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On the cephalic and pectoral girdle muscles of the deep sea fish *Alepocephalus rostratus*, with comments on the functional morphology and phylogenetic relationships of the Alepocephaloidei (Teleostei)

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Abstract

The muscles of the cephalic region and pectoral girdle of *Alepocephalus rostratus* are described and compared with those of other alepocephaloid and non-alepocephaloid teleosts. In what concerns the configuration of these muscles, the alepocephaloid fishes examined in the present work exhibit a mix of mainly plesiomorphic features with a few derived features, such as the direct attachment of the adductor mandibulae to the maxilla, the anterior extension of the anterodorsal portion of the hypaxialis, the presence of an undivided arrector dorsalis, the absence of the protractor pectoralis, and the subdivision, in *Alepocephalus rostratus*, of the levator arcus palatini into two bundles. The functional and phylogenetic implications of these derived features are discussed.

Keywords

Alepocephaloidei, *Alepocephalus*, functional morphology, muscles, phylogeny, Teleostei

Introduction

The alepocephaloids (fig. 1) are marine teleostean fishes that live in fairly deep to very deep water (e.g. Gegenbaur, 1878; Parr, 1951, 1960; Greenwood et al., 1966; Gosline 1969, 1973; Greenwood and Rosen, 1971; Markle, 1980; Markle and Merrett, 1980; Markle and Krefft, 1985; Matsui and Rosenblatt, 1987; Begle, 1992; Sanford, 2000; Nelson, 2006). They are usually classified in three families, the Alepocephalidae with about 24 genera, the Platytroctidae with about 13 genera, and the Leptoichilichthyidae with one genus, although the number of genera and even of families recognised varies among authors (see e.g. Johnson and Patterson, 1996; Nelson, 2006; Diogo, in press).

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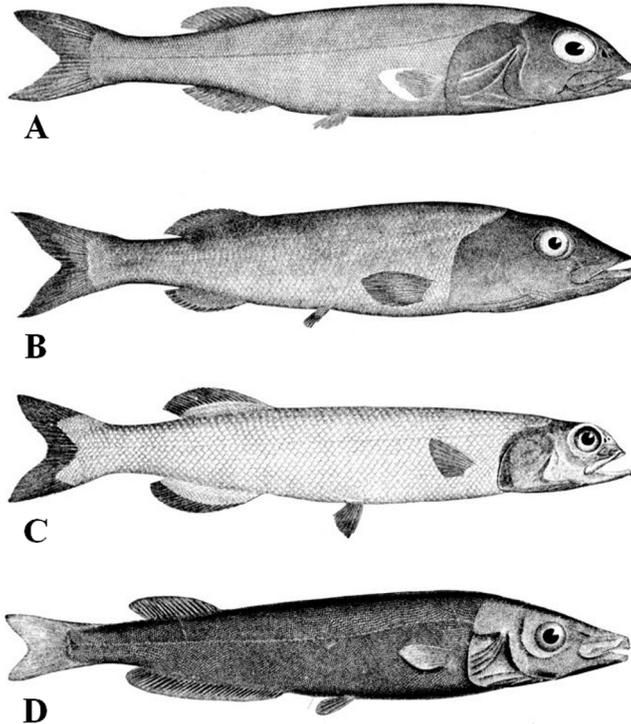


Figure 1. Examples of alepocephaloid fishes: A) *Alepocephalus agassizii*; B) *Alepocephalus bairdii*; C) *Alepocephalus productus*; D) *Conocara macropterus* (modified from Goode and Bean, 1896).

The phylogenetic position of the alepocephaloids within teleosts has been controversial. In Greenwood et al.'s (1966) overview of teleostean phylogeny, the alepocephaloids were placed within a clade named 'Salmoniformes'. This clade corresponded somewhat to the 'Protacanthopterygii' of recent works, including fishes such as salmoniforms, but also such as osmeriforms, esociforms and argentinoids (sensu Diogo, in press). Greenwood et al. (1966) recognised, however, that a review of the data available until that moment did not really allow solving the relationships of the Alepocephaloidei, and that the placement of this group within their 'Salmoniformes' was far from being strongly supported. In order to help to clarify the phylogenetic position of the alepocephaloids, Gosline (1969) promoted an anatomical study of these fishes and a comparison with other teleosts. Gosline (1969: 216) concluded that "by a process of elimination, it appears that the alepocephaloids are perhaps least unlike the osmeroids among modern fishes". However, as admitted by Gosline (1969: 216), the "characters held in common by the two groups are much too general in nature to more than suggest the possibility of such a relationship".

In 1971, Greenwood & Rosen undertook a further study on the anatomy and relationships of alepocephaloids, which was mainly focused on structures of the branchial apparatus and of the caudal skeleton. The observations of these authors strongly supported a sister-group relationship between the alepocephaloid and the argentinoid fishes,

the clade formed by these two groups being closely related to taxa such as the Esociformes, Salmoniformes and Osmeriformes (sensu Diogo, in press). The sister-group relationship between alepocephaloids and argentinoids proposed by Greenwood and Rosen (1971) was followed and/or further supported in works such as Rosen (1974, 1985), Fink and Weitzman (1982), Fink (1984), Begle (1991, 1992), Johnson (1992), Patterson and Johnson (1995), Johnson and Patterson (1996), Sanford (2000) and Springer and Johnson (2004). However, two recent molecular analyses have proposed a rather different hypothesis. Based on a cladistic mitogenomic analysis including a few representatives of the major extant non-neoteleostean groups, Ishiguro et al. (2003) concluded that the alepocephaloid fishes are not closely related to the argentinoid fishes or to fishes such as esociforms, salmoniforms and osmeriforms, but are, instead, closely related to otocephalans (clupeomorphs + ostariophysans). More precisely, according to these authors the alepocephaloids form a monophyletic group with the clupeomorphs, this group being in turn the sister-group of the Ostariophysi. In a cladistic mitogenomic analysis mainly focused on the phylogenetic relationships of the ostariophysan order Gonorynchiformes, Lavoué et al. (2005) also supported a close relationship between the alepocephaloids and the otocephalans. However, in the cladogram obtained by Lavoué et al. (2005), the Alepocephaloidei appear as the sister-group of the Ostariophysi, the Clupeomorpha being the sister-group of the clade formed by these two taxa. Thus, according to the results of these two molecular studies, two of the four major groups of extant teleosts defined in general textbooks such as e.g. Nelson (2006), namely the Otocephala and Euteleostei (the others are the Osteoglossomorpha and Elopomorpha) are not monophyletic. The Otocephala, defined as a clade including ostariophysans and clupeomorphs, is not monophyletic because some otocephalans appear to be more closely related to alepocephaloids than to other otocephalans. The Euteleostei is not monophyletic because the euteleostean alepocephaloids appear to be more closely related to fishes such as clupeomorphs and ostariophysans than to other euteleosts.

One can understand therefore why the Alepocephaloidei play a crucial role in discussions on the phylogeny, systematics and evolution of the Teleostei (see e.g. Ishiguro et al., 2003; Lavoué et al., 2005; Nelson, 2006; Diogo, in press). Curiously, despite the importance of alepocephaloids in such discussions, and despite the efforts that have been made to clarify the phylogenetic position of these fishes, their myology continues to be poorly known. In fact, within the published studies that have dealt with alepocephaloid anatomy only a few have described, with some detail, the configuration of certain muscles of these fishes (e.g. Gosline, 1969; Greenwood and Rosen, 1971; Markle, 1980; Markle and Merrett, 1980; Markle and Krefft, 1985; Sanford, 2000). Moreover, these descriptions are mainly concerned with lateral cephalic muscles such as the adductor mandibulae, the configuration of the ventral cephalic muscles and of the pectoral muscles of these fishes being thus practically unknown. Such a scarce knowledge of the myology of alepocephaloids hinder not only the study of topics such as the functional morphology and, consequently, the evolution of these fishes, but also the comparison between these fishes and other teleosts.

In the present study I describe the muscles of the cephalic region (branchial and extrinsic eye musculature excluded) and pectoral girdle of *Alepocephalus rostratus* and

compare these muscles with those of other alepocephaloid and non-alepocephaloid teleosts (either examined by the author or described in the literature). A discussion of certain aspects of the functional morphology of these fishes, as well as of their phylogenetic position within teleosts, is also given. It is hoped that this work could thus not only increase the knowledge of the anatomy and functional morphology of alepocephaloids, but also pave the way for future works concerning the comparative anatomy, functional morphology, evolution, ecomorphology and phylogeny of teleosts in general.

Materials and methods

Anatomical descriptions are made after dissection of adult, alcohol-preserved specimens (alc). Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. A list of the teleostean specimens examined for this work is given below (AMNH: American Museum of Natural History; ANSP: Academy of Natural Sciences of Philadelphia; CAS: California Academy of Sciences; FMNH: Field Museum of Natural History; INHS: Illinois Natural History Survey; LFEM: Laboratory of Functional and Evolutionary Morphology of the University of Liège; MNCN: Museo Nacional de Ciencias Naturales; MNHN: Museum National d'Histoire Naturelle; MRAC: Musée Royal de l'Afrique Centrale; UNB: Université Nationale du Bénin; USNM: National Museum of Natural History):

Osteoglossomorpha: *Hiodon tergisus*: MNCN 36019, 3 (alc). *Mormyrus niloticus*: LFEM, 1 (alc). *Mormyrus tapirus*: MNCN 80593, 3 (alc); MNCN 85283, 1 (alc). *Pantodon buchholzi*: MNCN 73493, 4 (alc). *Xenomystus nigri*: MNCN 227824, 25 (alc).

Elopomorpha: *Albula vulpes*: MNCN 52124, 2 (alc). *Anguilla anguilla*: MNCN 41049, 3 (alc). *Elops lacerta*: LFEM, 2 (alc). *Elops saurus*: MNCN 48752, 2 (alc). *Conger conger*: MNCN 1530, 5 (alc). *Eurypharynx pelecanooides*: AMNH 44315, 1 (alc); AMNH 44344, 1 (alc). *Megalops cyprinoides*: MNCN 48858, 3 (alc). *Notacanthus bonaparte*: MNCN 107324, 3 (alc).

Otocephala *Bagrus bajad*: LFEM, 1 (alc). *Bagrus docmak*: MRAC 86-07-P-512, 1 (alc). *Barbus guiraonis*: MNCN 245730, 3 (alc). *Brachyhyopomus brevirostris*: LFEM, 2 (alc). *Brachyhyopomus* sp.: INHS 89761, 2 (alc). *Brycon guatemalensis*: MNCN 180536, 3 (alc). *Brycon henni*: CAS 39499, 1 (alc). *Callichthys callichthys*: USNM 226210, 2 (alc). *Catostomus commersonii*: MNCN 36124, 10 (alc). *Cetopsis coecutiens*: USNM 265628, 2 (alc). *Chanos chanos*: USNM 347536, 1 (alc), LFEM, 1 (alc). *Chrysichthys auratus*: UNB, 2 (alc). *Citharinus* sp.: 86-016-P-72, 3 (alc). *Cobitis paludica*: MNCN 248076, 7 (alc). *Cromeria nilotica*: MRAC P.141098, 2 (alc). *Danio rerio*: LFEM, 5 (alc). *Denticeps clupeoides*: MRAC 76-032-P-1, 5 (alc). *Diplomystes chilensis*: LFEM, 3 (alc). *Distichodus notospilus*: MRAC A0-048-P-2630, 3 (alc). *Engraulis encrasicolus*: MNCN 68048, 2 (alc); MNCN 65097, 8 (alc); MNCN 1099, 3 (alc). *Engraulis* sp.: MNCN 48896, 3 (alc). *Ethmalosa fimbriata*: MNCN 48865, 3 (alc). *Gonorynchus gonorynchus*: LFEM, 2 (alc). *Gonorynchus greyi*: FMNH 103977, 1 (alc). *Grasseichthys gabonensis*: MRAC 73-002-P-264, 3 (alc). *Gymnotus carapo*: ILNS

35493, 2 (alc); MNCN 115675, 2 (alc). *Ilisha fuerthii*: MNCN 49338, 8 (alc). *Kneria wittei*: MRAC P-33512, 2 (alc). *Nematogenys inermis*: USNM 084346, 2 (alc). *Opsariichthys uncirostris*: MNCN 56668, 3 (alc). *Parakneria abbreviata*: MRAC 99-090-P-703, 3 (alc). *Phractolaemus ansorgii*: MRAC P.137982, 3 (alc). *Pimelodus blochii*: LFEM, 2 (alc). *Pristigaster cayana* LFEM, 2 (alc). *Silurus aristotelis*: LFEM, 2 (alc). *Silurus glanis*: LFEM, 2 (alc). *Sternopygus macrurus*: CAS 48241, 1 (alc); INHS 62059, 2 (alc). *Trichomycterus areolatus*: LFEM, 2 (alc). *Thryssa setirostris*: MNCN 49294, 2 (alc). *Xenocharax spilurus*: MRAC A0-048-P-2539, 3 (alc).

Euteleostei: *Alepocephalus rostratus*: MNCN 108199, 4 (alc). *Argentina brucei*: USNM 239005, 2 (alc). *Argentina sphyraena*: MNCN 001134, 12 (alc); MNCN 78530, 5 (alc). *Astronesthes niger*: MNCN 1102, 1 (alc). *Aulopus filamentosus*: MNCN 1170, 6 (alc). *Bathylagus euryops*: MNCN 124597, 1 (alc). *Bathylagus longirostris*: USNM 384823, 2 (alc). *Bathylagus tenuis*: MNHN 2005-1978, 2 (alc). *Chlorophthalmus agasizi*: MNCN 1193, 3 (alc); MNCN 1182, 5 (alc). *Coregonus lavaretus*: MNCN 75424, 1 (alc). *Coregonus tugun*: MNCN 75422, 2 (alc). *Esox lucius*: MNCN 197706, 5 (alc). *Galaxias maculatus*: USNM 344889, 2 (alc). *Osmerus eperlanus*: MNCN 193795, 11 (alc). *Osmerus mordax*: USNM 32565, 2 (alc). *Plecoglossus altivelis*: MNCN 192036, 1 (alc). *Retropinna retropinna*: AMNH 30890, 1 (alc). *Salmo trutta*: MNCN 136179, 2 (alc); MNCN 16373, 2 (alc); MNCN 40685, 2 (alc). *Salmo* sp.: MNCN 48863, 2 (alc). *Searsia koefoedi*: USNM 206896, 3 (alc). *Stokellia anisodon*: AMNH 31037, 1 (alc). *Stomias boa*: MNCN 74444, 8 (alc); MNCN 74456, 4 (alc). *Thymallus thymallus*: MNCN 115147, 1 (alc); MNCN 114992, 1 (alc). *Umbra limi*: MNCN 35672, 2 (alc); 36072, 2 (alc). *Umbra krameri*: MNCN 36659, 3 (alc). *Xenodermichthys copei*: MNCN 78950, 3 (alc); MNCN 1584, 2 (alc); USNM 215527, 2 (alc).

Results

As can be seen in the list above, besides the alepocephaloid *Alepocephalus rostratus*, a representative of the family Alepocephalidae (*Xenodermichthys copei*) and one of the other multi-generic alepocephaloid family, the Platytroctidae (*Searsia koefoedi*), have been dissected for this work. Thus, the myological descriptions given below are based on *Alepocephalus rostratus*, but in those cases in which there are significant differences between the configuration described for this species and that found in these two latter taxa, these differences will be mentioned. Unless otherwise stated, the nomenclature of the myological and osteological structures mentioned in this paper follows that of Diogo (in press).

Cheek musculature

Adductor mandibulae. The adductor mandibulae (figs. 2, 3) is differentiated into two bundles, A2 and A ω . The A2 originates on the preopercle, hyomandibula, quadrate and metapterygoid. It exhibits two anterior, thick tendons: one, more lateral, inserts on the maxilla (fig. 2); the other, more mesial, mixes with the posterior portion of the A ω and attaches on the coronomeckelian bone (fig. 3). The broad A ω attaches anteriorly

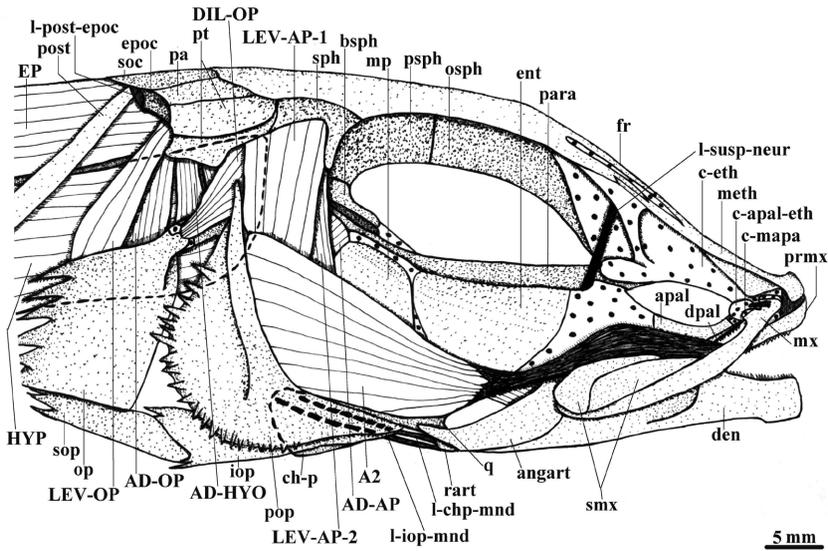


Figure 2. Lateral view of the cephalic musculature of *Alepocephalus rostratus*. The pectoral girdle muscles are not illustrated; most elements of the pectoral girdle, as well as the nasals and infraorbitals, were removed. A2, adductor mandibulae A2; AD-AP, adductor arcus palatini; AD-HYO, adductor hyomandibulae; AD-OP, adductor operculi; angart, angulo-articular; apal, autopalatine; bsph, basisphenoid; c-apal-eth, cartilage between autopalatine and ethmoid region; c-eth, ethmoid cartilage; c-mapal, small cartilage between maxilla and autopalatine; ch-p, posterior ceratohyal; den, dentary bone; dpal, dermopalatine; DIL-OP, dilatator operculi; ent, entopterygoid; EP, epaxialis; epoc, epioccipital; fr, frontal; HYP, hypoaxialis; iop, interopercle; l-chp-mnd, ligament between posterior ceratohyal and mandible; l-iop-mnd, ligament between interopercle and mandible; l-pri, primordial ligament; l-post-epoc, ligament between posttemporal and epioccipital; l-susp-neur, ligament between suspensorium and neurocranium; leth, lateral-ethmoid; LEV-AP-1, 2, sections of levator arcus palatini; LEV-OP, levator operculi; meth, mesethmoid; mp, metapterygoid; mx, maxilla; op, opercle; osph, orbitosphenoid; pa, parietal; para, parasphenoid; mp, metapterygoid; post, posttemporal; prmx, premaxilla; psph, pterosphenoid; pt, pterotic; q, quadrate; rart, retroarticular; smx, supramaxillae; soc, supraoccipital; sop, subopercle; sph, sphenotic.

on the mesial surface of both the anguloarticular and dentary bones and posteriorly on the tendon of the A2 (fig. 3).

Levator arcus palatine. This muscle (fig. 2) comprises an anteromesial bundle and a posterolateral bundle. It runs from the pterotic and sphenotic to the hyomandibula and quadrate. In *Xenodermichthys copei* and *Searsia koefoedi* the levator arcus palatini comprises a single bundle, not two bundles, as in *Alepocephalus rostratus*.

Adductor arcus palatine. The adductor arcus palatini (fig. 2) is a broad muscle extending from the lateral sides of the parasphenoid, pterosphenoid, pterotic and sphenotic to the mesial medial side of the hyomandibula.

Adductor hyomandibulae. This is small muscle (fig. 2) situated anteriorly to the adductor operculi and posteriorly to the adductor arcus palatini. It originates on the pterotic and inserts on the posterodorsomesial surface of the hyomandibula.

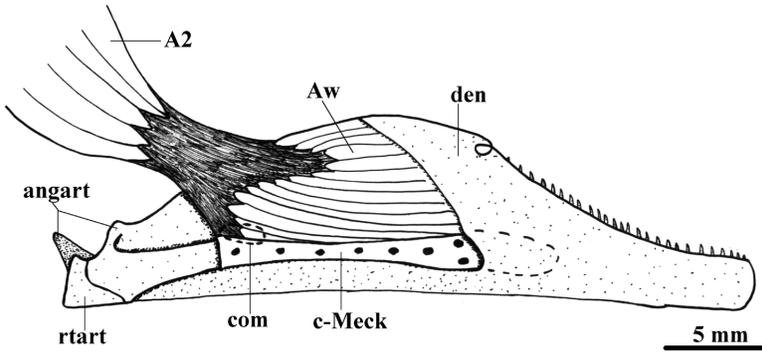


Figure 3. Mesial view of the left mandible and adductor mandibulae of *Alepocephalus rostratus*. A2, A ω , sections of adductor mandibulae; angart, angulo-articular; c-Meck, Meckel's cartilage; com, coronomeckelian bone; den, dentary bone; rtart, retroarticular.

Levator operculi. The levator operculi (fig. 2) originates on the ventrolateral margin of the pterotic and inserts on the dorsomesial edge of the opercle, laterally to the insertion of the adductor operculi on this latter bone.

Dilatator operculi. This muscle (fig. 2) originates medially to the levator arcus palatini, on the lateral surfaces of the sphenotic, pterotic and hyomandibula, and inserts on the anterodorsal margin of the opercle, laterally to the articulation between this latter bone and the hyomandibula.

Adductor operculi. The adductor operculi (fig. 2) originates on the pterotic and inserts on the dorsomesial surface of the opercle, mesially to the insertion of the levator operculi on this latter bone.

Although the epaxialis and hypaxialis are not included, by definition, on the lateral cephalic musculature, it is worthy to refer here the peculiar configuration of the hypaxialis, which was noticed by Gosline (1969) in *Alepocephalus rostratus*. This peculiar configuration is effectively found in the specimens of *Alepocephalus rostratus* analyzed in the present work, as well as in the specimens analyzed of *Xenodermichthys copei* and *Searsia koefoedi*. In all these specimens the anterodorsal portion of the hypaxialis is peculiarly extended anteriorly (see fig. 2), covering a great part of the neurocranial floor and reaching the ventral surface of bones such as the sphenotic. The functional implications of this peculiar configuration are discussed below.

Ventral cephalic musculature

Protractor hyoidei. The muscle protractor hyoidei (formed by the posterior intermandibularis and the interhyoideus: see e.g. Edgeworth, 1935; Kesteven, 1942; Kirchhoff, 1958; Jarvik, 1963; Vrba, 1968; Greenwood, 1971, 1977; Winterbottom, 1974; Lauder, 1980; Lauder and Liem, 1980, 1983; Adriaens and Verraes, 1997; Diogo and Chardon, 2000b; Diogo and Vandewalle, 2003; Diogo, 2004a) is divided into two sections (fig. 4). The ventral section connects the anterior ceratohyal and the ventral hypohyal to the ventromesial surface of the dentary bone. The left and right sides of

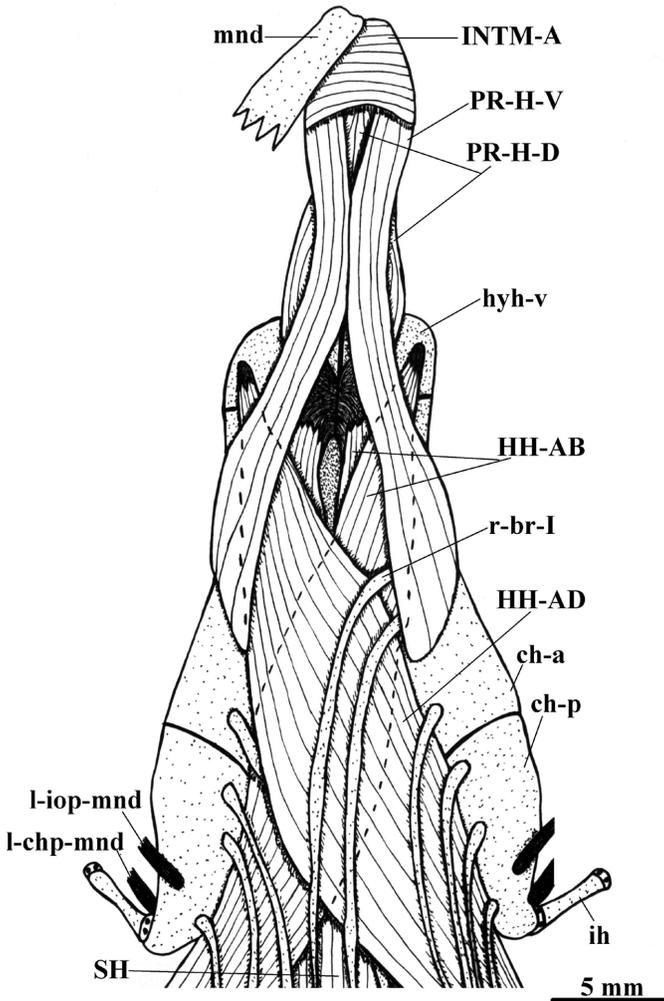


Figure 4. Ventral view of the ventral cephalic musculature of *Alepocephalus rostratus*. On the right side, the mandible was removed; on the left side, the mandible was cut. ch-a, ch-p, anterior and posterior ceratohyals; HH-AB, hyohyoideus abductor; HH-AD, hyohyoidei adductores; hyh-v, ventral hypohyal; ih, interhyal; INTM-A, anterior intermandibularis; l-chp-mnd, ligament between posterior ceratohyal and mandible; l-iop-mnd, ligament between interopercle and mandible; mnd, mandible; PR-H-D, PR-H-V, sections of protractor hyoidei; r-br-I, branchiostegal ray I; SH, sternohyoideus.

this ventral section fuse in the midline. With respect to the dorsal section, it runs from the anterior ceratohyal and the ventral hypohyal to the ventromesial margin of the dentary and situates dorsally to the ventral section.

Intermandibularis. As mentioned above, the posterior intermandibularis forms, together with the interhyoideus, the protractor hyoidei. Concerning the anterior intermandibularis (fig. 4), this is a broad structure running from one dentary bone to the dentary bone of the opposite side, thus joining the two mandibles.

Hyohyoideus abductor. The two sides of the hyohyoideus abductor (fig. 4) are mainly attached posteriorly to the first branchiostegal ray of the respective side. Anteriorly, they attach, by means of a small tendon, to the ventral hypophyal of the opposite side, and, by means of a broad tendon, to the ventral hypophyal of the respective side and to their counterpart mesially (fig. 4). The hyohyoideus inferior is not present as a separate structure. In the specimens analyzed of *Xenodermichthys copei* and *Searsia koefoedi* only a few fibers of each side of the hyohyoideus abductor attach on the ventral hypophyal of the respective side; the remaining fibers attach on the ventral hypophyal of the opposite side.

Hyohyoidei adductores. The hyohyoidei adductores (fig. 4) connect the branchiostegal rays, the opercle, the interopercle and the subopercle of the respective side of the fish.

Sternohyoideus. The sternohyoideus (fig. 4) is a broad muscle running from the anterior margin of the cleithrum to the posterior and posterolateral margins of the urohyal. It does not contact posteriorly with the anteroventromesial fibers of the hypoxialis.

Pectoral girdle musculature

Adductor superficialis and profundus. The adductor of the pectoral fin is formed by the adductor superficialis and adductor profundus (fig. 5). It originates on the cleithrum, scapula, coracoid, mesocoracoid arch and dorsal surfaces of the proximal radials and inserts on the anterior margin of the dorsal part of the pectoral fin rays.

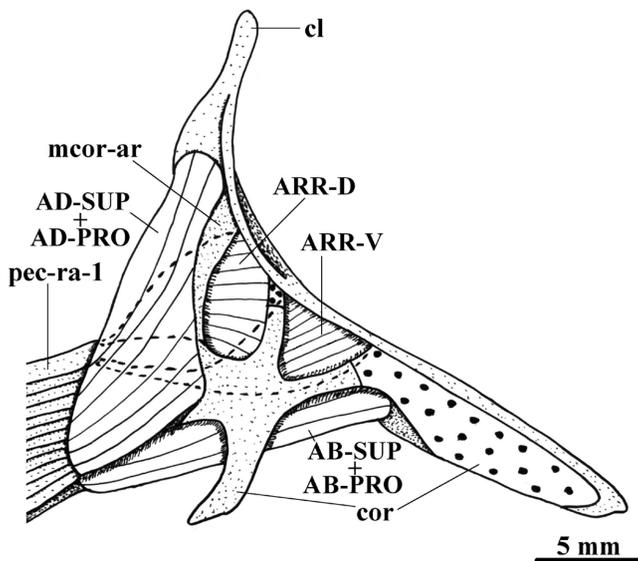


Figure 5. Mesial view of the pectoral girdle musculature of *Alepocephalus rostratus*. AB-SUP+AB-PRO, abductor superficialis and abductor profundus; AD-SUP+AD-PRO, adductor superficialis and adductor profundus; ARR-D, arrector dorsalis; ARR-V, arrector ventralis; cl, cleithrum; cor, coracoid; mcor-ar, mesocoracoid arch; pec-ra-1, pectoral ray 1.

Abductor superficialis and profundus. The abductor of the pectoral fin is formed by the abductor superficialis and abductor profundus (fig. 5). It originates on the cleithrum, coracoid and ventral surfaces of the proximal radials and inserts on the anterior margin of the ventral part of the pectoral fin rays.

Arrector dorsalis. The arrector dorsalis (fig. 5) is a large, undivided muscle that originates on the mesial surfaces of the cleithrum and coracoid, passes laterally to the mesocoracoid arch, and attaches on the anteromesial margin of the first pectoral ray.

Arrector ventralis. The arrector ventralis (fig. 5) is a broad muscle that originates on the coracoid and cleithrum and inserts on the anterior margin of the first pectoral ray. The protractor pectoralis (see. e.g. Winterbottom, 1974; Brosseau, 1978; Greenwood and Lauder, 1981) is not present as a separate structure.

Discussion

In major lines, it can be said that the configuration of the cephalic and pectoral muscles of the alepocephaloid fishes analyzed in the present work do not differ significantly from the configuration found in basal teleosts. If one compares for example the overall configuration of the *Alepocephalus rostratus* muscles listed above to the plesiomorphic teleost condition hypothesized by Diogo (in press), it can be inferred that only five of these muscles seemingly exhibit a derived configuration.

One of these muscles is the arrector dorsalis. The plesiomorphic condition for teleosts seems to be that in which the arrector dorsalis is divided into two well-separated bundles attaching respectively on the first and second pectoral rays (Diogo, in press). In *Alepocephalus rostratus*, as well as in the other alepocephaloids examined, the arrector dorsalis is constituted by a single bundle (fig. 5), which attaches on the first pectoral ray. The functional implication of this is that in the alepocephaloids analyzed the second pectoral ray cannot be adducted by a well-separated bundle exclusively promoting its adduction. Instead, the adduction of this ray is promoted by the contraction of the adductor superficialis and adductor profundus, which also promote the adduction of all but the first pectoral rays. Apart the alepocephaloids examined, the only teleostean fishes analyzed in the present work exhibiting an arrector dorsalis formed by a single bundle are those of the ostariophysan orders Cypriniformes and Siluriformes.

Another derived configuration concerns the protractor pectoralis. The plesiomorphic condition for teleostean fishes is seemingly to have a recognizable protractor pectoralis (Greenwood and Lauder, 1981; Diogo, in press). However, as explained above, in *Alepocephalus rostratus*, as well as in the other alepocephaloids examined, there is no recognizable protractor pectoralis. The functional implication of this is that in these alepocephaloids there is no well-differentiated muscle promoting the protraction of the pectoral girdle. Within the teleosts analyzed in the present study a recognizable protractor pectoralis is also lacking in fishes such as aulopiforms, most ostariophysans, and the clupeiform *Ethmalosa*.

A third derived configuration concerns the levator arcus palatini. As mentioned above, in *Alepocephalus rostratus* there are two well-differentiated levator arcus palatini bundles associated with the abduction of the suspensorium: an anteromesial bundle and a posterolateral bundle (fig. 2). In the other alepocephaloid fishes examined the levator arcus palatini is undivided. According to Diogo (in press), the plesiomorphic condition for teleosts is to have an undivided levator arcus palatini. A divided levator arcus palatini similar to that of *Alepocephalus rostratus* is found, within the teleosts dissected, in argentinoids, in clupeoids, and in the cypriniform *Opsariichthys*.

A fourth derived configuration concerns the peculiar anterior extension of the anterodorsal portion of the hypaxialis (fig. 2) (see above). Apart the alepocephaloids, within the teleostean fishes examined in this work a similar configuration is only found in argentinoids, in aulopiforms and in stomiiforms. As explained by e.g. Allis (1903), Edgeworth (1935), Kesteven (1942), Weisel (1960), Jarvik (1963), Alexander (1964, 1965), Gosline (1973), Vandewalle (1975, 1977), Lauder (1980) and Lauder and Liem (1980, 1983), in many teleosts exhibiting a high mobility between the anterior vertebrae and the neurocranium, the insertion of the epaxialis on the posterodorsal margin of the neurocranium may allow this muscle to elevate the neurocranium and, consequently, to help opening the mouth. The insertion of the anterodorsal portion of the hypaxialis on a significant part of the posteroventral margin of the neurocranium, ventrally to the articulation point between the neurocranium and the anterior vertebrae, may thus eventually allow this muscle to lower the neurocranium and, consequently, to help closing the mouth. This functional hypothesis should, however, as all the other functional hypotheses advanced in this work, be tested in future studies using techniques such as e.g. the electromyographical recording of muscle activity.

The other derived configuration concerns the direct attachment of the adductor mandibulae on the maxilla (fig. 2). This feature is found in *Alepocephalus rostratus* and in the other alepocephaloids dissected. It is also found in other alepocephaloid fishes in which the muscle adductor mandibulae has been studied (see e.g. Gosline, 1969; Greenwood and Rosen, 1971; Markle, 1980; Markle and Merrett, 1980; Markle and Krefft, 1985; Sanford, 2000). Functionally, the direct attachment of the adductor mandibulae on the maxilla allows this muscle to directly adduct the maxilla. This adduction is indirectly associated, in turn, with the raising of the mandible, due to the thick ligamentous tissue connecting the mesial surface of the maxilla to the lateral surface of the mandible. The plesiomorphic condition for teleosts is seemingly that in which there is no direct attachment of the adductor mandibulae on the maxilla (Diogo, in press). Such a direct attachment is however found in various teleostean taxa, being for example found, within the teleostean fishes examined, in taxa such as the stomiiforms, the aulopiforms, the argentinoid *Bathylagus*, the clupeiforms *Engraulis* and *Thryssa*, most ostariophysans, the elopiforms *Albula* and *Notacanthus* and the osteoglossiforms *Pantodon* and *Mormyrus*.

According to Gosline (1969), regarding their osteological structures the alepocephaloid fishes exhibit a mix of mainly plesiomorphic features with a few derived features. From the discussion above, it seems that this statement may also apply to the configuration of their cephalic and pectoral muscles. The few derived myological features mentioned

in the discussion above do however seem to provide some useful phylogenetic information for discussing the position of alepocephaloids within teleosts. For instance, the peculiar anterior extension of the anterodorsal portion of the hypoaxialis (see above) constitutes, very likely, a synapomorphy uniting the alepocephaloid and argentinoid fishes (see fig. 6). As explained in the Introduction, since the publication of Greenwood and Rosen (1971), many researchers have considered the Argentinoidei to be the sister-group of the Alepocephaloidei. However, the molecular analysis of Ishiguro et al. (2003) and Lavoué et al. (2005) have contradicted this view. According to these molecular analyses, the Alepocephaloidei is the sister-group of the Clupeomorpha or of the Ostariophysi. But in an extensive cladistic analysis including more than 70 extant and fossil teleostean terminal taxa and more than 270 morphological characters, Diogo (in press) has strongly supported a sister-group relationship between argentinoids and alepocephaloids (see fig. 6). Six synapomorphies support, in that analysis, the clade formed by argentinoids and alepocephaloids, one of these synapomorphies concerning precisely the peculiar configuration of the hypaxialis referred above. The other five synapomorphies are: 1) posterodorsal portion of mesethmoid appearing markedly compressed transversally when seen in dorsal view (independently acquired in some teleostean groups as e.g. characiforms, gymnotiforms and siluriforms); 2) both autopterotic and dermopterotic bones present as independent, distinct ossifications (homoplasy free within the numerous teleostean taxa examined by Diogo, in press); 3) primordial ligament attaching posteriorly on dorsal surface of coronoid process (independently acquired in some teleostean groups as e.g. some catfishes); 4) peculiar dorsoventral enlargement of posterior portion of autopalatine (only occurring independently in a few teleosts such as osmeroids); 5) presence of peculiar accessory cartilage of the fifth ceratobranchial (homoplasy free within the teleostean taxa examined by Diogo, in press) (see fig. 6).

One specific aspect that is particularly controversial within the conclusions of the molecular analysis of Ishiguro et al. (2003) is the fact that in the cladogram obtained by these authors the argentinoids and alepocephaloids do not appear closely related but, instead, appear separated by a great number of teleosts (note: Lavoué et al.'s 2005 molecular analysis did not include the argentinoids). As can be seen in figure 6, in the tree obtained in Diogo's (in press) cladistic analysis, the Alepocephaloidei + Argentinoidei clade appears as the most basal euteleostean group. In this sense, to postulate that this clade might eventually be more closely related to certain otocephalans than to other euteleostean groups would eventually not seem too unsound. But to postulate that the Alepocephaloidei are placed inside the Otocephala but the Argentinoidei not, and that these two suborders are in fact separated by many teleostean taxa, this does seem rather unsound in face of the large amount of data (provided by various authors and by various kinds of morphological characters) available to support the monophyly of the clade Alepocephaloidei + Argentinoidei (e.g. Greenwood and Rosen, 1971; Rosen, 1974; Begle, 1991, 1992; Johnson and Patterson, 1996; Sanford, 2000; Diogo, in press). One point in which I agree with Ishiguro et al. (2003) is that the results of their molecular work do not contradict directly the results of most morphological cladistic analyses done so far. This because most of these morphological cladistic analyses unfortunately

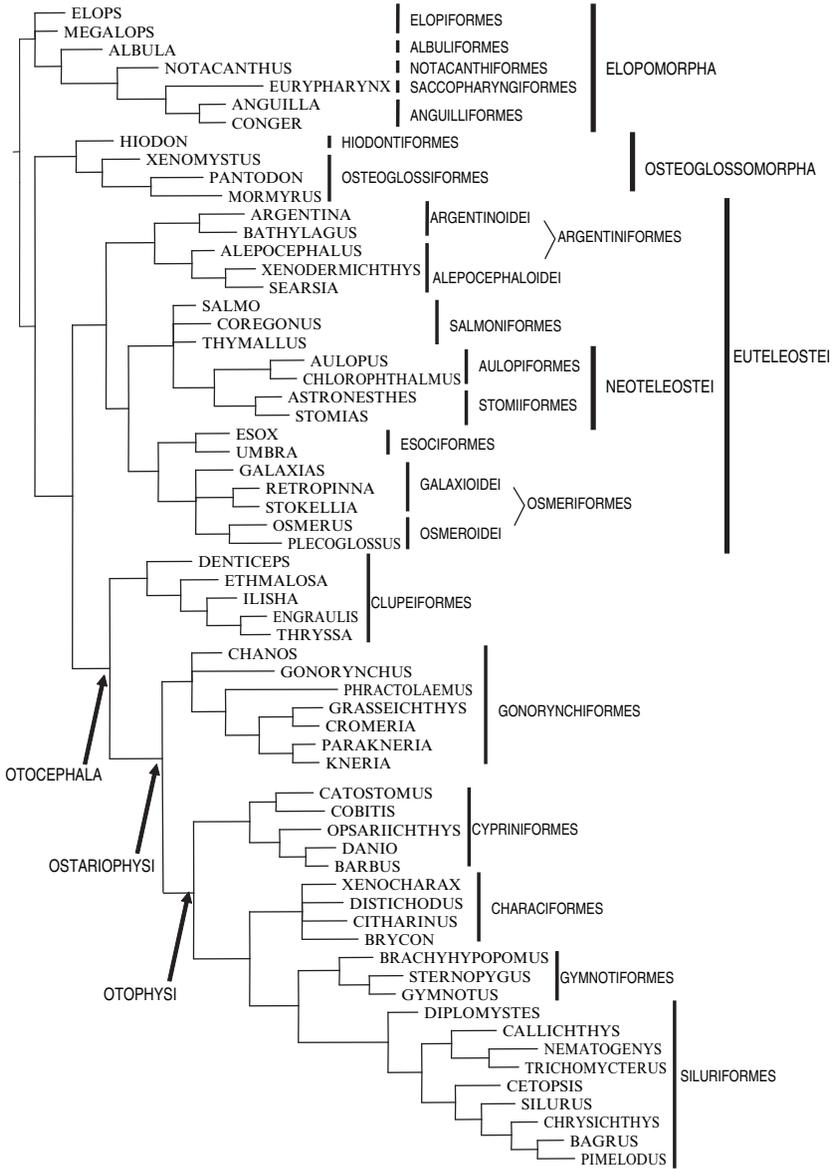


Figure 6. Phylogenetic relationships among extant teleosts, modified from Diogo (in press) (for more details, see text).

did not include, in a same matrix, representatives of the Clupeomorpha, of the Ostariophysii, of the Alepocephaloidei, and of other teleostean taxa to which these three groups should be compared. However, it should be noted that, with Diogo's (in press) recent work, there are already three extensive morphological cladistic analyses that have included these three groups together with many other teleostean taxa in a same matrix and that have supported a sister-group relationship between alepocephaloids and argentinoids (Patterson and Johnson, 1995; Sanford, 2000; Diogo, in press).

Apart the peculiar anterior extension of the anterodorsal portion of the hypaxialis, the myological observations and comparisons of the present study revealed two features that may eventually constitute additional synapomorphies of a clade including the argentinoids and alepocephaloids. One of these features concerns the division of the levator arcus palatini in anteromesial and posterolateral bundles (fig. 2). As explained above, within the teleosts examined in the present work such a configuration is found in *Alepocephalus rostratus*, in argentinoids, in clupeoids, and in the cypriniform *Opsariichthys*. Thus, if one takes in consideration the phylogenetic scenario shown in figure 6, this feature might have been acquired independently in argentinoids and in alepocephaloid fishes such as *Alepocephalus rostratus* or, instead, might have been acquired in the node leading to argentinoids + alepocephaloids and then subsequently lost in the clade including alepocephaloid fishes such as *Xenodermichthys* and *Searsia*. In this latter case, this feature would thus constitute a synapomorphy uniting argentinoids and alepocephaloids. The other feature concerns the direct attachment of the adductor mandibulae on the maxilla. As referred above, within the teleosts dissected, this feature is found in alepocephaloids, in stomiiforms, in aulopiforms, in the argentinoid *Bathylagus*, in the clupeiforms *Engraulis* and *Thryssa*, in most ostariophysans, in the elopiforms *Albula* and *Notacanthus* and in the osteoglossiforms *Pantodon* and *Mormyrus*. Thus, this feature might have been acquired independently in alepocephaloids and in argentinoids such as *Bathylagus*, or, instead, it might have been acquired in the node leading to argentinoids + alepocephaloids and then subsequently lost in argentinoid fishes such as *Argentina* (see fig. 6). In this latter case, this feature would thus constitute a further synapomorphy uniting argentinoids and alepocephaloids.

In summary, it can be said that, as is the case with other teleostean groups (see e.g. Alexander, 1964, 1965; Greenwood, 1968; Chardon and De la Hoz, 1973; De la Hoz, 1974; Gosline, 1975, 1986, 1989; Howes, 1976, 1983, 1985; Lauder and Liem, 1983; De la Hoz and Chardon, 1984; Aguilera, 1986; Bornbush, 1995; Diogo and Chardon, 2000a,b; Diogo et al., 2001; Diogo, 2004a,b; Springer and Johnson, 2004; Wu and Shen, 2004), the analysis of alepocephaloid myology might eventually provide useful data to help clarifying the phylogenetic relationships of these fishes. However, it should be noted that the phylogenetic hypotheses postulated in the paragraph above need to be tested in future works. For instance, it would be important to include, in future phylogenetic studies, myological features such as those referred above and, at the same time, a great number of alepocephaloid and argentinoid fishes in order to adequately represent the diversity of these groups. Future studies using techniques such as e.g. the electromyographical recording of muscle activity should also be done in order to test the functional hypothesis advanced in the present paper. It is precisely hoped that this paper will not only contribute to the knowledge of alepocephaloid anatomy, but also stimulate, and pave the way for, future works concerning the comparative anatomy, functional morphology, phylogeny and evolution of alepocephaloids and of teleosts in general.

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