MECHANISM OF THE JAW AND BODY MUSCLES OF ORTHRAGORISCUS MOLA L.

by

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There are several descriptions of the anatomy of *Orthragoriscus mola* L., but no authors except Van Dobben (1935) have given a functional treatise concerning the mechanism of the jaw.

Unfortunately the fish described by Van Dobben seems to have been abnormal. The description which follows is based on anatomical study of two sunfishes which stranded on the Dutch coast and were placed at our disposal by the Rijksmuseum van Natuurlijke Historie, Leiden.

Specimen A, a female, stranded December 10, 1935 near Burgh, in the neighbourhood of Haamstede, on the Isle of Schouwen. It has been used for a cast in the Leiden Museum and was dissected by Dr N. Tinbergen and J. J. ter Pelkwijk December 13 and 14, 1935 at the Zoological Laboratory at Leiden.

Specimen B, a male, stranded December 13, 1938, between Wassenaarsche Slag and Katwijk in Holland. It was dissected by J. M. van Roon and J. J. ter Pelkwijk on December 14 and 15, 1938 at the Leiden Museum. The dissected specimen was kept in a 50 % solution of alcohol and was further studied on February 14, 1939.

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External features (fig. 1a and 1b)	A 1935	B 1938
Total length	100 cm	120 cm
Total height of the body	65	75
Total height from tip of anal fin to tip of dorsal fin	137	150
Height of tail fin	63	75
Distance from tip of snout to gill-slit	29	36
Distance from tip of snout to front of pectoral fin	33	47
The tip of the snout protudes over the upper jaw	1	3
Distance from tip of snout to front of dermal opening of the eye	15	17
Length of dermal opening of the eye	4,5	5,6
Height of dermal opening of the eye	3,5	4,3
Distance from bottom of eye to the lower border of body, mesured vertically	35	34
Distance from back of eye to gill-slit	14	13
Straight distance from tip of snout to front of dorsal fin	67	74
The width at base of dorsal fin	20	26
Height of dorsal fin	42	45
Straight distance from tip of snout to anus	67	80
Distance from anus to front of anal fin	7	7
Length of tail fin	13	13
Width at the base of anal fin	21	23
Height of anal fin	42	43
Width at base of pectoral fin	8	8,5
Length of pectoral fin	15	17
Height of gill-slit	5,5	9
Width of skin-lobe covering gill-slit	3	4,4

Muscles of the body.

The muscles of the body have been described by Gregory and Raven (1934) from one specimen only. Therefore a short description follows here (fig. 1b).

The dorsal fin in moved by a complex of muscles, tapering rostraly and fastened to the skin, to the vertebral column and to the skull. (measures of specimen A: 60—20 cm, specimen B: 70—20 cm). To the left and right 17 tendons pass through the cartilaginous zone at the base of the dorsal fin, corresponding with certain parts of the fin and with parts of the muscular system. Undulating movements of the dorsal fin are thus possible and of the anal fin also (see below).

The anal fin is moved by a complex of muscles, extending caudally of the visceral cavity and fastened at the sides along the vertebral column (measures of specimen A: 30—30 cm, of B: 32—40 cm). To the left and right 19 tendons (specimen A. 18 tendons?) pass through the cartilaginous zone at the base of the fin, here also corresponding with parts of this fin and parts of the muscular system.

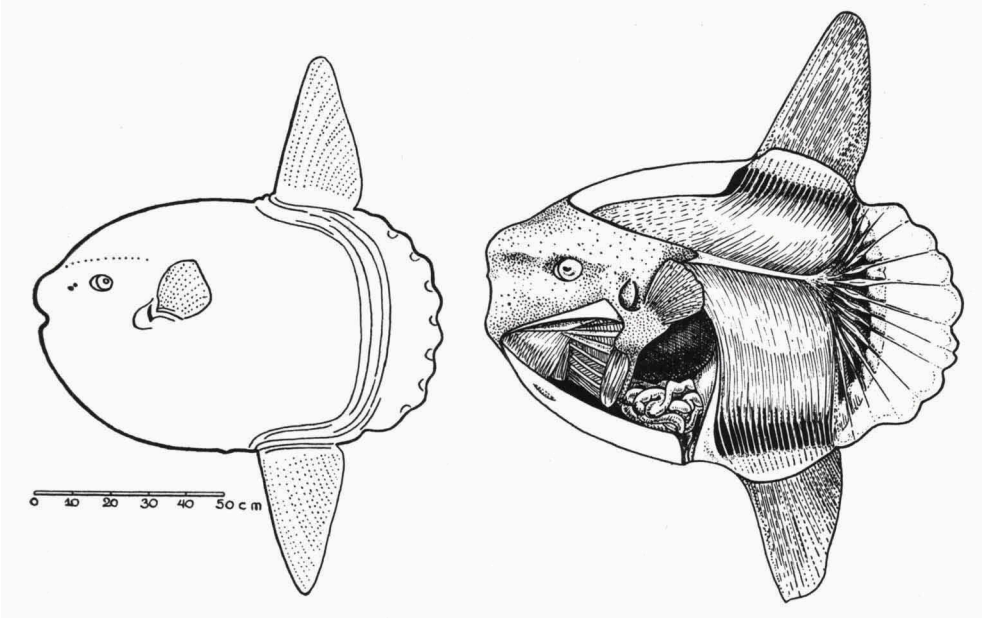

Fig. 1. *Orthragoriscus mola* L. Specimen A (left) and specimen B (right), the skin partly removed.

The tail fin, contrary to the anal and dorsal fin, is rather restricted in its movements. Then separate muscles connect the caudal part of the spinal column with scalloped parts of the tail (specimen B: 12 muscles, specimen A: 8 muscles?). The ventral part of the tail fin of specimen B. was injured, so that the scalloping in the lower part was less distinct.

The pectoral fin can be pulled horizontally by the musculus abductor profundus and the musculus abductor superficialis, which are fastened to the lower part of the cleithrum and the whole of the coracoid. When these muscles are relaxed, the pectoral fin springs up against the body, presumably by the elasticity of the skin. Specimen B showed a muscle, most probably the musculus retractor postclavicularis, extending through the visceral cavity in the direction of the anus.

The skin.

The skin is made rough by small denticle-like structures. There is a layer of subcutanous tissue from four to six cm thick. At the base of the fins and around the gill-slits the skin is thinner. Above the mouth the skin forms a nose-like protrusion, which extends into a swelling above the eye. Below the mouth the skin is only one cm thick. Thus movement of the mouth is made possible. Still lower the skin becomes very thick forming a keel. Here is found a tube-like ossification (Specimen B: 6,5—1 cm).

In several places the skin is attached to the muscles and bones which play a part in the opening and closing of the mouth. The skin has fused with the braincase to form a whole. Tendonlike connections of the skin with the back of the pectoral girdle, the middle of the praeoperculum, the back of the praeoperculum (where it hinges with the hyomandibular) and with the median of the musculus geniohyoideus inferior can be found. A considerable length of the musculus hyohyoideus is attached to the skin arround the gill-slit.

Bones of the jaw-mechanism.

A figure of the skull has been given by W. K. Gregory (1933) and here we will use his nomenclature. For the movements of the jaw the following bones are important:

A. Palatinum, mesethmoid, praefrontale, frontale, supraoccipetale, epioccipetale, sphenoticum, pteroticum, parasphenoid and enteropterygoid forming a solid brain-case, in strong connection with the skin, vertebral column and pectoral girdle.

B. Quadratum, symplecticum and hyomandibulare are united. The ventral border of this complex is firmly attached to the praeoperculum. The components of this complex can only move in relation to each other as far as torsion in their cartilaginous parts will admit. Through a ligament, 3 cm long and 1 cm in diameter, this complex is suspended to the pteroticum by means of the hyomandibulare. In front the quadratum has a joint with the articulare which together with dentale and angulare form the lower jaw. The praeoperculum is connected by a tendon with the epihyale (forming a whole with cerato- and basihyale: the "hyale"). The hyomandibulare has a joint with the operculum by means of a ball and socket joint. The measures of this complex from specimen B were: from the joint of the quadratum with the dentale to the connection with the epihyale 10 cm; from the connection of the praeoperculum with the epihyale to the rear corner of the operculum 13 cm; from this corner to the connection with the skin 5,5 cm.

C. At the left and the right the solid upper jaw consists of praemaxillare and maxillare. This complex is attached to the braincase at the left and right by joints which make it possible for the upper jaw to turn

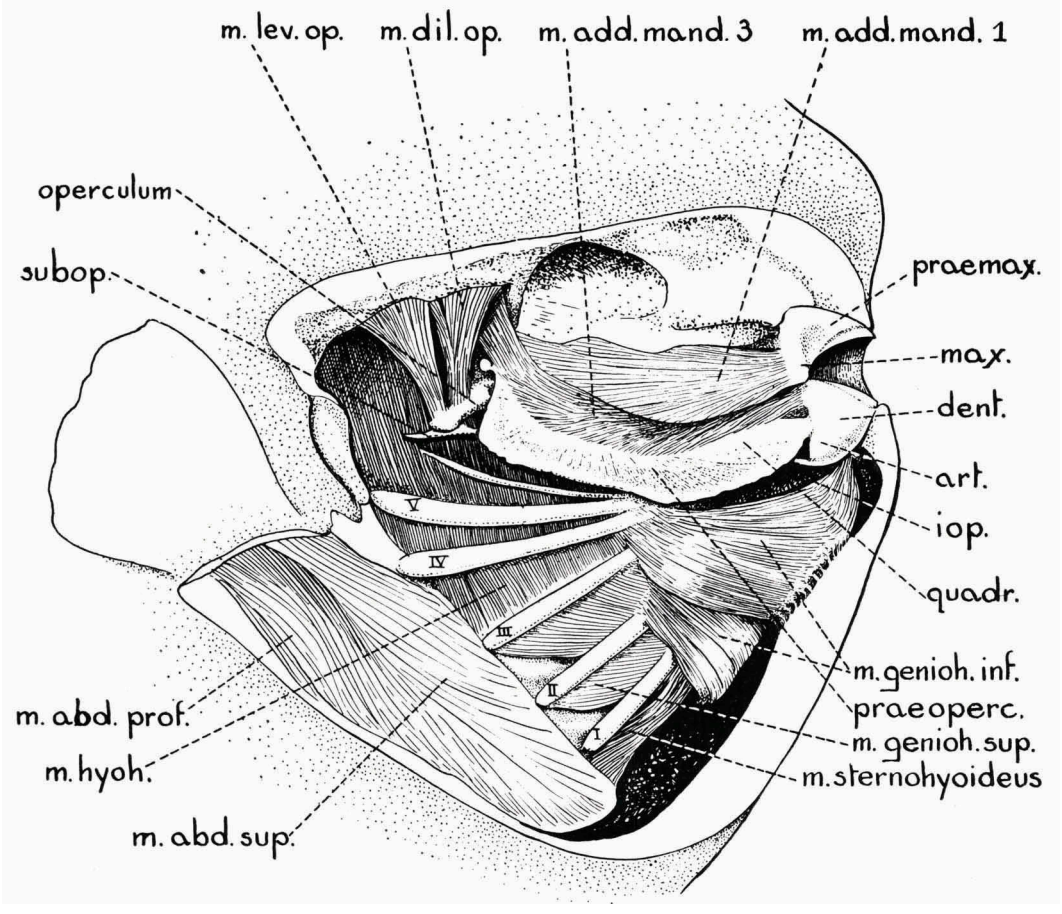

Fig. 2. *Orthragoriscus mola* L. Muscles and bones of the head of specimen B, seen from the right.

upwards. The back of the maxillare partly incloses the dentale and is connected with this bone by tendons. At the caudal border of the maxillare the musculus adductor mandibulae is attached. When the mouth is closed, the lower edge of the upperjaw rests in front in a groove of the lowerjaw. The measures of the upperjaw of specimen B were: from the joint with the braincase to the foremost point of the latter 7,5 cm; from this point to the joint with the dentale 10 cm. Distance between the joints with the lower jaw 9,5 cm.

D. The lower jaw consists of a firmly united dentale, angulare and articulare. The articulare hinges with the quadratum (we found this joint not so low as drawn by Greory and Raven (1934). Maxillare and dentale are connected by a broad ligament, also extending from the backpart of the dentale to the palatinum. By this ligamentary connection upper and lower jaw are moved simultaneously. Left and right from the median of the dentale the lobes of the musculus geniohyoideus are fastened. Along the border of the mouth the dentale is closely fused with the skin. A long ligament connects the interoperculum. The measures of the lower jaw of specimen B were: from the front of the lower jaw to the connection with the maxillare 8 cm; from this connection to the articulare 6 cm.

E. Interoperculum and subopercuIum form a connection between angulare and operculum. This connection passes through a tunnel in the membraneous tissue medial of the praeoperculum. In specimen B the total length of this connection was 21,5 cm. Under the angulare we saw first a ligament 3 cm long then the bone of the interoperculum 8 cm long, a ligament 6 cm long and finally the bone of the subopercuIum, which is 3,5 cm long to the connection with the operculum and protudes another 4 cm caudally.

F. The operculum is jointed with the hyomandibulare by a ball and socket joint. The socket lying in the operculum and is connected with the subopercuIum by a number of ligaments. Dorsally three muscles connect the operculum with the braincase. In specimen B the length of the operculum was 6 cm; the greatest width 2 cm. Where the left operculum was connected with the subopercuIum there is a knob about 0,4 cm thick.

G. Basi-, cerato- and epihyale form a solid whole, the hyale. The epihyale is connected with the praeoperculum by a joint which makes it possible to turn round the horizontal axis. Series of joints connect the ceratohyale with the branchiostegalia. To the left and right two layers of the musculus geniohyoideus inferior are fastened to the ceratohyale. In specimen B the basihyale is 5,5 cm long, the ceratohyale 7 cm, the epihyale 3 cm. The height of this bone measures on the joint of basi- and ceratohyale 6,5 cm and on the joint of cerato- and epihyale 4,5 cm.

H. There are six branchiostegalia. The most dorsal branchiostegale (number VI) is considerably thinner and less ossified than the rest. Apparently it was absent in Van Dobben's specimen. Three of the branchiostegalia hinge in front with the ceratohyale, the other three are fastened to the epihyale by a less prominent joint. Caudally the branchiostegalia were not as Van Dobben describes fastened to the cleithrum by „sehnenartige Bildungen". Between the outer ends of the branchiostegalia and the pectoral girdle we found a loose tissue. Over the branchiostegalia

and the muscles between them there is a strong membrane, fastened along the pectoral girdle to the skin over a length of 15 cm. The branchiostegalia are mutually connected by the musculus geniohyoideus superior and the musculus hyoideus. The measurements in specimen B were:

branchiostegale	I	length	14 cm,	breadth 1 cm
	II		13	1
	III		14	1,5
	IV		15	1,5
	V		15,5	1
	VI		13	0,4

I. The pectoral girdle consists of the cleithrum, coracoid and scapula, forming a solid whole which is somewhat movably connected with the braincase via subcleithrum and postcleithrum. In the median left and right cleithrum are connected with each other by a strong ligament. The coracoid is movably connected with the skin by series of tendons. At the front the cleithrum is connected with the branchiostegalia by a membrane. At the back the musculus protractor clavicularis connects the pectoral girdle with the skin.

Muscles of the jaw mechanism.

The muscles of the head are completely symmetrical (fig. 2).

A. The musculus adductor mandibulae 1 extends from the back part of the upper jaw to the strong membranes around the eye. When contracting it pulls the ventricaudal part of the upper jaw caudad. In specimen B this muscle was 10 cm long and fully 1 cm thick. A musculus adductor mandibulae 2, as found in many fishes, is not to be separated from the musculi adductores mandibulae 1 and 3.

B. The musculus adductor mandibulae 3 extends from the dorsocaudal part of the lower jaw and the tendon between lower and upper jaw to the praeoperculum, the symplecticum and along the hyomandibulare to the pteroticum (underneath the musculus dilatator operculi). When contracting it pulls the dorsocaudal corner of the lower jaw caudad. In specimen B the total length was 17 cm, the thickness 2 cm.

C. The musculus dilatator operculi extends from the operculum to the pteroticum and sphenoticum. A small lobe is fastened caudally to the musculus levator operculi. When contracting it pulls the caudal part of the operculum dorsad and somewhat laterad. In specimen B the length was

6 cm, the breadth near the pteroticum 3,5 cm, the breadth near the operculum 0,5 cm and the thickness 1,5 cm.

D. The musculus levator operculi extends from the pteroticum to the operculum. When contracting it pulls the operculum dorsad and somewhat laterad. In specimen B the length was 6 cm, the breadth near the pteroticum 4 cm, the breadth near the operculum 1 cm, the thickness 2 cm.

E. A third muscle extends from the operculum to the pteroticum and the sphenoticum, medial from the musculus dilatator operculi and the musculus levator operculi. When contracting it pulls the operculum dorsad and somewhat laterad. In specimen B the length was 7 cm, the breadth near the pteroticum 6,5 cm, the breadth near the operculum 1,5 cm and the thickness 1 cm.

F. The uppermost lobe of the musculus geniohyoideus inferior is a more or less triangular muscle. To the left and right this muscle is attached to the ceratohyale (near the joints with the branchiostegalia) and to the third branchiostegale. In front the muscle is attached left and right to the inside of the dentale. Some tendons are fastened to the membrane in the bottom of the mouth. In the ventral median the left and right muscle come together and are fused with the skin. When contracting the hyale is pressed upwards. In specimen B the measures were, from the attachment to the dentale to the most caudal point of the attachement to the skin 11 cm, from the attachment of the skin to the joint at the branchiostegalia 15 cm.

G. A second lobe of the musculus geniohyoideus inferior is situated under the first and entirely free from it. Between the two lobes there is a loose tissue. Left and right part form one muscle. This lobe is fastened to the basihyale and the ceratohyale and to the first and second branchiostegalia. Ventrally there is to the left and right a small tendonlike connection with the musculus sternohyoideus, 3,5 cm broad and 1,5 cm long. When this muscle contracts the hyale is pressed upwards. In specimen B the breadth was 12,5 and the height 9,5 cm.

H. The musculus geniohyoideus superior extends between the branchiostegalia I and II, II and III. When it contracts the branchiostegalia turn with their ventral ends somewhat caudad. Between the branchiostegalia I and II the muscle was 0,3 cm thick, between the branchiostegalia II and III the muscle is 0,4 cm thick.

I. The musculus hyohyoideus extends from the praeoperculum along the branchiostegalia VI, V, IV and III over the membrane covering the gills. This muscle is attached to the inside of the praeoperculum (from de point where the epihyale is jointed to the praeoperculum) and more

caudally to one point of the hyomandibulare. Ventrally it curves around the gills. When it contracts the gill cavity deminishes. In specimen B the thickness above the branchiostegale VI was 0,3 cm, between branchiostegale VI and V 0,5 cm, between branchiostegale V and IV 0,2 cm and between IV and III 0,6 cm.

J. The musculus sternohyoideus connects the left and right of the pectoral girdle with the front border of the hyale. It lies within the musculus hyohyoideus. This muscle is fastened to the basihyale and to the foremost part of the ceratohyale. A number of smaller bundles extend from the ceratohyale to the first branchiostegale. A thick bundle extends along the first branchiostegale, dividing into a left and a right bundle, which extend to the left and the right cleithrum. Ventrally this muscle is connected by two small tendons with the musculus geniohyoideus. When it contracts the hyale is pulled caudad. In specimen B the length was 15 cm, the thickness 2,5 cm.

K. A muscle above the mouth cavity is fastened over the full length of the praeoperculum and the membraneous roof of the mouth extending between the left and right dentale, quadratum, symplecticum and hyomandibulare. When this muscle contracts, the mouth cavity is demimshed.

L. Above the cavity of the throat a muscle extends from the spinal column and the braincase to the oesophagus. When contracting this muscle widens the cavity of the throat behind the teeth.

Mechanism of the jaw.

From the shape of skeleton and muscles we have tried to reconstruct the manner in which they move:

I. Manner of opening.

1. Musculus levator and dilatator operculi pull the caudal half of the operculum dorsad and somewhat laterad. Sub- and interoperculum convey this movement to the lower jaw, which turns downwards at its joint with the quadratum. A ligamentlike connection between upper and lower jaw conveys this movement to the upper jaw, which turns upwards at its joint with the braincase (the mouth opens). Consequently praeoperculum and quadratum move a little in relation to the braincase by torsion.

2. The musculus protractor clavicularis internus pulls the pectoral girdle caudal. This movement is conveyed to the hyale via the branchiostegalia (mouth cavity enlarges).

3. The musculus sternohyoideus pulls down the hyale (mouth cavity enlarges). By turning of the hyale at its joints with the praeoperculum the

proximal parts of the branchiostegalia IV, V and VI move somewhat dorsad. They stay in place near the pectoral girdle. The proximal ends of the branchiostegalia I, II and III turn dorsad and at the same time laterad (gill cavity enlarges). Their outer ends near the pectoral girdle stay in place. The muscles between the cavity of the throat, the spinal column and the braincase pull open this cavity.

II. Manner of closing.

1. Musculus adductor mandibulae 1 and 3 pull respectively the upper jaw and the connection between upper and lower jaw caudad (the mouth closes). A sickle-like fold from the skin in the lower jaw closes the slit between upper and lower jaw, when water presses from within.

2. Musculus geniohyoideus inferior pulls the hyale dorsad (mouth cavity deminishes) and turns it at it's joints with the opercula, by which the branchiostegalia move mediad (gill cavity diminishes).

3. Musculus geniohyoideus superior pulls the branchiostegalia I and II and III together and increase the effect of the musculus geniohyoideus inferior.

4. Musculus hyohyoideus pulls the branchiostegalia together and directly deminishes the gill cavity.

5. The muscle above the roof of the mouth probably presses it downwards (mouth cavity smaller).

Comparison with the specimen, described by van Dobben.

While the jaw muscles of specimens examined by us proved to be almost indentical and agreed with the description of Gregory and Raven (1934) we found many differences from the specimen described by Van Dobben.

In this specimen were absent:

1° All the muscles at the left side of the head.

2° Several muscles at the right side of the head:

a. A part of the musculus adductor mandibulae. Strangely enough a part that neither morphologically nor functionally is to be separated from the rest of the muscle.

b. All the muscles between the branchiostegalia.

c. The musculus geniohyoideus inferior.

d. The musculus sternohyoideus.

3° Branchiostegale 1.

Van Dobben's specimen was entirely fresh and undamaged, which makes it seem improbable that these parts were indistinguishable after death.

The length agrees with that of our specimens (127 cm) and that of Gregory's specimen (118 cm), so that differences in age seem unlikely. It remains an open question, whether more of these strange deviations occur among the sunfishes and what may be the cause of this important degeneration.

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