CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

PART II. THE FEEDING MECHANISM OF THE ANGLER-FISH, *LOPHIUS PISCATORIUS* LINNAEUS

J. G. FIELD

Zoology Department, University of Cape Town
(Present address: C.S.I.R. Oceanographic Research Unit, U.C.T.)

INTRODUCTION

Lophius piscatorius Linnaeus is a species of wide distribution. It is commonly trawled from depths of ten fathoms and more around the South African coast and is also trawled off the coast of Europe. Fossils of the genus *Lophius* date back to the Upper Eocene (Gregory 1951). It is included in the family Lophiidae of the order Pediculati by Regan (Lophiiformes of Berg).

The mode of life of *Lophius* is quite well known. It lies still on the sea-bed (usually mud) camouflaged by its dark green to dark grey colour, its flat shape and by processes of skin which hang out like pieces of cloth around the edges of its flat ventral surface. By patient angling by means of its 'lure' (*illicium*) prey is attracted to its mouth and swallowed.

Chadwick (1929) and Wilson (1937) have observed the living fish in an aquarium. The latter author reviews the knowledge of the feeding behaviour up to his time. The only work which directly mentions the feeding mechanism is that of van Dobben (1935). This author describes only the principle of the mechanism for the protrusion of the upper jaw. His opinion of the muscular action bringing about the protrusion is criticised below. Van Dobben mentions the special skull-vertebral articulation. The only other aspect of the feeding mechanism dealt with by him is the principle behind the sucking-in of water during opening of the mouth. This is dealt with fully below and criticised.

MATERIALS

Two trawled *Lophius* were used for dissection. The first, 70 cm. long, was presumably adult as only the largest reach four feet (120 cm.) (Smith 1953). This was dissected fresh in order to judge the extent of movement of the parts. The second fish, only 45 cm. long was preserved in formalin and then dissected to confirm the observations made on the first. All measurements given are those of the larger specimen.

GENERAL DESCRIPTION

Lophius has a wide dorso-ventrally flattened head, about as wide as it is long. Medially are borne three modified dorsal fin rays, the anterior one being called the 'lure' or *illicium* (Fig. 1).

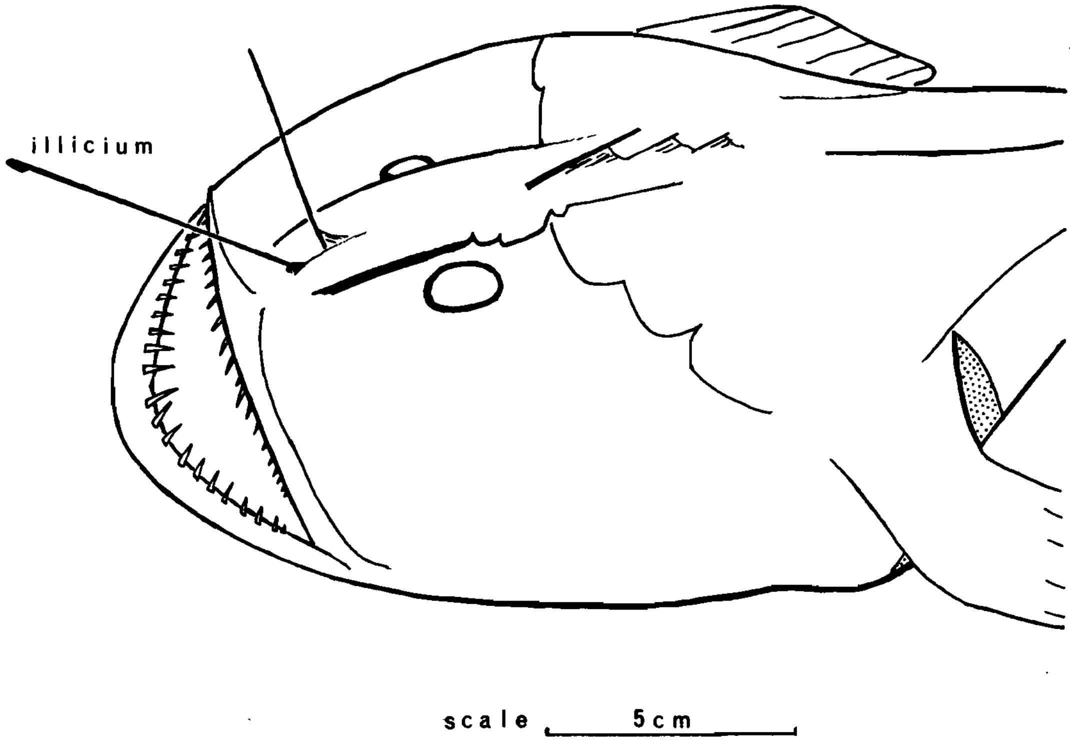

Fig. 1. *Lophius piscatorius* in its 'angling' position. Note the limb-like pectoral fins and the opening of the opercular tube which can be seen behind the left pectoral fin.

The flattened and widened skull forms a dorsal boundary to the head. Wide upper and lower jaws form the antero-lateral border. The eyes are dorsally directed and set about 5 cm. apart. The mouth is also directed upwards and when the mouth is fully opened the animal cannot see directly ahead.

The opercular apparatus forms the dorso-lateral border of the head. Behind this lies the dorsal and posterior part of the pectoral girdle. Behind the girdle and in the axis of the fin is situated the opercular opening. This is the aperture of an elongated opercular chamber passing backward from the gills under the medial surface of the opercular bones, across the lateral surface of the cleithrum and below the pectoral fin. Its muscular wall is supported ventrally by greatly elongated branchiostegal rays projecting from the hyoid arch.

The ventral surface of the fish is completely flat. All the lower portions of the arches (mandibular, hyoid and branchial) and also the lower part of the pectoral girdle lie in forwardly-directed U's flat on the substratum. The pelvic girdle is attached to the medial, anteriorly-directed part of the pectoral girdle. It supports two muscular, very leg-like pelvic fins. The lateral extremities of the pectoral girdle bear pectoral fins which are also muscular and somewhat leg-like. Both sets of fins are believed to lever the fish up during the capture of prey (Wilson 1937; Gregory 1933). The thick, fleshy tail contributes much muscle to the operation of the feeding mechanism.

THE STRUCTURE OF THE 'LURE' AND ITS MECHANISM (Fig. 2)

Lophius has three dorsal fin rays which have migrated forwards to take up a position on top of the skull. The first two rays share a common supporting plate which is partly bone and partly, posteriorly, cartilage. It is possible that even the larger specimen was not fully adult and the basal plate may become completely ossified in older specimens. The ray used in 'angling', the illicium, the first of the three, is attached at the anterior end of the basal plate called by Gregory (1951) the *pterygiophore.*

The flexible illicium forms at its base an almost complete ring of bone, the bottom of the ring being completed by a ligament. The ring fits through a hole in the median dorsal ridge of the pterygiophore. The articulation provides freedom for almost 180° of rotation in an anterior-posterior arc so that the illicium can be moved in any direction from back flat against the head to directly forwards. It also allows considerable lateral movement.

The second dorsal ray has a slightly different articulation. Its proximal end bears two prongs which fit on either side of the dorsal ridge on the pterygiophore. The ray is held in position by connective tissue and also the muscles which move it. The same type of articulation is found in all the other dorsal rays.

The third ray can be erected to about 30° only from its position flat on the skull. It is supported on a separate dorsal plate. This suggests that the pterygiophore is formed by the fusion of two basal plates.

Both the pterygiophore and the ascending processes of the premaxillae (see p. 51) rest in a longitudinal trough on the dorsal surface of the skull. The trough is bounded laterally by serrate ridges of the frontal bones and it is floored by the frontals and the vomer. The anterior part of the pterygiophore overlaps the ascending processes above a groove between the right and left processes. The basal plate of the third dorsal ray is situated above the otic region of the skull.

Muscles

The pterygiophore is operated by two pairs of muscles. A posterior pair of retractors originates in the trough of the skull on either side of the third ray and inserts by a tendon onto the pterygiophore on either side of the second ray. Each of a very thin lateral pair of muscles originates on the skull on the medial side of the ridge formed by the frontal and runs obliquely backwards towards the midline to insert on the underside of the pterygiophore about 1 cm. behind the second ray. These lateral muscles probably function as protractors. Connective tissue strands anchor the anterior end of the pterygiophore to the underlying connective

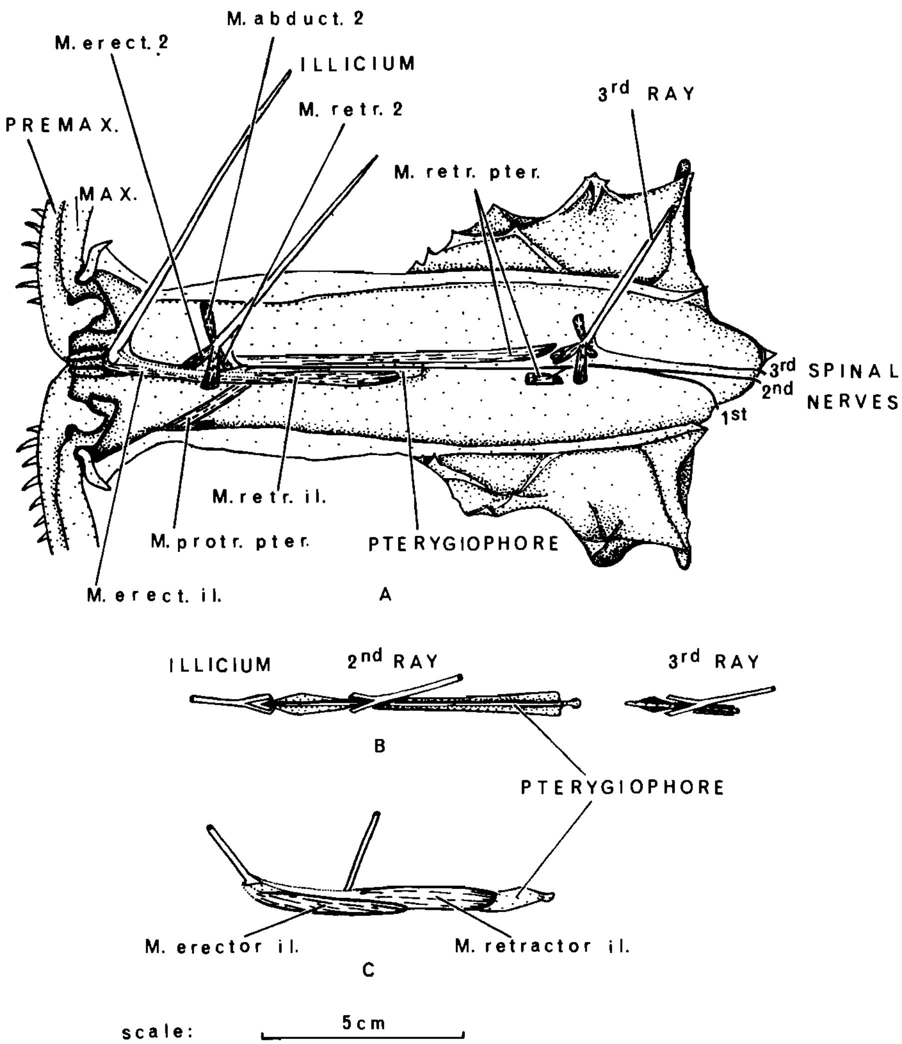

Fig. 2. ILLICIUM AND DORSAL RAYS.

A. Latero-dorsal view of the angling apparatus. The left pterygiophore retractor muscle has been cut to show the nerves of the left side. The third dorsal ray has been erected more than is normal in the living fish.

B. Dorsal view of the first three rays and their basal plates with all the muscles removed.

C. Lateral view of the illicial muscles after removal of the other muscles.

For abbreviations see p. 65.

tissue sheet above the ascending processes of the premaxillae. Movement of the pterygiophore is quite independent of that of the upper jaw.

The second and third rays are moved by three pairs of muscles in the same manner as the normal dorsal fin-rays of teleosts (Gregory 1951). In the case of the second ray an anterior pair of erector muscles originates on the sides of the pterygiophore about 2 cm. in front of the ray and mesial to the tendons of the illicial retractors and inserts onto the front of the fork in the ray. Their contraction raises the ray from its resting position flat on the skull. A pair of lateral abductor muscles originates on the skull on either side of the pterygiophore and inserts on the sides of the fork in the ray. This pair of muscles moves the ray from side to side. The retractor muscles are very small and short, originating on the basal plate behind the articulation and inserting on the ray above the articulation. These serve to lower the rays. The muscles of the third ray are similar.

The illicium is attached at the extreme front of the pterygiophore above the sliding ascending processes of the premaxillae. Two pairs of illicial muscles are well developed and run down the sides of the pterygiophore. The retractor muscles originate along the sides of the pterygiophore behind the second ray and run forward to insert by tendons on the posterior surface of the illicial articulatory ring. These pull the illicium back to lie flat on the skull. The erector muscles originate on the medial ventral keel of the pterygiophore. They lie under the pterygiophore and under the retractor muscles on either side and run forwards to short tendons inserting on the *anterior* surface at the top of the illicial articulatory ring. Contraction of the erectors pulls the illicium up and forwards through an arc of 180° from the resting position flat on the skull. The arrangement of the illicial muscles and the ring articulation of the illicium permit nearly 90° of extra rotation as compared to the second ray.

The two pairs of illicial muscles are theoretically capable of moving the freely articulated illicium to almost any position because lateral movement could be achieved by contraction of only the right or left muscle of a pair. Observation of the living animal is necessary to determine whether the illicium is in fact moved from side to side as well as backward and forward.

The muscles of the first two dorsal rays and the pterygiophore are innervated by a nerve derived from elements of the first and second spinal nerves (Fig. 2). This supports the generally accepted view that the illicium is derived from a spine of the dorsal fin which has migrated forwards.

THE JAW-OPERCULAR COMPLEX

The Upper Jaw

The maxillae and premaxillae are long curved bones forming the front edge of the upper jaw. The maxilla articulates with the anterior surface of the skull. No attempt will be made here to discuss the homologies of the bones of the skull. Suffice it to say that the modifications in *Lophius* appear to be an extension of those described by Gregory (1933) for *Antennarius.* In the latter species Gregory states that the 'small mallet-like lacrymal' is fused with the anterior part of the pterygo-palatine arch or palatine bone. This appears to be the case in *Lophius* too, and it is against this composite lacrymal bone that the maxilla articulates and

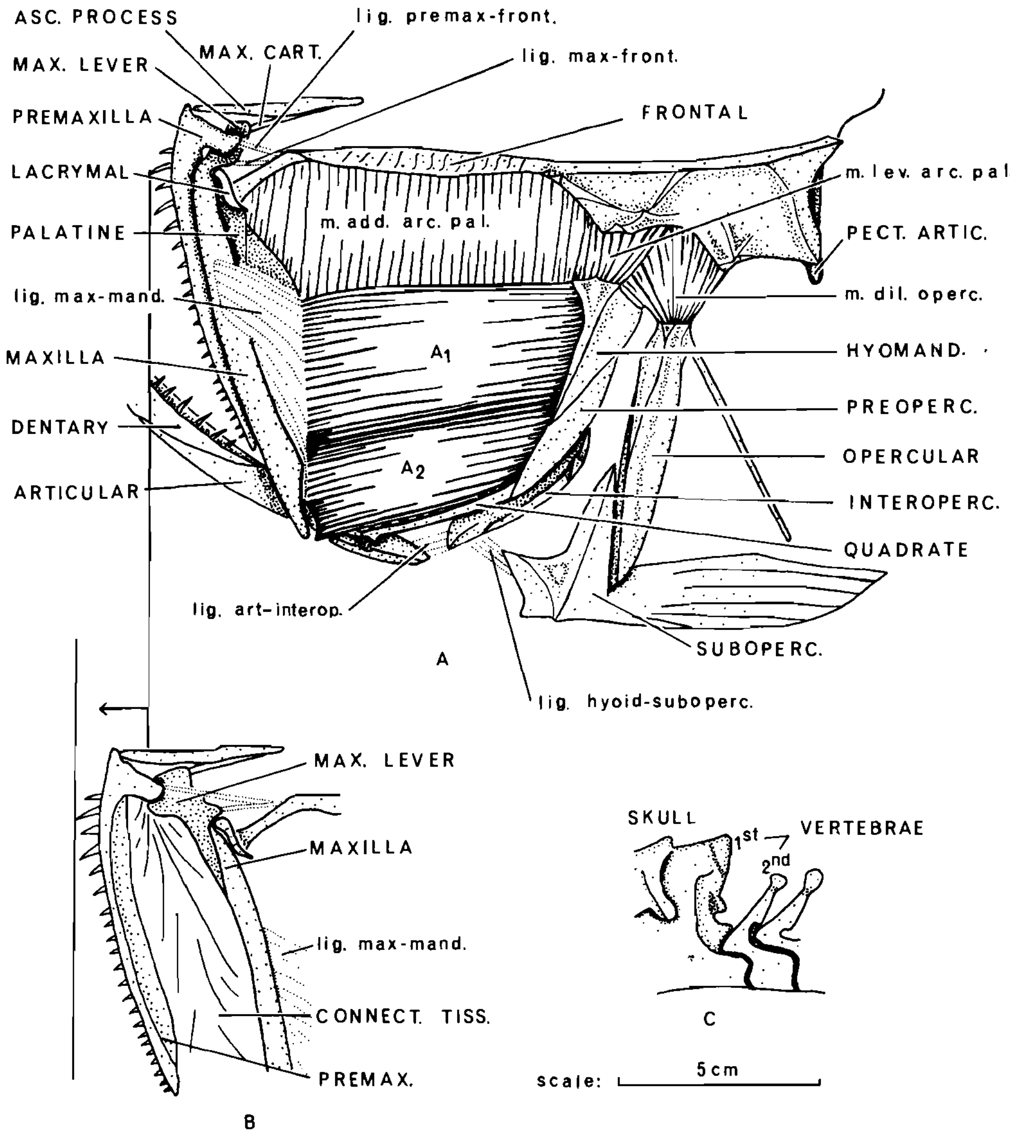

Fig. 3. **THE SKULL, OPERCULAR APPARATUS AND JAWS.**
A. Dorso-lateral view of the left side of the head in the resting position, showing superficial muscles.
B. The premaxilla protruded from the resting position, showing the action of the maxillary lever.
C. Lateral view of the skull-vertebral articulation. Note that the first vertebra is fused to the skull.
For abbreviations see p. 65.

to which it is held strongly by connective tissue (Figs. 3A and 3B). There is also a ligament connecting the maxilla with the frontal, probably homologous with one of the 'crossed ligaments' described by Eaton (1935). The proximal end of the maxilla, medial to its articulation with the lacrymal, is curved sharply downwards and slightly backwards in the resting position. If the maxilla is rotated backwards about a transverse horizontal axis, this downward projection rotates forward through an arc of about 60°. It will be referred to as the maxillary lever. The alveolar process of the maxilla is attached to the lower jaw by the maxillo-mandibularis ligament which will be described later.

The right and left premaxillae are held together by connective tissue in the midline. This junction allows some movement between them, as during protrusion of the lower jaw. The ascending processes of the premaxillae are strongly developed and separately ossified. They are bound to one another by connective tissue and slide in the trough on the front of the skull, lubricated by a jelly-like substance. Dorso-ventral movement is prevented by connective tissue which anchors the processes to the floor and sides of the trough and by a transverse bridge of connective tissue stretching between the lacrymals above the processes. The latter sheet also provides a floor on which the pterygiophore of the first two dorsal rays slides. The ascending processes, thus, can slide only forwards and backwards during protrusion and retraction of the upper jaw. This ensures that the teeth on the premaxillae maintain a constant angle and cannot be rotated outwards. Between the maxillary lever and the posterior end of the ascending process of the premaxilla is a section of what appears to be cartilage, possibly chondrified ligament, this will be referred to as the maxillary cartilage.

The articular process of the premaxilla, situated lateral to the ascending process, fits against the maxillary lever and is held to it by connective tissue. Its movement is controlled by a ligament attached to the skull.

The arrangement of the upper jaw bones is such that if the maxilla is rotated backward around its transverse axis, the maxillary lever rotates forward through 60° resulting in a forward displacement of about 2 cms. The maxillary lever pushes forward the articular process of the premaxilla and at the same time exerts a forward pull on the ascending process through the medium of the maxillary cartilage. Since rotation of the premaxilla is prevented as described above, the whole bone shifts forward, its ascending process sliding in the trough of the skull (Figs. 3A and 3B).

In the upper jaw teeth are borne on the premaxilla, vomer and palatine bones. The larger, proximal teeth on the premaxilla are reflexible.

The Lower Jaw

The two halves of the lower jaw are held to one another firmly in the midline by connective tissue, permitting a change in the angle between them, as occurs with the narrowing of the buccal cavity.

The posterior end of the jaw is connected to the interopercular by a ligament (Fig. 4). The articular surface of the quadrate is shaped like a bent rolling pin and fits into a groove on the dorsal surface of the articular. This articulation permits only a limited up and down movement of the lower jaw through an angle of about 30°. Immediately in front of the

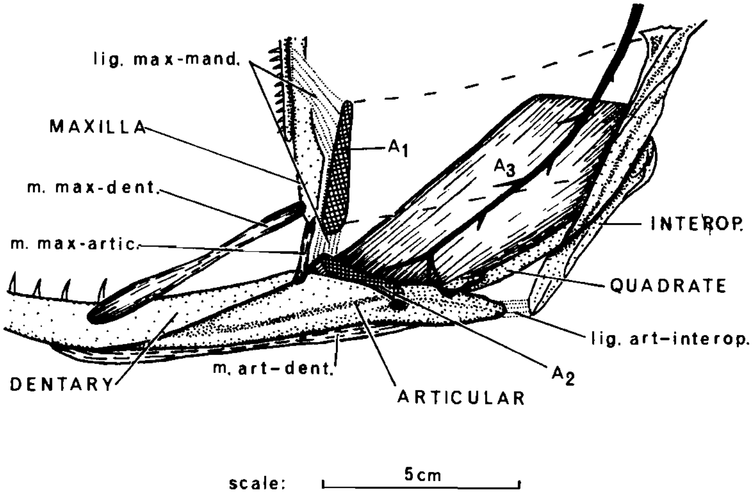

Fig. 4. Lateral view of the left side of the jaw with the upper jaw raised to show the maxillo-mandibular muscles. The broken line indicates the position of muscle A_1 which has been cut at its insertion on the maxillo-mandibular ligament. Muscle A_2 has been cut at its insertion on the coronoid process of the mandible. The ramus mandibularis of the Vth cranial nerve is superficial to muscle A_3.
For abbreviations see p. 65.

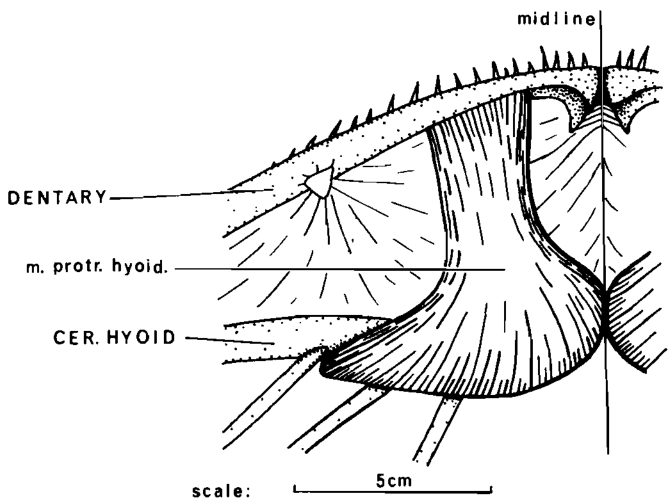

Fig. 5. Anterior view of the right protractor hyoidei. The mandible has been lifted up and the hyoid arch pulled back and down to extend the protractor hyoidei. The first three branchiostegal rays can be seen near their origin on the ceratohyoid.
For abbreviations see p. 65.

articulation the articular bone bears a low coronoid process for the insertion of adductor mandibulae muscles and the maxillo-mandibularis ligament.

The dentary bone bears teeth, of which the innermost ones are reflexible.

Hyoid arch and opercular bones

In association with the great enlargement and flattening of the head, the hyomandibular and opercular complex is directed out laterally instead of vertically downwards as in most fish.

The hyomandibular articulates with the skull by a wide facet in the otic region and together with the quadrate and preopercular forms a curved arch reaching outwards and forwards to the jaw articulation. All four opercular bones are present (Fig. 3A). The opercular is a forked bone with a stout anterior limb and a very slender posterior limb. The subopercular in both specimens was only firmly ossified anteriorly. Its posterior end consisted of flexible rays.

The ventral part of the hyoid arch is normal in position and structure. Along its length the ceratohyal bears six long branchiostegal rays (Figs. 6 and 7) which support the lateral and ventral sides of the pumping respiratory tube which runs under the cleithrum and opens behind the pectoral fin. Its opening is supported by a ray projecting from the cleithrum above and by branchiostegal rays beneath.

The muscles

Three sections of the *adductor mandibulae* are present, of which two are superficial and one deep. Of the former the more medial represents A_1 (Vetter's terminology). It originates on the front of the hyomandibular and inserts on the maxillo-mandibularis ligament (Fig. 3A). The muscle is about 0·5 cm. thick near its medial edge and about 1 cm. thick near the lateral edge. The maxillo-mandibular ligament has a broad attachment to the maxilla, partly along the *dorsal* surface of the latter (the medial part) and partly along its posterior border (the lateral part). The other end of the ligament attaches to the coronoid process of the lower jaw (in front of the articulation). Thus contraction of muscle A_1, pulling on the ligament, will not only pull the lower jaw up but will also rotate the maxilla backwards and thus protrude the premaxilla.

The lateral superficial part of the adductor represents section A_2 (Fig. 3A). It originates on the front of the hyomandibular and on the quadrate and inserts partly on the maxillo-mandibularis ligament but mainly on the coronoid process of the lower jaw (Fig. 4). Its deepest part is inseparable from the intramandibularis section of the adductor ($A\omega$ of Vetter) situated in the hollow of the lower jaw. Contraction of these muscles will enhance the effect of A_1 in raising the lower jaw.

A thin, deep part of the adductor represents section A_3 (Fig. 4). It originates on the metapterygoid, symplectic and quadrate bones and has a tendinous insertion on the inner side of the coronoid process of the lower jaw. Its fibres are more oblique than those of A_1 and A_2 and contraction raises the lower jaw and also pulls it towards the midline.

The adductor muscles are innervated by branches of the ramus mandibularis of the trigeminal nerve, which on its course runs internal to A_1 and A_2 but superficial to A_3.

A set of small tendinous muscles around the jaw articulation are of particular interest as they have not, to my knowledge, been reported in other fish. They are possibly derived from the ventral part of the masticatory muscle plate.

Of these a slender maxillo-dentary muscle stretches from the distal end of the maxilla to the outer surface of the dentary about 8 cm. in front of the articulation. A shorter, very slender and largely tendinous maxillo-articular muscle stretches from the distal part of the maxilla to the dorsal edge of the articular at the highest point of the latter bone (Fig. 4). These two muscles may perhaps be homologous with the palato-mandibularis muscle reported in *Amia* and *Lepidosteus* (Edgeworth 1935, pp. 49–50). They would appear to replace the anterior section of the maxillo-mandibularis ligament (van Dobben 1935) and to function during the closing of the mouth instead of during the opening. In *Clupea* and most Perciformes the two sections of the maxillo-mandibularis ligament are responsible for transmitting the force of the lower jaw to the maxilla so bringing about its rotation and the protrusion of the premaxilla during the *opening* of the mouth. In *Lophius*, as has been shown above, the adductor muscle (A_1) and the section of the maxillo-mandibularis ligament inserting on the maxilla can rotate the maxilla, and this would occur during the *closing* of the mouth. This action would be enhanced by the simultaneous contraction of the maxillo-dentary and maxillo-articular muscles which would assist in raising the lower jaw.

A third and largely tendinous muscle, the articulo-dentary, stretches between the articular and the dentary on the ventral surface of the lower jaw (Fig. 4). Slight movement is possible between the articular and the dentary and this may be brought about by the maxillo-dentary and the articulo-dentary muscles acting as an antagonistic pair.

The *adductor arcus palatini* originates along the ventro-lateral edge of the skull (mainly on the parasphenoid) and inserts onto the edges of the metapterygoid and endopterygoid (Fig. 3A). Contraction helps pull the jaw-opercular complex inwards and upwards. This narrows the angle between the mandibles, pushes them forward a little and may help lower the jaw. Continuous with this is a small adductor hyomandibulae, inserting onto the underside of the hyomandibular.

The *levator arcus palatini* originates on the sphenotic ridge and inserts on the outer surface of the hyomandibular (Fig. 3A). It probably serves as an attachment muscle because it does not have enough leverage to raise the long hyomandibular and its associated complex outwards.

The opercular bone has the usual dilatator muscle originating on the pterotic and the posterior surface of the hyomandibular and inserting on the outer surface of the opercular. Internally there are two fused levators and a small adductor which are antagonistic to the dilatator. They pull the opercular inwards, narrowing the opercular cavity a little.

Muscles of the ventral surface

The *intermandibularis anterior* is a diffuse muscle consisting of some short, transverse fibres connecting the two halves of the lower jaw immediately behind their junction.

The *protractor hyoidei* is represented by a wide thick band of muscle attached anteriorly to the dentary. Posteriorly it widens and approaches its counterpart to insert on a fascia near

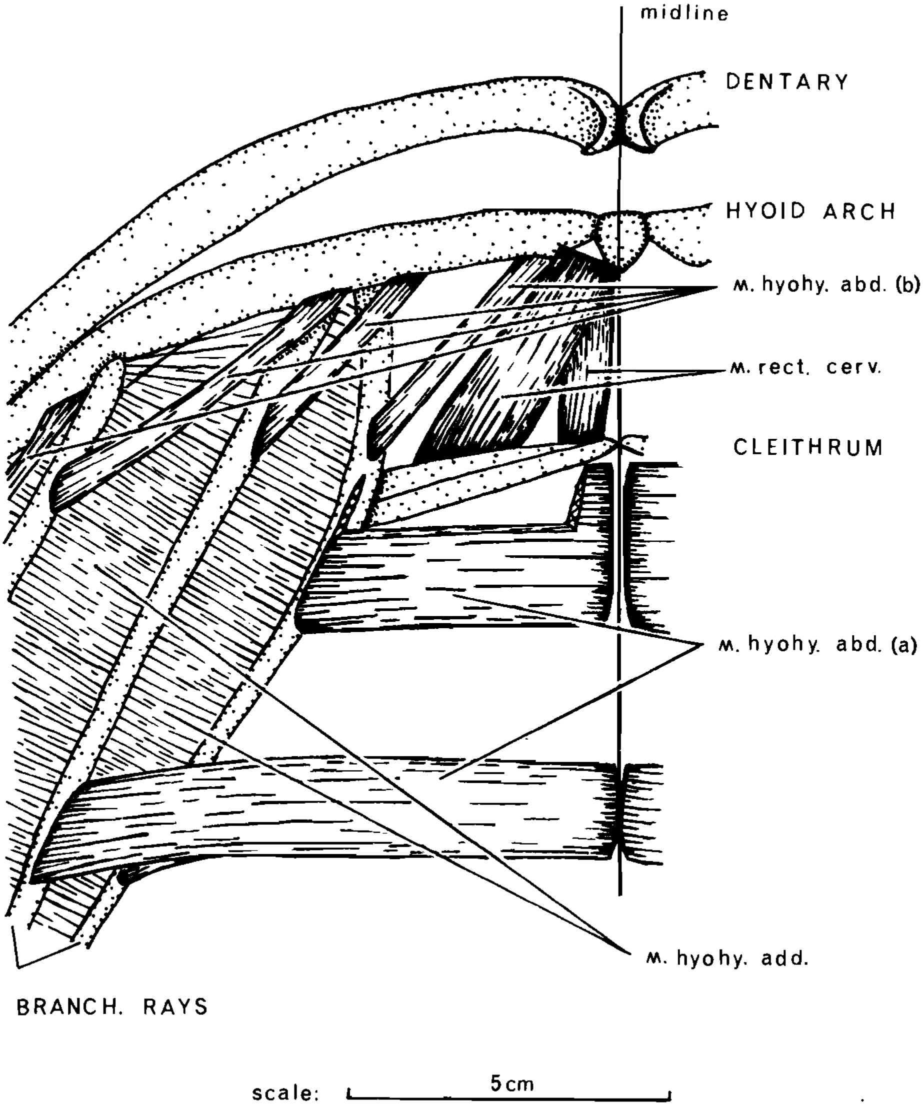

Fig. 6. Ventral view of the ventral superficial muscles of the right side after removal of the protractor hyoidei. The branchiostegal rays are in abduction.

For abbreviations see p. 65.

the midline and laterally on the ceratohyoid (Fig. 5). Contraction of this muscle could either lower the jaw if the hyoid arch were fixed, or protract and raise the hyoid arch if the lower jaw were fixed. Since the movement of the lower jaw is somewhat limited and unimportant during prey capture (see p. 63) it is unlikely that it would require a muscle of this size to aid gravity in lowering the jaw. The more probable function is to raise the hyoid arch. When the head is raised above the substratum and the mouth open, as during prey capture, the hyoid arch sags below the jaw leaving a considerable gap between them. Contraction of the protractor hyoidei as the mouth closes would reduce this space.

The protractor hyoidei has a double innervation from cranial nerves V and VII. This is in agreement with Edgeworth's hypothesis (1935) that the muscle is derived partly from the intermandibularis posterior and partly from the interhyoideus.

The *rectus cervicis* (sternohyoid) stretches between the pectoral girdle and the hyoid arch and is split into two sections on each side (Figs. 6 and 7). The lateral section is the larger of the two and inserts onto a ligament uniting the ventral parts of the hyoid arch. The medial section inserts onto the basihyoid dorsal to the lateral section.

Contraction of the rectus cervicis pulls together the pectoral girdle and hyoid arch. Therefore this muscle also has two possible functions, either to protract the girdle during closing of the mouth or to retract and lower the hyoid arch during opening of the mouth. The former action could take place automatically owing to the weight of the sinking body on the girdle whereas the latter action would seem to require definite muscular action in order to create the suction necessary for ingestion. It is therefore considered that the function of the rectus cervicis is to retract and lower the hyoid arch and so increase the cavity of the mouth.

The rectus cervicis is innervated by the hypoglossal branch of the first spinal nerve.

The *hyohyoideus* muscle is complex and differentiated in a number of different parts responsible for moving the branchiostegal rays (Fig. 6).

The *hyohyoidei abductores* on contraction spread the rays apart and enlarge the opercular tube. They include:

(*a*) Two transverse bands of muscle originating on a connective tissue fascia in the midline and inserting on the more ventral rays. An interior band originates at the level of, and ventral to, the cleithrum and inserts on the first ray. A more posterior band originates behind the cleithrum and inserts on the first and second rays.

(*b*) Four small bands of muscle originating on the ceratohyoid and passing obliquely outwards to insert on the first four rays.

The *hyohyoidei adductores* on contraction draw the branchiostegal rays together and reduce the size of the opercular tube. They are thin muscle sheets stretching transversely between successive rays and from the sixth ray to the ventral surface of the subopercular bone and together contribute to the ventral wall of the opercular tube.

The hyohyoideus muscle is innervated by the ramus hyoideus of the facial nerve.

THE BRANCHIAL ARCHES

Description

The branchial skeleton has spread out laterally in accordance with the general widening

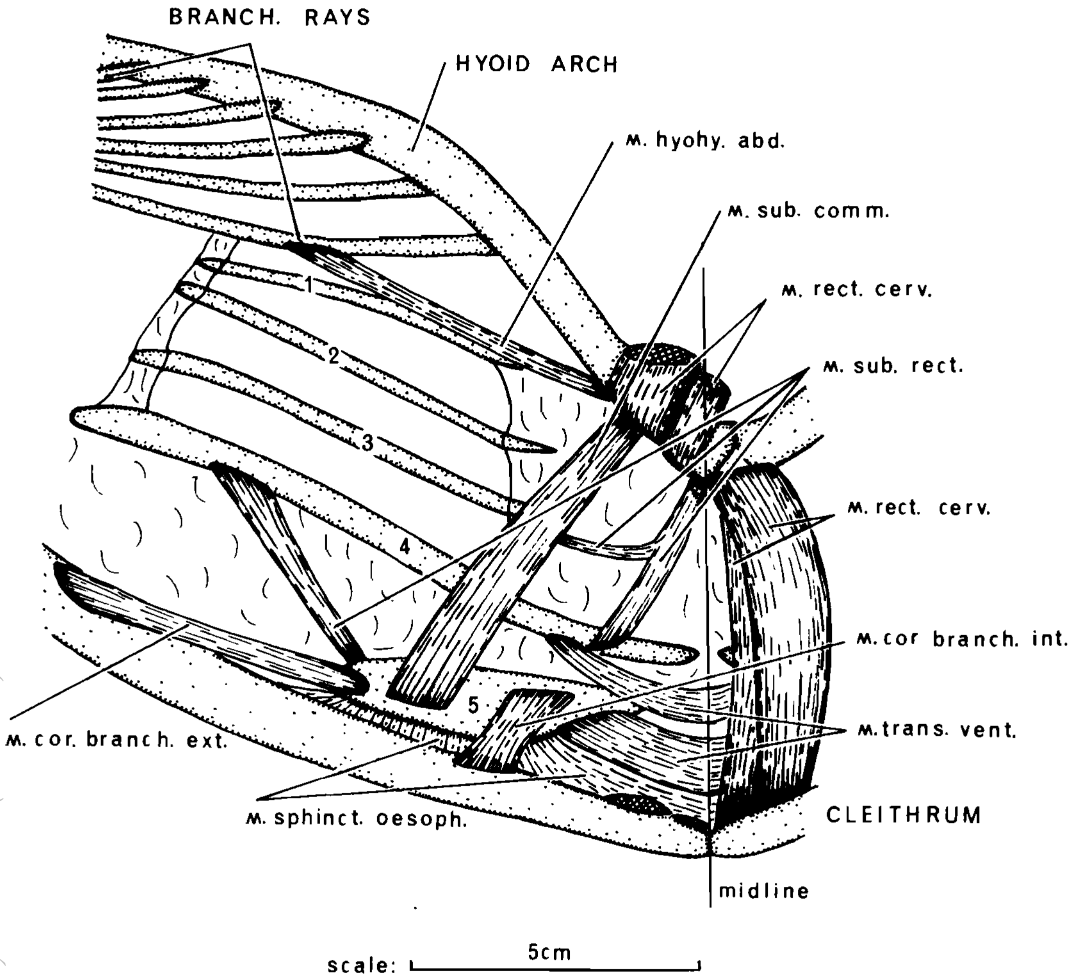

Fig. 7. Ventral view of the branchial apparatus of the right side. The branchiostegal rays have been displaced laterally to expose the branchial arches and their muscles. Both hyoid arch and pectoral girdle have been pulled backwards as far as they will go. The dorsal ends of the ceratobranchials have been shifted forwards and outwards. Right rectus cervicis muscle removed.

For abbreviations see p. 65.

and ventral flattening of the head. Five branchial arches can be recognised; of these only the fourth is complete and the fifth is represented by a ceratobranchial only. The ventral ends of the first three arches do not meet in the midline but are held by elastic tissue. A median copula is likewise absent. This provides the necessary elasticity for the great enlargement of the mouth cavity, particularly during the lowering of the floor. Only three sets of gills are present, borne on the ceratobranchials of the first to third arches which lie parallel to one another on the floor of the mouth behind the ceratohyoid (Fig. 8).

The fifth arches are represented only by their cerato-elements, which are flat tooth-bearing plates 6 cm. long lying close to one another near the midline. Their anterior ends are close together and the posterior ends diverge from the midline slightly. The ventral parts of the other arches lie parallel to the fifth ceratobranchial on each side, the first arch being furthest from the midline.

The fourth arches are complete and their ventral ends are loosely connected to one another. Their epi-elements are strongly developed for the support of the pharyngobranchials of arches two to four.

The second and third arches consist of cerato-elements, very slender epi-elements and short flat pharyngo-elements.

The first arch has a normal cerato-element and, dorsal to this, a triangular plate representing a reduced epi-element. No basibranchials occur in the first three arches but hypobranchials may be represented by the narrowed ventral ends of the cerato-elements of these arches.

The pharyngobranchials of the second to fourth arches are short, flat plates closely attached to one another and bearing curved pharyngeal teeth. The whole apparatus can be moved on the epibranchials to swing the teeth from their retracted position forwards into a functional position.

The muscles

The branchial muscles are concerned in movements of the branchial arches during respiration and the dorsal ones are particularly well-developed and modified in relation to the pharyngeal teeth.

The ventral muscles include (Fig. 7):

(*a*) *Transversi ventrales:* two muscles stretching from a fascia in the midline to the fourth and fifth branchial arches respectively. The second muscle is continuous with the *sphincter oesophagi* at its posterior end. Some transverse fibres between the ventral ends of the first three arches may represent transversi ventrales but they are not differentiated into distinct muscles.

(*b*) *Obliquus ventralis:* this may be represented by a muscle continuous with the sphincter oesophagi and stretching between the fourth epi- and cerato-branchials and the only element of the fifth arch (Fig. 8).

(*c*) *Coraco-branchialis:* a muscle stretching from the fifth ceratobranchial to the cleithrum and including both internal and external parts (Fig. 7).

(*d*) *Subarcuales recti:* four muscles are represented. The first and second originate together on the ventral part of the hyoid arch and pass obliquely backwards separate from one another to insert on the third and fourth arches respectively. The third muscle is more lateral and stretches from the fourth ceratobranchial obliquely back-

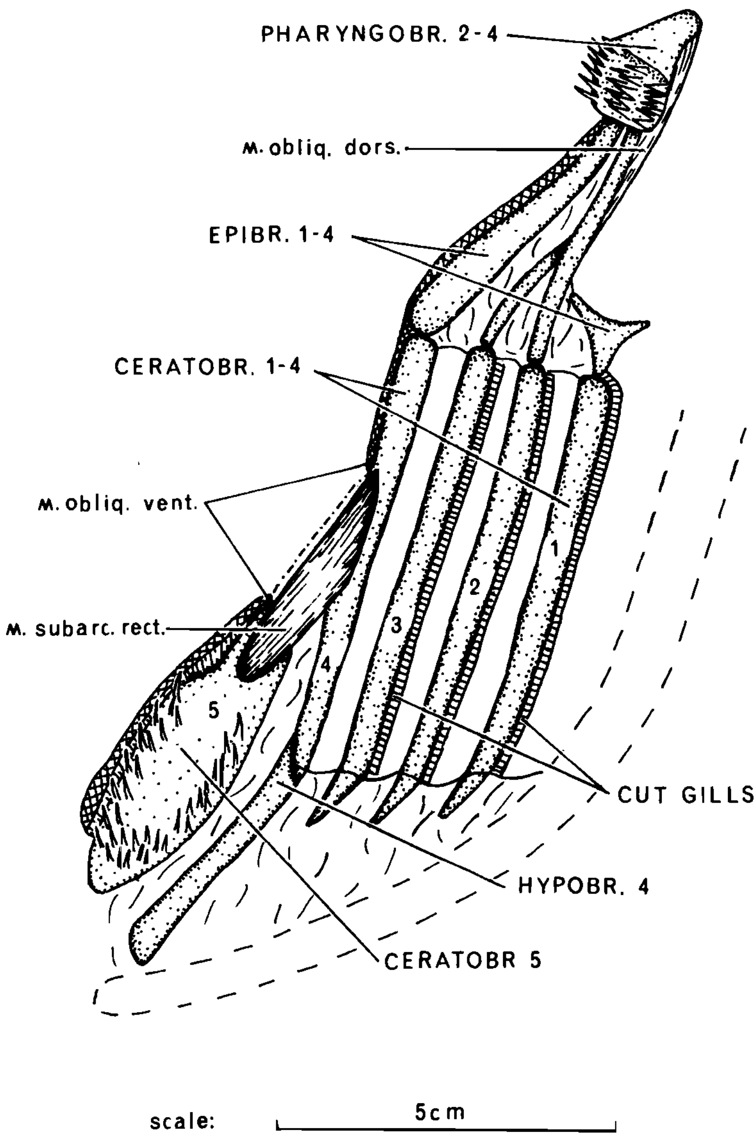

Fig. 8. Dorsal view of the branchial arches of the left side removed from the animal. The dorsal parts of the arches are shown pulled back- and lateralwards and some muscles have been removed to expose the arches. The obliquus ventralis muscle has been cut. The broken line indicates the position of the left ceratohyoid relative to the ventral parts of the gill arches in the live fish.

For abbreviations see p. 65.

wards and inwards to the fifth ceratobranchial. The fourth muscle stretches from the ceratohyoid to the fifth ceratobranchial and represents a *subarcualis rectus communis* (Fig. 7).

The dorsal muscles include:

(*a*) *Levatores arcuum branchialium:* the levators all originate on the ventral surface of the skull. The levator of the first arch is missing in accordance with the reduction of the dorsal part of this arch. The second levator is divided into internal and external sections, the former inserting onto the pharyngobranchial and the latter onto the epibranchial of the second arch. The third levator is undivided and inserts onto the third pharyngobranchial. The fourth levator, also undivided, inserts on the fourth epibranchial (Fig. 9).

(*b*) *Transversus dorsalis:* stretching from a fascia in the dorsal midline to the branchial arches. An anterior section inserts on pharyngobranchials 2 and 3 and a posterior section on epibranchial 4 (Fig. 9).

(*c*) *Obliquus dorsalis:* only one muscle occurs stretching from the epibranchial to the dorsal surface of pharyngobranchial 2 (Fig. 8).

(*d*) *Epiarcualis rectus:* only one muscle occurs stretching from epibranchial 4 to pharyngobranchial 3 (Fig. 9).

(*e*) *Retractor arcus branchialis:* a well-developed muscle originating on the ventral surface of the vertebral column and passing forwards to insert on the ventral parts of the third and fourth pharyngobranchials (Fig. 9).

(*f*) *Attractor arcus branchialis:* one representative stretching between the epi- and ceratobranchial of the fourth arch (Fig. 9).

Mechanism

The dorsal pharyngeal teeth and their supporting bones (the 2nd to 4th pharyngobranchials) form a complex which can articulate on the corresponding epibranchials to rotate the teeth into a functional position and which can also be shifted backwards and forwards in the roof of the pharynx. These teeth bite against the tooth-bearing lower pharyngeal bones, the fifth ceratobranchials.

The erection of the dorsal teeth is brought about as follows (Fig. 9B): the dorsal ends of the pharyngobranchials are pulled backwards by contraction of the obliquus dorsalis 2 and the levator arcus branchialis 2 (internal part) and 3, thus rotating the whole apparatus on the joint with the epibranchials and swinging the teeth forwards. The food can thus be grasped between the erected dorsal and ventral pharyngeal teeth.

Contraction of the retractor arcus branchialis pulls the whole apparatus, including the food, backwards in the pharynx.

Depression of the teeth is due to the contraction of the epiarcualis rectus which inserts on the third pharyngobranchial ventral to its articulation.

Forward movement of the apparatus could be brought about by the expansion of the pharynx in the next respiratory cycle.

Movement of the ventral tooth-bearing bone could similarly be by muscles such

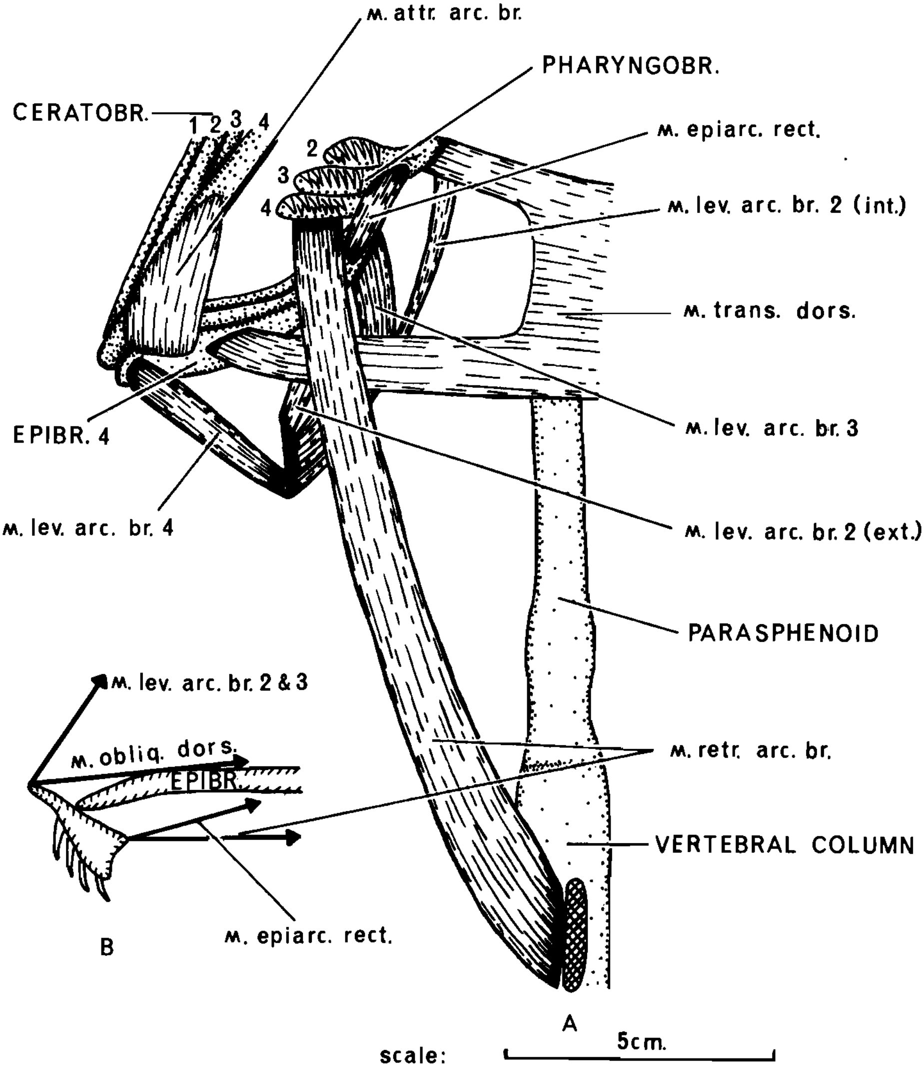

Fig. 9. A. Ventral view of the dorsal parts of the branchial arches of the right side. The levator muscles all originate on the ventral surface of the skull.

B. Diagrammatic lateral view of the dorsal pharyngeal apparatus showing the effects of the more important muscles on the articulation between the tooth-bearing pharyngobranchials 2 - 4 and epibranchials 2 - 4.

For abbreviations see p. 65.

as the coraco-branchialis, the subarcualis communis and the transversus ventralis 5.

Undoubtedly all the small branchial muscles have a part to play in adjusting the position and movement of the pharyngeal teeth during the feeding and respiratory cycle, but although some of these functions can be guessed at, it is not yet possible to correlate them with the correct phases of the cycle.

OTHER PERTINENT FEATURES OF THE ANATOMY

The attachment between the pectoral girdle and the skull

In the Lophiidae the short and broad posttemporal bone is incorporated in the skull roof and firmly attached to the epiotic, pterotic and exoccipital. Against its ventral surface articulates the upper bone of the pectoral girdle, the supracleithrum. The dorsal surface of the supracleithrum bears a groove into which fits a rounded lateral process of the posttemporal. This articulation permits the transversely oriented supracleithrum to rotate about a horizontal axis, so bringing the whole girdle from a forwardly-directed position into an almost vertical position under the body. This movement is due to contraction of hypaxial body muscles inserted onto the posterior surface of the cleithrum.

The articulation between skull and vertebral column (Fig. 3C)

In the Lophiidae the first vertebra is fused onto the posterior region of the skull, thereby, according to Gregory 1933, reinforcing the occiput against the forces exerted by the long suspensorium and pectoral girdle. Between the first and second vertebrae there exists an articulation which permits upward movements of the head but no sideways movement. The enlarged centrum of the first vertebra projects backwards as a shelf which fits into a transverse groove on the anterior surface of the second centrum. Since the neural arch of the first vertebra is vertically orientated and that of the second slopes backwards at an angle of about 30° a gap is left between them permitting raising of the head.

The upward movement of the head is due to contraction of epiaxial body muscles which insert on the posterior surface of the skull by strong, wide tendons.

DISCUSSION

Almost all the anatomy of *Lophius* is specialised towards feeding. As van Dobben (1935) says "Das Tier lebend zu erhalten".

From a study of the anatomy of *Lophius* and from observations by Chadwick (1929), van Dobben (1935) and Wilson (1937), the following hypothesis on the feeding mechanism is put forward.

At rest the animal lies flat and camouflaged on the sea bottom with its illicium retracted in the dorsal trough, flat against the head (Chadwick, Wilson). The lower jaw projects, resting flat on the bottom, below the upper jaw. The upper jaw rests against the skull medially in the retracted position and the mouth is slightly open because the upper jaw does not meet the projecting lower jaw. The gills, in the floor of the mouth, are freely exposed to the respiratory water current.

Van Dobben observed no movements of the jaws or, surprisingly, of the operculum during respiration. From the anatomy this is not surprising considering the weak development of the opercular muscles and levator arcus palatini. These muscles probably act mainly as fixation muscles. The creation of the respiratory current is taken over by the well-developed hyohyoideus muscle in the wall of the tubular opercular cavity. Contraction of the abductor elements enlarges the opercular cavity and sucks water in through the gills. Contraction of the adductor elements reduces the size of the chamber and expels water through the opercular opening.

Chadwick and Wilson observed that when prey was sighted the animal raised its illicium and flicked it about. The dark fold of skin at the end of the illicium evidently attracted prey which approached the lure. Subsequent movement of the fish was quicker than the eye could follow and the prey was next seen protruding from the mouth. The illicium is supplied by a pair of nerves which may well be sensory, but the eyes are equally capable of judging the distance of the prey because they are wide-set and face forwards and upwards.

Lophius differs from most of the Acanthopterygii in that it cannot open its mouth by dropping the lower jaw, since the latter rests on the sea-bed. Instead the head must be raised. This is achieved partly by the action of the epiaxial muscles pulling the skull upwards and backwards and partly by the backward rotation of the pectoral girdle. The use of the epiaxial muscles in raising the head is normal in fishes feeding on large prey (Tchernavin 1948) but in *Lophius* the purpose is rather different and the angle of movement appears to be larger than usual (about 20°). The contraction of the hypaxial muscles pulls the ventral part of the pectoral girdle backwards into a vertical position and with the help of the paired fins levers the body forwards and upwards off the substratum. At the same time contraction of the rectus cervicis muscle depresses the hyoid arch so that the whole mouth cavity is deepened and its volume increased.

At this stage it would theoretically be possible for the lower jaw to drop, but the nature of the articulation allows for little movement further than that caused by the raising of the head because the retro-articular part of the lower jaw locks against the quadrate. Since the retro-articular process is in a straight line with the axis of the lower jaw in front and with the base of the interopercular bone behind, it is unlikely that van Dobben's hypothesis (van Dobben, 1935, pp. 3–5) for jaw opening could apply here. The force applied through the interopercular would need to be diagonally upward rather than backward and inward, as is the case. It is more feasible that the lower jaw, if it moves at all, does so through the indirect action of connective tissue and muscles connecting it to the pectoral girdle.

As van Dobben shows (1935, Figs. 30 and 31) when the mouth opens the hyomandibular and operculum move towards the centre unlike most fish where they move away from the centre. Van Dobben thus argues that the adductor arcus palatini functions during opening and the levator arcus palatini during closing of the mouth which is the reverse of the condition in other fish. While this might apply to the former of the two muscles, it is felt that the levator arcus palatini and also the opercular muscles have little function in the feeding mechanism and act mainly as fixation muscles. The inward movement of the hyoid/opercular apparatus could be brought about automatically as a result of the deepening of the mouth. In fresh material inward movement of the opercular apparatus results in the lowering of the mandible but the converse lowering of the mandible also results in inward movement of the operculum. Experimental work on live *Lophius* is needed to show which is responsible for the movement of the other. In contrast to van Dobben's hypothesis, *inward* movement would be conveyed to the mandible via the interopercular if inward movement of the opercular apparatus does cause lowering of the mandible.

The sudden forward and upward movement of the fish together with the suction created by the increase in volume of the mouth-cavity would create an inward current of water amply sufficient to engulf the prey.

Closure of the mouth presents some problems as the teeth of the upper jaw in the resting position do not meet those of the lower jaw which projects further forward (Fig. 1). The only way in which the teeth can meet and the mouth close fully is by protrusion of the upper jaw. It is thus maintained that protrusion occurs during the closing of the mouth and not during the opening of the mouth as in most Perciformes. This is in direct contrast to the statement of van Dobben, namely "Bei *Lophius* erfolgt beim Öffnen des Mundes automatisch ein Drehen des Maxillare und ein Vorstülpen des Praemaxillare" (1935, p. 45). Van Dobben's statement is not borne out by his diagram (Fig. 33) which shows the fish with the mouth open and the upper jaw retracted.

This hypothesis that protrusion occurs during the closing of the mouth is supported by the following features of the anatomy and does not require a reversal of the phase at which the muscles contract.

1. The limited movement of the lower jaw would not be sufficient to rotate the maxilla during opening of the mouth in the normal way. Moreover the coronoid process on the lower jaw is not high enough for insertion of the anterior section of the maxillo-mandibularis ligament to give the necessary forward component to any rotation brought about in this way.

2. The insertion of section A_1 of the adductor mandibulae onto the maxillo-mandibularis ligament (posterior section) and of the ligament onto the maxilla is such that contraction of the muscle would, at the same time, raise the lower jaw and rotate the maxilla. Furthermore it seems improbable that section A_1 would contract during the opening of the mouth to protrude the upper jaw when A_2 and A_3 of the same ontogenetic origin and innervated by branches of the same nerve bring about closure of the mouth.

3. The extra muscles in the angle of the jaw (maxillo-dentary and maxillo-articular) appear to replace the anterior section of the maxillo-mandibularis ligament in providing the forward component of the rotation and thus assist the adductor mandibulae during *closure* of the mouth.

Closure of the mouth occurs rapidly by contraction of the adductor mandibulae and probably while the head is still raised. Escape of the prey is prevented by the sharp hinged teeth. The simultaneous contraction of the protractor hyoidei pulls the hyoid arch upwards and forwards, reducing the size of the buccal cavity. If the prey is small it will be swept back into the pharynx and gripped by the pharyngeal teeth. If large it will be moved back in the next cycle of movements.

Together with, or immediately after, the closing of the mouth relaxation of the epiaxial and hypaxial body muscles allows the head and pectoral girdle to sink down into the resting position, which can occur automatically under the weight of the body and needs no special muscles. Finally relaxation of the adductor mandibulae allows the premaxilla to be retracted by the elastic ligament connecting it to the skull and by the ligamentous tissue between it and the maxilla.

Closure of the mouth and reduction of the buccal cavity (the buccal pump: Hughes 1960) forces the surplus water through the gills, and this is followed by contraction of the opercular tube which ejects the water through the opercular opening. Similarly enlargement of the buccal cavity when the mouth opens is followed by enlargement of the opercular cavity (the suction pump: Hughes, 1960) which also draws water through the gills and helps to prevent a reversal of current through the mouth and escape of the prey.

The modification of the opercular "tube" and its independent musculature is thus closely correlated with the modifications in the feeding apparatus and it is difficult to see how one could develop without the other.

SUMMARY

The anatomy of the bones and muscles concerned with feeding in the angler-fish, *Lophius piscatorius* is described in relation to its specialised mode of life. The mechanism of the "angling apparatus" or illicium and the mechanism of the protrusion of the upper jaw are of particular interest.

From a consideration of the anatomy together with some records of the animal's observed behaviour, proposals are made as to how the muscles function during the feeding cycle.

Evidence is given to show that the protrusion of the upper jaw occurs, not during opening of the mouth as is the case in most fish, but during closing of the mouth.

ACKNOWLEDGEMENT

I wish to thank Dr. N. A. H. Millard for her helpful criticism and encouragement throughout this work.

ABBREVIATIONS FOR TEXT FIGURES

ASC. PROC. – Ascending process of premaxilla;
BRANCH. RAYS – Branchiostegal rays;
CONNECT. TISS. – Connective tissue;
CER. HYOID – Ceratohyoid;
CERATOBR. – Ceratobranchials;
EPIBR. – Epibranchials;
HYOMAND. – Hyomandibular;
HYPOBR. – Hypobranchial;

INTEROPERC.—Interopercular;

Ligaments:

lig. premax-front.—Premaxilla-fróntal ligament;
lig. max-front.—Maxilla-frontal ligament;
lig. hyoid-suboperc.—Hyoid-subopercular ligament;
lig. art-interop.—Articular-interopercular ligament;
lig. max-mand.—Maxillo-mandibular ligament;
MAX.—Maxilla;
MAX. CART.—Maxillary cartilage;
MAX. LEVER—Maxillary lever;

Muscles:

A_1, A_2, A_3—Adductor manidibulae, see text.
M. abduct. 2—Abductor of 2nd dorsal ray;
M. art-dent.—Articular-dentary;
M. attract. arc. br.—Attractor arcus branchialis;
M. cor. branch. int. (or ext.)—Coraco-branchialis internal (or external);
M. dil. operc.—Dilatator operculi;
M. epiarc. rect.—Epiarcualis rectus;
M. erect. 2—Erector of 2nd ray;
M. erect. il.—Erector of illicium;
M. hyohy. abd.—Hyohyoidei abductores;
M. hyohy. add.—Hyohyoidei adductores;
M. lev. arc. br.—Levator arcus branchialis (internal or external);
M. lev. arc. pal.—Levator arcus palatini;
M. max-artic.—Maxillo-articular;
M. max-dent.—Maxillo-dentary;
M. obliq. vent. (or dors.)—Obliquus ventralis (or dorsalis);
M. protr. hyoid.—Protractor hyoidei;
M. protr. pter.—Pterygiophore protractor;
M. rect. cerv.—Rectus cervicis;
M. retr. 2—Retractor of 2nd ray;
M. retr. il.—Retractor of illicium;
M. retr. arc. br.—Retractor arcus branchialis;
M. sphinct. oesoph.—Sphincter oesophagi;
M. sub. comm.—Subarcualis rectus communis;
M. sub. rect.—Subarcuales recti;
M. trans. vent. (or dors.)—Transversus ventralis (or dorsalis);
PHARYNGOBR.—Pharyngobranchials;
PECT. ARTIC.—Articulation of skull with pectoral girdle;
PREMAX.—Premaxilla;
PREOPERC.—Preopercular;
SUBOPERC.—Subopercular.

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