Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 135-157 — Brussels 1993

MORPHOLOGY OF THE PECTORAL GIRDLE IN *POMATOSCHISTUS LOZANOI* DE BUEN, 1923 (GOBIIDAE), IN RELATION TO PECTORAL FIN ADDUCTION

by

DOMINIQUE ADRIAENS, DOMINIEK DECLEYRE and WALTER VERRAES
University of Ghent, Institute of Zoology
Ledeganckstraat, 35, B-9000, Gent (Belgium)

SUMMARY

Like most gobies, *Pomatoschistus lozanoi* is a benthic fish species. During locomotion the pectoral fin adduction is of great importance in generating a forward propulsion. Several specimens of *Pomatoschistus lozanoi* were dissected, cleared with staining and sectioned with staining, in order to examine the morphology of the pectoral girdle-apparatus. In this paper a detailed description is given of the skeletal elements, the musculature and the ligaments of the pectoral girdle-apparatus. The pectoral fins of gobies seem better adapted to powerful adduction than a generalised teleost. The proximal radials form a large rigid shoulder plate with a long distal margin on which a high pectoral fin articulates. The fin muscles are strongly developed and assure, together with the large pectoral fin, powerful — drag based — pectoral propulsion. The morphological adaptations for powerful adduction, however, are at cost of the maneuvering abilities of the pectoral fins.

Keywords : Pomatoschistus lozanoi, morphology, pectoral fin, adaptation, locomotion.

INTRODUCTION

Pomatoschistus lozanoi (Fig. 1) is one of the most abundant fishes in the European coastal waters, occuring from the Wadden Sea up to South-Portugal and around the British Isles (HAMERLYNCK *et al.,* 1990).

Related to its benthic life style, locomotion occurs by short hops and darts, remaining close to the bottom and frequently resting on it between darts. Propulsion is generated by combined adduction of the pectoral fins and tail beating. Aquarium observations show that pectoral fin adduction is especially important in generating the lift needed for leaving the bottom. The pectoral fins also serve as supporting structures when lying on the bottom, preventing the body from rolling over. The present study provides a description of the pectoral girdle-apparatus and discusses some functional aspects of its adduction.

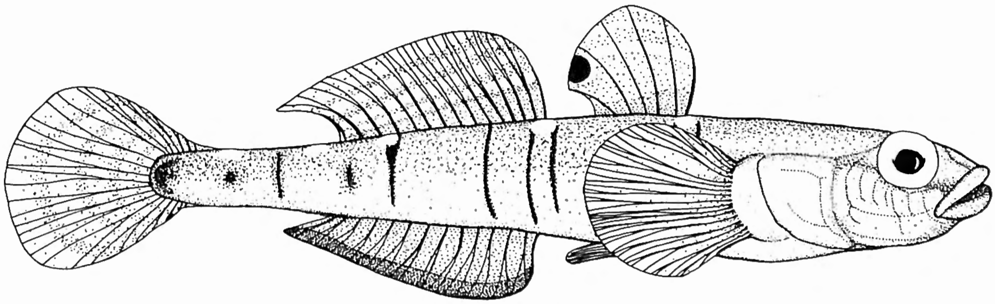


Fig. 1. — Habitus of *Pomatoschistus lozanoi.*

MATERIAL AND METHODS

Four specimens of *Pomatoschistus lozanoi* were identified according to HAMERLYNCK (1990), sexed and measured.

Specimen 1 (male, SL = 51.30 mm, TL = 60.55 mm), specimen 2 (female, SL = 50.70 mm, TL = 59.65 mm), specimen 3 (female, SL = 45.00 mm, TL = 54.00 mm), specimen 4 (male, SL = 44.40 mm, TL = 52.25 mm), specimen 5 (female, SL = 48.65, TL = 56.10) and specimen 6 (male, SL = 50.15 mm, TL = 59.95 mm) were dissected, after being stained with alizarin red S and alcian blue.

Specimen 7 (male, SL = 47.30 mm, TL = 56.90 mm) was cleared and the skeletal elements were stained with alizarin red S and alcian blue, as described by HANKEN and WASSERSUG (1981), but the trypsin was replaced with a 2 % KOH solution.

Specimen 8 (female, SL = 48.10 mm, TL = 56.70 mm) was embedded in Technovit 7100. Serial cross sections (5 µm) were made and stained with toluidin.

Specimens 1 to 7 were studied using a stereoscopic microscope (WILD M5) and specimen 8 was examined using a light microscope (WILD M12).

RESULTS

Osteology

In the skeletal part of the pectoral girdle-apparatus three functional units can be distinguished : (1) the shoulder girdle, which is dorsally attached to the skull and functions as the suspension unit for the shoulder- and finplate ; (2) the shoulder plate, firmly attached to the former element and (3) the actual fin plate, consisting of fin rays that articulate with the shoulder plate.

These skeletal elements consist of cartilage, with corresponding perichondral ossifications, and dermal bones. These elements may be fused or interconnected with short collagen fibres.

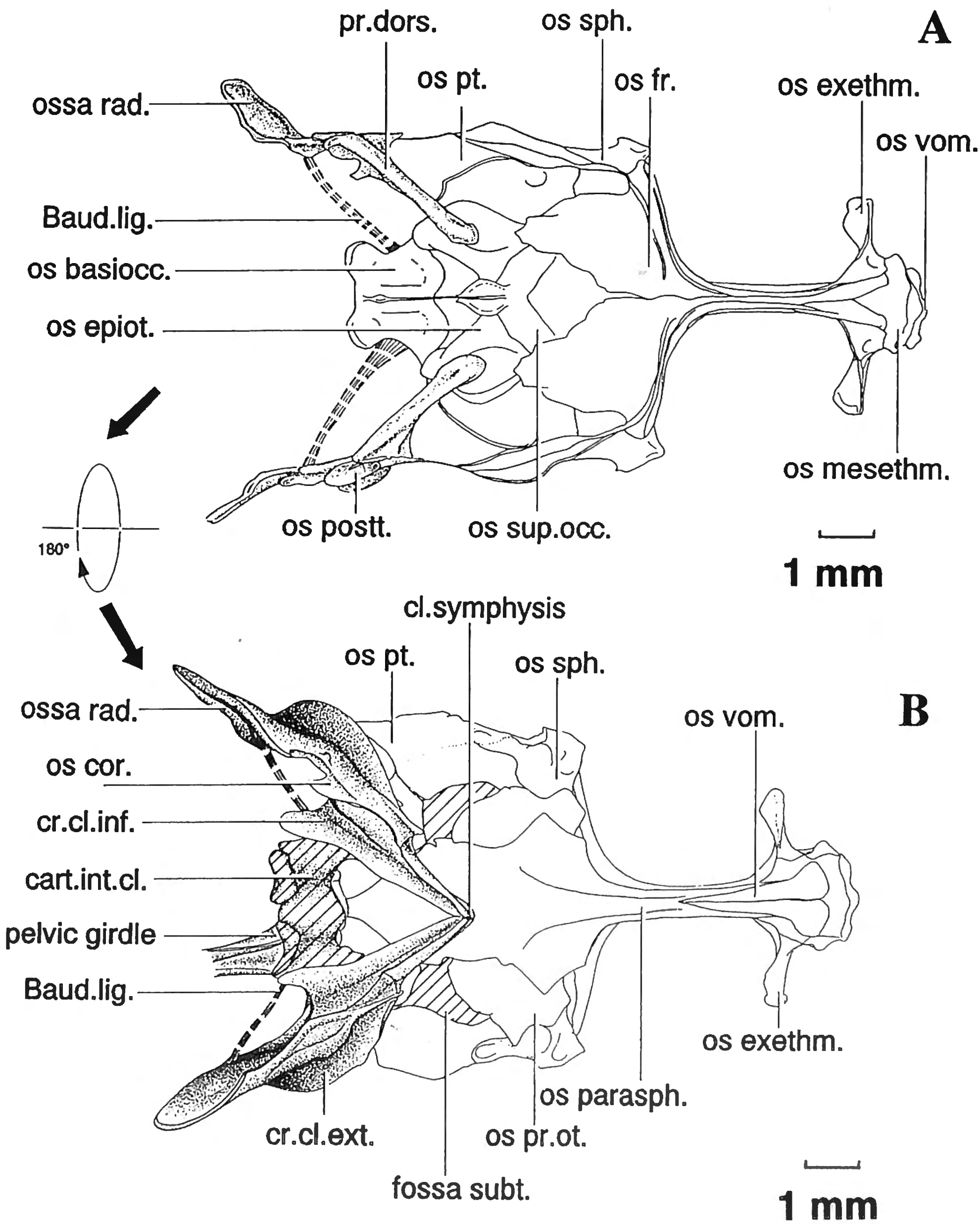


Fig. 2. — Dorsal (A) and ventral (B) view of the neurocranium and pectoral girdle-apparatus in *Pomatoschistus lozanoi* (shaded areas : cartilage). (Abbreviations : see list on p. 153).

The shoulder girdle

os posttemporale (Fig. 2A-B, 3C, 4A-C, 5A-B). The suspension of the pectoral girdle to the skull occurs through the posttemporal bone (Fig. 2A-B) (supraclaviculare I in EGGERT, 1929). This is a dermal bone bearing the posterior oculo-scapular canal of the canalis lateralis system (AKIHITO, 1986). Some authors describe this bone as a part of the otic region (MESTERMANN and ZANDER, 1984). Although the posttemporal bone seems to be part of the skull in some primitive fishes (*e.g. Amia calva,* Holostei), according to JARVIK (1980) it is considered as being part of the exoskeletal shoulder girdle.

In *Pomatoschistus,* the posttemporal bone is situated caudolaterally to the skull. It consists of a basal plate with two rostrally directed processes (proc. dorsalis and proc. ventralis). On its lateral face the basal plate bears the oculo-scapular canal. The dorsal and ventral process form a fork with a dorsal and a ventral attachment to the skull (Fig. 2A-B). The rostral tip of the dorsal process is flattened and is firmly connected to the epiotic bone via a syndesmosis (terminology of ANKER, 1989). The processus ventralis is situated at the ventral side of the neurocranium. This process extends rostrally into the ligamentum posttemporalo-intercalare, which is attached to the neurocranium at the intercalar bone (Fig. 5B).

The posttemporal-epiotic syndesmosis allows restricted rotation around a dorsoventral axis. The ligamentum posttemporalo-intercalare allows movements of the ventral process in all directions relative to the neurocranium. The posttemporal and hence the shoulder girdle can thus rotate to a limited extent around a dorsoventral axis.

Among the Gobiidae differences in relative length of the ventral process and the ligamentum posttemporalo-intercalare occur (SPRINGER and FREIHOFER, 1976; SPRINGER, 1983). A possible explanation for these variations is that the ventral process of the posttemporal bone is an ossification of the ligamentum posttemporalo-intercalare.

The supracleithral-posttemporal syndesmosis is situated on the medial side of the basal plate (Fig. 3C). Two attachment zones can be distinguished. The larger one is situated at the lateral side of the supracleithral bone and allows some rotation in the plane of the shoulder girdle. The smaller one forms a rostral border preventing the supracleithrum to slide forward.

os supracleithrum (Fig. 3A-B, 4B-C, 5B). EGGERT (1929) named this dermal bone the supraclavicularia II. The supracleithrum is a dermal bone connecting the posttemporal to the cleithral bone (the major element of the shoulder girdle). In lower actinopterygians it is a sensory canal bone through which the connection between the cranial sensory system and the body lateral sensory system passes (JARVIK, 1980).

In *Pomatoschistus lozanoi,* no sensory canal is situated in the supracleithral bone nor does a lateral line exist (MILLER, 1986). The lateral face of the supracleithral bone is attached to the medial side of the posttemporal bone. The ventromedial side of the supracleithrum is connected to the dorsolateral face of the cleithrum via the

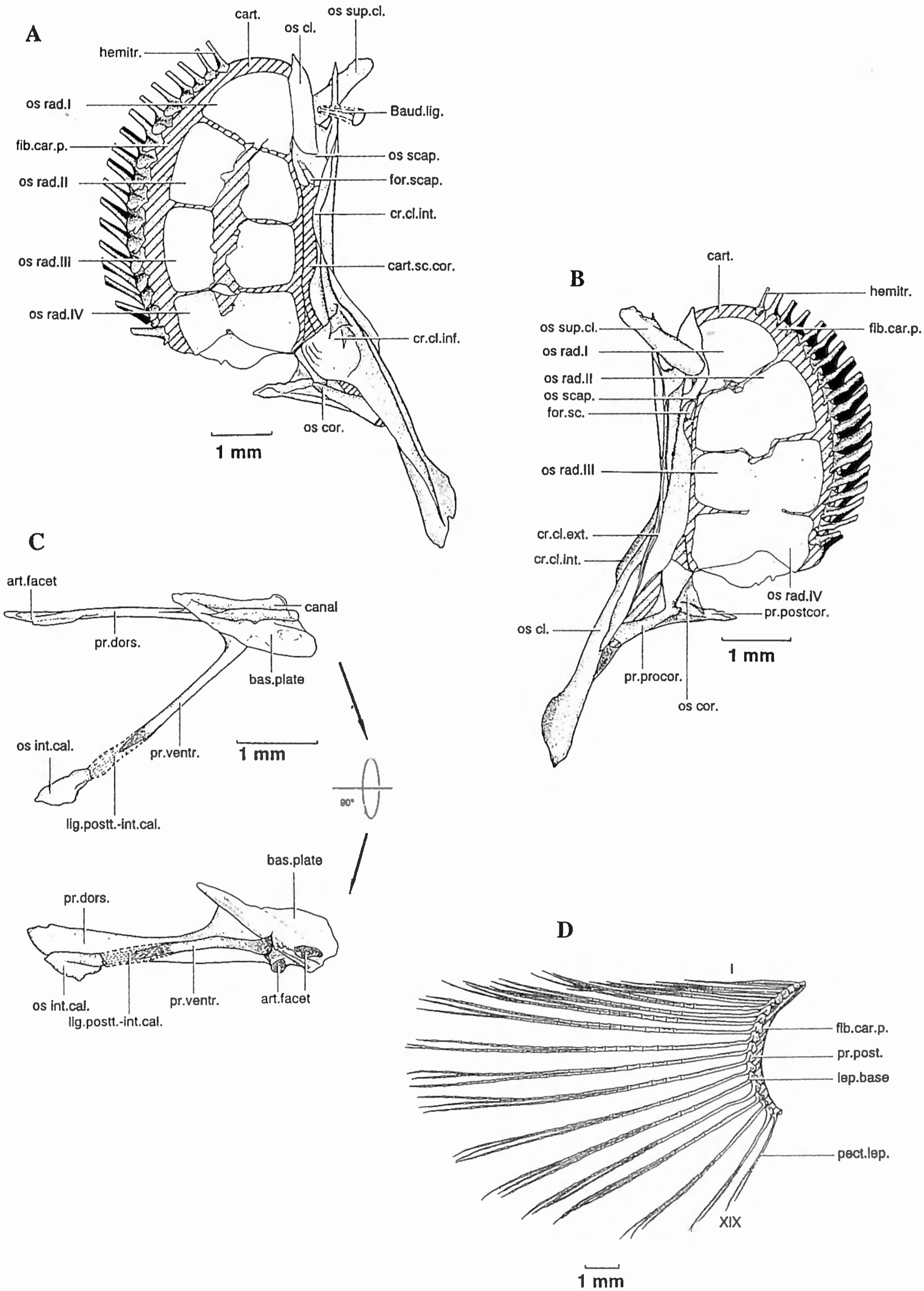


Fig. 3. — Bony elements of the pectoral girdle-apparatus in *Pomatoschistus lozanoi.* — A. Medial view of the shoulder girdle and shoulder plate. — B. Lateral view. — C. Lateral and ventral view of the os posttemporale with the os intercalare. — D. Lateral view of the fin plate. (Shaded areas : cartilage).

supracleithral-cleithral syndesmosis (Fig. 3B). Near the latter, Baudelot's ligament is attached (see below).

os cleithrum (Fig. 2B, 3A + B, 4A-C, 6A-C, 7A + B, 7E + F). This element constitutes the main part of the shoulder girdle. It suspends the endoskeletal elements of the pectoral girdle-apparatus and the pelvic girdle-apparatus. The cleithral bone forms the caudal margin of the branchial cavity, thereby protecting the heart. Dorsally it is attached to the supracleithral bone. Ventrally it forms a symphysis with the ventral tip of the contralateral cleithral bone (Fig. 2B, 6C), this symphysis is lying subdermally (Fig. 4B-C, 6A-C).

Rostral to the supracleithral-cleithral syndesmosis an incision is present through which runs Baudelot's ligament (Fig. 3A ; see below). At the rostral edge of the cleithrum bone three crests are present. The lateral crest (lateral crista cleithralis externa) is situated along the whole length of the cleithral bone, except for the most ventral part (Fig. 3B). The upper medial crest (crista cleithralis interna) extends between the dorsal incision and the coracoid bone. The lower medial crest (crista cleithralis inferior) is situated along the ventral half of the cleithrum. This crest is much higher than the internal cleithral crest (Fig. 3A). The medial faces of the left and right inferior cleithral crest are interconnected by the intercleithral cartilage, thus forming a second connection between the cleithra. The pelvic girdle articulates with the pectoral girdle by the intercleithral cartilage.

The cleithral bone forms a caudal furrow in which the scapulo-coracoidal cartilage is enclosed. This cartilage and its ossifications are attached to the cleithrum by means of collagen fibres.

This cleithral bone is also named the clavicula by MATSUBARA and IWAI (in BIRDSONG, 1975). The os cleithrum and the os claviculum, however, are not homologous : in some primitive Crossopterygians, both can be present (*e.g. Eusthenopteron*) (ROMER and PARSONS, 1986 ; JARVIK, 1980).

os postcleithrum. This dermal element has not been found in *Pomatoschistus lozanoi,* although in other gobiid species it can be present (AKIHITO, 1969, 1986). In *Eusthenopteron* (Crossopterygii) an os anocleithrum is present but whether this bone is homologous to the os postcleithrum remains uncertain (JARVIK, 1980).

Shoulder plate

During ontogeny a single cartilaginous shoulder plate develops. Later on this plate is subdivided into the proximal scapulo-coracoid cartilage and the distal radials (MERTENS, 1971, unpublished document).

cartilago scapulo-coracoideum (Fig. 3A-B, 7F). This cartilage is fixed in the distal furrow of the cleithral bone by collagen fibers. In this hyaline cartilage two ossification centres are present : a dorsal os scapulum and a ventral os coracoideum. In gobies the central part of the cartilage is not ossified, thus separating the scapular bone from the coracoid bone (AKIHITO, 1963, 1967).

os scapulum (Fig. 3A). This perichondral bone, which is perforated by a foramen scapulae, is the dorsal ossification of the scapulo-coracoid cartilage. In gobiid fishes a gradation in the ossification of the dorsal part of the scapulo-coracoid cartilage occurs. According to AKIHITO (1963, 1967) four types of scapular bones can be distinguished within the Gobiidae. In *Pomatoschistus lozanoi,* the ventral border of the foramen scapulae is not lined with an ossification (Fig. 3A), corresponding with type II in AKIHITO (*op. cit.*).

Distally the scapular bone articulates with the ventral part of the uppermost proximal radial bone and the dorsal part of the second proximal radial bone of the shoulder plate (Fig. 3A).

The scapular foramen is situated just below the overlapping dorsal part of the cleithral bone (Fig. 3B). Through this foramen runs a trunk of three connected nerve fibers, i.e. the spinal nerves I, II and III (MERTENS, 1971, unpublished document).

os coracoideum (Fig. 2B, 3A-B, 6C, 7B, 7E-F). Lateral to the lower medial crest lies this ventral ossification centre of the scapulo-coracoid cartilage. The perichondral ossification starts early during the ontogeny (JOLLIE, 1983).

The triangular coracoid bone consists of a vertical plate possessing two ventral processes (Fig. 3A-B). The processus procoracoideus is pointed ventrorostrally, articulating with the caudal side of the cleithral bone. The processus postcoracoideus is directed caudally, up to almost half the length of the shoulder plate. This process forms the ventral border for the coracoradial muscle fibers.

The dorsal non ossified part of the coracoid borders onto the rostral side of the ventralmost radial bone. The number of radial bones articulating with the coracoid bone is species specific (SPRINGER and FRASER, 1976 ; JARVIK, 1980 ; MERTENS, 1971, unpublished document).

ossa radialia proximalia (Fig. 2A-B, 3A-B, 7F). The four radial bones in *Pomatoschistus lozanoi* form the major part of the shoulder plate. Variable terminology has been used to describe these perichondral bones. Generally the term 'radialia' is used (MERTENS, 1971, unpublished document; BIRDSONG, 1975; SPRINGER and FRASER, 1976; JARVIK, 1980; MESTERMANN and ZANDER, 1984). Other authors use 'actinost' to indicate these elements (GOSLINE, 1971 ; HUSSAIN, 1981 ; AKIHITO, 1969). Also used is the name 'pterygophore' which is very much confusable with the term 'pterygiophore', the latter refering to the basal bony elements supporting the unpaired fins (LAGLER *et al.,* 1962).

The radial bones are the ossifications of the cartilaginous radials (see above) (JOLLIE, 1983). In *Pomatoschistus lozanoi,* the ossification is not complete, in such a way that the central region of the medial side of the three ventralmost radial bones remains cartilaginous (Fig. 3A).

In most fishes these radial bones are bar-like. In *Pomatoschistus lozanoi,* however, these bones are laterally compressed, and form plates instead of bars. The ventralmost and dorsalmost radial bones are triangular, the former bearing a ventral bony lamella (Fig. 3B-C). The two central bones are somewhat rectangular.

The radial bones are interconnected by collagenous fibres, thus forming one rigid plate.

Both lateral and medial fin muscles lie on the proximal radial bones, running from the cleithral or coracoid bone to the fin rays.

ossa radialia distalia. These small spherical structures are perichondral bones, situated distally to the proximal radial bones. They are completely surrounded by the fibrocartilage pad (hence they are not visible on the drawings), thus acting as supporting structures for this pad.

fibrocartilage pad (Fig. 3A-B, 7F). This pad forms a pliable but firm articulation border for the fin rays, situated along the distal margin of the proximal radial bones. Due to the curvature of the pad it is possible for the marginal fin rays to make a large angle between each other (GEERLINK, 1989).

Fin plate

lepidotrichia (Fig. 3A-B, 3D, 7D). In *Pomatoschistus lozanoi,* only soft, segmented fin rays are present, which are connected to each other by a dermal membrane. The number of pectoral fin rays varies at least between species. In *Pomatoschistus lozanoi,* nineteen pectoral fin rays are present. They act as supporting structures for the propulsion-generating fins.

The fin rays consist of two hemitrichia, each of which can be subdivided in three parts : a basal element, an unsegmented stem and a distal part, which is segmented into hemisegments.

In a transverse section, the hemitrichs are curved with their convex sides facing to each other. Opposite hemitrichs are connected by collagenous intra-lepidotrich ligaments, except at their base where they remain separated (GEERLINK and VIDELER, 1987).

At their base the hemitrichs are flattened and are provided with a processus posterior and a processus internus. The posterior process serves as an insertion site for the abductor and adductor muscles of the fin plate. The internal process which is situated at the medial sides of the hemitrichs, anchors the fin ray into the fibrocartilage pad (GEERLINK, 1989).

In *Pomatoschistus lozanoi,* the pectoral (and pelvic) fin rays are dichotomously branched (Fig. 3D, 6A). In the pectoral lepidotrichs maximally two branching points are present. Starting dorsally, the first and second rays are not branched. The third and nineteenth fin rays both have one braching point, all the others have two. The branching in those hemitrichs follows a certain pattern : in fin rays four to eleven the second branching point is situated in the ventralmost branch. The second branching point in fin ray twelve to eighteen is situated on the dorsal branch.

The attachment of the fin rays to the fibrocartilage pad allows the rays to rotate around two axes. Restricted rotation is possible around a horizontal axis going through the base of each fin ray. This rotation enables a dorsoventral motion of the pectoral fin rays resulting in enlarging and reducing the fin surface. The second rotation axis runs through the fibrocartilage pad between the bases of the fin ray. Rotation around this axis results in adduction and abduction of the fin plate.

Myology

In this publication nomenclature is used as in WINTERBOTTOM (1974). For synonymy we refer also to WINTERBOTTOM (1974).

Body muscles attached to the shoulder girdle-apparatus

Epaxial and hypaxial body muscles are attached to the pectoral girdle : dorsally the musculus lateralis superficialis and ventrally the musculus obliquus inferioris.

m. lateralis superficialis (Fig. 4A-C, 7A). This part of the body musculature lies ventrolaterally to the epaxial muscles, attaching to the dorsocaudal side of the posttemporal bone. These lateral muscles extend to the tail region. Contraction of these muscles will presumably rotate the shoulder girdle backwards.

m. obliquus inferioris (Fig. 4A-C, 6A-B, 7A). This ventralmost body muscle runs along the pelvic girdle-apparatus and joins the contralateral oblique muscle at the ventral tip of the cleithral bone.

Ontogenetically the oblique muscle arises from those fibers of the hypaxial muscles which are orientated in an anteroventral to a posterodorsal direction. The medial fibers of this muscle are attached to the caudal side of the ventral tip of the cleithral bone (Fig. 7A). The lateral fibers insert on a myocomma, separating the inferior oblique muscle from the sternohyoid muscle (Fig. 6A-B) (WINTERBOTTOM, 1974).

Some dorsolateral fibers of the inferior oblique muscle (on the second myomere starting rostrally) insert anteriorly on the postcoracoid process of the coracoid bone (Fig. 4B-C, 6A-B).

In *Pomatoschistus lozanoi,* the fibers of the inferior oblique muscles lie lateral to those of the superior oblique muscle, which seems contradictory. According to WINTERBOTTOM (1974), the position of these two muscles, in relation to each other, can vary in teleost fishes. In general the inferior oblique muscle is situated medially to the superior one. Both muscles fuse at the tail region.

Muscles between the shoulder girdle-apparatus and the neurocranium

m. levator pectoralis (Fig. 4B-C, 5A-B, 7A-B). This muscle arises from the epaxial muscles and becomes completely separated from them. In some primitive fishes the medial fibers are still continuous with the epaxial muscles (WINTERBOTTOM, 1974). In *Pomatoschistus lozanoi,* two subdivisions are distinguishable : a pars lateralis and a pars medialis. Both are situated at the lateral side of the caudoventral region of the skull.

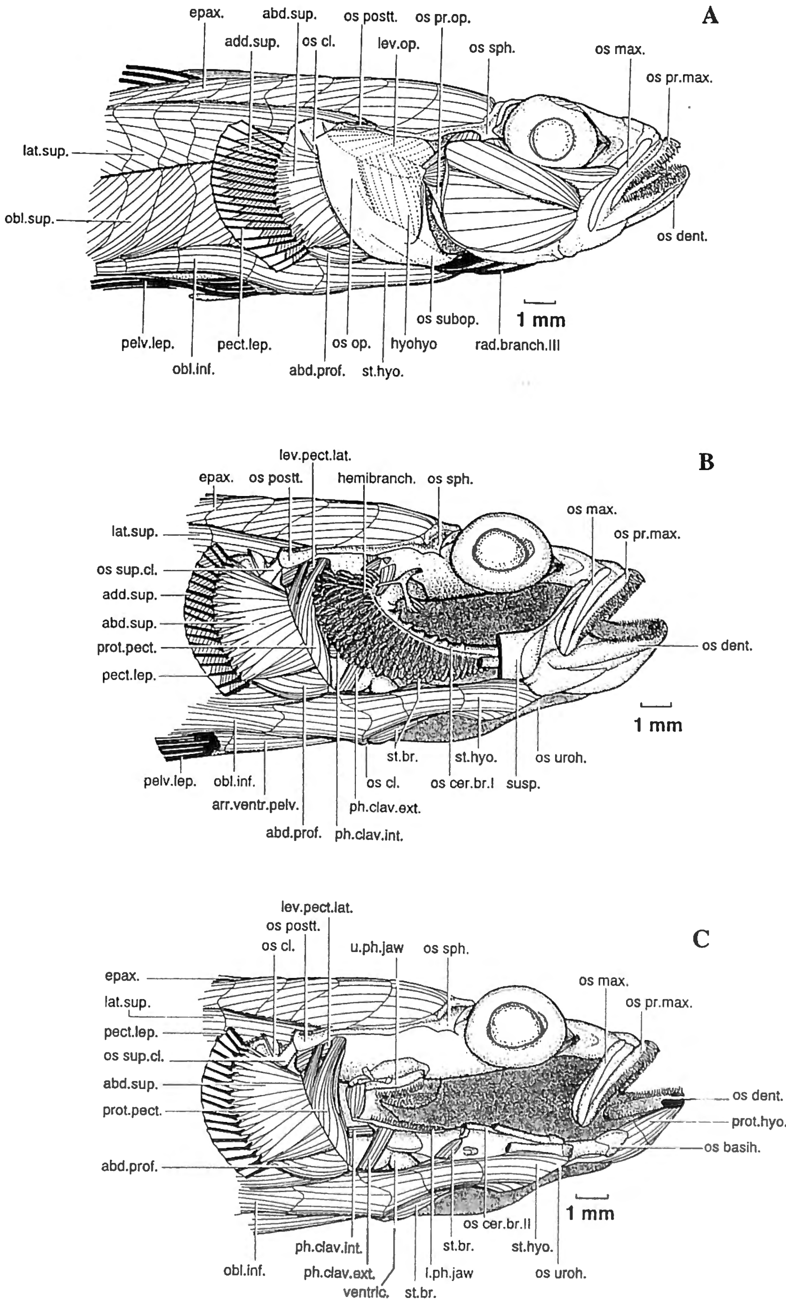


Fig. 4. — Lateral view of the body muscles and the muscles of the pectoral girdle-apparatus.

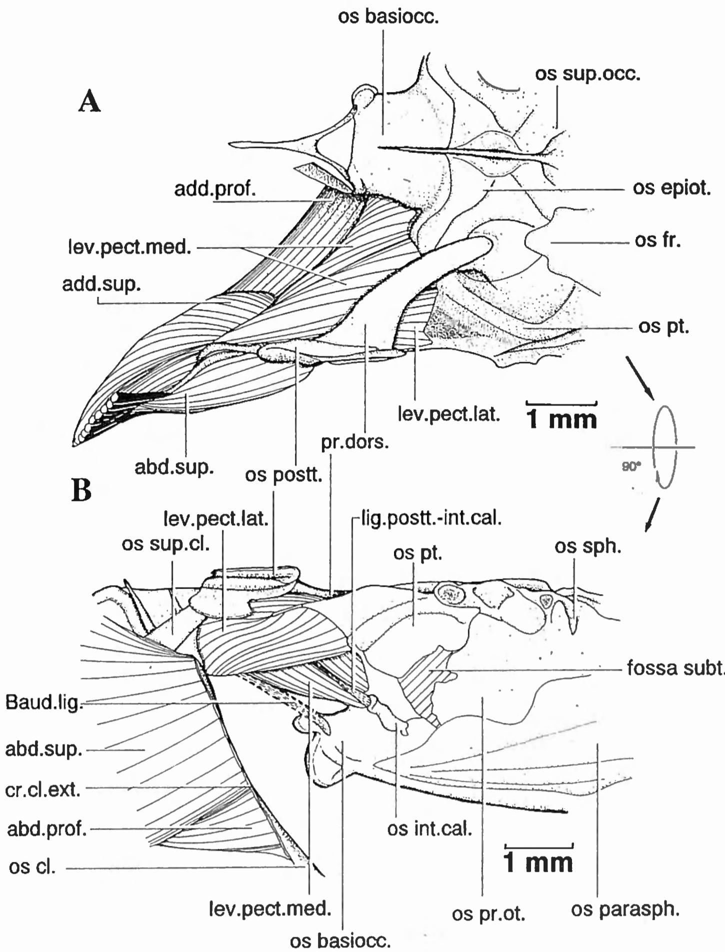


Fig. 5. — Detailed view of the musculus levator pectoralis in dorsal view (A) en lateral view (B). (Shaded areas : cartilage).

The shorter musculus levator pectoralis pars lateralis originates from the caudal margin of the pterotic bone of the neurocranium (Fig. 5A-B). This bundle runs medially to the basal plate of the posttemporal bone, ventrally to the dorsal process and laterally to the ventral process. It inserts on the rostral margin of the cleithral bone. At the caudalmost tip of the pterotic bone a small tendon is present on which the fibers of the lateral part insert.

The musculus levator pectoralis pars medialis originates more ventrally to the base of the skull, at the exoccipital bone, close to the intercalar bone (Fig. 5B). Distally, this muscle encloses the ventral process of the posttemporal bone as well as the distal part of Baudelot's ligament. The fibers are attached to the medial side of the supracleithral bone and the rostral side of the cleithral bone, just before the insertion site of the superficial adductor muscle of the pectoral fin.

m. protractor pectoralis (Fig. 4B-C, 7B). This muscle connects the rostral side of the shoulder girdle with the lateral side of the neurocranium.

During ontogeny the protractor muscle arises from the levator arcuum branchialum 'Anlage' (WINTERBOTTOM, 1974). This sheet-like muscle is attached to the rostrolateral margin of the crista cleithralis externa of the cleithral bone. The insertion is spread over the total length of the crest. Dorsally, the muscle is separated into two smaller bundles, a rostral one inserting on the ventral side of the lateral margin of the pterotic bone of the neurocranium, and a caudal one inserting on the basal plate of the posttemporal bone (Fig. 4B-C). Contraction of this protractor muscle will presumably generate a forward rotation of the pectoral girdle-apparatus around a horizontal axis.

Muscles between the shoulder girdle-apparatus and the hyoid arch

m. sternohyoideus (Fig. 4A-C, 6A-B, 7A). This muscle lies ventrally between the ventral tip of the cleithral bone and the urohyal bone.

The sternohyoid muscle develops from the ventral part of the hypobranchial muscle plates of the first few spinal myomeres (WINTERBOTTOM, 1974). The fibers of the sternohyoid are musculously attached to the lateral sides of the urohyal bone (Fig. 4B-C, 6B). This dermal bone is the ossification of the tendon plate between the rostral tips of the contralateral sternohyoid muscles (VERRAES, 1973). It is connected to the distal tips of the hyoid bars by ligaments (MERTENS, 1971, unpublished document; LELE and KULKARNI, 1939).

Caudally, the lateral fibers of the sternohyoid muscle are separated from the inferior oblique muscle by a myocomma (Fig. 4B-C, 6A-B). The medial fibers insert on the rostral side of the ventral tip of the cleithral bone (Fig. 7A). This muscle forms the ventral border of the branchial cavity, lying between the two hyoid rami. The basal elements of the branchial arches meet just above the sternohyoid muscle.

Ventrally the sternohyoid muscle is subdivided by one myocomma. However, on the lateral side of the muscle a middle third muscle segment is present. The myocommata separating this subdivision are continuous with the ventral myocomma.

The sternohyoid muscle, together with the cleithral bone and the inferior oblique muscle, participates in a four bar system which is used in suction feeding (AERTS and VERRAES, 1984; MULLER, 1987).

Muscles between the shoulder girdle-apparatus and the branchial arches

m. sternobranchialis (Fig. 4B-C, 6A-C). In some fishes the medial and mediodorsal fibers of the sternohyoid muscle become separated forming the sternobranchial muscle (WINTERBOTTOM, 1974).

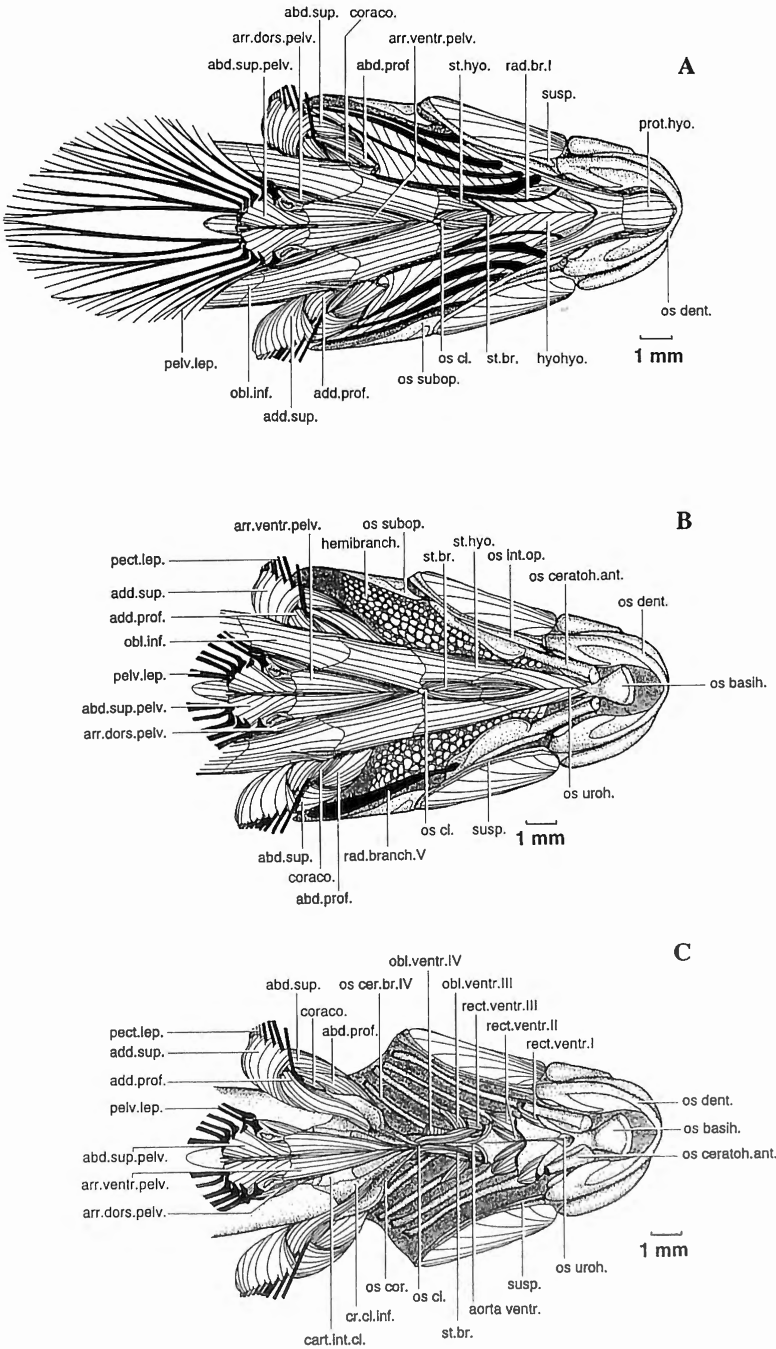


Fig. 6. — Ventral view of the body muscles and the muscles of the pectoral girdle-apparatus.

Caudally the muscle is attached to the ventral tip of the cleithral bone, medially to the attachment of the fibers of the sternohyoid muscle (Fig. 6C). In *Pomatoschistus lozanoi,* the fibers of the sternobranchial muscle rostrally form two separate bundles : a dorsal one inserting on the hypobranchial bone III (Fig. 6C), and a ventral one inserting on the caudal border of the urohyal bone (Fig. 6B). The latter lies between the two sternohyoid muscles and is subdivided by a myocomma.

m. pharyngoclavicularis externus (Fig. 4B-C). This muscle is the first of two muscles connecting the lower pharyngeal jaws to the pectoral girdle.

According to WINTERBOTTOM (1974), during ontogeny the pharyngoclavicular muscle becomes divided from the fifth branchial arch muscle plate. Later during development this muscle becomes separated in an external portion (pharyngoclavicularis externus) and an internal portion (ph. clav. internus). In *Pomatoschistus lozanoi,* the external muscle attaches on the ventrorostral part of the external crest of the cleithral bone, ventral to the insertion site of the pectoral protractor muscle. The small external muscle bundle runs anterodorsally, attaching to the lateral side of the lower pharyngeal jaw, lateral to its ventrolateral crest (Fig. 4C).

m. pharyngoclavicularis internus (Fig. 4B-C, 7A). Medially to the external pharyngoclavicular muscle passes the internal muscle. It also connects the lower pharyngeal jaw with the shoulder girdle.

The fibers are attached to the rostral side of the external crest of the cleithral bone, medially to the ventral fibers of the pectoral protractor muscle. The fibers are directed horizontally. They insert on the ventral side of the lower pharyngeal jaw, medially to the ventrolateral crest of the jaw.

Muscles between the shoulder girdle and the fin plate

m. abductor superficialis (Fig. 4A-C, 5A-B, 6A-C). The lateralmost muscle plate of the shoulder plate is the superficial abductor muscle.

According to WINTERBOTTOM (1974), during ontogeny a muscle plate develops laterally to the shoulder plate. The lateral fibers become separated from the medial ones, forming the superficial abductor muscles. In some primitive fishes the lateral fibers are not completely separated from the medial ones (*e.g. Elops*) (WINTERBOTTOM, 1974). The medial fibers form the musculus adductor profundus.

In *Pomatoschistus lozanoi,* the superficial abductor muscle originates along the upper three quarters of the margin of the external cleithral crest. Caudally the muscle is tendinously attached to the posterior process of the lateral hemitrichs, except for the ventralmost fin ray where there is no insertion.

Contraction of this abductor muscle, together with the deep abductor muscle, will generate a forward rotation of the fin rays. When the pectoral fins are used to support and stabilise the fish on the bottom, the fin rays are in an abducted position.

Within the Gobiidae a subdivision of this superficial muscle may be present in a pars superficialis and a pars profundus (Eggert, 1929). This division is also present in other fish groups (*e.g.* Labridae) (Geerlink, 1989). In *Pomatoschistus lozanoi,* a clear subdivision could not be distinguished.

m. abductor profundus (Fig. 4A-C, 5B, 6A-C, 7A). Medially to the superficial abductor muscle and more oblique directed is the deep abductor muscle.

In *Pomatoschistus lozanoi,* the insertion of this muscle on the cleithral bone is situated medially to the attachment of the superficial muscle on the external crest (Fig. 7A). This insertion site is spread over the lower half of the crest. The fibers run posterodorsally to the base of each lateral hemitrich. Contraction will result in the abduction of the fin rays.

m. adductor superficialis (Fig. 4A-C, 5A, 6A-C, 7B-D). This medialmost ('medial' is relative to the body axis, not to the shoulder plate) muscle of the shoulder plate originates dorsally on the shoulder girdle, adjacent to the insertion of the m. levator pectoralis pars medialis, and inserts on the fin rays.

During ontogeny a muscle plate is formed at the medial side of the shoulder plate. Its medial fibers form the superficial adductor muscle, whereas the lateral ones form the deep adductor muscle. The adductor muscle may not be completely subdivided (*cfr.* abductor) in some primitive fishes (*e.g. Elops*) (Winterbottom, 1974).

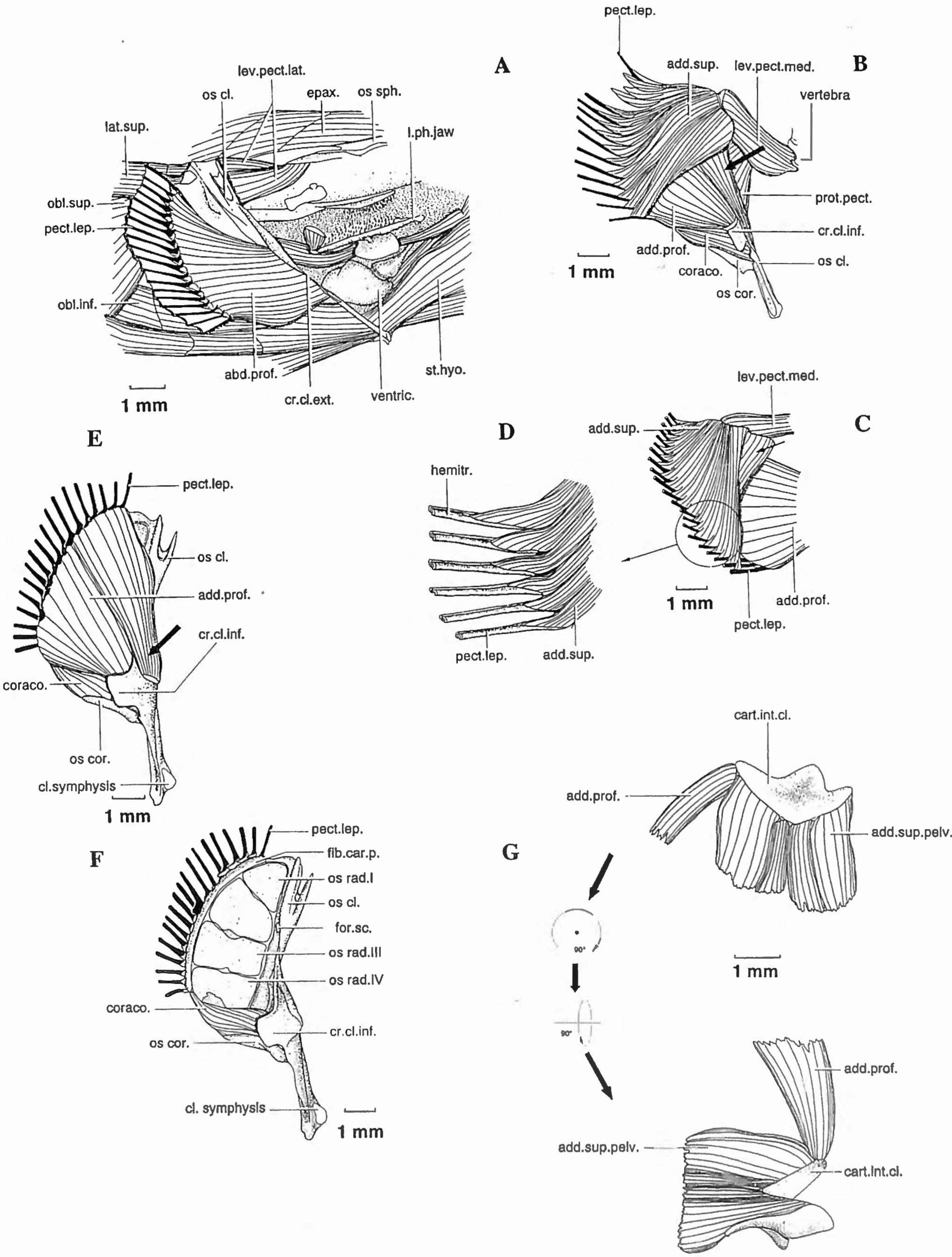
In *Pomatoschistus lozanoi,* the insertion site of the superficial adductor muscle is situated caudally to the insertion of the medial part of the pectoral levator muscle. It comprises the medial side of the basal plate of the posttemporal bone, the anteromedial side of the supracleithral bone and the dorsomedial side of the cleithral bone. Distally the fibers of the adductor muscle are attached to the medial side of the fin ray stem. This insertion is situated at some distance from the base of the ray (Fig. 4A, 7C-D), resulting in a larger lever for the adductor muscle compared to a basal insertion. Thus the momentum on the fin increases which enlarges the adduction force.

In *Pomatoschistus lozanoi* and some other fishes the superficial fibers are differently orientated with regard to the deeper ones. The dorsal superficial fibers are attached to the more ventral fin rays whereas the ventral, deeper fibers run to the more dorsal fin rays (Fig. 7C, small arrow).

Contraction of this muscle is believed to rotate the fin rays backward.

m. adductor profundus (Fig. 5A, 6A-C, 7B-C, 7E-G). This muscle is situated between the superficial adductor muscle and the shoulder plate. The caudal insertion is at the bases of the medial hemitrichs. The deep adductor muscle is rostrally attached at two different places, thus dividing the muscle in two parts.

The ventral part of the muscle originates from the coracoid and the cleithral bones (Fig. 6C, 7B, 7E). The dorsal fibers are attached to the dorsorostral tip of the intercleithral cartilage (Fig. 7E, 7G). Rostrally, these two muscle parts are separated by the crista cleithralis inferior.


A
lat.sup.
os cl.
lev.pect.lat.
epax.
os sph.
l.ph.jaw
obl.sup.
pect.lep.
obl.inf.
abd.prof.
cr.cl.ext.
ventric.
st.hyo.
1 mm
B
pect.lep.
add.sup.
lev.pect.med.
vertebra
prot.pect.
cr.cl.inf.
os cl.
add.prof.
coraco.
os cor.
1 mm
C
lev.pect.med.
add.sup.
add.prof.
pect.lep.
1 mm
D
hemitr.
pect.lep.
add.sup.
E
pect.lep.
os cl.
add.prof.
cr.cl.inf.
coraco.
os cor.
cl.symphysis
1 mm
F
pect.lep.
fib.car.p.
os rad.I
os cl.
for.sc.
os rad.III
os rad.IV
coraco.
os cor.
cr.cl.inf.
cl. symphysis
1 mm
G
cart.int.cl.
add.prof.
add.sup.pelv.
90°
90°
1 mm
add.prof.
add.sup.pelv.
cart.int.cl.

m. coracoradialis (Fig. 6A-C, 7B, 7E-F). This ventralmost muscle of the shoulder plate connects the coracoid bone with the ventralmost radial bone.

According to WINTERBOTTOM (1974) no data are available concerning the ontogeny of this muscle. Possibly it arises from a part of the hypaxial muscles.

In *Pomatoschistus lozanoi,* the muscle lies ventrally to the shoulder plate, between the deep abductor and deep adductor muscles (Fig. 6A-C). The fibers of the coracoradial muscle originate from the dorsal side of the coracoid bone and the caudal side of the cleithral bone, medially to its inferior medial crest (Fig. 7E-F). Distally the fibers insert on the ventrocaudal tip of the ventralmost radial bone, right below the ventralmost fin ray.

As yet, it is difficult to suggest a possible function for this muscle, since it inserts on, in our opinion, firmly connected and hardly movable skeletal elements.

Ligaments

Ligamentum posttemporalo-intercalare (Fig. 3C, 5B). This ligament is continuous with the ventral process of the posttemporal bone (Fig. 3C). The ligament is attached to the intercalar bone of the neurocranium. The length of this ligament, in relation to the length of the ventral process varies interspecifically, as already stated in the description of the ventral process of the posttemporal bone.

Baudelot's ligament (Fig. 2A-B, 3A, 5B). In Pomatoschistus lozanoi, this strong ligament is situated between the medial side of the shoulder girdle and the caudoventral side of the neurocranium. It is attached medially on the shoulder girdle, on that part of the supracleithral bone that is left uncovered by the cleithral incision (Fig. 3A). The attachment site on the neurocranium is the ventromedial side of the basioccipital bone (Fig. 5B).

In the literature not many functions for this ligament are proposed. In cyprinids this ligament functions as a rotation axis for the lower pharyngeal jaws SIBBING (1976). However, in gobies the pharyngeal jaws do not 'articulate' with this ligament.

Fig. 7. — Muscles of the shoulder plate. — A. Lateral view of the musculus abductor profundus. — B. Medial view of the adductor muscles (arrow indicating the position of the profound adductor muscle fibers attaching to the intercleithral cartilage). — C. Idem as B. but showing the crossing of muscle fibers of the musculus adductor superficialis (small arrow). — D. Detailed view of the insertion of the musculus adductor superficialis on the fin ray stem. — E. Medial view of the musculus adductor profundus (arrow indicating the dorsal muscle fibers that insert on the intercleithral cartilage). — F. Medial view of the musculus coracoradialis. — G. Detailed view of the insertion of the dorsal fibers of the musculus adductor profundus on the intercleithral cartilage. (Shaded areas : cartilage).

DISCUSSION

As the pectoral fins are very important in locomotion and as supporting structures when resting on the bottom, some morphological adaptations are discussed below.

Forward propulsion through pectoral fin adduction is exerted according to a drag based mechanism (WEBB and BLAKE, 1985). Contraction of the pectoral fin adductor muscles results in a backward rotation of the fin during the powerstroke. A forward rotation is generated during the non-propulsive recovery stroke through contraction of the abductor muscles. In some other teleost fishes, a dorsoventral movement of the pectoral fins produces the forward propulsion (*e.g.* Labridae, Pomacentridae). In these lift based propulsion mechanisms the pectoral fin rays show an undulating motion which requires a large mobility of the rays and its supporting structures (WEBB and BLAKE, 1985).

During the powerstroke in pectoral fin adduction, large forces are exerted on the skeletal elements of the pectoral girdle. In order to withstand such forces, some strengthening morphological adaptations are present. In generalised teleosts, the radial bones are bar-like structures, attached to each other with connective tissue. GEERLINK (1983) showed that in *Coris formosa* (Labridae) the proximal radials have a considerable degree of movability with the scapulo-coracoid plate and with each other.

In *Pomatoschistus lozanoi* and some other benthic fishes (Gobiidae : EGGERT, 1929 ; AKIHITO, 1986, Cottidae : GREGORY, 1933 and Bleniidae : BRANDSÄTTTER *et al.,* 1990), the radials are plate like structures that are firmly connected to each other and to the scapulo-coracoid plate by short collagen fibers. Thus a rigid shoulder plate is formed. However, the rigidity of the radials considerably reduces the ability for precise maneuvering.

The propulsion force can be increased by altering several parameters such as enlarging the propulsion generating surface, enlarging the proportion of adductor muscles or increasing the contraction power of the adductor muscles. According to AKIHITO (1986 : Fig. 6) and GEERLINK (1983 : Fig. 1B) the proximal radials in gobies are greatly enlarged compared to generalised teleosts. Thus the distal border of the shoulder plate and hence the fin base are relatively larger in gobies. The shape of the fin is trapeziform (compared to triangular in *Coris formosa*). A broader fin base implicates a larger resistance against torque along a proximal-distal axis during powerful fin adduction. In *Pomatoschistus lozanoi,* the surface of the pectoral fin is also strongly enlarged by the branching of the fin rays. The enlarged plate-like shoulder plate provides ample space for large fin muscles (ab- and adductors). The contraction force of the superficial adductor muscle is increased through a distally moved insertion site on the fin rays. The insertion of the superficial adductor muscles is musculous on the stem of the fin rays, in contrast to a tendinous insertion in *Coris formosa* (GEERLINK, 1989). The rather distal attachment will create a large momentum on the fin rays, resulting in a large adduction force. Together with the large reaction force on the fin plate, this results in a strong forward propulsion. The musculous insertion on the fin rays may be an indication that the extent to which the individual rays can be moved independently is smaller in gobies than in *Coris formosa* (Geerlink, 1989). Again this is in favour of powerful fin adduction and at cost of maneuvrability of the fin rays.

CONCLUSIONS

The pectoral fins of gobies seem to be better adapted to powerful adduction than those of generalised teleosts. The proximal radials form a large rigid shoulder plate with a long distal margin on which a high pectoral fin articulates. The fin muscles are strongly developed and assure, together with the large pectoral fin, powerful drag-based pectoral propulsion. The morphological adaptations for powerful adduction, however, are at cost of the maneuvering abilities of the pectoral fins.

ABBREVIATIONS TO THE FIGURES

Skeletal elements

art.facet	= articulation facet
bas.plate	= basal plate
cart.	= cartilago
cart.int.cl.	= cartilago intercleithralis
cart.sc.cor.	= cartilago scapulo-coracoideum
cl.symphysis	= cleithral symphysis
cr.cl.ext.	= crista cleithralis externa
cr.cl.int.	= crista cleithralis interna
cr.cl.inf.	= crista cleithralis inferior
fib.car.p.	= fibrocartilage pad
for.sc.	= foramen scapulae
fossa subt.	= fossa subtemporalis
hemitr.	= hemitrichium
l.ph.jaw	= lower pharyngeal jaw
lep.base	= lepidotrichium base
os basih.	= os basihyale
os basiocc.	= os basioccipitale
os cer.br.	= os ceratobranchiale
os ceratoh.ant.	= os ceratohyale anterior
os cl.	= os cleithrum
os cor.	= os coracoideum
os dent.	= os dentale
os epiot.	= os epioticum
os exethm.	= os exethmoideum
os fr.	= os frontale
os int.cal.	= os intercalare
os int.op.	= os interoperculare
os max.	= os maxillare
os mesethm.	= os mesethmoideum

os op.	= os operculare
os parasph.	= os parasphenoideum
os postt.	= os posttemporale
os pr.max.	= os praemaxillare
os pr.op.	= os praeoperculare
os pr.ot.	= os prooticum
os pt.	= os pteroticum
os rad.	= os radiale
os scap.	= os scapulum
os sph.	= os sphenoideum
os subop.	= os suboperculare
os sup.cl.	= os supracleithrum
os sup.occ.	= os supraoccipitale
os uroh.	= os urohyale
os vom.	= os vomerale
ossa rad.	= ossa radialia
pect.lep.	= pectoral lepidotrichia
pelv.lep.	= pelvic lepidotrichia
pr.dors.	= processus dorsalis of the os posttemporale
pr.post.	= processus posterior of the lepidotrichium base
pr.postcor.	= processus postcoracoideus
pr.procor.	= processus procoracoideus
pr.ventr.	= processus ventralis of the os posttemporale
rad.branch.	= radius branchiostegus
susp.	= suspensorium
u.ph.jaw	= upper pharyngeal jaw

Muscles

abd.prof.	= musculus abductor profundus
abd.sup.	= musculus abductor superficialis
abd.sup.pelv.	= musculus abductor superficialis pelvicus
add.prof.	= musculus adductor profundus
add.sup.	= musculus adductor superficialis
add.sup.pelv.	= musculus adductor superficialis pelvicus
arr.dors.pelv.	= musculus arrector dorsalis pelvicus
arr.ventr.pelv.	= musculus arrector ventralis pelvicus
coraco.	= musculus coracoradialis
epax.	= epaxial muscles
hyohyo.	= musculus hyohyoideus
lat.sup.	= musculus lateralis superficialis
lev.op.	= musculus levator operculi
lev.pect.lat.	= musculus pectoralis pars lateralis
lev.pect.med.	= musculus pectoralis pars medialis
obl.inf.	= musculus obliquus inferioris
obl.sup.	= musculus obliquus superioris
obl.ventr.	= musculus obliquus ventralis
ph.clav.ext.	= musculus pharyngoclavicularis externus
ph.clav.int.	= musculus pharyngoclavicularis internus
prot.hyo.	= musculus protractor hyoidei

prot.pect. = musculus protractor pectoralis
rect.ventr. = musculus rectus ventralis
st.br. = musculus sternobranchialis
st.hyo. = musculus sternohyoideus

Ligaments

Baud.lig. = Baudelot's ligament
lig.postt.-int.cal. = ligamentum posttemporalo-intercalare

Other

hemibranch. = hemibranchium
ventric. = ventriculus
aorta ventr. = aorta ventralis

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