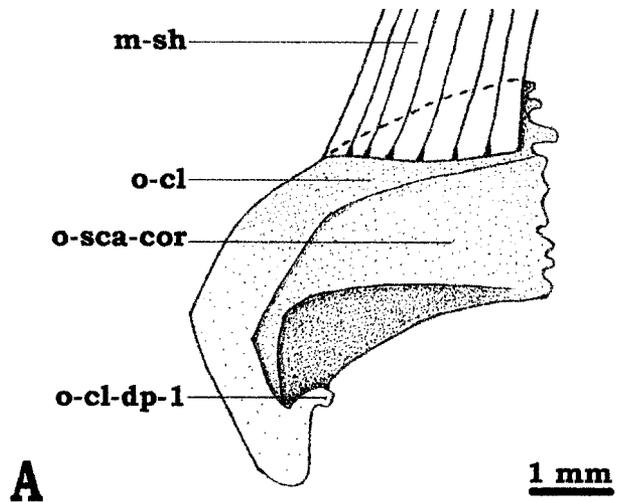
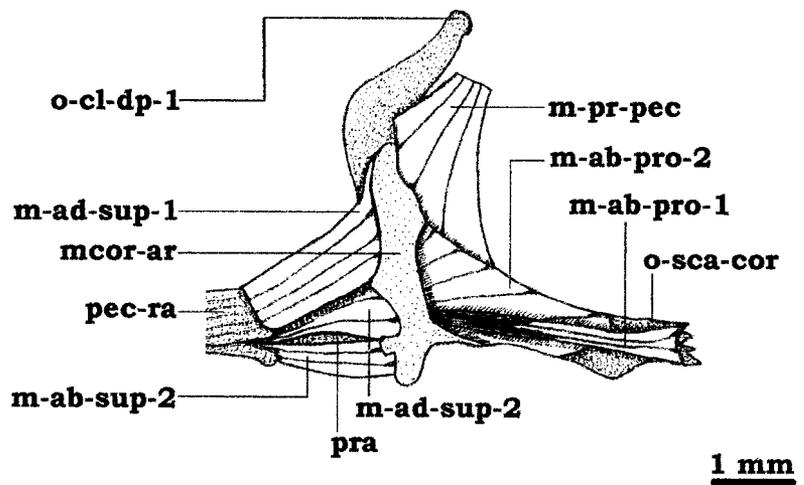
**A****1 mm****B****1 mm**

Fig. 10. Pectoral girdle of *Amphilius brevis*, all muscles exposed. **A**: Dorsal view. Pectoral fin and posttemporo-supracleithrum removed. **B**: Posterior view, posttemporo-supracleithrum removed. m-ab-pro-1, m-ab-pro-2, sections of musculus abductor profundus; m-ab-sup-2, section 2 of musculus abductor superficialis; m-ad-sup-1, m-ad-sup-2, sections of musculus adductor superficialis; m-pr-pec, musculus protractor pectoralis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-cl-dp-1, dorsal process 1 of cleithrum; o-sca-cor, os scapulo-coracoid; pec-ra, pectoral rays; pra, proximal radial.

represent the plesiomorphic condition for these fishes. We will discuss whether such a plesiomorphic condition is shared by the catfishes and other nonsiluriform teleosts, or would represent a symplesiomorphy of the Siluriformes; that is, is exclusively present in these fishes. It should be noted that, in order to facilitate and to simplify this discussion, we will often refer to “generalized” catfishes. We should specify that this designation is mainly based on articles such as those of Eigenmann (1890), Regan (1911b), Nawar (1954, 1955), Alexander (1965), Saxena and Chandy (1966), Chardon (1968), Gosline (1975), Mo (1981), Ghiot et al. (1984), Grande (1987), etc., but also is based on our own morphological observations and/or phylogenetic results (Diogo and Chardon, 1998, 2000a,b, in press, a,b; Diogo et al., 1999b, 2000a,b, in press), and that it refers to catfishes lacking a large number of specialized morphological features, including catfishes such as diplomystids, ictalurids, bagrids, claroteids, austroglanidids, cranoglanidids, silurids, arriids, plotosids, doradids, pimelodids, cetopsids, hypsidorids,

etc. (vs. highly specialized catfishes such as sisorids, amphiliids, doumeids, clariids, heteropneustids, callichthyids, loricariids, astroblepids, or scoleplacids) (see Eigenmann, 1890; Regan, 1911b; Nawar, 1954, 1955; Alexander, 1965; Saxena and Chandy, 1966; Chardon, 1968; Gosline, 1975; Mo, 1981; Ghiot et al., 1984; Grande, 1987; Diogo and Chardon, 1998, 2000a,b, in press, a,b; Diogo et al., 1999ab, 2000a,b, in press; etc.).

Posttemporo-supracleithrum

The identity of this bone has been the subject of considerable discussion in the past (see, e.g., Lundberg, 1975a; Fink and Fink, 1981, 1996; Jollie, 1986; Arratia and Gayet, 1995). It has been identified as a supraclavicle (Eigenmann, 1928), a posttemporal (Bridge and Haddon, 1893; Bamford, 1948; Nawar, 1954; Alexander, 1965; Chardon, 1968; etc.), a supraclavicle (Regan, 1911a; Merriman, 1940; Lundberg, 1975a; Gosline, 1977; etc.) or a supratemporale (Cerny, 1988), but it is presently accepted

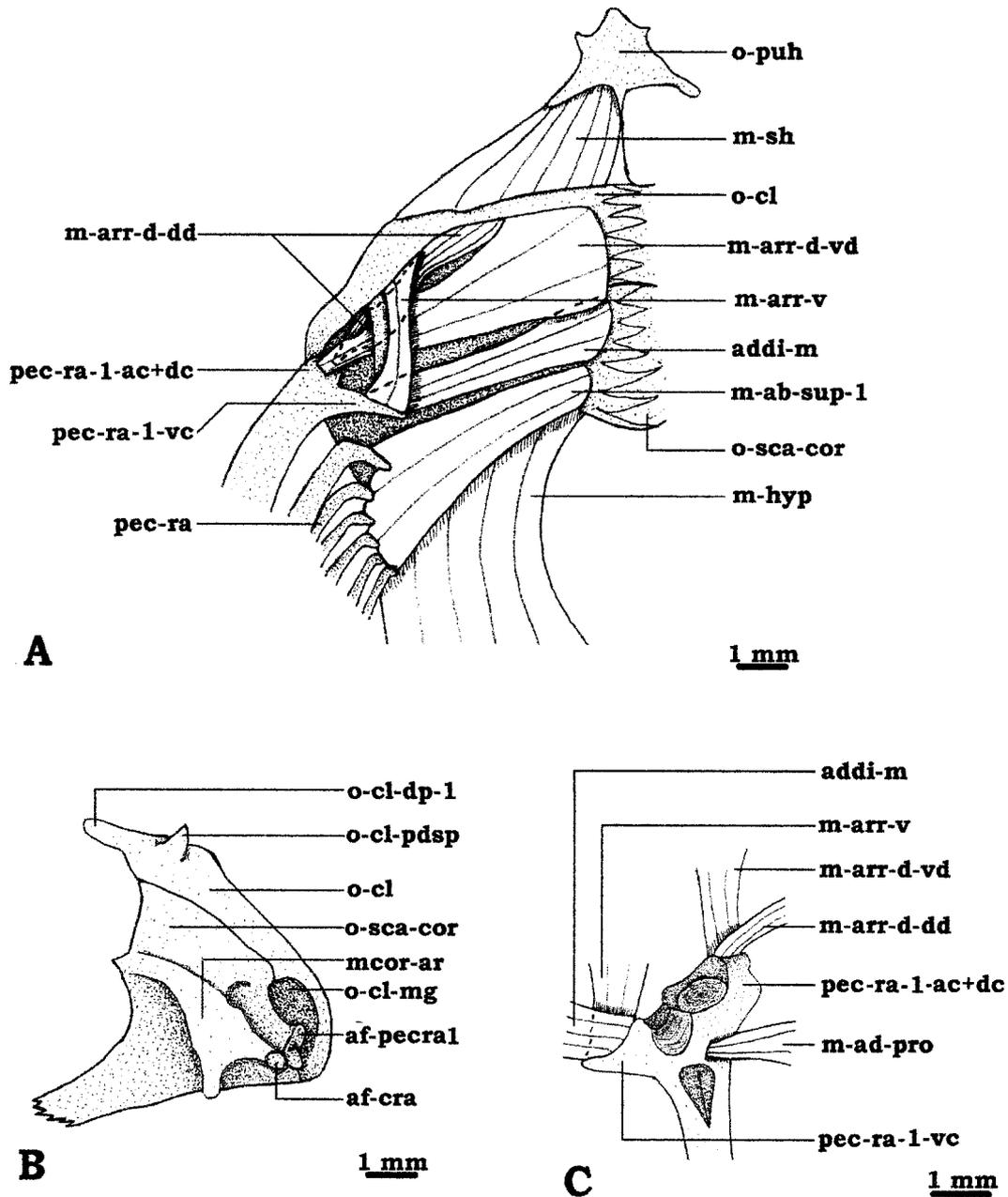


Fig. 11. *Phractura brevicauda*. **A**: Ventral view of the pectoral girdle, all muscles exposed. **B**: Posterior view of the pectoral girdle. Pectoral fin, posttemporo-supracleithrum and all muscles removed. **C**: Median view of the anterior region of the first pectoral ray, showing the insertions of the muscles responsible for its movement. addi-m, additional muscle; af-cra, articular facet for complex radial; af-pecra1, articular facet for first pectoral ray; m-ab-pro, musculus abductor profundus; m-ab-sup-1, section 1 of musculus abductor superficialis; m-arr-d-dd, m-arr-d-vd, dorsal and ventral divisions of musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-cl-dp-1, dorsal process 1 of cleithrum; o-cl-mg, medial groove of cleithrum; o-cl-pdsp, postero-dorsal spine of cleithrum; o-puh, os parurohyale; o-sca-cor, os scapulo-coracoide; pec-ra, pectoral rays; pec-ra-1, first pectoral ray; pec-ra-1-ac+dc, pec-ra-1-vc, anterodorsal and ventral condyles of first pectoral ray.

(Schaefer, 1990, 1998; Howes and Fumihito, 1991; Arratia and Gayet, 1995; Adriaens, 1997; Adrianes and Verraes, 1998; Gayet and Meunier, 1998; Cabuy et al., 1999; He et al., 1999; etc.) that it probably corresponds to the posttemporal plus supracleithrum of other teleosts.

In a large number of catfishes (see Results and also descriptions of Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1982; Gosline, 1977; Howes, 1983a, 1985; Arratia, 1987; Grande, 1987; Cerny, 1988; Grande and Lundberg, 1988; Mo, 1991; etc.), the posttemporo-supracleithrum is a strong, well-

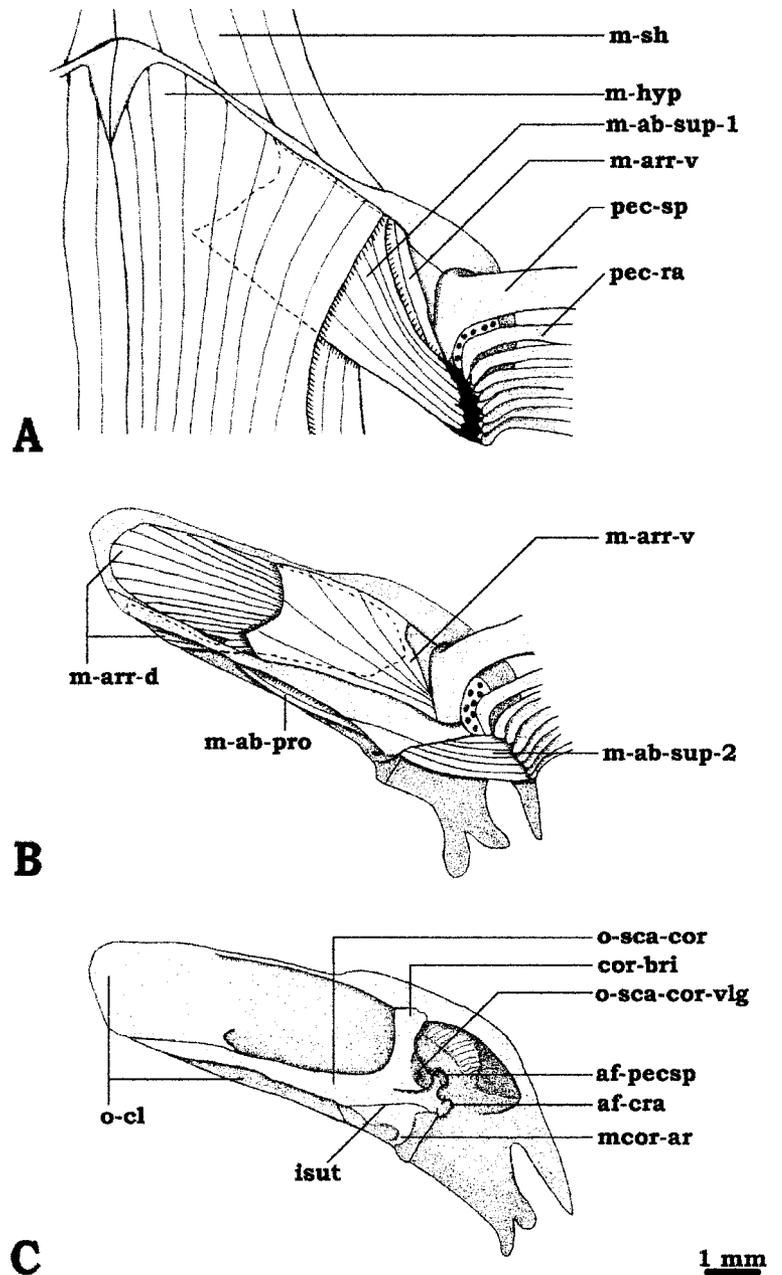


Fig. 12. Ventral view of the pectoral girdle of *Diplomystes chilensis*, posttemporo-supracleithrum removed. **A:** All muscles exposed. **B:** Hypoaxialis, sternohyoideus and section 1 of abductor superficialis removed. **C:** All muscles, as well as pectoral fin and pectoral spine, removed. af-cra, articularity facet for complex radial; af-pecsp, articularity facet for pectoral spine; cor-bri, coracoid bridge; isut, incomplete suture; m-ab-pro, musculus abductor profundus; m-ab-sup-1, m-ab-sup-2, sections of musculus abductor superficialis; m-arr-d, musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-hyp, musculus hypoaxialis; m-sh, musculus sternohyoideus; mcor-ar, mesocoracoid arch; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; o-sca-cor-vlg, ventro-lateral groove of scapulo-coracoide; pec-ra, pectoral rays; pec-sp, pectoral spine.

ossified bone, with three (dorsomedian, median, and posteroventrolateral: see below) well-developed limbs.

In many catfishes, the dorsomedian limb attaches to the posterior region of the cranium by means of extensive ligamentous tissue (Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1982; Gosline, 1977; Howes, 1983a, 1985; Arratia, 1987; Grande, 1987; Mo, 1991). This is the case in all claroteids (Fig. 3A), bagrids, diplomystids, and plotosids studied in this work. However, in the clariids (Fig. 8), ariids, amphiliids, and doumeids studied, as well as in several other catfishes (Regan, 1911a; Alexander, 1965; Chardon, 1968;

Howes, 1983a,b, 1985; Schaefer, 1990; Mo, 1991; De Pinna, 1993, 1998; etc.), this limb is firmly sutured to cranial elements. In the astroblepids, loricariids, callichthyids, and scoloplacids, it is completely fused to the pterotic (Alexander, 1965; Chardon, 1968; Howes, 1983a,b, 1985; Schaefer, 1990; Mo, 1991; De Pinna, 1993, 1998; etc.). The plesiomorphic condition of the dorsomedial limb of catfish posttemporo-supracleithrum seems to be that in which this limb is only loosely (not firmly) attached to the neurocranium by means of ligamentous tissue. In fact, this is not only the case in the Diplomystidae (the most primitive siluriform family: Alexander, 1965; Chardon, 1968; Arratia,

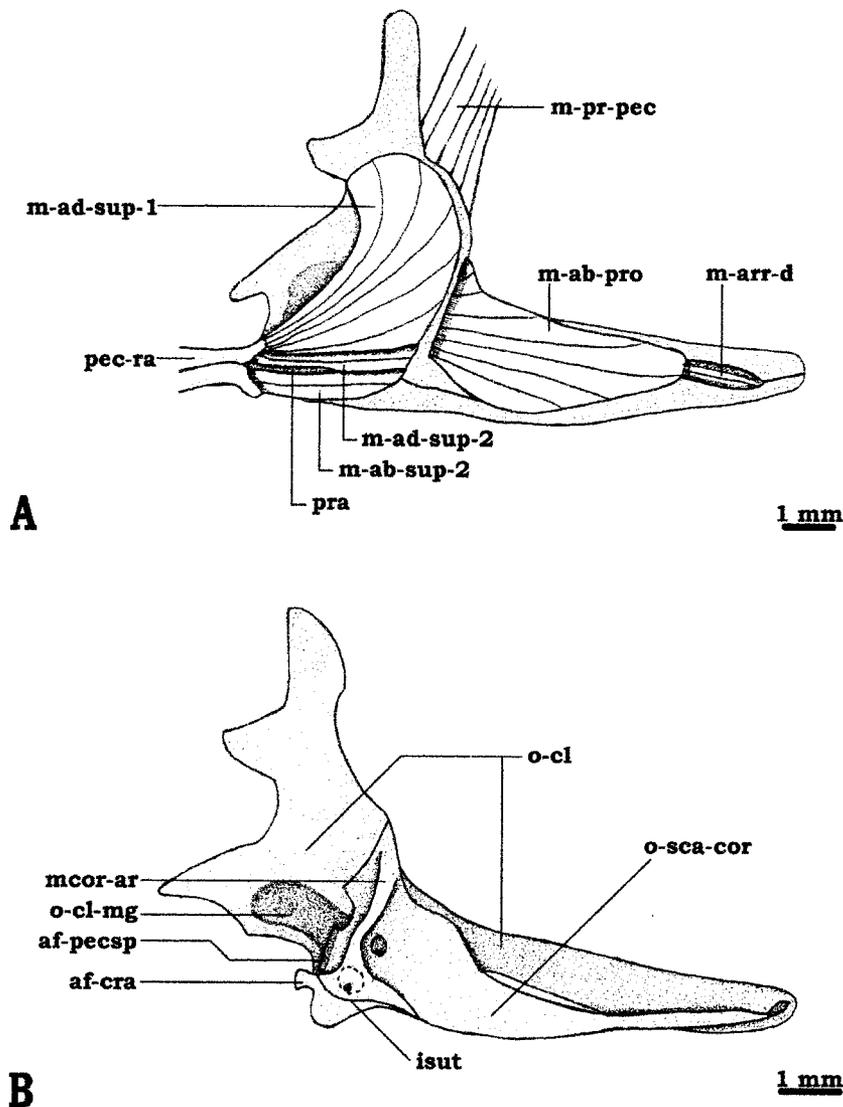


Fig. 13. Posterior view of the pectoral girdle of *Diplomystes chilensis*, posttemporo-supracleithrum removed. **A:** All muscles exposed. **B:** All muscles, as well as pectoral fin and pectoral spine, removed. af-cra, articular facet for complex radial; af-pecsp, articular facet for pectoral spine; isut, incomplete suture; m-ab-pro, musculus abductor profundus; m-ab-sup-2, section 2 of musculus abductor superficialis; m-ad-sup-1, m-ad-sup-2, sections of musculus adductor superficialis; m-arr-d, musculus arrector dorsalis; m-pr-pec, musculus protractor pectoralis; mcor-ar, mesoracoid arch; o-cl, os cleithrum; o-cl-mg, medial groove of cleithrum; o-sca-cor, os scapulo-coracoide; pec-ra, pectoral rays; pra, proximal radial.

1987, 1992; Mo, 1991; De Pinna, 1993, 1998; Diogo and Chardon, 1998, Fink and Fink, 1996; Arratia, 1992).

In relation to the mesial limb of the posttemporo-supracleithrum, in all nonariid catfishes studied, as well as in many other siluriforms described in the literature (Regan, 1911a; Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1975a, 1982; Howes, 1983a, 1985; Arratia, 1987; Cerny, 1988; Schaefer, 1990; Mo, 1991; De Pinna, 1993, 1998; etc.), it attaches, by means of ligamentous tissue to the basioccipital and/or exoccipital bones. However, in the ariids studied here, and also in other catfishes such as mochokids, doradids, and auchenipterids, this limb could be firmly sutured to these bones (Alexander, 1965; Chardon, 1968; Britski, 1972; Taverne and Aloulou-Triki, 1974; Mo, 1991; Higuchi, 1992; etc.). In a reduced number of siluriforms, such as clariids, heteropneustids, akysids, and astroblepids, this limb is absent (see Results and also descriptions of

Srinivasachar, 1958; Alexander, 1965; Chardon, 1968; Mo, 1991; etc.). The plesiomorphic siluriform condition of the median limb of the posttemporo-supracleithrum seems to be that of *Diplomystes* and of many other generalized catfishes in which this limb is a well-developed structure connected, by means of a short, strong ligament, to the basioccipital and/or exoccipital bones. However, it is somewhat difficult to support this hypothesis with an outgroup comparison, since the configuration of this limb is different from that of any other structure of the posttemporal and/or supracleithrum of other Ostariophysi, including the characiforms and gymnotiforms (see, e.g., Fink and Fink, 1981, 1996). Such a plesiomorphic condition would, thus, represent a symplesiomorphy of the Siluriformes; that is, it is exclusively present in these fishes.

The posteroventrolateral limb of the posttemporo-supracleithrum is usually bifurcated (see, e.g., Figs. 1B, 2A) to receive the dorsal part of the cleithrum,

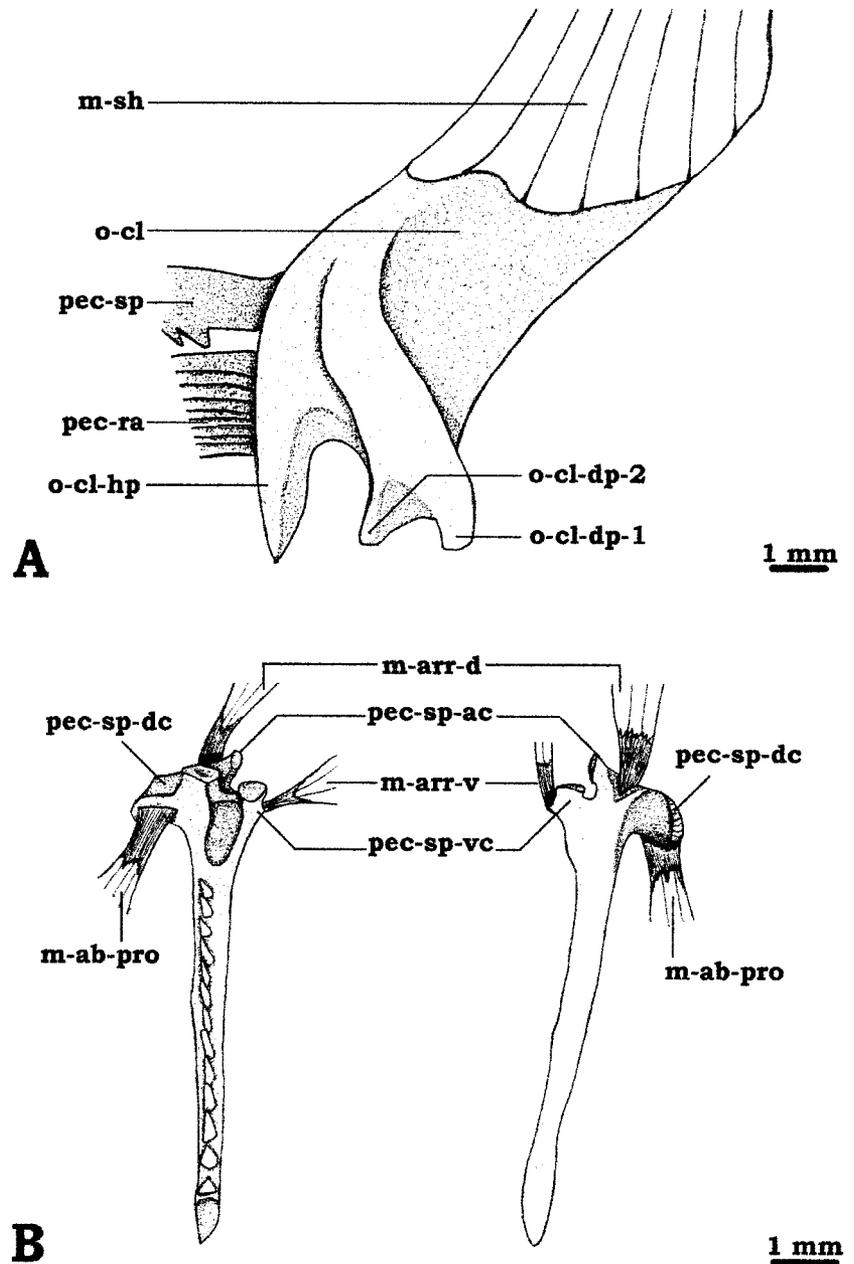


Fig. 14. *Diplomystes chilensis*. **A**: Dorsal view of the pectoral girdle. All muscles exposed; posttemporo-supracleithrum removed. **B**: Mesial (in left) and lateral (in right) view of the pectoral spine, showing the insertions of the muscles responsible for its movement. m-ab-pro, musculus abductor profundus; m-arr-d, musculus arrector dorsalis; m-arr-v, musculus arrector ventralis; m-sh, musculus sternohyoideus; o-cl, os cleithrum; o-cl-dp-1, o-cl-dp-2, dorsal processes of cleithrum; o-cl-hp, humeral process of cleithrum; pec-ra, pectoral rays; pec-sp, pectoral spine; pec-sp-ac, pec-sp-dc, pec-sp-vc, anterior, dorsal, and ventral condyles of pectoral spine.

with this bifurcation being particularly deep in the amphiliids studied (see Results and also the descriptions of Regan, 1911a; Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1975a, 1982; Howes, 1983a, 1985; Arratia, 1987; Cerny, 1988; Schaefer, 1990; Mo, 1991; De Pinna, 1993, 1998; etc.). In some catfishes, for example, the bagrids, claroteids, doumeids, and clariids studied, the dorsal edge of the cleithrum passes through a dorsal foramen of the posttemporo-supracleithrum (see, e.g., Figs. 1B, 2A). However, in the other catfishes studied in this work, as well as in a large number of other catfishes (Alexander, 1965; Chardon, 1968; Howes, 1983a, Howes, 1983b, 1985; Schaefer, 1990; Mo, 1991; De

Pinna, 1993, 1998; etc.), the dorsal surface of the posttemporo-supracleithrum is not pierced, being the dorsal edge of the cleithrum lodged between the anterior process of the fourth parapophysis, the posttemporo-supracleithrum, and the posterior region of the neurocranium. In some siluriforms, such as the loricariids and scoloplacids, the upper part of the cleithrum articulates in a large, globular ventral groove of the pterotic-posttemporo-supracleithrum complex (Schaefer, 1990). The plesiomorphic condition for siluriforms (which represents a sympleisomorphy of the siluriforms, since it is exclusive of these fishes; see below) seems to be that of *Diplomystes* and many other generalized catfishes, in

which the posteroventrolateral limb of the posttemporo-supracleithrum is bifurcated (but not as deeply bifurcated as in amphiliids), and in which the dorsal edge of the cleithrum is lodged between the posterior region of the neurocranium, the fourth parapophysis, and the posttemporo-supracleithrum. It is difficult to argue this hypothesis with an out-group comparison, since the articulation between the cleithrum and the posttemporo-supracleithrum of catfishes is quite different from that between the cleithrum and the supracleithrum of other ostariophysine fishes, including the Gymnotiformes and the Characiformes (see, e.g., Weitzman, 1962; De La Hoz, 1974; Gosline, 1977).

Cleithrum

In most species studied in this work, as well as in many other catfishes (Regan, 1911a; Alexander, 1965; Chardon, 1968; Lundberg, 1970, 1975a, 1982; Howes, 1983a, 1985; Arratia, 1987; Grande, 1987; Grande and Lundberg, 1988; Schaefer, 1990; Mo, 1991; De Pinna, 1993, 1998; etc.), the upper limb of the cleithrum bears a roughly triangular, pointed process directed posteriorly, the humeral process (see, e.g., Fig. 3A). However, in the amphiliids, plotosids, clariids (Fig. 8), and doumeids studied, and also in certain other siluriforms (e.g., nematogenyids, callichthyids, loricariids, trichomycterids, astrolepids, amblycipitids, some sisorids, etc.), this process is rudimentary, or even completely absent (Tilak, 1963; Alexander, 1965; Mo, 1991; Schaefer, 1990; De Pinna, 1996; Reis, 1998; etc.). According to most authors (Tilak, 1963; Alexander, 1965; Chardon, 1968; Mo, 1991; De Pinna, 1996; etc.), the presence of a well-developed humeral process is the primitive condition for siluriforms. We fully agree with this opinion, since such a process is present in the diplomystids and hypsidorids, as well as in many other generalized catfishes. Although this is not the case for most Ostariophysini (Weitzman, 1962; Alexander, 1964; Gijssen and Chardon, 1976; Vandewalle, 1975; Howes, 1976, 1978; Gosline, 1977; Brosseau, 1978; etc.), in *Sternopygus* (De La Hoz, 1974; De La Hoz and Chardon, 1984), as well as in many other Gymnotiformes (see, e.g., De La Hoz, 1974; Mago Leccia, 1978) (the sister-group of the Siluriformes; see above), the upper limb of the cleithrum presents a broad, posteriorly directed triangular process, which is comparable to the catfish humeral process (see, e.g., De La Hoz and Chardon, 1984: fig. 22).

Anteroventrally to the humeral process, in the vast majority of catfishes in which the pectoral girdle bones have been studied in detail, the cleithrum bears a deep, crescentic, roughed, medially faced groove to accommodate the thick crescentic dorsal condyle of the pectoral spine, forming an anterior-posteriorly mobile articulation (osteological base of the friction-locking mechanism of the pectoral spine)

(see, e.g., Fig. 1B). However, in a few highly-specialized siluriforms, such as the doumeids (Fig. 11A,B), amphiliids (Fig. 9A,B), and sisorids (Tilak, 1963; De Pinna, 1996; He, 1996, 1997), the cleithrum only bears an articulatory facet for the pectoral spine (first pectoral ray in the amphiliids and doumeids, in which there is no true pectoral spine; see above), this median groove being rudimentary or absent (consequently, the friction-locking mechanism is lost). Although a deep crescentic, roughed medial groove of the cleithrum is not present in other Ostariophysini (see, e.g., Regan, 1911a; Weitzman, 1962; Alexander, 1965; De La Hoz, 1974; De La Hoz and Chardon, 1984; etc.), the taxonomic distribution of this character within catfishes clearly seems to indicate that it represents, in fact, the plesiomorphic condition for these fishes (and, thus, a symplesiomorphy of the siluriforms).

Curiously, in many catfishes in which there is no well-developed cleithral medial groove, such as the amphiliids (Figs. 9A,B, 10A), doumeids (Fig. 11A), and some, but not all, sisorids (Tilak, 1963; He, 1996, 1997; etc.), but also in some other specialized siluriforms (e.g., scoloplacids: Schaefer, 1990), each cleithrum meets its counterpart in an interdigitation of several strong serrations. However, this is not the case for the vast majority of catfishes described in the literature or studied by us, in which the cleithra meet only by means of ligamentous tissue (see, e.g., Fig. 1B). This latter condition clearly represents the plesiomorphic situation for Siluriformes, not only because the cleithra interdigitate in only some few specialized catfishes, but also since such an interdigitation is missing in other ostariophysine fishes, including the characiforms and the gymnotiforms (see, e.g., Regan 1911a; Weitzman, 1962; Alexander, 1965; De La Hoz, 1974; Gosline 1977; De La Hoz and Chardon, 1984; etc.).

Scapulo-coracoid

In almost all siluriforms studied by us and/or described in the literature (see Results and also descriptions of Alexander, 1965; Lundberg, 1970, 1982; Arratia, 1987; Grande, 1987; Cerny, 1988; Grande and Lundberg, 1988; Mo, 1991; etc.), the anterolateral surface of the scapulo-coracoid presents a well-developed coracoid bridge, which extends ventrally to the ventrolateral surface of the cleithrum, fusing to an anteroventral ridge of this bone (see, e.g., Fig. 1B). In catfishes such as clariids (Fig. 7B), this bridge is very thin and small, and is fused dorsally with the main body of the ventrolateral surface of both the cleithrum and the scapulo-coracoid bones. Therefore, the tunnel usually formed by the coracoid bridge is closed (Fig. 7B, c.f. Fig. 1B). However, the condition in clariids is clearly a derived one. In fact, although in other Ostariophysini, including Gymnotiformes and Characiformes, there is no coracoid bridge (see Alexander, 1965), the taxonomic distri-

bution of this character within the Siluriformes indicates that a well-developed coracoid bridge represents, very likely, a catfish plesiomorphy (and, thus, a symplesiomorphy of the Siluriformes).

Posteriorly to the coracoid bridge, in the ariids, diplomystids (Fig. 12B), claroteids (Fig. 1B), and bagrids (Fig. 5A) studied in this work, there is a ventrolateral groove in the scapulo-coracoid, which accommodates the ventral condyle of the pectoral spine when this spine is erected. In the amphiliids, doumeids, plotosids, and clariids examined, this groove is absent. It is somewhat difficult to determine the taxonomic distribution of this character, as well as its plesiomorphic condition. In fact, the osteological descriptions available in the literature concerning catfish pectoral girdle are not sufficiently detailed to answer this question. Moreover, the quite different configuration of the articulation between the pectoral spine and the pectoral girdle in catfishes and that of the pectoral girdle and the first pectoral ray of other Ostariophysi (a stout pectoral spine with an irregular, multiarticulated proximal end is exclusive of the Siluriformes; see above) renders any outgroup comparison difficult. It can only be speculated that the existence of a scapulo-coracoid ventrolateral groove in the diplomystids, hypsidorids (a ventrolateral groove of the scapulo-coracoid, comparable to that described in this work, is illustrated in fig. 5B of Grande, 1987) and in some generalized catfishes, such as the claroteids, bagrids, and ariids (see Eigenmann, 1980; Alexander, 1965; Gosline, 1975; Chardon, 1965; Diogo et al., 1999b; Diogo and Chardon, 2000a, in press) could indicate that the presence of this groove represents a symplesiomorphy of the Siluriformes. A quite similar problem arises when one discusses the phylogenetic significance of the scapulo-coracoid posterolateral foramen that accommodates the anterior condyle of the pectoral spine in some siluriforms (see Results), which is present in the diplomystids, claroteids, bagrids, plotosids, clariids, but not in the other catfishes studied in this work, nor in the other Ostariophysi (see, e.g., Weitzman, 1962; Alexander, 1965; Saxena and Chandy, 1966; De La Hoz, 1974; Gijzen 1974; Brosseau, 1978; Vari, 1979; De La Hoz and Chardon, 1984).

In a large number of catfishes (see Results and also descriptions of Alexander, 1965; Lundberg, 1970, 1982; Arratia, 1987; Grande, 1987; Grande and Lundberg, 1988; Mo, 1991; etc.), there is a mesocoracoid tunnel (see, e.g., Fig. 2B) between the anterior margin of the mesocoracoid and the posterior surface of the main body of the scapulo-coracoid (see Results). However, in certain catfishes, such as ariids (Fig. 3B), akysids, doradids, achenipterids, ageneiosids, or aspredinids (Tilak, 1963; Alexander, 1965; Gainer, 1967; Mo, 1991; etc.), the mesocoracoid tunnel is absent (see, e.g., Fig. 3B). Since such a tunnel is present in the Diplomystidae, Hypsidoridae (Grande, 1987; Grande and De Pinna, 1998),

and in many other generalized catfishes, as well as in most other Ostariophysi, including the Gymnotiformes and the Characiformes (see, e.g., Weitzman, 1962; Alexander, 1965; De La Hoz, 1974; Gijzen, 1974; Gosline, 1977; De La Hoz and Chardon, 1984), it clearly seems that the plesiomorphic condition for siluriforms is that in which the mesocoracoid tunnel is present.

As for the overall aspect of the scapulo-coracoid, in the vast majority of the catfishes in which this bone has been studied this is a broad, irregular bony plate visible either in ventral or in dorsal view, suturing with the cleithrum along its anterolateral edge and meeting its counterpart in an interdigitation of several strong serrations (see, e.g., Figs. 1B, 2A). However, in the diplomystids (Figs. 12C, 13B, 14A), as well as in catfishes such as trichomycterids, nematogenyids, astroblepids, cetopsids, and silurids (Tilak, 1963; Gosline, 1977; Arratia et al., 1978; Arratia and MenuMarque, 1984; Mo, 1991; Bornbusch, 1995; Grande and De Pinna, 1998), the scapulo-coracoid is a slender bone, not visible in dorsal view, which does not interdigitate with its counterpart mesially (see, e.g., Figs. 12C, 13B, 14A). Mo (1991) and Bornbusch (1995) consider that a slender scapulo-coracoid with no medial suture with its counterpart represents the plesiomorphic condition for catfishes. Grande and De Pinna (1998) suggested that a scapulo-coracoid with no medial interdigitation with its counterpart represents a catfish plesiomorphy and that a scapulo-coracoid medially sutured with its counterpart could probably constitute either a Siluroidea (all catfish families except Diplomystidae) synapomorphy or a synapomorphy of non-diplomystid and noncetopsid catfishes (if both Diplomystidae and Cetopsidae were basal groups to Hypsidoridae and other siluroids; see Grande and De Pinna, 1998: 471). According to these authors, the slender scapulo-coracoid with no mesial suture with its counterpart of catfishes such as trichomycterids and nematogenyids is probably a homoplastic character. This is also the opinion of Bornbusch (1995), who considers that the slender scapulo-coracoid of most silurids probably represents a homoplastic reversion. We fully agree with Mo (1991), Bornbusch (1995), and Grande and De Pinna (1998) in that the overall configuration of the scapulo-coracoid of diplomystids probably represents the plesiomorphic condition for siluriforms. In fact, the complex constituted by both the scapula + coracoid + mesocoracoid of Gonorynchiformes, Cypriniformes, Characiformes, and particularly of Gymnotiformes clearly resembles to the scapulo-coracoid of diplomystids (Figs. 12C, 13B, 14A), being a slender structure with a very thin median process, which does not suture with its counterpart mesially (see, e.g., Regan, 1911b; Monod, 1963; Alexander, 1964, 1965; Roberts, 1969; De La Hoz, 1977; Gijzen, 1974; Gijzen and Chardon, 1976; Gosline, 1977; Howes, 1978; Mago Leccia, 1978; De La Hoz and Chardon,

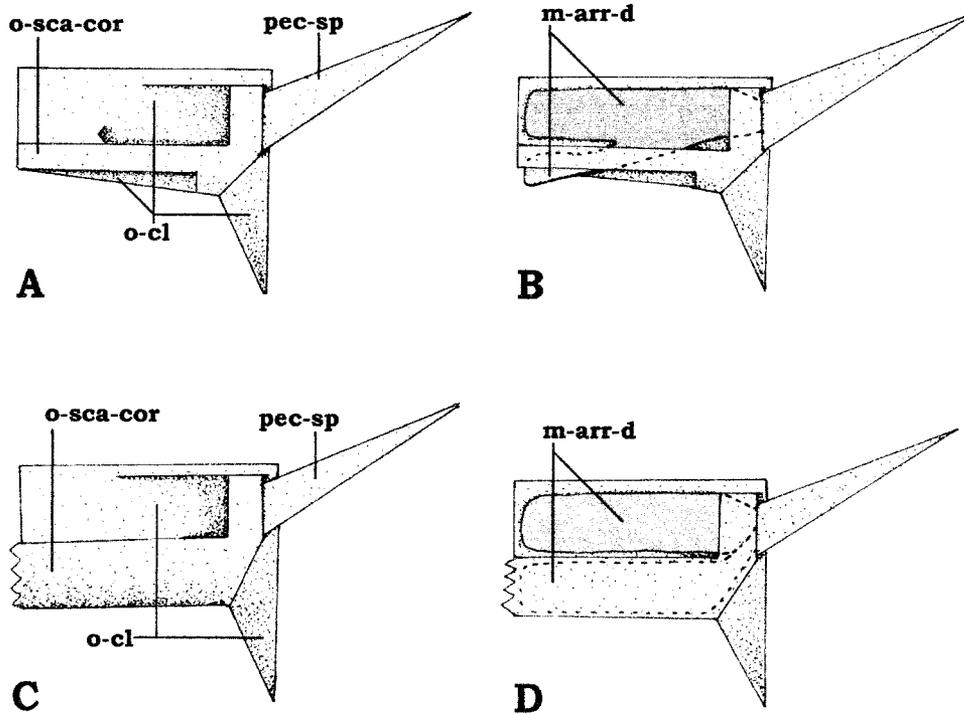


Fig. 15. Scheme illustrating the main morphological differences between the pectoral girdle (A) and arrector dorsalis muscle (B) of diplomystids and the pectoral girdle (C) and arrector dorsalis muscle (D) of a large number of other catfishes (see Discussion). m-arr-d, musculus arrector dorsalis; o-cl, os cleithrum; o-sca-cor, os scapulo-coracoide; pec-sp, pectoral spine.

1984; Mago Leccia et al., 1985). We also agree that a well-developed scapulo-coracoid, visible in dorsal view, meeting its counterpart in a strong median interdigitation probably represents either a Siluroidea synapomorphy or a synapomorphy of all non-diplomystid and noncetopsid catfishes (if both Diplomystidae and Cetopsidae were basal groups all other Siluriformes). The main morphological transformations between the plesiomorphic siluriform configuration of the scapulo-coracoid and the derived configuration present in a great number of catfishes (see above) were: 1) a more pronounced ankylosis (Fig. 15A,C) between the anterior margin of the scapulo-coracoid and the posterior margin of the cleithrum; 2) a broad posterodorsal expansion (Fig. 15A,C) of the mesial surface of the scapulo-coracoid; and 3) the interdigitation (Fig. 15A,C) between this broad posterodorsal expansion and that of the scapulo-coracoid of the other side.

Arrector Ventralis

The identity of this muscle has been, and still is, a subject of much confusion. It has been called several names, such as “abductor of spine” (Alexander, 1965), “adducteur superficiel de l'épine pectorale” (Taverne and Aloulou-Triki, 1974), “abductor superficialis internus” (Dubale and Rao, 1961), “abductor profundus” (McMurrich, 1884), “abductor pectoralis superficialis” (Saxena and Chandy, 1966), “abducteur du rayon osseux” (Jaquet, 1898), “erector spini ventralis” (Nawar, 1955), and “arrector ventralis superficialis” (Schaefer, 1991). However, it is most

commonly identified as “arrector ventralis” (e.g., Winterbottom, 1974; Howes, 1985, 1987; Bornbusch, 1995). In fact, it clearly corresponds to the arrector ventralis of other teleosts, which inserts “on the anteromedial base of the medial half of the marginal (first) fin ray” (see Winterbottom, 1974:273, 274). This muscle is present in all catfishes examined in this work (Figs. 1A, 3B, 4A, 5, 6, 7A,D, 9A,C, 11A,C, 12A,B, 14B), and also in all other catfishes in which the pectoral muscles have been described (see, e.g., McMurrich, 1884; Jaquet, 1898; Nawar, 1955; Dubale and Rao, 1961; Alexander, 1965; Saxena and Chandy, 1966; Taverne and Aloulou-Triki, 1974; Howes, 1985). Usually it is a thin muscle visible in ventral view, whose fibers are anteroposteriorly directed (see, e.g., Fig. 1A). However, in the diplomystids (Fig. 12B) studied in this work, this is a large, somewhat oblique muscle. This is also the case in the amphiliids examined (Fig. 9A), with the difference that in these fishes the large arrector ventralis is deeply bifurcated laterally. In the hypoptomatina loricariids (Schaefer, 1991), the arrector ventralis is almost invisible in ventral view, since it is “partially or entirely enclosed by a ventral lamina” of the scapulo-coracoid (Schaefer, 1991). The plesiomorphic condition for catfishes is probably similar to that found in the diplomystids, not only since these are the most plesiomorphic siluriforms (see above), but principally since the arrector ventralis is a “fairly well developed” muscle in other teleosts, including in the Characiformes and Gymnotiformes (see, e.g., Alexander 1965; Saxena and Chandy, 1966; De La Hoz, 1974; Gijzen 1974; Winterbottom 1974).

Arrector Dorsalis

Several names have been used to identify this muscle, such as “extensor” (Alexander, 1965), “abductor profundus” (McMurrich, 1884), “adductor superficialis” (Dubale and Rao, 1961), “ventral arrector” (Brosseau, 1978), “erector pectoralis” (Saxena and Chandy, 1966), “arrector ventralis profundus” (Schaefer, 1991), or “erector spini” (Nawar, 1955). We agree with Winterbottom (1974), Howes (1985), and Bornbusch (1995), in that this muscle corresponds to the arrector dorsalis of other teleosts, which usually originates on the “posteroventromesial face of the cleithrum and the adjoining area of the coracoid” and inserts “on the base of the medial half of the marginal (first) pectoral ray” (Winterbottom, 1974). The plesiomorphic condition for catfishes seems to be that found in the diplomystids in which, like in almost all the nonsiluriform teleosts, including the Characiformes and Gymnotiformes (see, e.g., Alexander, 1965; De La Hoz, 1974; Gijssen, 1974; Winterbottom, 1974; De La Hoz and Chardon, 1984), the arrector dorsalis is a well-developed, undivided muscle (Fig. 12A). In almost all nondiplomystid catfishes in which the pectoral girdle muscles have been studied (see Results and also descriptions of Jaquet, 1898; Alexander, 1965; Saxena and Chandy, 1966; Gainer, 1967; Taverne and Aloulou-Triki, 1974; Bornbusch, 1995) the arrector dorsalis is differentiated into two (dorsal and ventral) well-developed divisions. In the vast majority of these fishes, the ventral division, situated on the ventral surface of the pectoral girdle (see, e.g., Fig. 1A), inserts on the anterolateral edge of the pectoral spine (see, e.g., Fig. 3B), and the dorsal division, situated on the dorsal surface of the pectoral girdle (see, e.g., Fig. 2A), inserts on the anterior edge of the dorsal condyle of the pectoral spine (see, e.g., Fig. 3B). However, in the clariids (Fig. 7C) studied in this work both divisions lie in the dorsal side of the pectoral girdle. Contrarily, in the amphiliids (Fig. 9A,B) and doumeids (Fig. 11A) examined, both divisions situate on the ventral surface of this girdle.

In the plotosids studied in this work (Fig. 6) there is only one division of the arrector dorsalis, which seems to correspond to the dorsal division of other catfishes, but which inserts on the anteroventral surface of the pectoral spine, and not in the anterior margin of the dorsal condyle of the this spine (see above). This configuration of the arrector dorsalis is clearly a derived one since, although there is only a division of this muscle, like in the diplomystids and in nonsiluriform teleosts, this division does not lie on the ventral (the plesiomorphic condition; see above), but on the dorsal side of the pectoral girdle.

The main morphological transformations between the plesiomorphic configuration of the arrector dorsalis of diplomystids and that of catfishes in which this muscle is differentiated into ventral and dorsal divisions situated, respectively, on the ventral and

dorsal sides of the pectoral girdle, could probably be directly related to the morphological transformations of the scapulo-coracoid bone (see above). In fact, in the diplomystids the arrector dorsalis, although constituted by a single section, is bifurcated medially, its anteromesial fibers being situated ventrally to the cleithrum, and its posteromesial fibers situated dorsally to the scapulo-coracoid bone (Fig. 15B). This mesial bifurcation of the arrector dorsalis is due to the firm contact between the anteromesial edge of the scapulo-coracoid and the posteroventromesial margin of the cleithrum (Fig. 15A). Therefore, a much more pronounced ankylosis (Fig. 15A,C) between the anterior margin of the scapulo-coracoid and the posterior margin of the cleithrum (see above) would contribute to a more pronounced differentiation between the anteromesial and the posteromesial fibers of the arrector dorsalis (Fig. 15B,D). In addition, a broad posterior expansion (Fig. 15A,C) of the ventromesial surface of the scapulo-coracoid (see above) would allow a posterior expansion of the posteromesial fibers of this muscle, dorsally to the scapulo-coracoid (Fig. 15B,D).

Abductor Superficialis

Several names have been used to identify this muscle, such as “abductor of rays” (Alexander, 1965), “abductor superficialis” (McMurrich, 1884), “abductor superficialis externus” (Dubale and Rao, 1961), “depressor pinnae” (Nawar, 1955), “abductor pectoralis superficialis” (Saxena and Chandy, 1966), or “extenseur superficiel des lépidotriches pectoraux” (Taverne and Aloulou-Triki, 1974). However, it corresponds to the abductor superficialis of other teleosts (Winterbottom, 1974; Bornbusch, 1995).

In all siluriforms studied in this work, the abductor superficialis is differentiated into a larger, ventral section (section 1), which inserts on the anteroventral surface of the ventral part of the pectoral fin rays (see, e.g., Fig. 1A), and a smaller, dorsal section (section 2) which inserts on the anterodorsal surface of the ventral part of the pectoral fin rays (see, e.g., Fig. 2B). In almost all catfishes examined, as in most other siluriforms described in the literature (see, e.g., McMurrich, 1884; Alexander, 1965; Taverne and Aloulou-Tricki, 1974; Saxena and Chandy, 1966; Bornbusch, 1995), section 1 of the abductor dorsalis is well developed (see, e.g., Fig. 1A). However, in *Plotosus lineatus* (but not in the plotosids *Tandanus rendahli* and *Paraplotosus albilabris*) (Fig. 6A), as well as in the clariids studied (see Fig. 7A), this section is relatively small, being confined to the ventrolateral surface of the pectoral girdle. The plesiomorphic condition for catfishes clearly seems to be that in which the abductor superficialis is a large, well-developed muscle, since this is the case in diplomystids and in the vast majority of the other catfishes in which this muscle has been studied, as

well as in most other teleosts, including in gymnotiforms and characiforms (see, e.g., Alexander 1965; De La Hoz, 1974; Gijzen 1974; Winterbottom, 1974; Bornbusch, 1995).

In some catfishes, such as the claroteids (Fig. 1A), ariids (Fig. 4A), and doumeids (Fig. 11A) studied in this work, as well as in some sisorids (Saxena and Chandy, 1966) and some mochokids (Taverne and Aloulou-Triki, 1974), section 1 of the abductor superficialis lies anteriorly to the fore end of the hypoaxialis muscle. However, in several other catfishes (see Results and also descriptions of Alexander, 1965; Saxena and Chandy, 1966; Gosline, 1977; Howes, 1985; etc.) the hypoaxialis muscle invades a great portion of the ventral surface of the pectoral girdle (e.g., Fig. 12A). As a result, in these fishes the mesial portion of section 1 of the abductor superficialis lies dorsal to the hypoaxialis muscle (e.g., Fig. 12A). The invasion of the ventral surface of the pectoral girdle by the hypoaxialis muscle probably represents the plesiomorphic condition for catfishes, not only since this is the case in the diplomystids and many other siluriforms, but also since this is equally the case in most other teleostean and ostariophysine fishes, including the gymnotiforms and characiforms (e.g., De La Hoz, 1974; Winterbottom, 1974; Gijzen, 1974; Vandewalle, 1975; Gijzen and Chardon, 1976; De La Hoz and Chardon, 1984).

Abductor Profundus

The identity of this muscle has been, and still is, controversial. It has been called several names, such as “adductor of spine” (Alexander, 1965), “adductor profundus” (Dubale and Rao, 1961; Bornbusch, 1995), “retractor pectoralis dorsalis” (Saxena and Chandy, 1966), “depressor spini” (Nawar, 1955), “adducteur du rayon osseux” (Jaquet, 1898), “adductor muscle of the spine” (Gainer, 1967), or “adducteur profond de l'épine” (Taverne and Aloulou-Triki, 1974). We follow here the nomenclature of Winterbottom (1974), which has synonymized the “depressor spini pectoralis” of Nawar (1955) and the “retractor pectoralis dorsalis” of Saxena and Chandy (1966) (both correspond to this muscle; see above) with the abductor profundus of other teleosts (see Winterbottom, 1974:273). However, Howes (1985) suggested that this muscle corresponds either to part of the abductor superficialis or to part of the adductor superficialis plus adductor profundus of other teleosts. A somewhat similar opinion is that of Bornbusch (1995), who identified this muscle as the adductor profundus of other teleostean fishes. In our opinion, however, this muscle does indeed correspond to the abductor profundus since, in catfishes, it exclusively inserts on the pectoral spine (which corresponds to the first pectoral ray), and neither the adductor superficialis nor the adductor profundus attach to the first pectoral ray in teleosts (see Winterbottom, 1974).

In almost all catfishes studied in this work, and also in almost all other catfishes in which the pectoral girdle muscles have been studied (e.g., Jaquet, 1898; Alexander, 1965; Saxena and Chandy, 1966; Gainer, 1967; Taverne and Aloulou-Triki, 1974; Howes, 1985; Bornbusch, 1995; etc.), the abductor profundus is a large, undivided muscle, which originates on the posterior margin of the scapulo-coracoid and passes anteriorly to the mesocoracoid, to attach on the dorsal condyle of the pectoral spine (see, e.g., Figs. 2B, 3B). This is also the case in most other teleosts, including the gymnotiforms and characiforms (see, e.g., De La Hoz, 1974; Gijzen, 1974; Winterbottom, 1974; De La Hoz and Chardon, 1984). This plesiomorphic configuration is only slightly altered in a few catfishes, such as ariids (and probably also in the other catfishes where a mesocoracoid tunnel is missing; see above), in which this muscle passes posteriorly to the mesocoracoid (see Results), and amphiliids (Fig. 10B), in which this muscle is differentiated in two well-developed sections.

Adductor Superficialis

Several names have been used to identify this muscle, such as “releveur de la nageoire” (Jaquet, 1898), “abaisseurs profonds des lépidotriches” (Taverne and Aloulou-Triki, 1974), “deep adductor” (Brosseau, 1978), “dilatator posterior” (Dubale and Rao, 1961), “dorsal section of the adductor superficialis” (Howes, 1985), or “adductor of rays” (Alexander, 1965). However, we agree with Winterbottom (1974) and Bornbusch (1995) in that it clearly corresponds to the abductor superficialis of other teleosts, which usually attaches to “the antero-dorsomesial faces of the fin rays, some distance distal to their bases” (see Winterbottom, 1974). The configuration of this muscle is rather conservative within siluriforms. In fact, in all siluriforms studied in this work, including the primitive diplomystids, and also in the few other catfishes in which this muscle has been studied with some detail (see, e.g., Taverne and Aloulou-Triki, 1974; Howes, 1985), the adductor superficialis is a broad muscle, differentiated in two well-developed sections. The larger, dorsal section originates on the posterior surface of the cleithrum and on the posterolateral surface of the scapulo-coracoid, and the smaller, ventral section originates on the lateral margin of the mesocoracoid arch and on the dorsal margin of the pectoral proximal radials (e.g., Fig. 13A). Both sections pass posteriorly to the abductor profundus muscle, inserting on the anterior edge of the dorsal part of the pectoral fin rays (e.g., Fig. 13A). Although this configuration of the abductor superficialis clearly seems to represent the plesiomorphic condition for catfishes (it is present in all catfishes examined and also in all the other catfishes in which this muscle has been studied in some detail), the lack of detailed descriptions available in

the literature concerning the configuration of this muscle in other teleosts, and particularly in gymnotiforms and characiforms, renders it difficult to discriminate whether this configuration is exclusively present in the Siluriformes or is shared by these fishes and some other noncatfish teleosts.

CONCLUSIONS

Within the Siluriformes there is a great morphological diversity of the pectoral girdle structures. In fact, each of these structures often presents several different configurations within these fishes and it is, thus, sometimes difficult to discriminate which of these configurations represents the plesiomorphic siluriform condition. Moreover, many of the morphological characters analyzed in this discussion are exclusively present in catfish, thus complicating the discussion on which is the plesiomorphic state of these characters (this plesiomorphic state, exclusively present in the siluriforms, thus representing a symplesiomorphy of these fishes). However, despite this difficulty, as is the case with several other complex structures, such as the palatine-maxillary system (Diogo et al., 1999a, in press; Diogo and Chardon, in press a), the adductor mandibulae complex (Howes, 1983a, 1985; Schaefer and Lauder, 1986; Diogo and Chardon, 2000b) or the Weber apparatus (e.g., Chardon, 1968; Arratia, 1987), the configuration of the pectoral girdle structures of diplomystids seems to represent, in most, if not all, cases the plesiomorphic siluriform condition, representing inclusively, in some cases (e.g., the configuration of the arrector ventralis and arrector dorsalis muscles), the intermediate between that of catfish outgroups and that of the nondiplomystid siluriforms.

We hope that the discussion given in this article on the morphological diversity of the different pectoral girdle structures within the catfishes, as well as on which of the different types of configuration of these structures represents the plesiomorphic condition for these fishes, will not only increase the knowledge on the myology and osteology of catfish pectoral girdle, but also pave the way for future works concerning the comparative anatomy, functional morphology, paleontology, eco-morphology, and principally the phylogeny of the Siluriformes.

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