CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

PART I. INTRODUCTION

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During recent years the functional anatomy of the head region of fishes has been the subject of a number of projects by Honours students in the University of Cape Town performed under the supervision of the author. Due partly to the University's unique position on the southern tip of Africa, and partly to the facilities offered by various sources, it has been possible to obtain a wide variety of material. Some of this has been collected by the University research vessel, the *John D. Gilchrist*, some has been contributed by the South African Museum and the Oceanographic Research Institute, Durban, and some has been obtained from commercial trawlers belonging to Messrs. Irvin and Johnson. Additional specimens have been collected on University expeditions to places such as St. Lucia Estuary, Knysna Estuary and Langebaan Lagoon, and the students themselves have foraged material in many ways.

In these projects the emphasis has been laid on the functional aspect of the problem and whenever possible anatomical data have been supported by observations on the feeding, respiratory and other mechanisms of living fish. This is an aspect which was sadly neglected by the earlier workers who have, however, laid an invaluable foundation of anatomical knowledge on which we can work. It is an aspect which is coming more and more into prominence in our Universities and research institutions today and which is essential for a satisfactory interpretation of anatomy.

During these projects valuable information is emerging and it is intended to publish some of them as a series of papers during the next few years. They will not appear in any systematic order as the choice of subject is left largely to the student and is influenced by the material and facilities available at the time. It is hoped, however, that they will contribute to a better understanding of the anatomy of the head and that with time the very varied and often spectacular adaptations will sort themselves into a pattern compatible with accepted theories of evolution and classification. It is already apparent that useful information of this nature will emerge.

Although it was originally planned to concentrate on the head region of teleosts it has inevitably happened that problems of peculiar interest have presented themselves in other parts of the fish body, and because of their value to functional morphology as a whole will be included in the series.

This paper is intended to introduce the series and includes a brief review of the relevant literature.

It is not proposed to review the osteology of the head region as this aspect has been adequately covered by other authors. In this respect Gregory's book on fish skulls (1933) has

been invaluable as a reference. It includes an account of the fish skull from a comparative and evolutionary point of view with particular emphasis on the skull as a 'natural mechanism'. Unfortunately it touches but lightly on the muscles.

The most comprehensive work on cranial muscles in recent years is that of Edgeworth (1935), who summarised the knowledge on comparative anatomy and embryology which had accumulated up to his time and added much valuable information from his own findings. It would be superfluous to review papers published before this date. Edgeworth has attempted to standardise the terminology, replacing some of the older names by more appropriate ones, but emphasises the difficulties which arise as a result of convergence and the 'homoplastic' nature of muscles. Although it may appear in the course of this work that some of Edgeworth's conclusions need revision, it is necessary to have a basis on which to work and, since his book remains the most complete thesis on the subject, his terminology will be adopted.

In the same year (1935) two other significant papers appeared—by Eaton and by van Dobben. Both have approached the problem in the 'modern' manner, that is, from the functional aspect.

Eaton concentrated on the mechanism of the protrusible jaw and also gave due consideration to the muscles and ligaments concerned. The interpretation of the muscles, and particularly the sections of the adductor mandibulae, is in many cases different from that of Edgeworth.

Van Dobben, interested in the functional significance of the jaw mechanism, described a wide variety of types mostly from living material available in Holland, starting with a detailed account of the mechanism in *Perca fluviatilis*. His experimental approach to the problem is refreshing and the thoroughness of his work impressive.

Lubosch, in 1938, produced a concise account of the cranial muscles based mainly on the work of Edgeworth and earlier workers, but omitting any reference to Eaton and van Dobben and without adding significantly to the functional aspect of the problem.

Kesteven, in 1942–45, in a study of the comparative morphology and evolution of the cephalic muscles, assumes that the relationship between nerve and muscle is a constant one and uses this association for the identification of the muscles. He thus differs from Edgeworth who maintains that the innervation of homologous muscles may change. To quote, ' . . . neither the origin of a nerve within the central nervous system nor its peripheral path is an infallible guide to the place of development or the source of the muscle it innervates. Both vary.' (Edgeworth 1935, p. 220.)

Which of these views is correct is a problem which requires investigation. Unfortunately Kesteven's work is not very liberally illustrated and it does not have a functional approach. Moreover his application of mammalian terms to the mandibular adductors is inadvisable and merely complicates still further an already complex situation.

Recently papers have appeared by Schaeffer and Rosen, 1961, and Patterson, 1964, in which the evolution of the feeding mechanism in the Actinopterygii has been discussed. These authors have shown how the mobility of the bony structures in the head of teleosts has been attained and has made possible the adaptive radiation of feeding mechanisms in this group, so well illustrated in the Acanthopterygii or 'spiny-rayed' forms.

There have also been papers describing the feeding mechanisms of particular groups or species of teleosts. Thus Matthes, 1963, has dealt with the Cyprinidae and, incidentally, includes a useful table on the muscle nomenclature of previous authors. Alexander, 1964, has dealt with the Characinoidei. *Orthagoriscus mola* was described by van Roon and ter Pelkwijk, 1940, *Chauliodus sloani* by Tchernavin, 1948–49 and 1953, and *Labeo horie* by Girgis, 1952, to mention only some.

THE DEVELOPMENT AND ANATOMY OF THE VISCERAL
MUSCLES IN TELEOSTS

The account which follows has been extracted mainly from the work of Edgeworth, who is the authority quoted unless otherwise stated.

1. *The Mandibular muscles*

The mandibular muscle-plate becomes attached to Meckel's Cartilage at an early stage of development and separates into the masticatory muscle-plate above it and the inter-mandibularis muscle below it.

The *intermandibularis* remains ventral and its fibres stretch transversely between the two halves of the lower jaw. In most teleosts it separates into anterior and posterior parts, the latter often becoming longitudinally orientated with its posterior end attached to elements of the hyoid arch or associated with the hyoid musculature.

The masticatory muscle-plate of Teleostomes becomes divided by the palatoquadrate into a dorsal part originating on the skull, the *constrictor dorsalis*, and a ventral part inserting on Meckel's Cartilage, the *adductor mandibulae*.

In most adult 'ganoids' the *constrictor dorsalis* has already spread backwards external to the hyomandibular and separated into an anterior and a posterior part.

In Teleosts the anterior part, the *levator arcus palatini*, originates on the postorbital region of the skull and inserts on the metapterygoid and sometimes on the hyomandibular as well, or even on the hyomandibular alone.

The posterior part, the *dilatator operculi*, originates on the otic region of the skull and upper end of the hyomandibular and its insertion is on the dorsal external edge of the oper-culum and thus entirely in the hyoid region. These two muscles may, however, not be distinct from one another (e.g. in the Anacanthini: Eaton 1935).

The adductor mandibulae is the main masticatory muscle and, primitively stretching from the palatoquadrate to Meckel's Cartilage, its origin tends to shift backwards towards the hyoid arch and even onto the skull, and part of its insertion upwards onto the palato-quadrate. It can thus be used not only for jaw-closing but also for retraction of the upper jaw when this is free and movable.

In *Lepidosteus* and some Isospondyli the muscle is in the form of a simple sheet, but in most Teleosts it becomes divided into several sections. Edgeworth and most other authors, adopting Vetter's terminology (1878), recognise A_1, A_2 and A_3.

A_1 is distinguished by its insertion, which tends to shift dorsally from the lower jaw along

the maxillo-mandibularis ligament, often becoming inserted solely on the maxilla. Van Dobben (1935) shows that in some Percomorphs (e.g. *Perca*) a separate tendon for A_1 may differentiate from the rest of the maxillo-mandibularis ligament which latter then remains responsible for protrusion of the upper jaw (see p. 40).

Occasionally the origin of A_1 may even shift partially (e.g. *Cyprinus carpio*) or completely (e.g. *Ammodytes tobianus*) onto the lower jaw. In such cases van Dobben postulates a change in function, this section being used to *protrude* the upper jaw and thus acting antagonistically to the rest of the adductor. In *Gadus* and *Lophius* also, A_1 is said to act antagonistically to the rest of the adductor.

Edgeworth maintains that the position of A_1 varies and that in development it may separate from the dorsal edge of the fore part of the adductor (e.g. *Caranx*), from the internal surface of the adductor (e.g. *Amiurus*) or from the external surface of the adductor (e.g. *Amia*).

A_2 and A_3 insert on the lower jaw and represent external and internal components respectively of the adductor.

The arrangement of these three adductor sections is certainly very variable. One section may be absent (A_1 in *Salmo*, *Scomber* and *Esox* according to Edgeworth), two sections may be combined (A_2 and A_3 in *Amiurus* and other genera according to Edgeworth, and in *Eupomotis* according to Eaton; A_1 and A_2 in *Anguilla* according to Kesteven, in *Pseudoscarus* according to van Dobben, partly in *Osmerus*, *Clupea*, *Esox* and *Epinephalus* according to Eaton), or extra sections may be developed (Edgeworth mentions the intramandibularis, quadrato-mandibularis, retractor maxillae and retractor palatini; Eaton and van Dobben both use the term A_4 but in different senses). The result is that the interpretation of different authors is often quite different for one form. *Gadus* is a case in point. This genus has an extra section inserted on the maxilla in addition to A_1. According to Edgeworth and Lubosch this represents a deep component of A_1, according to Eaton it is A_3 which has shifted its insertion onto the maxilla, and according to van Dobben it represents a new section which, following Vetter, he calls A_4.

Kesteven, 1943, in an attempt to homologise the adductors of bony fish with the jaw muscles of tetrapods, includes A_1 and A_2 in a 'temporo-masseteric group' which inserts lateral to the ramus mandibularis V, and A_3 in a 'pterygoid group' which inserts medial to the nerve. His identification of the muscles, based on their relation to this nerve as it is, is thus often completely at variance to that of the authors so far mentioned.

Kesteven's viewpoint is attractive because of its simplicity, but preliminary anatomical work in this Department has suggested that the path of the ramus mandibularis V is not a reliable guide to the identification of the adductor sections. The relationship between the two varies intergenerically and probably interspecifically as well. Edgeworth states that the ramus mandibularis may lie external to the complete adductor, internal to A_2, or internal to A_3. Lubosch states that the usual position is between A_1 and A_2. It seems therefore that Kesteven's change in terminology is not justified at this stage of our knowledge.

Finally Lubosch maintains that the variable nature of the adductor in Teleosts is an indication of a multiple evolutionary origin of the group.

2. *The Hyoid muscles*

The hyoid muscle-plate develops from a continuous dorso-ventral sheet, which spreads backwards into the opercular fold and becomes the *constrictor hyoideus*. It differentiates into a dorsal part, the *constrictor hyoideus dorsalis*, situated behind the hyomandibular and a ventral part, the *constrictor hyoideus ventralis*.

The *constrictor hyoideus dorsalis* retains its primitive position in adult Chondrostei where the anterior part, originating on the auditory region of the skull, functions as a retractor of the hyomandibular, but in Holostei and Teleostei the anterior edge spreads forwards internal to the hyomandibular to function as an adductor. Among Teleosts in the Isospondyli (*Salmo* and *Clupea*) part of the insertion has shifted onto the metapterygoid, and in other orders this anterior part has become distinct as the *adductor arcus palatini*. The latter originates on the parasphenoid and auditory region of the skull and inserts on the metapterygoid and sometimes the palatine. A section inserting on the hyomandibular may be distinct as the *adductor hyomandibulae*. In its final position, thus, the anterior part of the constrictor hyoideus dorsalis is anterior to, though more internal than, the constrictor mandibularis dorsalis which has shifted backwards. Eaton, however, following Allis (1903) believes that this muscle is derived from the levator arcus palatini and represents an anterior component of it.

The posterior part of the constrictor hyoideus dorsalis forms the *opercularis*, stretching from the skull to the dorsal edge of the operculum. In Chondrostei it is still undifferentiated from the retractor hyomandibulae. In Holostei it is a distinct muscle and in Teleosts it may differentiate into the *adductor* and *levator operculi* situated posterior to the dilatator operculi derived from the mandibular muscle-plate.

The *constrictor hyoideus ventralis* is primitively a sheet of transverse fibres stretched between the two halves of the hyoid arch and situated ventral to the hypobranchial musculature. In Teleosts it differentiates into an anterior part, the *interhyoideus*, in front of the hyoid arch, and a posterior part, the *hyohyoideus*, behind the hyoid arch.

The fibres of the *interhyoideus* tend to swing forwards so that they stretch obliquely forwards between the hyoid arch and a median raphé, the lower jaw or the floor of the mouth. In this position some of the fibres may cross those of the intermandibularis dorsally or acquire a more intimate association with this muscle. Thus, in certain genera a *protractor hyoidei* is formed, which is a compound muscle derived partly from the longitudinally orientated intermandibularis posterior and partly from the interhyoideus. As such it stretches from the lower jaw to the hyoid arch.

This muscle was known as the *geniohyoideus* by older workers and the name is still retained by many recent ones (Gregory, Girgis, van Roon and ter Pelkwijk), who assign to it the function of lowering the jaw. It was renamed the *protractor hyoidei* by Holmqvist in 1910 (followed by van Dobben) in accordance with its function of protracting the hyoid arch during expiration. Edgeworth uses Holmqvist's name but retains the old idea of its function.

The *hyohyoideus* primitively forms an oblique muscle-sheet stretching from the opercular bones to the ventral mid-line or ventral part of the hyoid arch, e.g. *Amia*. Generally it is subdivided by the branchiostegal rays into a number of sections, and Edgeworth distinguishes a *hyohyoideus superior* above the lowest ray and a *hyohyoideus inferior* below the lowest ray.

However, among advanced Teleosts the muscle is exceedingly variable and modified to control the movement of the branchiostegal rays. As a result Edgeworth's terminology becomes quite inadequate. Kesteven distinguishes four sets of muscles: the pars anterior, partes abductores, partes adductores and pars dorsalis. Even these do not meet with all the requirements and it is proposed to use just two terms, the *hyohyoidei abductores*, which spread the rays and enlarge the opercular cavity, and the *hyohyoidei adductores*, which close the rays and reduce the opercular cavity, and to describe the variations as they occur in individual species.

3. *The Branchial muscles*

Branchial muscle-plates are present early in development external to the branchial arches. In Teleosts the dorsal part of each normally forms a *levator arcus branchialis*, and the ventral part a *transversus ventralis*.

The *levatores arcuum branchialium* originate on the skull and normally insert on the epibranchials. The fifth one may, according to Edgeworth, be the derivation of the '*cephalo-clavicularis*' and the *cucullaris*.

The '*cephalo-clavicularis*' (better termed *cephalo-cleithralis*), present in many genera of Teleosts, apparently represents the last levator in which the insertion has shifted onto the pectoral girdle.

The *cucullaris*, only occasionally present in Teleosts, stretches from the skull to the pectoral girdle (cleithrum and occasionally supracleithrum) and is situated external to the last levator, from which it was formed.

One or more small *attractores arcuum branchialium*, developed as downgrowths from the levators, may stretch from epi- to ceratobranchials on the inner sides of the skeletal arches.

In the primitive condition (retained in *Lepidosteus*) each *transversus ventralis* stretches from the ventral part of its branchial arch to a median, ventral raphé. In Teleosts, however, the inner ends of part or all of the first four muscles may be secondarily attached to the branchial (or hyoid) arches as the *obliqui ventrales*. Although the transversi ventrales have a similar position to the intermandibularis and interhyoideus, Edgeworth maintains that they are not serially homologous due to the early interruption of the branchial muscle-plates by the pericardium.

In addition to the transversi ventrales the ventral ends of the branchial muscle-plates give rise to the *coraco-branchiales* and the *subarcuales recti*.

In Teleosts only one *coraco-branchialis* (pharyngo-clavicularis of Dietz) is formed. It develops from the outer end of the last transversus ventralis and lies ventral to it. It originates on the ventral end of the last branchial arch and inserts on the pectoral girdle, and it generally differentiates into external and internal parts.

The *subarcuales recti* are a series of longitudinal muscles primitively connecting the ventral end of each branchial arch with the one in front (or with the hyoid arch in the case of the first). The first four are usually normal in position, while the fifth may be produced forwards for a variable distance as the *subarcualis rectus communis* below the transversi ventrales.

Also associated with the branchial region are muscles derived from the *sphincter oesophagi*.

The sphincter develops as a backgrowth from the fifth pair of transversi ventrales and spreads around the oesophagus and forwards over the dorsal surface of the branchial region. Here it forms the *transversus dorsalis* and acquires attachments to the branchial arches. From its lateral edges differentiate the *obliqui dorsales* (anterior and posterior) and from its dorsal surface grows back the *retractor arcus branchialium* to its origin on the ventral surface of the vertebral column.

4. *The Hypobranchial muscles*

In Teleostomes the hypobranchial muscle-mass is formed from the ventral ends of a number of spinal myotomes which grow down behind the branchial region and forwards below it. In Teleosts this mass reaches the level of the hyoid arch, thus forming the *rectus cervicis* muscle (*sternohyoideus* of most authors). It originates on the pectoral girdle, fuses with its fellow in the ventral mid-line and, crossing the constrictor hyoideus ventralis dorsally, inserts on the hyoid arch. Unlike most ganoids no geniohyoideus or geniobranchialis is developed, these mucles when present being formed from the forward growth of the hypobranchial mass beyond the level of the hyoid arch. Thus the normal muscles responsible for lowering the jaw are absent in Teleosts and the main function of the rectus cervicis is to retract the hyoid apparatus.

THE FEEDING AND RESPIRATORY RHYTHM

The feeding mechanism of a fish is dependent on, and co-ordinated with, the respiratory rhythm. Indeed in many forms the same muscles are used for both. In recent years the respiratory mechanism has received considerable attention from such workers as Hughes and Shelton in 1958, Hughes in 1960 and Ballintijn and Hughes in 1965, but the physiology of the feeding mechanism is still relatively unknown.

Hughes in 1960 and Saunders in 1961 supported the concept of a buccal force-pump and an opercular suction-pump co-operating to drive the water across the gills (these terms being used in reference to passage through the gills only) and showed that the movements of the operculum lag behind those of the buccal cavity, i.e. enlargement of the opercular cavity (the suction-pump) follows enlargement of the buccal cavity, and reduction of the opercular cavity follows reduction of the buccal cavity (the force-pump). The buccal cavity enlarges as the mouth opens and reduces as the mouth closes.

In 1965, by a very beautiful series of experiments, Ballintijn and Hughes showed that since the mechanism of both pumps is very intricately linked "it is clearly necessary that the two pistons should be coupled together by a spring of varying stiffness" (p. 361). These authors, working on the trout, have also determined the time in the respiratory cycle at which the various muscles come into action and have thus solved many of the problems outstanding. For instance it is conclusively shown that the protractor hyoidei contracts during the closing of the mouth and reduction of the buccal cavity and does not lower the jaw as previously supposed. For a full account of the contribution of the various muscles to the respiratory cycle the reader is referred to this paper.

Briefly the three most important muscles involved are the adductor mandibulae, the adductor arcus palatini et operculi (which is undifferentiated in the trout) and the levator hyomandibulae et arcus palatini. These muscles contract in sequence during shallow respiration so that closure of the mouth is followed by adduction of the palatal complex and operculum (reducing the size of the buccal and opercular cavities) and then by levation of the palatal complex (expanding the buccal and opercular cavities). Since the phases of contraction of the three sets of muscles overlap, a smooth flow of water through the gills is ensured. By an intricate arrangement of couplings (joints and ligaments) the jaw is automatically opened and the ventral part of the hyoid arch adducted and abducted at the right phases.

During deeper respiratory movements various other muscles are brought into action, including the hyohyoideus, protractor hyoidei, rectus cervicis (sternohyoid) and dilatator operculi. The first two òf these function during mouth-closing and the last two during mouth-opening.

Ballintijn and Hughes emphasise the fact that the couplings between different parts of the skeleton are complex and ". . . a particular movement of part of the skeleton may be produced by several different patterns of muscular co-ordination. Correspondingly, the contraction of a given muscle affects many different parts of the system" (p. 358–359). What is more the details of the mechanism are not necessarily the same in different fish.

It is clear then that two "intensities" of rhythm are possible even in respiration. The deeper intensity would presumably suffice for feeding in suction-feeders, the food being retained in the pharynx with the aid of gill-rakers and directed towards the oesophagus. It appears that in macrophagous feeders a third and deeper intensity of rhythm is possible for increasing the gape to accommodate large prey. Such movements, though based on and correlated with the fundamental respiratory rhythm, may require the use of additional muscles or the reorganisation of existing ones. Thus, van Dobben describes two positions of the mouth in *Cyprinus carpio*, one for the normal rhythm and one for seeking out food on the bottom. As an extreme example the case of the deep-sea fish *Chauliodus* can be quoted (Tchernavin 1948–49 and 1953), where the gape is increased by the upward rotation of the skull on the vertebral column accompanied by a backward rotation of the front end of the hyoid arch through almost 180°.

In macrophagous feeders it is also necessary for the food to be grasped and manipulated on its passage through the buccal cavity. This can be achieved with the aid of premaxillary, vomerine and pharyngeal teeth, which grip the food at the correct phase and work it backwards, possibly over several "respiratory" cycles. The development of movable pharyngeal teeth has involved specialisation of parts of the branchial skeleton and its muscles. Girgis, 1952, describes the manner in which the pharyngeal bones grip and masticate the food in *Labeo horie*, and Matthes, 1963, describes the process in various genera of Cyprinidae.

The latter author also gives an account of the "spitting" or "coughing" action by which unwanted matter is ejected through the mouth. Hughes maintains that this is due to a sudden increase in pressure in the opercular cavity causing a reversal of flow through the gills. Matthes postulates a contraction of the pharynx together with the opening of the mouth and thus apparently the simultaneous contraction of muscles which do not normally act together.

One of the most interesting features of the feeding apparatus of Teleosts is that no direct mechanism exists for opening the mouth. One gains the impression that this process was not of sufficient survival value to have influenced the evolution of the head muscles. A jaw after all falls open under its own weight. Mechanisms for opening the mouth appear to have evolved fortuitously and in different ways. This was noticed by Tchernavin in 1953, who could find no general rule for a method of opening the mouth in bony fishes, as it varies according to the structure of the head and jaws. Ballintijn and Hughes have shown that in the trout the opening of the jaw is brought about indirectly as a result of couplings with several different muscle systems. It is reasonable therefore to expect great variety in jaw-opening mechanisms in the more specialised fishes.

THE MECHANISM OF THE PROTRUSIBLE JAW*

Gregory as early as 1933 pointed out that in early bony fish the dermal bones of the upper jaw formed part of the 'facial mask' and were firmly attached to the cartilage bones below. Both premaxilla and maxilla were marginal and tooth-bearing. In later ganoids and teleosts, however, these bones became 'movably pivoted on the ethmo-vomer block' so that their posterior ends could rotate forward as the mouth opened. This condition has been achieved in some of the Isospondyli (Clupeiformes) which most authorities consider the most primitive group of Teleosts. The associated modifications which made this change possible have been described by Schaeffer and Rosen, 1961. Van Dobben, 1935, shows that the rotation in *Clupea* is accompanied by the division of the maxillo-mandibularis ligament into an anterior and a posterior section, the former stretching from the coronoid process of the dentary to the posterior outer edge of the maxilla and the latter from the articular to the anterior dorsal edge of the maxilla. Eaton, 1935, shows how the movement in *Clupea* is controlled by a pair of 'crossed ligaments' (one from the palatine to the premaxilla crossing over another from the ethmoid to the maxilla).

In most other Teleosts the maxillae have withdrawn from the margin and lost the teeth. As Gregory has remarked, the initial freeing of the upper jaw has permitted the wide adaptive radiation in feeding mechanisms so characteristic of this group.

One of these adaptations has been the development of a protrusible mouth permitting both upper and lower jaw to be thrust forward in the capture of food. This mechanism is most advanced in the orders Ostariophysi (Cypriniformes) and Percomorphi (Perciformes) in which it has developed independently. In both, protrusion is effected by the depression of the lower jaw; the downward movement of the latter causing a rocking, twisting or lifting movement of the maxilla to which it is held by ligament, this movement in turn being transmitted to the premaxilla which is thrust forward.

The maxilla, thus, on being freed of its marginal and tooth-bearing function, has taken over a new one—that of transmitting movement from lower jaw to premaxilla—and is an important cog in the mechanism. In this way no new muscles are necessary, and those which

* In this section Regan's classification has been used, and Berg's quoted between brackets (*See* Norman · & Greenwood 1963).

originally depressed the lower jaw can now also protrude the upper jaw. The insertion of one section of the adductor mandibulae (A_1) on the maxilla permits its use in retraction of the mechanism.

Among the Ostariophysi the mechanism is best known for the carp, *Cyprinus carpio*, and is described by Gregory, 1933, Eaton, 1935, and van Dobben, 1935, among others. The forward movement of the premaxillae is brought about through the rocking action of the maxillae and rotation of the median 'tracker bone' clasped by the latter. It is controlled mainly by a median ligament stretching from the premaxillae to the mesethmoid (in which the tracker bone is ossified). According to Matthes the protrusible jaw has been secondarily lost or modified in some of the more specialised Cyprinidae, which have a highly developed pharyngeal masticatory apparatus.

In the Percomorphi the premaxillae bear long ascending processes which, on protrusion, slide downwards and forwards on the mesethmoid. This movement is brought about by the twisting of the maxilla on its axis, and is controlled by ligaments stretching from skull and palatine to premaxilla and maxilla. The Isospondylid 'crossed ligaments' have been further elaborated for the purpose (Eaton 1935; Schaeffer and Rosen 1961). Details and mechanics of the movement are fully described for *Perca* by van Dobben. This author also shows how a better control of the twisting movement of the maxilla is achieved in certain species by the separation of the maxillo-mandibularis ligament from the tendon of adductor A_1.

This type of protrusion is developed to extremes in the Labridae (Labridei), where not only upper jaw, but lower jaw as well, can be thrust forward. This is achieved by the forward rotation of the quadrate which is long and slender and articulates freely on the symplectic and short hyomandibular.

Eaton accepts these two types of protrusible jaw though extending the Percomorph type to include the Anacanthini (Gadiformes) and all Acanthopterygii or spiny-rayed fish. He adds a third ('Cyprinodont') type characteristic of the Microcyprini (Cyprinodontiformes), e.g. *Fundulus*, and the Mugiloidea (Mugiliformes), e.g. *Mugil*, in which no 'crossed ligaments' are present, but instead the mechanism is controlled by a hook on the maxilla which fits closely into a socket under the head of the premaxilla. Protrusion according to Eaton is due to the twisting of the maxilla about its axis in very much the same way as in *Perca*. Schaeffer and Rosen, 1961, seem to support the erection of a separate category for this group, but differ from Eaton in maintaining that protrusion of the premaxilla is effected through the direct connection of this bone with the coronoid process of the dentary by the anterior section of the maxillo-mandibularis ligament (the posterior section being absent: van Dobben), and 'without the intervention of the maxilla'. The function of the maxilla is thus limited to the control of the premaxilla.

However, the direct movement of the premaxilla has also been attained, and in a very similar way, in some of the Percomorphi (e.g. Gerridae: Schaeffer and Rosen 1961). It may be that we have here an example of parallel evolution and it is likely that many more examples of this phenomenon will be found. Van Dobben considers that the jaw mechanism in the 'Physoclysti' is so variable that no clear evolutionary picture emerges and there is no relation to classification.

Finally Patterson, 1964, shows that the evolution of the protrusible mouth in the Acanthopterygii is accompanied by a change from buccal dentition, with teeth on the parasphenoid, ecto- and endopterygoid and basibranchials, to pharyngeal dentition, with teeth on the pharyngo- and ceratobranchials of the posterior gill arches. 'Prey taken by a protrusible mouth would tend to be gulped straight into the pharynx, where the main dentition . . . is concentrated' (p. 457). This change is accompanied by modification of the posterior branchial muscles for manipulation of the pharyngeal teeth.

CONCLUSION

From this brief account it appears that in general the straight-forward anatomy of bones and muscles is fairly well known, at least for the more common species of Teleosts. In regard to muscle function it is a different story, most of the earlier workers having merely deduced function from anatomy. In recent years the contribution of various muscles to the respiratory cycle and the mechanism of the cycle itself have received a fair amount of attention from such workers as Hughes, Saunders and Ballintijn. However, there still remains much to be done on the feeding mechanism and its muscular control, preferably with a critical experimental approach such as that used by the above authors.

SUMMARY

This paper introduces a series to be published on the functional morphology of fishes, particularly on the feeding mechanisms of Teleosts, and presents some of the problems involved.

From current literature an account of the development and arrangement of the visceral muscles in Teleosts has been extracted.

The relation between the feeding mechanism and the respiratory rhythm is discussed with emphasis on the function of the muscles and their contribution to the process.

The mechanism of the protrusible jaw is discussed. It is considered that the attainment of a mobile premaxilla and maxilla in primitive Teleosts such as the Isospondyli has paved the way for extensive adaptive radiation in more advanced forms, involving further specialisations of bones, muscles and ligaments. Evidence of at least three such lines is indicated.

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