Chapter 10

The Deep-sea Alepocephaloid Fishes, A Key-Group for the Understanding of Teleostean Phylogeny and Evolution: An Insight on Their Myology and Functional Anatomy and Their Specializations to Life in Deep-water Environments

Rui Diogo

INTRODUCTION

The alepocephaloids (Fig. 10.1) are black, marine teleostean fishes living today in fairly deep to very deep water (e.g., Gegenbaur, 1878; Parr, 1951, 1960; Greenwood et al., 1966; Gosline, 1969, 1973; Greenwood and

Author’s address: Laboratory of Functional and Evolutionary Morphology, Institut de Chimil. Bât, B6, Université de Liege, B-4000 Sart-Tilman (Liege), Belgium. E-mail: R.Diogo@ulg.ac.be
Rosen, 1971; Markle, 1980; Markle and Merrett, 1980; Markle and Krefft, 1985; Matsui and Rosenblatt, 1987; Begle, 1992; Sanford, 2000; Nelson, 2006). These deep-sea fishes are often included in three families, the Alepocephalidae with about 24 genera, the Platytroctidae with about 13 genera, and the Leptochilichthyidae with one genus, although the number of genera and even of families recognized may vary according to different authors (Johnson and Patterson, 1996; Nelson, 2006; Diogo, in press).

According to authors such as Gosline (1969), in what concerns their osteology and their external anatomy, the alepocephaloids do not differ much, in the overall, from basal teleosts. However, they exhibit some derived features that seem to be related to specializations for the particular deep-sea environments in which they inhabit. For example, many alepocephaloids possess bioluminescent organs of various types, the most notable of which being the shoulder organ of fishes such as Searsia (Parr, 1951, 1960; Gosline, 1969). Also, they have lost the swimbladder, and their bones are relatively poorly ossified in comparison to those of many other teleosts (Gegenbaur, 1878; Gosline, 1969; Greenwood and Rosen, 1971). According to authors such as Gosline (1973), the rather generalized configuration of these fishes, associated with the fact that a significant portion of their few derived features seemingly concerns
specializations for deep-water environments, 'make it difficult to determine their phylogenetic relationships with assurance'. This is so because some of these specializations are also found in other deep-sea fishes such as stomiids, bathyalgids, gonostomatids or ophiids (Merrett and Haedrich, 1997; Randall and Farrell, 1997; Robison and Conner, 1999; Herring, 2002).

In fact, the phylogenetic position of the alepocephaloids within the Teleostei has effectively been the subject of much controversy. Greenwood et al. (1966) placed the alepocephaloids within a clade named 'Salmoniformes'. This clade somewhat corresponded to the 'Protacanthopterygii' of recent works, including fishes such as salmoniforms, but also such as osmeriforms, esociforms and argentinoids (sensu Diogo, in press). They recognized, 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. According to him, Gosline (1969) concluded that 'by a process of elimination, it appears that the alepocephaloids are perhaps least unlike the osmeroids among modern fishes' and admitted that 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, Rosen and Greenwood 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 and strongly supported a sister-group relationship between the alepocephaloids 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 Rosen and Greenwood (1991) 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 papers have proposed a rather different hypothesis. Ishiguro et al. (2003), on the basis of a cladistic
mitogenomic analysis, including a few representatives of the major extant non-neoteleostean groups, concluded that the alepocephaloidean fishes are not closely related to the argentinid fishes or to fishes such as esciforms, salmoniforms and osmeriforms, but are, instead, closely related to otocephalans (clupeomorphs + ostariophysans). More precisely, according to Ishiguro et al. (2003) the alepocephaloideans form a monophyletic group with the clupeomorphs, this group being in turn the sister-group of the Ostariophysii. Lavoué et al. (2005), in a cladistic mitogenomic analysis mainly focused on the phylogenetic relationships of the ostariophysian order Gonorynchiformes, also supported a close relationship between the alepocephaloideans and the otocephalans. However, in the cladogram obtained by these authors, the Alepocephaloidei appear as the sister-group of the Ostariophysii, 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, 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 since some otocephalans appear to be more closely related to alepocephaloideans than to other otocephalans; the Euteleostei is not monophyletic, since the euteleostean alepocephaloideans appear to be more closely related to fishes such as clupeomorphs and ostariophysans than to other euteleosts.

One can thus understand why the Alepocephaloidei have a crucial importance in discussions on the phylogeny, systematics and evolution of the Teleostei (Ishiguro et al., 2003; Lavoué, 2005; Nelson, 2006; Diogo, in press). Curiously, despite the importance of alepocephaloideans 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 deal with alepocephaloid anatomy only a few have described, with some detail, the configuration of certain muscles of these fishes (Gosline, 1969; Greenwood and Rosen, 1971; Markle, 1980; Markle and Merrett, 1980; Markle and Krefft, 1985; Sanford, 2000). Moreover, these descriptions are mainly concerned to 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 alepocephaloideans raises difficulties not
only for the study of topics such as the functional morphology and ecomorphology and, consequently, the evolution of these fishes, but also for the comparison between these fishes and other teleosts.

In order to contribute to the knowledge of this key-group, and, thus, it is hoped, to the knowledge of the comparative anatomy, phylogeny and evolution of teleosts in general, part of this work will be precisely dedicated to describe the musculature of these fishes. The reason being, as explained above, this constitutes one of the systems of these fishes that have been less studied. Moreover, an appropriate knowledge of the muscular system of these fishes is essential for a proper understanding of their functional morphology and of their ecomorphology. I will thus briefly 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 teleostean fishes (either examined by the author or described in the literature). This will allow a discussion of certain aspects of the functional morphology of these fishes and of their phylogenetic position within teleosts, as well as of their specializations to the particular deep-sea environments in which they inhabit. It is hoped that this work could thus not only increase the knowledge of the anatomy, functional morphology and ecomorphology of alepocephaloids, but also pave the way for future works concerning the comparative anatomy, functional morphology, ecomorphology, evolution, and phylogeny of teleostean fishes in general.

**FISHES EXAMINED AND METHODS USED**

The brief anatomical descriptions given in this work 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):


Myology of Alepocephalus rostratus, Xenodermichthys copei and Searsia koefoedii

As can be seen from the list above, apart the alepocephaloid Alepocephalus rostratus, another representative of the family Alepocephalidae (Xenodermichthys copei), as well as of the other multi-generic alepocephaloid family, the Platytroctidae (Searsia koefoedii), have been examined for this work. Thus, the myological descriptions given below are based on Alepocephalus rostratus, but in those cases where 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. 10.2, 10.3) is differentiated into two bundles, A2 and Aω. A2 originates on the preopercle, hyomandibula, quadrate and metapterygoid. It exhibits two anterior, thick tendons: one,
more lateral, inserts on the maxilla (Fig. 10.2); the other, more mesial, mixes with the posterior portion of the Aω and attaches on the coronomeckelian bone (Fig. 10.3). The broad Aw attaches anteriorly on the mesial surface of both the anguloarticular and dentary bones and posteriorly on the tendon of the A2 (Fig. 10.3).

**Levator arcus palatini**

This muscle (Fig. 10.2) is constituted by 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 is constituted by a single bundle, and not by two bundles, as is the case in *Alepocephalus rostratus*.

**Adductor arcus palatini**

The adductor arcus palatini (Fig. 10.2) 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 a somewhat small muscle (Fig. 10.2) 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.

**Levator operculi**

The levator operculi (Fig. 10.2) 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. 10.2) 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. 10.2) 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. 10.2), 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 will be discussed below.

Ventral Cephalic Musculature

Protractor hyoidei

The muscle protractor hyoidei (formed by the posterior intermandibularis and the interhyoideus: 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, 2006; Diogo and Vandewalle, 2003; Diogo, 2004a) is divided into two sections (Fig. 10.4). 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 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. 10.4), 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. 10.4) are mainly attached posteriorly to the first branchiostegal ray of the respective side. Anteriorly,
they attach, by means of a small tendon, on the ventral hypohyal of the opposite side, and, by means of a broad tendon, to the ventral hypohyal of the respective side and to their counterpart mesially (Fig. 10.4). 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 hypohyal of the respective side; the remaining fibers attach on the ventral hypohyal of the opposite side.

**Hyohyoidei adductores**

The hyohyoidei adductores (Fig. 10.4) connect the branchiostegal rays, the opercle, the interopercle and the subopercle of the respective side of the fish.

**Sternohyoideus**

The sternohyoideus (Fig. 10.4) 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 hypoaxialis.

**Pectoral Girdle Musculature**

**Adductor superficialis and profundus**

The adductor of the pectoral fin is formed by the adductor superficialis and adductor profundus (Fig. 10.5). 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.

**Abductor superficialis and profundus**

The abductor of the pectoral fin is formed by the abductor superficialis and abductor profundus (Fig. 10.5). 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.
Fig. 10.5 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; mcoc-ar, mesocoracoid arch; pec-ra-1, pectoral ray 1.

**Arrector dorsalis**

The arrector dorsalis (Fig. 10.5) 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. 10.5) is a broad muscle originating on the coracoid and cleithrum and inserting on the anterior margin of the first pectoral ray. The protractor pectoralis (Winterbottom, 1974; Brosseau, 1978; Greenwood and Lauder, 1981) is not present as a separate structure.

**DISCUSSION**

In major lines, it can thus be said that, concerning the configuration of the cephalic and pectoral muscles of the alepocephaloid fishes analyzed in the present work, these do not differ significantly from the configuration
found in basal teleosts. If one compares, for example, the overall configuration found in Alepocephalus rostratus to that found plesiomorphically in teleosts according to the results of a recent cladistic analysis promoted by the author (Diogo, in press), it can be inferred that only five of the muscles of this species exhibit rather derived configurations. A brief discussion of these derived configurations, as well as on their functional and phylogenetic implications, is given below.

One of these muscles is the arrector dorsalis. According to the results of Diogo’s (in press) cladistic analysis, the plesiomorphic condition for teleosts is to have an arrector dorsalis divided into two well-separated bundles attaching respectively on the first and second pectoral rays. In A. rostratus, as well as in the other alepocephaloids examined, the arrector dorsalis is constituted by a single bundle (Fig. 10.5), 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 the other pectoral rays, except the first one. 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 protactor pectoralis. Diogo’s (in press) cladistic analysis supported the hypothesis of Greenwood and Lauder (1981), according to which the plesiomorphic condition for teleostean fishes is to have a recognizable protactor pectoralis. However, as explained above, in A. rostratus, as well as in the other alepocephaloids examined, there is no recognizable protactor pectoralis. The functional implication of this is that in the alepocephaloids examined, there is no well-differentiated muscle promoting the protration of the pectoral girdle. Within the teleosts analyzed in the present work a recognizable protactor pectoralis is also lacking in fishes such as auropiforms, most ostariophysans, and the clupeiform Ethmalosa.

A third derived configuration concerns the levator arcurus palatini. As mentioned above, in A. rostratus, but not in the other alepocephaloids examined, this muscle is subdivided into an anteromesial bundle and a posterolateral bundle (Fig. 10.2). As these bundles exhibit a different orientation and are attached in different regions of the suspensorium, they might eventually promote a somewhat different type of abduction of this
latter structure. According to the results of the cladistic analysis of 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 A. rostratus is found, within the teleosts dissected, in argentinoids, in clupeoids, and in the cypriniform *Opsarichthys*.

A fourth derived configuration concerns the peculiar anterior extension of the anterodorsal portion of the hypaxialis (Fig. 10.2) (see above). Apart from 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 authors such as Allis (1903), Edgeworth (1935), Kesteven (1942), Weisel (1960), Jarvik (1963), Alexander (1964, 1965), Gosline (1973), Vandewalle (1975, 1977), Howes (1980), 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 promote the elevation of the neurocranium and, consequently, the opening of the mouth. The insertion of the anterodorsal portion of hypaxialis on a significant part of the posterovertral margin of neurocranium, ventrally to the articulation point between the neurocranium and anterior vertebrae may, thus, eventually allow this muscle to promote the lowering of the neurocranium and, consequently, the closing of 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 the electromyographical recording of muscle activity.

The other derived configuration concerns the direct attachment of the adductor mandibulae on the maxilla (Fig. 10.2). This feature is found in A. rostratus and in the other alepocephaloids examined. It is also found in other alepocephaloid fishes in which the muscle adductor mandibulae has been studied (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 promote the adduction of the maxilla. This adduction indirectly promotes, in turn, 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. According to the results of Diogo’s (in press) cladistic analysis, the plesiomorphic condition for teleosts is seemingly that in which there is no direct
attachment of the adductor mandibulae on the maxilla. Such a direct attachment is, however, found in many teleosts, being also found, within the teleostean fishes examined, in taxa such as the stomiiforms, 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), in what concerns their osteological and external 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. However, the few derived myological features mentioned in the discussion above do seem to provide some useful phylogenetic information for discussing the position of alepocephaloids within teleosts. For example, according to the results of Diogo’s (in press) recent cladistic analysis, the peculiar anterior extension of the anteriormost portion of the hypaxialis (see above) constitutes, very likely, a synapomorphy uniting the alepocephaloid and argentinoid fishes (see Fig. 10.6). As explained in the Introduction, since the publication of Greenwood and Rosen’s (work), many researchers have considered the Argentinoidae as the sister group of the Alepocephaloidei. However, the molecular works of Ishiguro et al. (2003) and Lavoué et al. (2005) contradict this view. According to these molecular works, the Alepocephaloidei is the sister group of the Clupeomorpha or of the Ostariophysi. But in an extensive cladistic 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. 10.6). In that analysis, six synapomorphies support the clade formed by the argentinoid and alepocephaloid fishes, with 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 the dorsal view (independently acquired in some teleostean groups such as characiforms, Gymnotiformes and siluriforms); (2) both autopterotic and dermopterotic bones present as independent, distinct ossifications (homoplasy free within the teleostean taxa examined by Diogo, in press); (3) primordial ligament attaching posteriorly on dorsal surface of coronoid process (independently acquired in some teleostean groups such as some catfishes); (4) peculiar dorsoventral enlargement of posterior portion of
Fig. 10.6 Phylogenetic relationships among extant teleosts, modified from Diogo (in press).

autopalatine (only occurring independently in a few teleosts such as e.g. osmeroids); and (5) the presence of peculiar accessory cartilage of the fifth
ceratobranchial (homoplasy free within the teleostean taxa examined by Diogo, in press) (see Fig. 10.6).

One specific aspect that makes me particularly reticent about 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: the molecular analysis by Lavoué et al. 2005 did not include the argentinoids). As can be seen in Figure 10.6, in the tree obtained in Diogo’s (in press) cladistic analysis, the Alepocephaloidei + Argentinoid one 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 Argentinoid one are not, and that these two suborders are, in fact, separated by many teleostean groups, 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 + Argentinoid one (Greenwood and Rosen, 1971; Rosen, 1974; Begle, 1991, 1992; Johnson and Patterson, 2000; 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, did not include, in a same matrix, representatives of the Clupeomorpha, of the Ostariophysi, 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 have supported a sister-group relationship between alepocephaloids and argentinoids (Patterson and Johnson, 1996; Sanford, 2000; Diogo, in press).

Apart from the peculiar anterior extension of the anterodorsal portion of the hypaxialis, listed as a synapomorphy uniting argentinoids and alepocephaloids in Diogo’s (in press) work (see above), the myological analysis of the present study revealed two features that may eventually constitute additional synapomorphies of a clade including these two groups. One of these features concerns the division of the levator arcus
palatini in anteromesial and posterolateral bundles (Fig. 10.2). As has been explained above, within the teleosts examined in the present study, such a configuration is found in *Alepocephalus rostratus*, in argentinoids, in clupeoids, and in the cypriniform *Opsariichthys*. Thus, if one takes into consideration the phylogenetic scenario shown in Figure 10.6, this feature might have been acquired independently in argentinoids and in alepocephaloid fishes such as *A. 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 *Searsi*. 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 *Bathyergus*, in the Clupeiformes *Engraulis* and *Thryssa*, in most ostariophysans, in the elopiforms *Albula* and *Notacanthus* and in the osteoglossiforms *Pantodon* and *Mormyris*. Thus, if ones takes again the phylogenetic scenario shown of Figure 10.6, this feature might have been acquired independently in alepocephaloids and in argentinoids such as *Bathyergus*, or, instead, it might have been acquired in the node leading to argentinoids + alepocephaloids and then subsequently lost in argentinoid fishes such as *Argentina*. In this latter case, this feature would, thus, constitute a further synapomorphy uniting argentinoids and alepocephaloids. To summarize, it can be said that, as is the case with other teleostean groups (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 to clarify the phylogenetic relationships of these fishes. However, it should be noted that the phylogenetic hypotheses postulated above clearly need to be tested in future works. For example, these phylogenetic hypotheses should be tested by including, in cladistic analyses, a great number of alepocephaloid and argentinoid fishes in order to adequately represent the diversity of these groups.

Concerning the specializations of the alepocephaloids to the particular deep-sea environments in which they inhabit, one question can
thus be made: are the derived myological features of these fishes discussed above directly related to such specializations? If one takes in consideration the functional implications of these features discussed above, the answer seems, at least at first sight, to be no. As explained above, these derived myological features seemingly concern functions such as the protraction of the pectoral girdle, the adduction of the second pectoral ray, the abduction of the suspensorium and the closing of the jaws, which do not seem directly related to specific specializations to a life in the deep-sea. In fact, four of the five derived myological features listed above are also found in other teleostean fishes that do not live in the deep-sea: an undivided arrector dorsalis is also found in fishes such as Cypriniformes and Siluriformes; the absence of protractor pectoralis is also found in many ostariophysans and the clupeiform Ethmalosa; a divided levator arcus palatini similar to that of Alepocephalus rostratus is also found in fishes such as clupeoids and the cypriniform Opsariichthys; a direct attachment of the adductor mandibulae on the maxilla is also found in many ostariophysans and the osteoglossiforms Pantodon and Moronius.

However, it is interesting to note that a configuration such as that found in alepocephaloids, in which a significant part of the body muscles is peculiarly extended anteriorly in order to attach well anteriorly on the neurocranial floor (Fig. 10.1), is only found, within the teleosts examined in the present work, in fishes such as argentinoids, stomiiforms and aulopiforms. And these three groups do include at least some deep-water fishes. Therefore, this peculiar derived myological feature might eventually be related to an existence in the deep-water. In fact, as explained above, the potential closing of the mouth by the contraction of body muscles attaching on a significant part of the posterior region of the neurocranial floor is only possible when there is a great mobility between the anterior vertebrae and the neurocranium. And in at least some members of the alepocephaloids, of the argentinoids, of the stomiiforms and of the aulopiforms there is, effectively, such a great mobility. And this may be related, at least partially, to an existence in the deep-sea since, as also explained above, deep-sea fishes normally exhibit a relatively poorly ossified skeleton. In many fishes with well-ossified skeletons, such as the ariid catfishes, there is often a strengthening between the anterior vertebrae, the pectoral girdle and the back of the skull, and, therefore, a reduction of the mobility between the anterior vertebrae and the neurocranium (Alexander, 1965; Chardon, 1968; Diogo, 2004a).
Other examples of derived anatomical features found in alepocephaloids that might well be related to specializations to an existence in deep-waters can be given. One example is the absence of swimbladder, as explained by authors such as Gosline (1969, 1973). Of course, as stressed by Gosline (1969), with the absence of the swimbladder the difficulty of attaining neutral buoyancy is increased, but this problem seems to have been precisely solved, at least in part, by the reduction of the quantity and density of bone (Gegenbaur, 1878; Greenwood and Rosen, 1971). According to Greenwood and Rosen (1971), ‘bone reduction in alepocephaloids is particularly evident in the opercular apparatus where the peculiar opercular seems to represent a residual ventral section of the bone’; ‘bone reduction is also evidenced in the caudal skeleton by the loss of the urodermal, reduction of the pleural flanges on the posterior neural and haemal spines, and of the supraneural laminae on the rudimentary neural arches on U1 (ural centrum 1) and PU1 (pleural centrum 1)’. According to Greenwood and Rosen (1971) ‘perhaps even the fact that the parietals are relatively small, and that they fail to meet in the midline’ (see Fig. 10.2) might be ‘related to similar reductional influences associated with a bathypelagic existence’. Also, as referred in the Introduction, some alepocephaloids have special light organs (Parr, 1951, 1960). Another example of anatomical features potentially related to a deep-water existence concerns the configuration of the fins. As explained by Gosline (1969), authors such as Denton and Marshall (1958) have stated that the fins of alepocephaloids are configured in a way to preclude strong, continuous swimming, but that these fishes may effectively dart short distances. Thus, ‘for a model of life of this sort abrupt acceleration from a standing start is advantageous; this would seem to be facilitated by a concentration of vertical fins at the rear of the body’ (Gosline, 1969). As noted Gosline (1969), ‘such a fin configuration and, presumably, mode of life has been adopted by fishes in various environments, e.g., Esox, Sphyraena, but seem to be particularly common among bathypelagic forms where, as in alepocephaloids, the dorsal fin is often far back on the body’ (see Fig. 10.1).

Alepocephaloid fishes, therefore, seem to effectively display, in what concerns their anatomical structures, a mix between rather plesiomorphic features and some few derived features, with at least part of these latter features being apparently related to potential specializations to the particular conditions of the deep-sea. It is however important to stress here that, as the other hypotheses advanced in this chapter, the functional
and ecomorphological hypotheses presented above should be seen as scientific hypotheses that clearly need to be tested in future studies. For example, future works using techniques like the electromyographical recording of muscle activity, as well as promoting direct observations and analyses of live specimens, may be done in order to test such functional and ecomorphological hypothesis. It is precisely hoped, as referred in the Introduction, that this paper will stimulate, and pave the way for, such future works on the comparative anatomy, functional morphology, ecomorphology, phylogeny and evolution of alepocephaloid fishes and of teleosts in general.

Acknowledgments


References


Allis, E.P. 1903. The skull and cranial and first spinal muscles and nerves of *Scomber scadus*. *Journal of Morphology* 18: 45-328.
280 Fish Life in Special Environments


Fish Life in Special Environments


