

Morphology and Function of Pectoral Fin Muscles in Lizardfishes (Actinopterygii: Aulopiformes: Synodontidae), with Comments on an Additional Muscle of the Fin

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The morphology of the pectoral fin muscles of lizardfishes (Synodontidae) is described. Members of this family commonly have six pectoral fin muscles: the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, and arrector dorsalis. An additional muscle, the arrector medialis (named in this study), was discovered on the mesial side of the pectoral fin in all nine examined species of *Synodus* and *Trachinocephalus*, but is absent in all four examined species of *Harpadon* and *Saurida*. It inserts on an anterior process of the base of the mesial half of the uppermost ray and appears to have a function similar to that of the arrector ventralis in supporting the protraction of the uppermost ray and the abduction of the pectoral fin. This muscle supports the division of the synodontids into two groups (present in *Synodus* and *Trachinocephalus* vs absent in *Harpadon* and *Saurida*). The function of the arrector medialis is morphologically discussed.

Key Words: lizardfishes, Synodontidae, pectoral fin, muscles, arrector medialis.

Introduction

The family Synodontidae, a member of the order Aulopiformes, comprises four genera and about 57 species (Nelson 2006). Species are commonly found on coral, rock, and sand bottoms in shallow coastal waters of temperate and tropical regions in the Atlantic, Indian, and Pacific Oceans (Russell 1999; Nelson 2006). The purposes of this study are to describe the pectoral fin muscles of the Synodontidae, to discuss their functions, and to review available comparative data. Although anatomical studies of the Aulopiformes, especially the family Synodontidae, have been conducted by several authors (Rosen 1973; Sulak 1977; Baldwin and Johnson 1996; Sato and Nakabo 2002), they have mostly focused on osteology and few authors have studied the myology of the order. Rosen (1973) examined the interrelationships among higher euteleostean fishes focusing on characters of the pharynx, jaw, and caudal regions. With regard to aulopiform myology, he described the pharyngobranchial and cheek muscles and made some use of these characters in inferring relationships among euteleostean orders. Sato and Nakabo (2002) examined the pectoral fin muscles of many aulopiforms, including the four synodontid genera, and used two transformation series including characters associated with the adductor profundus, an element of the pectoral fin muscles, to infer phylogenetic relationships within this order. Until recently, the myology of the family

Synodontidae has not otherwise been studied in detail. In this study, the pectoral fin muscles of representatives of this family were re-examined, and a unique muscular bundle was found that has never before been reported in fishes.

Materials and Methods

Preserved specimens were stained with alcian blue and alizarin red-S before dissection. Dissections and observations were undertaken with a Leica stereomicroscope fitted with a camera lucida attachment to facilitate illustrations. Osteological and myological terminology follows Sato and Nakabo (2002) and Winterbottom (1974) respectively. Specimen sizes are reported as standard length (SL). Institutional abbreviations follow Eschmeyer (1998), except for the Hokkaido University Museum, Hakodate (HUMZ).

Material examined. Synodontidae: *Harpadon nehereus* (Hamilton, 1822), HUMZ 201983, 162 mm SL; *Harpadon squamosus* (Alcock, 1891), MCZ 149098, 103 mm SL; *Saurida nebulosa* Valenciennes, 1850, HUMZ 124908, 107 mm SL; *Saurida tumbil* (Bloch, 1795), USNM 404394, 181 mm SL; *Synodus evermanni* Jordan and Bollman, 1890, AMNH 234786, 106 mm SL; *Synodus foetens* (Linnaeus, 1766), AMNH 80195, 131 mm SL; *Synodus hoshinonis* Tanaka, 1917, HUMZ 114357, 198 mm SL; *Synodus lucioiceps* (Ayres, 1855), HUMZ 113029, 162 mm SL; *Synodus sageneus* Waite, 1905, AMS I.22831-040, 141 mm SL; *Synodus saurus*

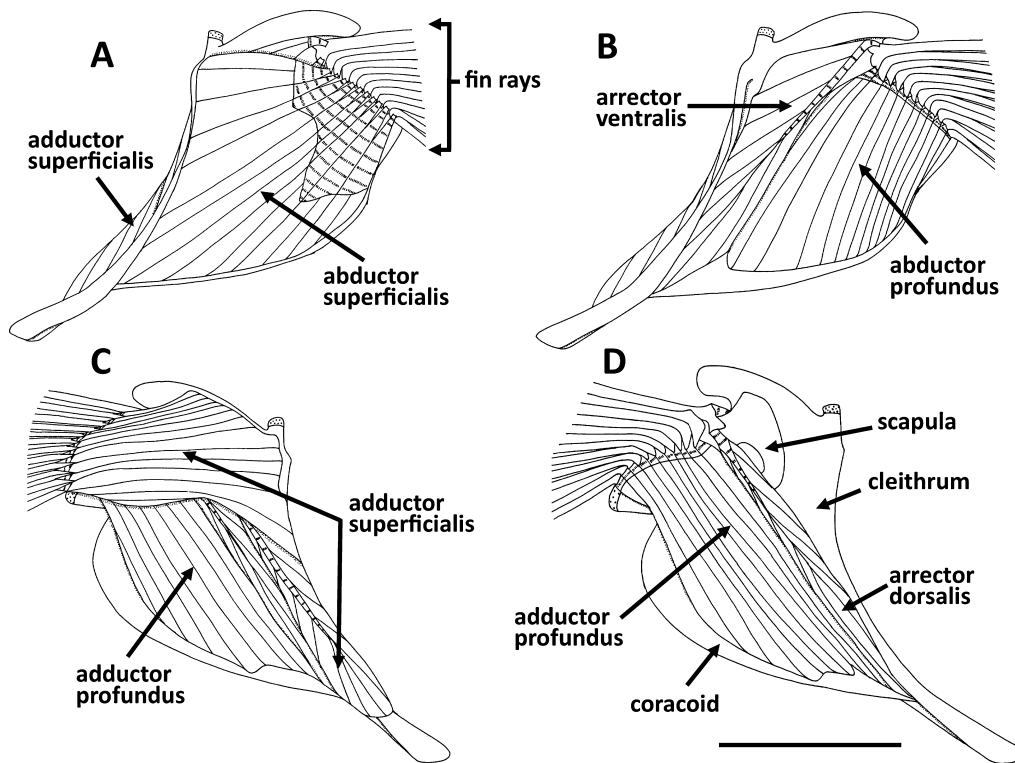


Fig. 1. Lateral (A and B) and mesial (C and D) views of pectoral fin muscles in *Saurida nebulosa*: (A) and (C) superficial view; (B) after removal of the abductor superficialis; (D) after removal of the adductor superficialis. Scale bar indicates 5 mm.

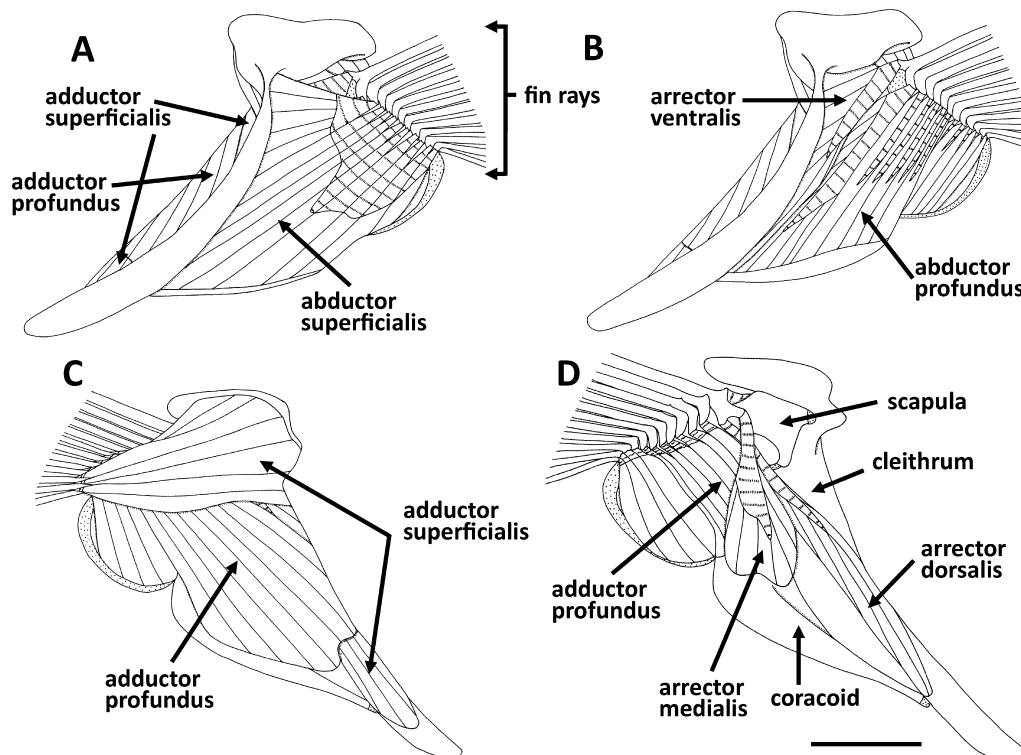


Fig. 2. Lateral (A and B) and mesial (C and D) views of pectoral fin muscles in *Synodus lucioceps*: (A) and (C) superficial view; (B) after removal of the abductor superficialis; (D) after removal of the adductor superficialis. Scale bar indicates 5 mm.

(Linnaeus, 1758), AMNH 210741, 137 mm SL; *Synodus synodus* (Linnaeus, 1758), AMNH 29882, 76 mm SL; *Synodus variegatus* (Lacépède, 1803), HUMZ 62811, 186 mm

SL; *Trachinocephalus myops* (Forster, 1801), HUMZ 103511, 172 mm SL.

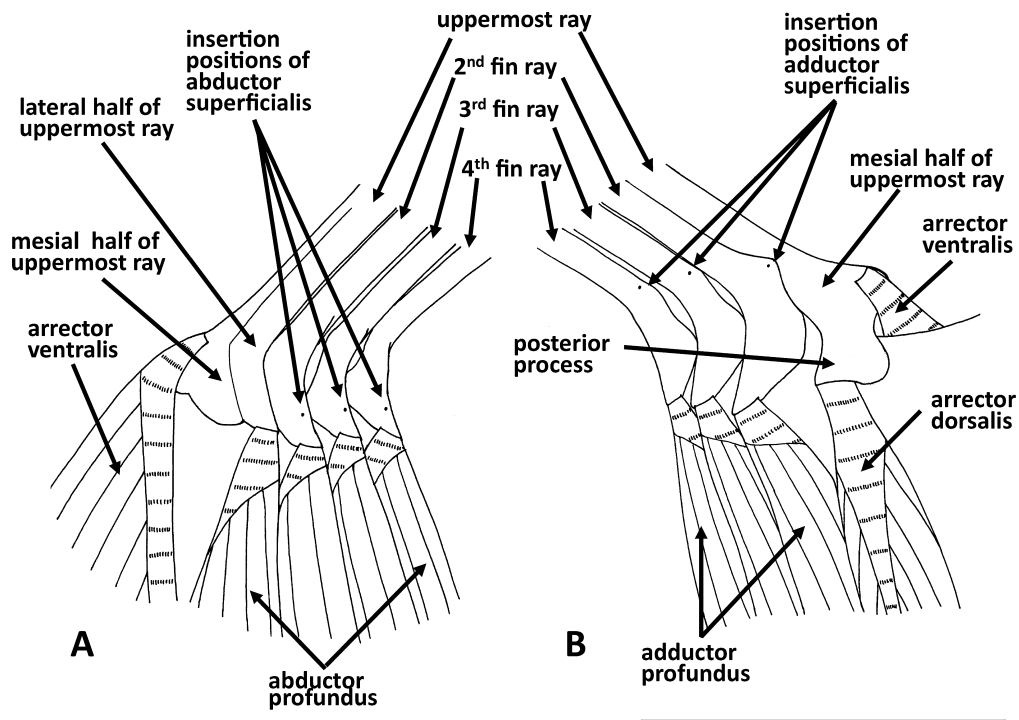


Fig. 3. Lateral (A) and mesial (B) views of pectoral fin muscles inserted on the uppermost and other fin rays in *Saurida nebulosa*. Scale bar indicates 2 mm.

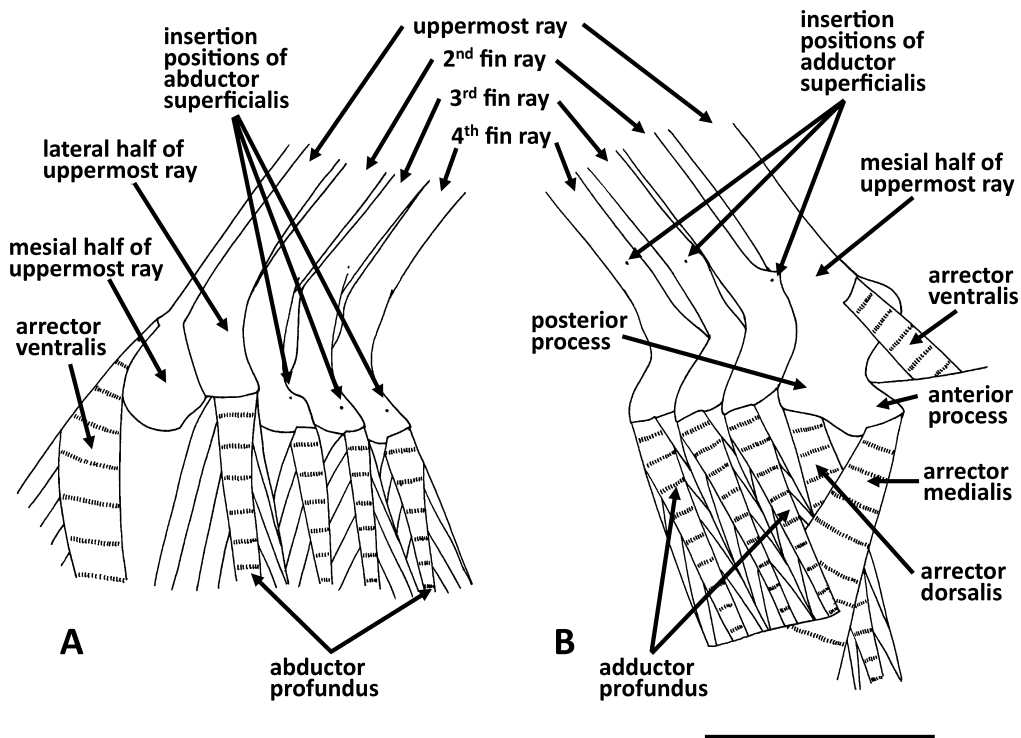


Fig. 4. Lateral (A) and mesial (B) views of pectoral fin muscles inserted on the uppermost and other fin rays in *Synodus sageneus*. Scale bar indicates 2 mm.

Results

Pectoral fin muscles in synodontids commonly consist of six elements: the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor

profundus, and arrector dorsalis. An additional muscle, the arrector medialis (newly named here), is present in the examined species of *Synodus* and *Trachinocephalus*, but absent in those of *Harpadon* and *Saurida*. These muscular elements are described as follows.

The abductor superficialis is a superficial muscle on the

lateral surface of the pectoral girdle. It originates on the posterior wing of the cleithrum and inserts via tendons on the upper portion of the base of the lateral half of each fin ray except the uppermost and lowermost rays (Figs 1A, 2A, 3A, 4A).

The abductor profundus is located medial to the abductor superficialis and occupies the posterior portion of the lateral side of the pectoral girdle. This muscle originates on the ventral half of the posterior wing of the cleithrum and the ventral surface of the coracoid. It inserts via tendons on the lower, distal portion of the base of the lateral half of each fin ray. The tendons of this muscle inserting on the pectoral fin rays are well developed in the examined species of *Synodus* and *Trachinocephalus* (Figs 1B, 2B, 3A, 4A).

The arrector ventralis is situated anterior to the abductor profundus. It originates on the posterior surface of the cleithrum and inserts via a tendon on the dorsal portion of the base of the mesial half of the uppermost ray. The tendon is particularly well developed in the examined species of *Synodus* and *Trachinocephalus* (Figs 1B, 2B, 3A, B, 4A, B).

The adductor superficialis is the dorsomedial muscle on the mesial side of the pectoral fin. It originates on the anterior part of the cleithrum and inserts via tendons on the surface dorsal to the base of the mesial half of each fin ray except the uppermost ray (Figs 1C, 2C, 3B, 4B).

The adductor profundus lies medial to the adductor superficialis. This muscle is separated into lateral and medial layers, which originate respectively on the anteroventral portion of the cleithrum and the mesial surface of the coracoid. The lateral and medial layers share common tendons for insertion on the lower, distal portion of the base of the mesial half of each fin ray except the uppermost ray (Figs 1C, D, 2C, D, 3B, 4B).

The arrector dorsalis is the muscle on the mesial surface of the pectoral girdle and is located anterior to the adductor profundus. It originates on the posteroventral corner of the cleithrum adjacent to the ventral tip of the coracoid. This muscle inserts on the posteroventral portion of the base of the mesial half of the uppermost ray in the examined species of *Harpadon* and *Saurida*, but on the posterior process of the base of the mesial half of the uppermost ray in the examined species of *Synodus* and *Trachinocephalus* (Figs 1D, 2D, 3B, 4B).

The examined species of *Synodus* and *Trachinocephalus* have an arrector medialis, which is located on the mesial surface of the pectoral girdle. This muscle is absent in the examined species of *Harpadon* and *Saurida*. It lies medial to the adductor superficialis, and between the lateral and medial layers of the adductor profundus. The upper part of this muscle crosses over the mesial portion of the arrector dorsalis. It originates on the dorsal part of the coracoid and on a membrane located between the cleithrum and coracoid. It inserts on the anterior process of the base of the mesial half of the uppermost ray (Figs 2D, 4B).

Discussion

A detailed examination of the pectoral fin muscles in synodontid fishes revealed their common possession of six major muscles typical of teleosts: the abductor superficialis, abductor profundus, arrector ventralis, adductor superficialis, adductor profundus, and arrector dorsalis (Winterbottom 1974). These pectoral fin muscles actuate the movement of the pectoral fin, including its downstroke and upstroke (Thorsen and Westneat 2005). The synodontids examined in this study are divisible into two groups based on the presence or absence of the arrector medialis and the prominent anterior process of the base of the mesial half of the uppermost ray on which this muscle is inserted. The muscle and process are absent in all examined species of *Harpadon* and *Saurida*, while they are present in all examined species of *Synodus* and *Trachinocephalus*.

Functional morphology. Species of *Harpadon* and *Saurida* have two muscles (the arrector dorsalis and arrector ventralis) that insert on the uppermost ray and work antagonistically to each other to control the movement of the leading edge of the pectoral fin formed by the uppermost ray (Druncker and Jensen 1997; Thorsen and Westneat 2005) (Fig. 3A, B). The arrector ventralis is reported to contract initially to rotate the uppermost ray forward and initiate the peeling of the leading edge of the fin away from the body. Then, the abductor muscles (the abductor profundus and abductor superficialis), which connect to each of the fin rays including the uppermost ray on the lateral side, become active and act in synchrony with the arrector ventralis to provide power for the downstroke (Westneat and Walker 1997; Westneat *et al.* 2004; Thorsen and Hale 2005). Meanwhile, the arrector dorsalis is inferred to relax and allow the distal base of the uppermost ray to rotate forward into the abduction of pectoral fin and initiate the downstroke (Fig. 5A). Immediately following the maximum abduction of the fin, the arrector dorsalis is hypothesized to contract, initiating the retraction of the uppermost ray to its original position. Then, the adductor muscles (the adductor superficialis and adductor profundus), which connect to the mesial side of each of the fin rays except the uppermost ray, become active and act in synchrony with the arrector dorsalis to provide the power for the upstroke (Westneat and Walker 1997; Westneat *et al.* 2004; Thorsen and Hale 2005) (Fig. 5B).

In contrast, species of *Synodus* and *Trachinocephalus* have three muscles (the arrector dorsalis, arrector ventralis, and arrector medialis) that insert on the uppermost ray and work antagonistically with each other to control the movement of the leading edge of the pectoral fin formed by the uppermost ray (Druncker and Jensen 1997; Thorsen and Westneat 2005) (Fig. 4A, B). In these genera, the tendons of these muscles are extremely well developed. The arrector ventralis and arrector medialis are likely to contract initially to rotate the uppermost ray forward and initiate the peeling of the leading edge away from the body. Then, the abductor muscles (abductor profundus and abductor superficialis), which connect to each of the fin rays on the lateral

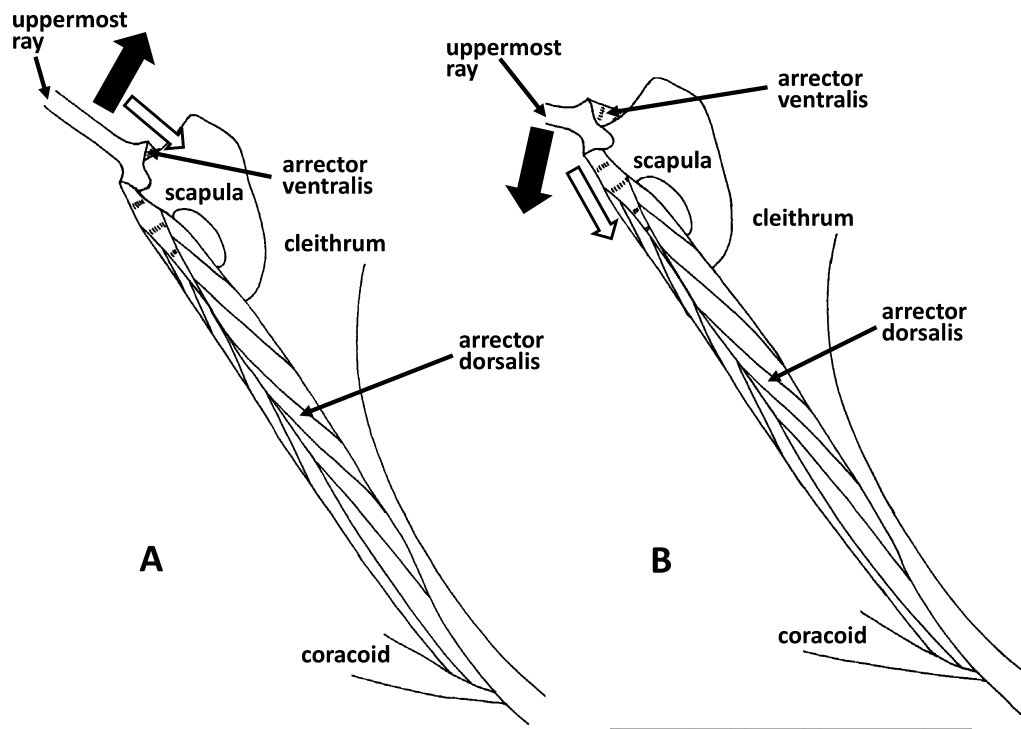


Fig. 5. Mesial views of pectoral fin muscles associated with the uppermost ray in *Saurida nebulosa*, showing abduction (A) and adduction (B) of the uppermost fin ray. Broad open and solid arrows show movement directions of the muscles and uppermost fin ray, respectively. Scale bar indicates 5 mm.

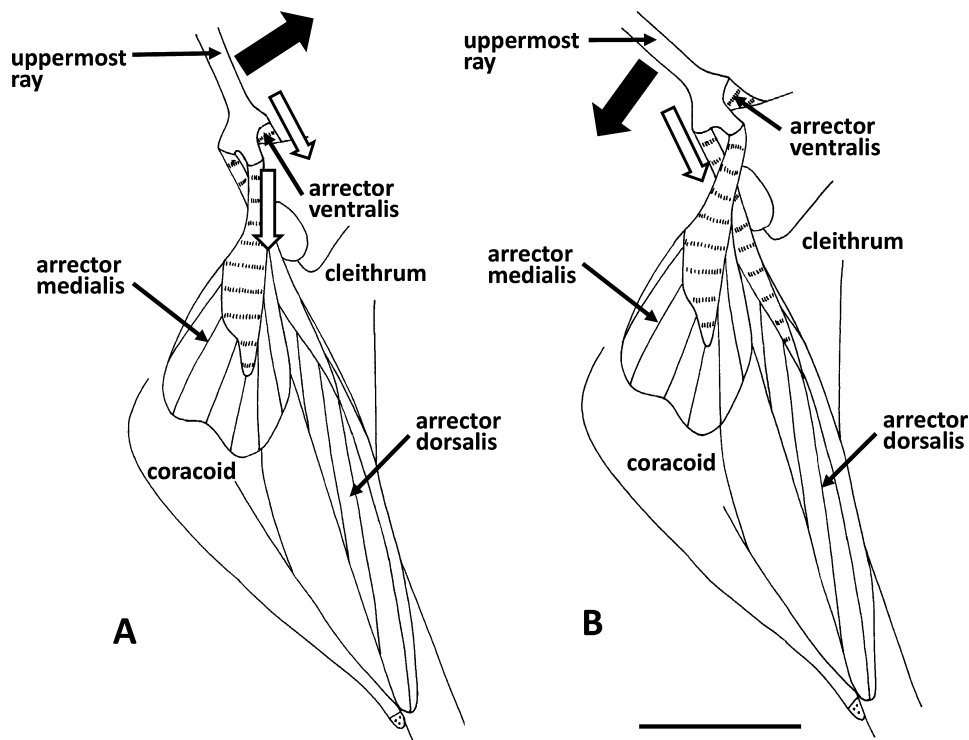


Fig. 6. Mesial views of pectoral fin muscles associated with the uppermost ray in *Synodus lucioceps*, showing abduction (A) and adduction (B) of the uppermost fin ray. Broad open and solid arrows show movement directions of the muscles and uppermost fin ray, respectively. Scale bar indicates 5 mm.

side, including the uppermost ray, become active and act in synchrony with the arrector ventralis and arrector medialis to provide power for the downstroke (Westneat and Walker

1997; Westneat *et al.* 2004; Thorsen and Hale 2005). Meanwhile, the arrector dorsalis is inferred to relax and allow the distal base of the uppermost ray to rotate forward into the

abduction of the pectoral fin and initiate the downstroke (Fig. 6A). Immediately following the maximum abduction of the fin, the arrector dorsalis is supposed to contract and initiate the retraction of the uppermost ray to its original position. Then, the adductor muscles (the adductor superficialis and adductor profundus), which are connected to the mesial side of each of the fin rays except the uppermost ray, become active and act in synchrony with the arrector dorsalis to provide the power for the upstroke (Westneat and Walker 1997; Westneat *et al.* 2004; Thorsen and Hale 2005) (Fig. 6B). The arrector medialis is inferred to function similarly to the arrector ventralis in supporting the forward rotation of the uppermost ray, which leads to the abduction of the pectoral fin. In addition, the presence of an anterior process at the base of the mesial half of the uppermost ray in *Synodus* and *Trachinocephalus* may be correlated with the presence of the arrector medialis. This process provides a larger area for a firm attachment of this muscle and thus permits a strong and rapid movement of the pectoral fin during the downstroke.

Some species of *Synodus* and *Trachinocephalus* (e.g., *Synodus foetens*, *Synodus lacertinus* Gilbert, 1890, *Synodus lucioceps*, *Synodus saurus*, *Synodus variegatus*, *Trachinocephalus myops*) are reported to burrow halfway into sand, or wholly with only the eyes exposed, as a means of camouflage, while they are waiting to capture a meal (Coleman 1980; Goodson 1988; Humann and DeLoach 1993; Allen *et al.* 2003; Soares *et al.* 2003; Cruz-Escalona *et al.* 2004; Randall 2005). It is also known that *Trachinocephalus myops* mainly uses its pectoral fins for burrowing (Yamada 1997). The unique structure of the pectoral fin muscles in *Synodus* and *Trachinocephalus* might be related to this burying behavior, although some species of *Saurida*, such as *Saurida flamma* Waples, 1982, are also known to habitually bury themselves into sandy bottoms (Scott and Schrichte 1993).

Phylogenetic considerations and homology. The presence and mode of function of the arrector medialis might be a derived character of *Synodus* and *Trachinocephalus*, since neither the muscle nor the specialized burrowing behavior it facilitates are generally found in other fishes. Winterbottom (1974) did not find a muscle which is identical with the arrector medialis, also suggesting the apomorphic status of the presence of this muscle. Accordingly, although the sister relationship of the two genera inferred by Baldwin and Johnson (1996) and Sato and Nakabo (2002) might be supported by the presence of the muscle, study of the phylogenetic relationships of the Synodontidae and analysis of the character evolution of this muscle based on the inferred relationships are needed to determine a strict polarity of presence and absence of this muscle in the Synodontidae. Some evidences may have been provided by Diogo and Abdala (2007) and Diogo (2008), who reported subdivided arrector dorsales muscles (arrector dorsalis 1 and 2) in some teleosts, such as *Elops saurus* Linnaeus, 1766 and *Chanos chanos* (Forsskål, 1775). However, discussion of any possible homology between the arrector medialis defined here and either of the arrector dorsales in these fishes would be premature. The extent of occurrence of the arrector medialis

among aulopiforms must first be confirmed, and detailed anatomical comparisons between aulopiforms and other fishes must be made.

To refer unambiguously to the new muscle found in the present synodontids, we have proposed the new name “arrector medialis”. This is a purely functional name, in as much as this muscle functions mainly to support the protraction of the uppermost ray and is located on the mesial side of the pectoral girdle. However, the ontogenetic and phylogenetic origins of the new muscle are still unclear. Further study is required to determine whether or not it originated as part of one of the other mesial pectoral fin muscles, such as the adductor profundus or arrector dorsalis.

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