CONTRIBUTIONS TO THE FUNCTIONAL MORPHOLOGY OF FISHES

PART III. THE FEEDING MECHANISM OF SYNGNATHUS ACUS LINNAEUS

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INTRODUCTION

Syngnathus acus, the pipe-fish, has a fairly wide distribution, being recorded from the west coast of South Africa and in the western Indian Ocean; its range extending as far as the West Indies. In European waters it is found in the Mediterranean and the East Atlantic (Smith 1949). It generally occurs in shallow waters, although one specimen has been dredged in sixty fathoms of water off Algoa Bay (Smith 1963).

In South Africa it is often found in large numbers, in beds of *Zostera*—a common estuarine weed. The fish is particularly suited to this habitat, for its slim elongate body is camouflaged among the long threads of *Zostera*. The colour of the fish varies, as *Syngnathus* has the ability to slowly alter its colour to suit that of its environment. Generally the ground colour is green or brown, with bands, spots, and stripes of green, brown and yellow. This colouring and pattern renders the fish inconspicuous in the *Zostera* beds. This deception is heightened by the slow swaying motion of the fish: for this resembles the way in which the weed is swirled about by the tidal waters. The fish moves quite slowly by undulations of the small dorsal fin, and more rapidly by a rhythmic wave-like motion of the elongate body, accompanied by spreading of the caudal fin.

The male carries the eggs in a covered brood-pouch situated on the tail. Specimens examined bore between 200 and 300 eggs, and one male "gave birth" to about 300 young fish in the aquarium.

Little work has been done on the functional anatomy of *Syngnathus*, although Kindred (1924) has studied the osteology and development of the skull of *S. fuscus*, and McMurrich (1883) that of *S. peckianus*. Gregory (1933) has investigated the skulls of allied species, and his work has been used to compare *S. acus* with related forms.

MATERIAL AND METHODS

Twenty-seven specimens of *S. acus* were captured in Knysna lagoon, by netting in about four feet of water amongst fairly thick beds of *Zostera*. Of these, ten were kept alive, and the others preserved in 7 per cent neutral formalin. The length of the fish varied from 4 cm. to 15 cm. The live specimens were kept in a sea-water aquarium at 18°C, and were fed on *Artemia* nauplii.

Most of the work was done by microdissection and the results verified by reconstruction of serial sections after the method of Pusey (1939). For sectioning, small specimens of about 4 cm. long were decalcified in 5 per cent nitric acid, and bulk-stained in Mayer's acid haemalum. Sections were cut at 15μ and counterstained with erythrosin. Muscle nomenclature follows that outlined in the introduction to this series (Millard 1966), unless otherwise stated.

<div align="center">OSTEOLOGY</div>

General considerations

The skull is modified by the development of an elongate snout, which bears the small mouth at its terminal end. The orbits are large and bounded dorsally by the cranial roof, and ventrally by the parasphenoid and anterior projections of the preopercular bones. The operculum is large and rounded, extending downwards so that the two opercular bones almost meet ventrally. The hyoid arch is small and the bones tend to be fused to one another.

Due to the development of bony rings around the body, the head is held rigid, and there is little need for articulation between the skull and the vertebral column. Consequently the occipital condyles are reduced. The immobility of the skull is increased by the fusion of the first three vertebrae.

The pectoral girdle is well developed but partially fused to the bony rings around the body. The cleithrum and post-temporal are fused to these rings, but the postcleithrum and coracoid are free and extend longitudinally. The scapula is small, but bears a pectoral fin. Both pelvic bones and pelvic fins are absent.

Osteology of the Head

The orbit is roofed by the frontal bones which also cover the neurocranium. The parietals are fused together medially and lie superficially over the epiotics, extending backwards to cover parts of the supraoccipital and the pterotics. The epiotics are thin scale-like bones situated almost superficially on the skull, while the pterotics, supraoccipitals, and frontals are fused and the sutures between them indistinct. The pterotics do not extend upwards to meet across the midline of the skull, as described for *S. peckianus* by McMurrich (1883).

The sphenotic is prolonged downwards behind the eye, and meets the preopercular, which lies beneath the orbit. Anteriorly a prefrontal and a suborbital complete the ring of circumorbital bones. Running medially below the orbit is the parasphenoid, which has lost its connection with the vomer, and ends at the front of the orbit, abutting against the mesethmoid.

The front of the head is produced forwards into an elongate cylindrical snout which tapers towards the small mouth. Laterally this snout is made up of enormously elongated quadrate bones, and dorsally it is roofed by the dermethmoid and vomer.

The preopercular (termed the infraorbital by McMurrich 1883) extends forwards from the operculum, underneath the snout (Fig. 1). The interoperculars have also been produced forwards in a similar manner and have lost their connection with the rest of the opercular complex: they lie ventrally medial to the quadrate bones (Figs. 2 and 10) and are attached by ligaments to the mandibles and the hyoid arch (Fig. 6). McMurrich considers the interopercular to be lacking in *S. peckianus*.
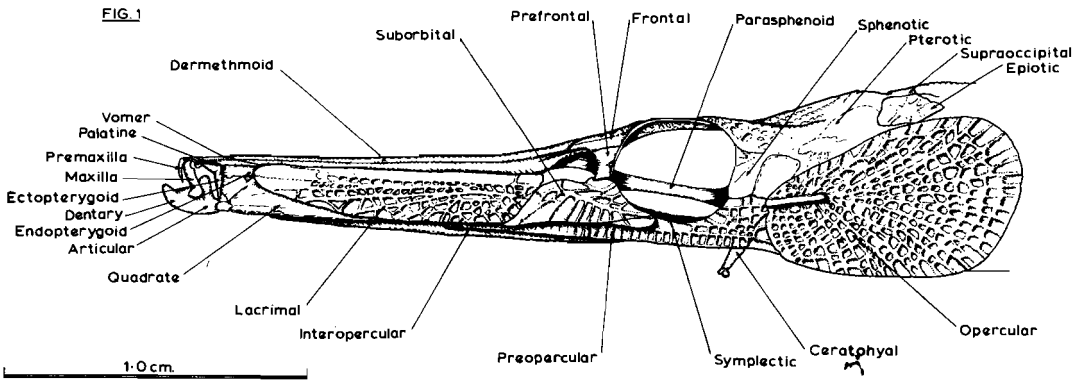
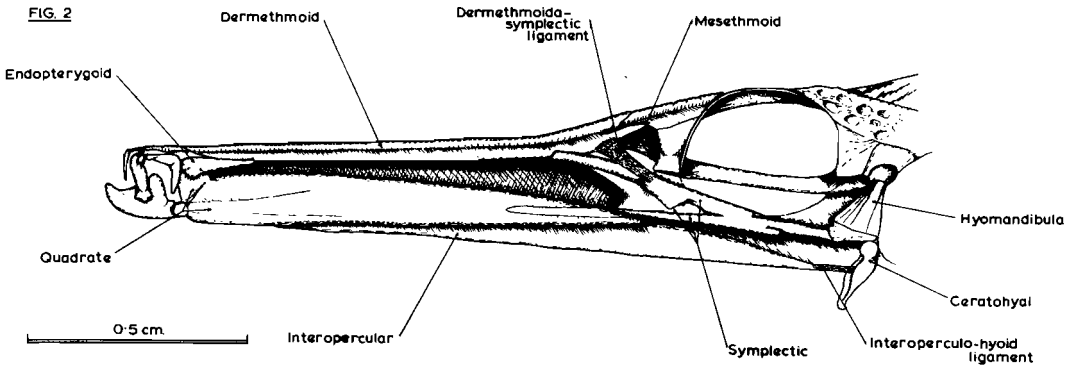Fig. 1 *Syngnathus acus.* Left lateral view of skull.

Fig. 2 *Syngnathus acus.* Left lateral view of skull after removal of lacrimal, suborbital, and preopercular bones.

The snout is further strengthened by two bones which encase the snout laterally. The homology of these bones is controversial and is discussed below (p. 73). In this work they are regarded as the lacrimal and suborbital which have lost their original position under the eye, and with protrusion of the skull to form a snout, have been carried forwards (Fig. 1). The nasals are lacking.

Due to the arrangement of the bones, and the large amount of dense connective tissue between them, the snout is a fairly rigid tube. There is little longitudinal movement of the bones, with the exception of the interopercular.

The premaxilla is considerably reduced and lies anterior to a larger (but also reduced) maxilla. The premaxilla is held in place by a ligament extending across the maxilla to the palatine bone (Fig. 4). A ligament also stretches between the maxilla and the palatine, and

from maxilla to vomer. The maxillo-mandibular ligament is well developed, being inserted on the upper inner edge of the maxilla, and running down to the dentary. The dentary and the articular are fused to such an extent that they are indistinguishable: the latter articulates with the quadrate bone. The retroarticular is a tiny loose bone at the base of the articular. Neither the mandible nor the premaxilla bear teeth.

The quadrate extends the whole length of the snout to meet the symplectic. A narrow limb of the latter is contained in a groove of the quadrate, while its upper portion abuts against the dermethmoid and is linked to it by a strong ligament (Fig. 2). Posteriorly the symplectic narrows and meets the hyomandibula, which articulates with the otic region of the skull. The hyomandibula has only a single articulatory facet with the skull, which increases its freedom.

The quadrate is held rigidly by the lacrimal and suborbital which encase it.

All the palatal bones are reduced in size, and the palatine, ectopterygoid, endopterygoid, and vomer, have been carried forward to the front of the snout (Figs. 1 and 4). The parasphenoid lies below the orbit and has lost contact with the other palatal bones.

S. acus has a comparatively large operculum, due to the size and shape of the opercular bone: this is an oval convex bone, which articulates anteriorly with the hyomandibula (Fig. 1). The subopercular is reduced and lies ventrally medial to the opercular, being loosely attached to it by connective tissue (Fig. 6). The preopercular and the interopercular constitute part of the snout, as discussed above.

The hyoid arch has several muscles inserted on it, and its action constitutes an important part of the respiratory cycle. The ceratohyoids are large, and each bears two long slender branchiostegal rays (Fig. 6). The median basihyoid is extended back as a long thin urohyal. Passing medially forwards is the embryonic copula communis, which extends from the first branchial arch, forwards between the two ceratohyoids, to form the os entoglossum of the adult. Cartilage persists in the interhyal which articulates with the hyomandibula. The cerato-hyoid can to a certain extent move on the interhyal, although this movement is somewhat restricted. Fusion has occurred between the hypohyal and the ceratohyoid, and the epihyal is apparently absent.

All the branchial arches are reduced to a certain extent, and are delicate slender structures. The first two bear their full complement of elements, except for the basibranchials which are missing. The copula communis links the hypobranchials of the first branchial arch, while those of the second arch extend ventrally to meet one another. Elongate pharyngobranchials pass over the top of the arch and link the first two arches together. The third arch has lost its pharyngobranchial, and the fourth lacks both pharyngobranchial and epibranchial. Of the fifth arch, only a rudimentary element remains, which Kindred (1924) maintains is the hypobranchial.

The ceratobranchials pass around the pharynx in an anteroventral direction, and provide the anterior support for each of the four gill slits.

None of the branchial arch elements bear teeth, but the endothelium covering the cerato-branchials—and thus bordering the gill slits—is thrown into papillae which project across the gill slit and prevent food from entering the branchial chamber.
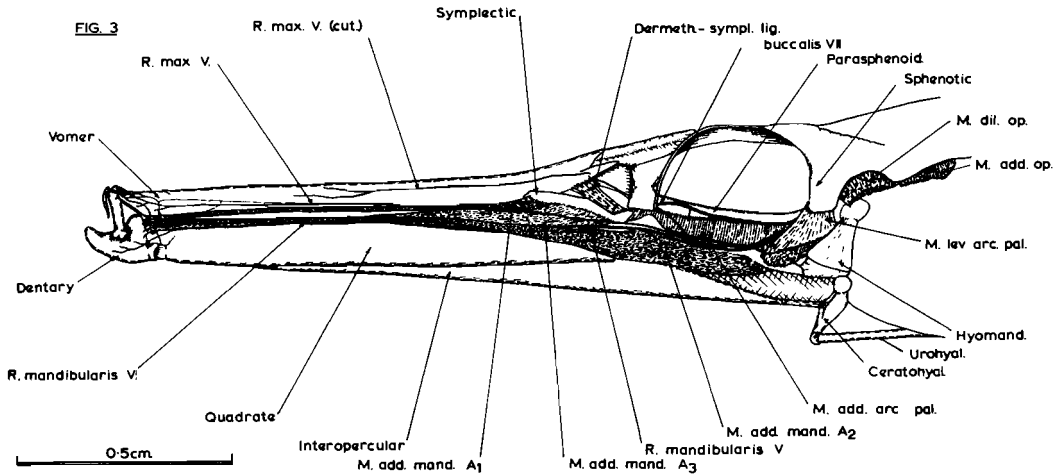
Fig. 3   *Syngnathus acus.* Dissection of cranial region to show muscles.

Dermeth.-sympl. lig.	Dermethmoido-symplectic ligament
Hyomand.	Hyomandibula
M. add. arc. pal.	Musculus adductor arcus palatini
M. add. mand. A1, A2 & A3.	M. adductor mandibulae A1, A2 & A3
M. add. op.	M. adductor operculi
M. dil. op.	M. dilatator operculi
M. Lev. arc. pal.	M. levator arcus palatini
R. max. V.	R. maxillaris V
R. max. V (cut).	R. maxillaris V (cutaneous)

Homologies of the Bones

Most of the bones in the skull, although extensively modified in some cases, have obvious counterparts in the skulls of other fishes. However, the homology of some remains uncertain.

Working on the allied genera *Phyllopteryx* and *Solenostomus*, Gregory (1933) and Jungersen (1910) conclude that the two bones encasing the quadrate in the snout region are metapterygoid bones, which have presumably ossified in two portions in the former case; and that the lacrimal and suborbital bones have been lost. Gregory maintains that these bones are specialisations of the Syngnathid skull, and with reference to *Phyllopteryx*, states that it has "leading specialisations . . . of its own, notably the presence of a row of 'antorbital plates' on the sides of the oral tube . . ." (p. 226).

The present author contends that these antorbital plates are not in fact metapterygoid bones, but a lacrimal and a suborbital that have been carried forward with the elongation of the snout into an oral cone.

It seems very likely that the antorbital plates are of dermal origin, in contrast with the cartilaginous origin of the metapterygoid. They are finely sculptured and pitted in a manner

that is characteristic of dermal bone. Sections cut of a young fish failed to show any cartilage in these bones, although it was obvious in all the recognised cartilage bones.

Although Kindred (1921 and 1924) has proved by embryological studies that the antorbital plates of *Syngnathus fuscus* are not cartilaginous in origin, he still regards the anterior of the two plates as the metapterygoid. His views are based largely on the relative position of this bone, for he states "I have regarded it as the homologue of the metapterygoid in other teleosts because it lies posterior to the pterygoid bone, postero-dorsal to the quadrate, postero-ventral to the short metapterygoid process of the pterygoquadrate cartilage, and in the position of the posterior flange in other teleosts". (1924, p. 427.)

The posterior of the two antorbital plates Kindred terms the infraorbital bone, which he and Swinnerton (1902) homologise with the anterior bones of the suborbitalia in *Gasterosteus*.

Further evidence that the antorbital plates are lacrimal and suborbital bones comes from a study of allied but less specialised forms included by Gregory in his order Thoracostei. According to Gregory (1933, p. 228) "in a general way, the gasterosteoids, the hemibranchs, and the lophobranchs form successive grades of organisation". Consequently it is reasonable to examine the less specialised gasterosteoids in an attempt to determine which bones are likely to form the antorbital plates.

Gasterosteus aculeatus represents the primitive stage in this group, showing no elongation of the front part of the skull: but it does have a large lacrimal and a prominent ring of sub-orbital bones (Gregory 1933, Fig. 102).

Gasterosteus spinachia has a partially elongated snout, and it is the lacrimal and first suborbital which extend forward over the snout, partially covering the quadrate (Gregory 1933, Fig. 103).

If this trend is continued further, it is easy to visualise how the long snout of *Syngnathus* can be formed, and how the lacrimal and suborbital could be carried forward from the margin of the orbit to form antorbital plates.

The condition of these plates in the Thoracostei lends further evidence for the phylogeny of the group, and this is discussed below (p. 88).

If these bones are the lacrimal and suborbital, it is difficult to say which bone is homologous with the metapterygoid. Starks (1902) states that the "pterygoid" bone becomes fused with the quadrate in *Fistularia*. In *S. acus* there is an upward extension of the anterior region of the quadrate (Figs. 2 and 3) which may be a fused "pterygoid". As the endopterygoid and the ectopterygoid are distinct and separate, this could be the metapterygoid. However, Starks has shown that the pterygoid of *Fistularia* can be separated from the quadrate by prolonged maceration: this is not the case in *S. acus*. Even after prolonged maceration this expansion of the quadrate remains attached, and there is no sign of a suture between it and the quadrate.

The fact that the metapterygoid is part of the mandibular arch supports the theory that the metapterygoid is fused to the quadrate.

The alternative is that the metapterygoid may have become fused to the symplectic, to form the upper limb of this bone—or at least part of it (Fig. 2). There is no dividing suture
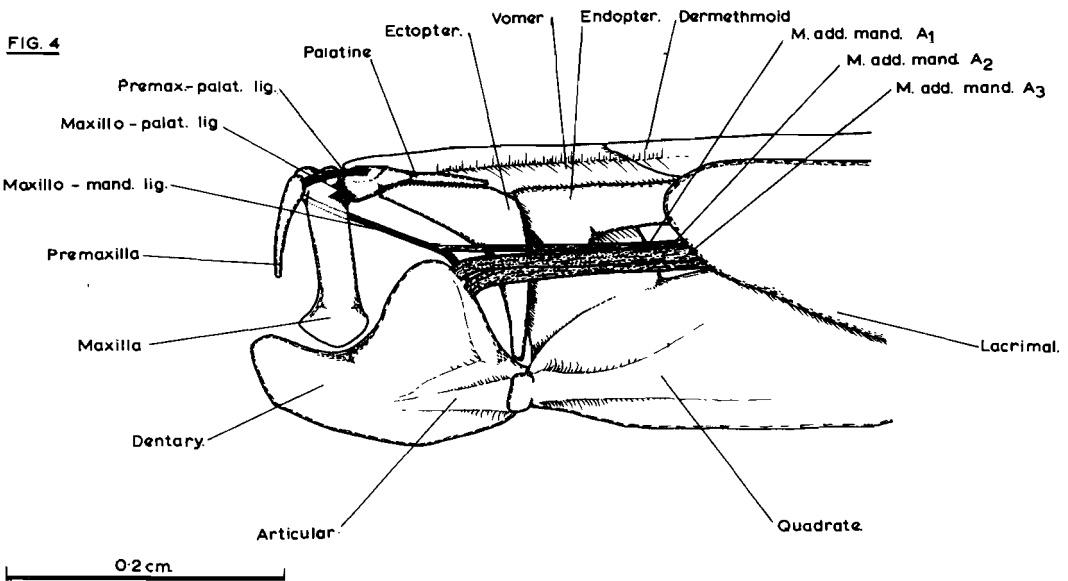
Fig. 4 *Syngnathus acus.* Left lateral view of mouth region, showing muscles and ligaments.

Ectopter.	:	Ectopterygoid
Endopter.	:	Endopterygoid
M. add. mand. A1, A2 & A3	:	Musculus adductor mandibulae A1, A2 & A3
Maxillo-mand. lig.	:	Maxillo-mandibular ligament
Maxillo-palat. lig.	:	Maxillo-palatine ligament
Premax.-palat. lig.	:	Premaxillo-palatine ligament

here, nor can one be demonstrated by maceration, although the metapterygoid normally occupies such a position.

Finally, it is possible that the metapterygoid may have been lost, for most of the palatal bones are reduced in size.

<div align="center">MUSCLES</div>

1. *Adductor mandibulae*

Three sections of the adductor are present, extending from beneath the orbit to their insertion on the lower jaw. They pass over the quadrate but lie beneath the antorbital plates (Figs. 3 and 4). This constitutes further evidence that these are lacrimal and suborbital bones, for it is unlikely that the adductor muscles would pass medial to the metapterygoid.

With the development of an elongate snout, the tendons of the adductor sections have elongated. The body of the muscle lies beneath and in front of the orbit, while the long tendons stretch along the snout to their insertion on the jaws.

Adductor A_1 originates on the upper limb of the symplectic (Fig. 3) and passes forwards to its insertion on the maxillo-mandibular ligament (Fig. 4). The insertion is characteristic of

this muscle, but its origin has shifted from its more normal position on the preopercular and metapterygoid, to the symplectic. Contraction exerts a tension on the maxillo-mandibular ligament, so that the maxilla and lower jaw are drawn backwards and inwards. Due to the connective tissue between the maxilla and the premaxilla, the latter is also pulled back. The mandible pivots at its articulation with the quadrate, and swings upwards and backwards, closing the mouth.

Sections A_2 and A_3 originate on the symplectic behind A_1 and extend to their insertion on the dentary. A_3 originates antero-dorsally to A_2, and then crosses under the latter half-way along the snout, to insert on the mandible ventrally to the insertion of A_2 (Fig. 3). The action of both these sections is to close the mouth by retracting the mandibles. The ligament between the maxilla and the mandible ensures a simultaneous retraction of the maxilla and the mandible.

The trigeminal nerve arises from the brain near to the facial nerve, and the two run together for a distance before diverging. The trigeminal divides into three principal rami. The superior ophthalmic passes forward over the orbit to supply the skin. The maxillary branch divides near the front of the orbit, one branch supplying the dorsal skin, and the other passing forwards to the mouth (Fig. 3).

The mandibular branch of the trigeminal nerve passes over A_3 and along its surface, under A_2, and after supplying twigs to the adductor, dives down to the lower jaw.

The position of this nerve in *S. acus* would thus support Kesteven's (1943) division of the muscle into a temperomasseteric group including A_1 and A_2, and situated superficial to the nerve, and a pterygoid group including A_3 situated medial to the nerve.

2. *Muscles of the palate*

(i) *Adductor arcus palatini.* Originating on the parasphenoid, this muscle passes downwards and outwards to its insertion on the symplectic (Figs. 3 and 5). It forms a thin sheet of short transverse fibres, which pass under the eye, bordering the orbit.

The action of the adductor arcus palatini is to pull the symplectic up and in, thus narrowing the buccal cavity. This movement is possible, as the symplectic can shift in the groove of the quadrate, and its posterior end is only loosely held to the hyomandibula.

From the back of the orbit the facial nerve gives off a thick branch, the buccalis, which passes along the parasphenoid, giving off very obvious twigs to the adductor arcus palatini. This is unusual, for the buccalis is usually a sensory somatic nerve and does not supply muscles.

(ii) *Levator arcus palatini.* This muscle originates from the inner surface of the sphenotic, and is inserted on the inside of the hyomandibula and the preopercular. As these bones are situated more medial than the sphenotic, the levator arcus palatini pulls the hyomandibula and preopercular outwards. Because the latter forms part of the snout rather than being associated with the operculum, its outward movement (and that of the hyomandibula) enlarges the buccal cavity. The action of the levator arcus palatini is therefore antagonistic to that of the adductor arcus palatini.

The mandibularis nerve of the trigeminal gives off a small twig at the back of the orbit, which innervates the levator arcus palatini.
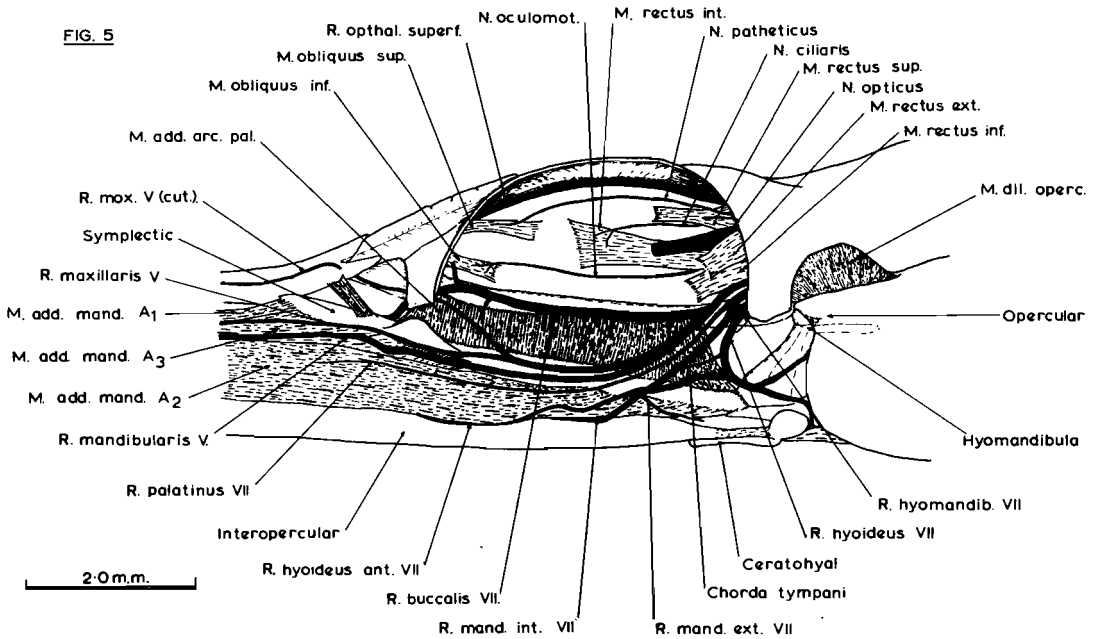
FIG. 5

R. opthal. superf.
M. obliquus sup.
M. obliquus inf.
M. add. arc. pal.
R. max. V (cut.)
Symplectic
R. maxillaris V
M. add. mand. A$_1$
M. add. mand. A$_3$
M. add. mand. A$_2$
R. mandibularis V.
R. palatinus VII
Interopercular
2·0 m.m.
R. hyoideus ant. VII
R. buccalis VII.
R. mand. int. VII

N. oculomot.
M. rectus int.
N. patheticus
N. ciliaris
M. rectus sup.
N. opticus
M. rectus ext.
M. rectus inf.
M. dil. operc.
Opercular
Hyomandibula
R. hyomandib. VII
R. hyoideus VII
Ceratohyal
Chorda tympani
R. mand. ext. VII

Fig. 5 *Syngnathus acus.* Muscles and nerves of the orbital region. Left lateral view.

M. add. arc. pal.	Musculus adductor arcus palatini
M. add mand. A1 A2 & A3	M. adductor mandibulae A1, A2 & A3
M. dil. operc.	M. dilatator operculi
M. obliquus inf.	M. obliquus inferioris
M. obliquus sup.	M. obliquus superioris
M. rectus ext.	M. rectus externus
M. rectus inf.	M. rectus inferioris
M. rectus int.	M. rectus internus
M. rectus sup.	M. rectus superioris
N. oculomot.	Nervus oculomotorius
R. hyoideus ant. VII	Ramus hyoideus anterioris VII
R. hyomandib. VII	R. hyomandibularis VII
R. mand. ext. VII	R. mandibularis externus VII
R. mand. int. VII	R. mandibularis internus VII
R. max. V (cut.)	R. maxillaris V (cutaneous)
R. ophthal. superf.	R. ophthalmicus superficialis

3. *Muscles of the ventral surface*

(i) *Rectus cervicis.* This muscle originates from the cleithrum and is inserted on the long urohyal, and its origin is partially confluent with the body muscles (Fig. 6). Contraction of the muscle pulls the urohyal back, rotating the hyoid arch backwards, so that instead of
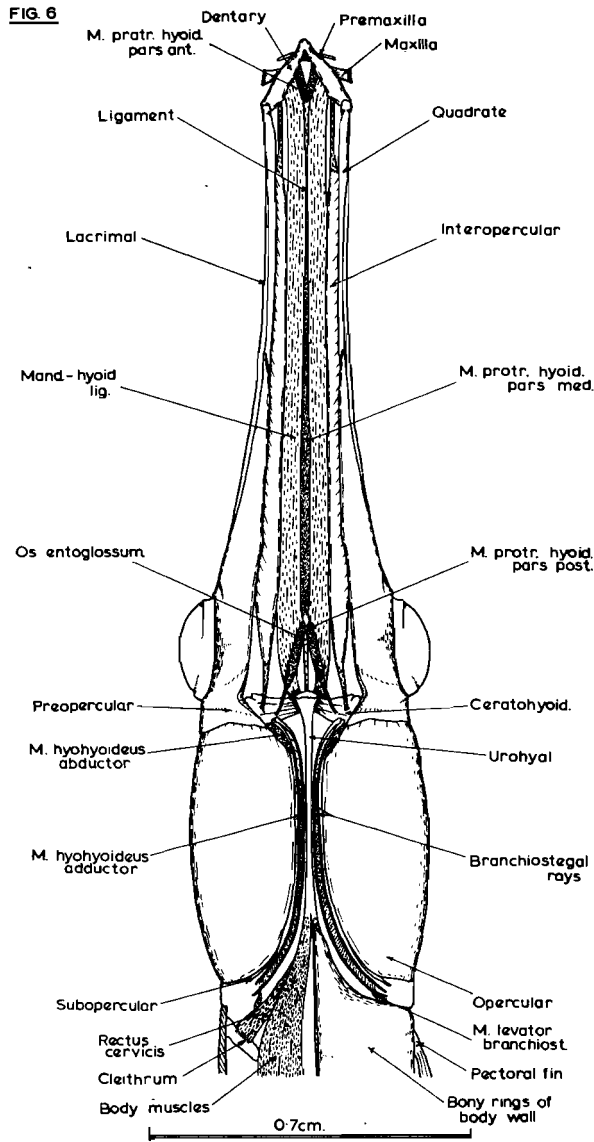
Fig. 6 *Syngnathus acus*. Ventral view of head dissected to show muscles. Bony rings of body wall removed on left.

Mand.-hyoid lig.	:	Mandibulo-hyoid ligament
M. levator branchiost	:	Musculus levator branchiostegalium
M. protr. hyoid. pars ant.	:	M. protractor hyoidei pars anterioris
M. protr. hyoid. pars med.	:	M. protractor hyoidei pars medialis
M. protr. hyoid. pars post.	:	M. protractor hyoidei pars posterioris

FIG. 7

Mandibulo-hyoid
ligament.

M. protr. hyoid.
pars med.

Preopercular

Interopercular

Branch of
R. hyoideus VII

M. protr. hyoid.
pars post.

Interop.-hyoid
lig.

Os entoglossum.

Basihyoid

Ceratohyal

Branch of
R. hyoideus VII

Urohyal.

M. interhyoid.

M. hyohyoideus
abductor.

Branch of
R. hyoideus VII

Branchiostegal
rays

Opercular

M. hyohyoideus
adductor

Connective
tissue

2·0mm.

Fig. 7 *Syngnathus acus.* Ventral view of the orbital region, dissected to show the muscles and their innervation.

Interop.-hyoid lig.	Interoperculo-hyoid ligament
M. interhyoid.	Musculus interhyoideus
M. protr. hyoid. pars med.	M. protractor hyoidei pars medialis
M. protr. hyoid. pars post.	M. protractor hyoidei pars posterioris
Branch of R. hyoideus VII	Branch of ramus hyoideus VII

lying flat against the skull, the arch is rotated through about 65° to lie at an angle to the skull (Fig. 3).

The rectus cervicis is a hypobranchial muscle and is therefore innervated by spinal nerves.

(ii) *Protractor hyoidei.* The protractor hyoidei is a compound muscle extending from the mandibles to the hyoid arch. It lies between the interopercular bones (Fig. 6) and is covered by a loose and extensible layer of skin (Fig. 10).

The formation of this muscle is described by Edgeworth (1935) and summarised by Millard (1966) in the introduction to this series. The muscle is compounded of a posterior slip of the intermandibularis, and the interhyoideus which extends forwards. The two are associated more or less intimately to form a single muscle system.

In *S. acus* the interhyoideus apparently divides into two portions. A deep portion extends forward from the inner surface of the ceratohyoid (Fig. 7), to insert on the dentary. In this portion the contractile tissue is replaced by a tendinous connective tissue, forming the mandibulo-hyoid ligament (Figs. 6 and 8).

A superficial and more ventral portion of the interhyoideus extends forwards and is associated with the intermandibularis posterior to form the protractor hyoidei muscle (Figs. 6 and 10). A slip of the interhyoideus retains its position between the ceratohyoids (Fig. 7). Its function appears to be largely connective, and it is reduced in size and incapable of pulling the two ceratohyoids together.

The embryonic copula communis develops for the attachment of muscles, and forms the os entoglossum of the adult (Figs. 6 and 7). In *S. acus* the intermandibularis posterior and the superficial interhyoideus form part of the same functional muscle system—the protractor hyoidei—but they are not fused together. The superficial interhyoideus extends from the outer surface of the ceratohyoid to the os entoglossum (Fig. 7), thus forming the protractor hyoidei pars posterioris (Fig. 6). The intermandibularis posterior originates on the tip of the os entoglossum (Fig. 7), and inserts on the mandible, superficial to the mandibulo-hyoid ligament (Fig. 8). This muscle tends to be replaced by ligamentous tissue, so that the muscle is split into two contractile units, the protractor hyoidei pars anterioris, and the protractor hyoidei pars medialis (Fig. 6).

In *S. acus* the superficial portion of the protractor hyoidei is in a maximal state of contraction when the jaws are closed, indicating that it is more likely to effect adduction of the hyoid arch than abduction of the jaws. Cutting of the protractor hyoidei of a dead fish had no effect on the opening of the jaw, for this occurred automatically when the rectus cervicis was pulled, whether or not the protractor hyoidei was cut. The indication is that the jaw opening is effected by way of the mandibulo-hyoid ligament and the interopercular ligaments, and that the action of the protractor hyoidei is unnecessary. On the other hand, when the jaws were forcibly closed, the mandibulo-hyoid ligament caused only partial protraction of the hyoid arch if the protractor hyoidei was cut. It seems that this muscle is needed for complete protraction of the hyoid arch.

The strong development of the mandibulo-hyoid ligament must partially take over the function of the protractor hyoidei, accounting for the poor development of the latter.

Having components of both mandibular and hyoid arch origin, the protractor hyoidei

is normally innervated by both facial and trigeminal nerves.

An anterior branch of the mandibularis V normally dives down to supply those parts of the protractor hyoidei which are of mandibular arch origin (Kesteven 1943), but no such nerve was found in *S. acus*. The hyoideus VII divides off from the hyomandibularis nerve, near the point where the latter energes from the back of the orbit, and gives off two branches. The hyoideus anterioris supplies the mandibulo-hyoid ligament, while the hyoideus posterioris passes back to the protractor hyoidei posterioris and the hyohyoideus muscles (Figs. 5 and 7).

(iii) *Intermandibularis anterioris*. Transverse fibres of this muscle stretch between the mandibles, and these hold the mandibles together (Figs. 8 and 9). When contraction occurs the mandibles are pulled together. The muscle is innervated by a small anterior branch of the mandibularis V.

4. Muscles of the Operculum

(i) *Dilatator operculi*. From its origin on the pterotic, the dilatator operculi passes over the articulation of the opercular with the hyomandibula, and inserts on the upper external surface of the opercular. Contraction enlarges the opercular chamber.

A fine posterior branch of the mandibularis V (which supplies the levator arcus palatini) gives off a twig innervating the dilatator operculi.

(ii) *Adductor operculi*. The adductor operculi originates from the pterotic underneath the opercular bone, and inserts on the inside of the latter. Its action is antagonistic to the dilatator operculi, and it pulls the opercular inwards, decreasing the volume of the branchial chamber.

Innervation is by the hyohyoideus posterioris, which gives off a twig passing up to the adductor operculi.

In *S. acus* no separate levator operculi can be distinguished.

5. Muscles of the Branchiostegal Rays

(i) *Hyohyoideus abductor*. This originates on either side from the base of the ceratohyoids, and passes back to be inserted on the outermost of the two pairs of branchiostegal rays (Fig. 7). The muscle is relatively small, and its function likely to be reduced. It pulls the branchiostegal ray nearer to the operculum, and as the second ray is pulled with it by the connective tissue, the rays of opposite sides are pulled apart. In conjunction with the expansion of the operculum, this aids in enlarging the branchial chamber.

(ii) *Hyohyoideus adductor*. This is a thin sheet of muscle stretched obliquely between the branchiostegal rays. The fibres are delicate and mixed with connective tissue (Figs. 6 and 7). Functionally this muscle is antagonistic to the abductor, for its contraction pulls the branchiostegal rays together, making the branchial chamber smaller.

Both hyohyoideus muscles are innervated by a posterior branch of the hyoideus VII (Fig. 7).

(iii) *Levator branchiostegalium*. This is the name applied to a small slip of muscle originating on the superficial fascia, medial and dorsal to the cleithrum, and inserting on the inner branchiostegal ray (Fig. 6). Its action is to pull the rays outwards, expanding the gill chamber.
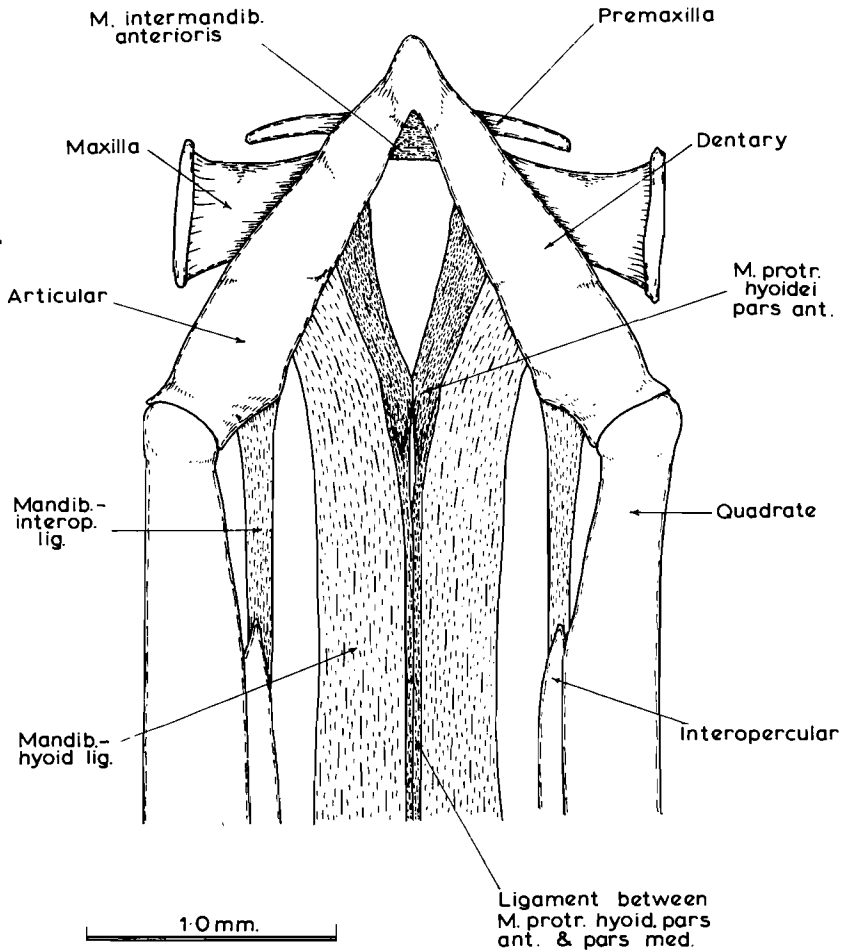
FIG. 8

Fig. 8 *Syngnathus acus*. Ventral view of jaws, revealing muscles and ligaments.

Mandib.-hyoid lig.	:	Mandibulo-hyoid ligament
Mandib.-interop. lig.	:	Mandibulo-interopercular ligament
M. intermandib. anterioris	:	Musculus intermandibularis anterioris
M. protr. hyoid. pars ant. & pars med.	:	M. protractor hyoidei pars anterioris & pars medialis

The levator occupies a similar position to the hyohyoideus dorsalis of Kesteven (1943), but is innervated by a spinal nerve and cannot therefore be considered one of the hyohyoideus group. There does not appear to be any homologous muscle in fishes described by other authors.

DISCUSSION

1. *Method of feeding*

From observation of aquarium specimens, *S. acus* is known to feed on small crustaceans, and will even accept fresh-water forms like *Daphnia*. Examination of the stomach contents of several specimens revealed little except a few unidentifiable fragments of crustacean limbs. Serial sections of one fish did, however, reveal two complete copepods in the stomach. As these were intact, it seems unlikely that the fish breaks up the prey in any way before swallowing it.

S. acus seems to depend largely on its sense of sight to detect its food, for its large protruding eyes are sensitive to any movement. The fish approaches a small crustacean slowly and then sucks the animal in by drawing a swift current of water into the mouth. In this way the fish is capable of capturing crustacea over a centimeter from its mouth.

2. *Muscle action during feeding*

In most teleosts, ligaments between the hyoid arch and the interopercular and between this and the retroarticular process of the jaw, transmit the movement of the hyoid arch and operculum to the lower jaw. Consequently the lower jaw is abducted when contraction of the rectus cervicis rotates the hyoid arch backwards (Holmqvist 1910; van Dobben 1935 and Ballintijn and Hughes 1965).

In *S. acus* the mandibulo-hyoid ligament is of far more importance than the mandibulo-interopercular ligament in transmitting the movement of the hyoid arch to the lower jaw. Ligaments are also present which suspend the interopercular between the hyoid arch and the mandible, and these also convey movement of the hyoid arch to the mandible. Cutting of the interopercular ligaments and the mandibulo-hyoid ligament respectively, indicates that the latter is of far more importance in lowering the mandible than are the former.

The pull of the mandibulo-hyoid ligament on the lower jaw has a strong backward component, but also a weaker outward component. As the mandibles are loosely joined together, this outward component causes them to swing apart at their articulation with the quadrate bones, thus widening the gape. The quadrate bones are in turn pushed apart, so that the whole snout is widened.

The downward swing of the mandible rotates the maxilla and premaxilla forwards to increase the gape. There is no real protrusion of the upper jaw, but the ligamentous connection between the jaw bones and the snout allow some degree of movement.

During respiration, water is drawn into the buccal cavity by contraction of the levator arcus palatini, which pulls the hyomandibula outwards, and contraction of the rectus cervicis which rotates the hyoid arch downwards. This increases the volume of the buccal cavity; the consequent decrease of pressure results in water being sucked in. The effect is aided by the widening of the snout as described above. Subsequently the water is directed into the branchial chamber by mutual action of the opercular and buccal muscles.
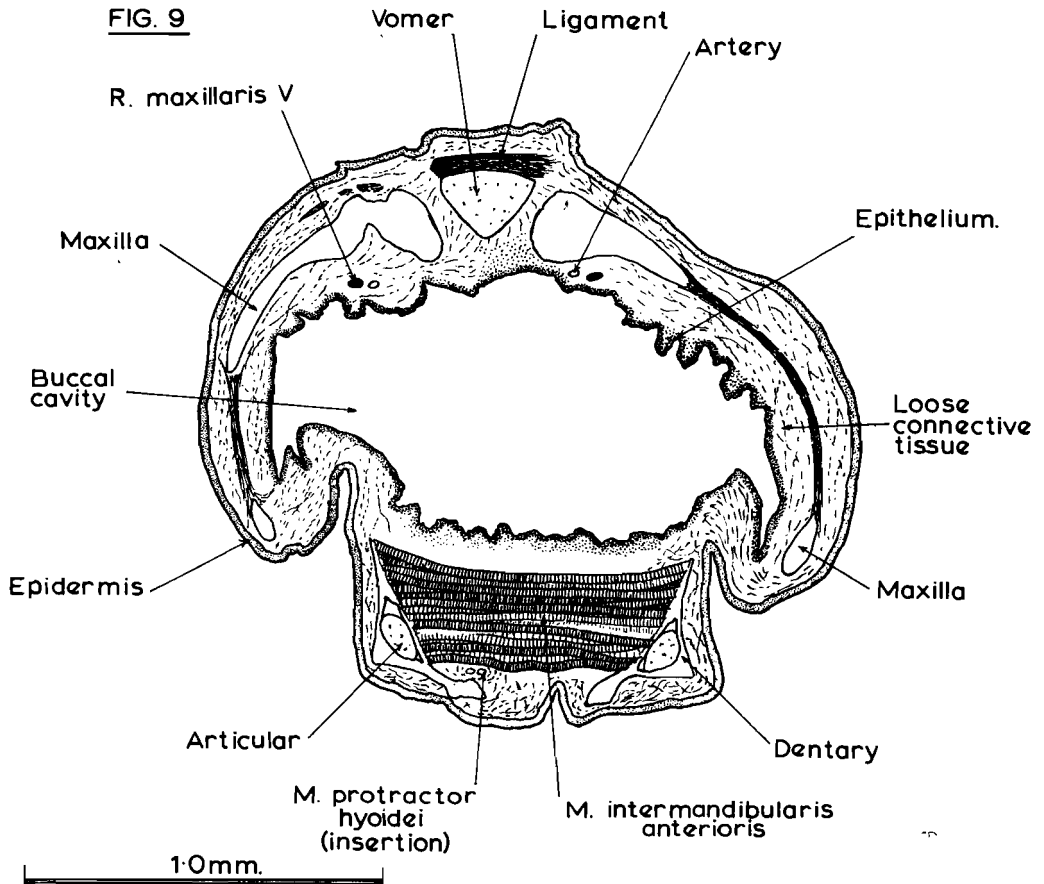
FIG. 9

Fig. 9 *Syngnathus acus.* Transverse secton through jaws.

The dilatator operculi, hyohyoideus abductor, and levator branchiostegalium lift the operculum outwards and spread the branchiostegal rays. The branchial chamber is consequently enlarged and the water passes through the gill slits and into the gill chamber. The branchial aperture acts as a valve, preventing water from entering through it, but allowing deoxygenated water to be forced out.

The mouth is then closed by the action of the adductor mandibulae. Contraction of the intermandibularis, which narrows the mouth and the snout, and the action of the adductor arcus palatini, decrease the volume of the buccal cavity. Retraction of the hyoid apparatus by the protractor hyoidei and the mandibulo-hyoid ligament occurs simultaneously, and the remaining water is forced from the buccal cavity into the branchial chamber.

The function of the protractor hyoidei is partially replaced by the mandibulo-hyoid ligament, which transmits the movement of the upper jaw to the hyoid apparatus, thus aiding

protraction of the hyoid arch when the jaws close. This explains the poor development of this muscle in *S. acus*. Partial protraction of the hyoid arch is therefore effected by the mandibulo-hyoid ligament, and the process supplemented by contraction of the protractor hyoidei muscle.

Evacuation of the gill chamber is brought about by contraction of the adductor operculi, and the hyohyoideus adductor, which pull the operculum inwards and the branchiostegal rays together respectively. The consequent decrease in volume forces the water out of the branchial aperture.

The action of the buccal cavity and the operculum can be likened to an interplay between a buccal pressure pump and an opercular suction pump. In the majority of teleosts it is the former which plays the predominant part (Saunders 1961), but in *S. acus* the reverse is true (Hughes 1960). This is principally due to the enlarged opercular cavity and the rigidity of the snout, for the former will increase the effectiveness of the opercular pump, while the latter inhibits the buccal pump. In addition, the opercular pump is aided by the almost complete closure of the opercular valve, which opens only at a small dorsal aperture.

The opercular pump is regulated by the opercular muscles and the branchiostegal muscles. In *S. acus* the branchiostegal muscles are of little importance; so much so that Hughes (1960, p. 42) states "there is no branchiostegal apparatus in this group". The branchiostegal apparatus is, however, present in *S. acus*, although admittedly it is relatively ineffective.

As these respiratory movements are continually performed without nearby particles of food being engulfed, it is obvious that the normal respiratory mechanism is inadequate for feeding. The additional suction necessary to engulf a crustacean is provided by the action of the rectus cervicis. This muscle normally pulls the hyoid arch backwards so that it rotates around at its articulation with the hyomandibula, and lies at an angle of about 65° to the skull, instead of flat against it. During prey capture the hyoid arch rotates even further, so that it lies almost perpendicular to the skull. This is presumably due to stronger contraction of the rectus cervicis than is normally experienced during respiration. Superimposed on the additional backwards rotation, the hyoid arch also twists outwards, forcing the hyomandibula bones apart. The net result is that the buccal and branchial chambers are expanded more than usual, creating sufficient suction to draw the prey in.

After the prey has been drawn into the mouth, the accompanying water is forced into the gill chamber by the usual expiratory muscles. Endothelial papillae stretch across the gill slits, and these act like a sieve, retaining any food. The food thus remains in the pharynx, and is passed down into the oesophagus.

The whole action of suction feeding is extremely rapid, and the fish must discriminate between desirable and undesirable objects before sucking anything into the snout. Food in the pharynx passes into the oesophagus, presumably forced there by a subsequent influx of water. The anterior end of the oesophagus and stomach is lined by a striated muscle, the sphincter oesophagi. Apparently it is not usual for striped fibres to extend over the stomach of fishes (Barrington 1957). Passage of the food into the oesophagus is aided by contraction of the pharynx while the sphincter oesophagi relaxes (Matthes 1963).
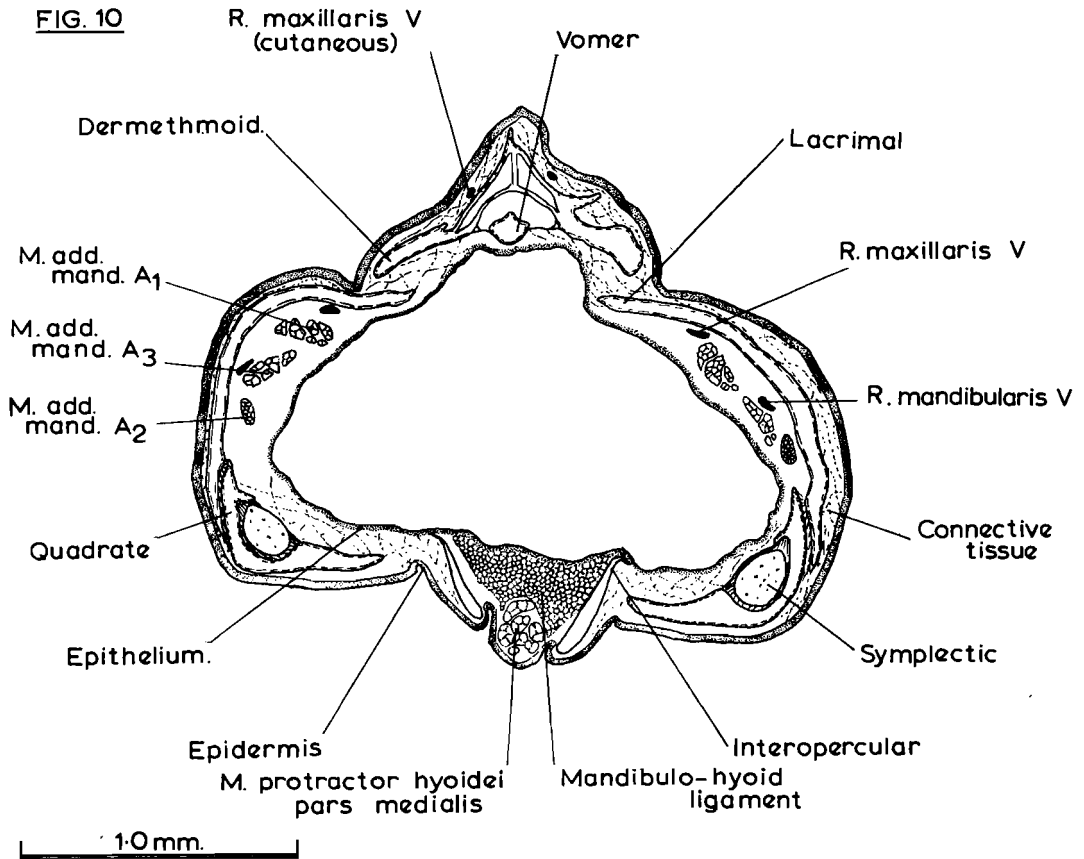
FIG. 10

Fig. 10 *Syngnathus acus.* Transverse section through mid-region of snout.
M. add. mand. A1 A2 & A3   :   Musculus adductor mandibulae A1 A2 & A3

3. *Adaptations of the head for feeding*

Judging from the method of feeding in this fish, it is likely that the snout has been developed in association with the sucking mechanism employed. An elongate and narrow snout with a small mouth not only increases the speed with which water can be sucked in, but also makes it possible for the fish to be more selective about what it sucks in.

The relative rigidity of the buccal cavity reduces the action of the buccal pump, but this is compensated for by the large branchial chamber, which enables a predominance of the opercular pump and increases the suction possible.

With the elongation of the snout, it is necessary for the muscles to shift their origins and become longer. In *S. acus* some of the muscles have changed their origins, such as the three sections of the adductor mandibulae. Increase of the length of the muscles is due to the

development of long tendons in those muscles which lie longitudinally. The adductor mandibulae has extremely long tendons, and the protractor hyoidei is partially replaced by tendinous tissue.

Elongation of the fibres of longitudinal muscles will increase the speed of their contraction, a factor which is of some importance in this type of sucking mechanism.

The lack of teeth on the jaws and branchial arches is a reflection on the type of feeding habits, for the prey is swallowed whole. The filtering action of the branchial arches is aided by the development of epithelial papillae on the arches.

Selection of food before feeding seems to be of importance, for *S. acus* is very specific in the choice of particles·that it swallows. Towards this end, the eyes are well developed. The nasal sacs are large and lined with a well developed epithelium, and it seems that both optic and olfactory senses play a part in food selection.

Many of the modifications of the head are therefore primarily aids to the method of feeding.

4. Phylogenetic significance of the cranial anatomy

As has been outlined in the introduction (Millard 1966), Eaton (1935) has suggested that the phylogeny of fishes is indicated by the arrangement of their cranial muscles, and the type of protractile mechanism which they possess. Four basic types of protractile mechanism are distinguished:

1. The non-protrusible mechanism of the Isospondyli.

2. The acanthopteran (Perciform) type where protrusion is controlled by crossed ligaments.

3. The cyprinodont type. The maxilla bears an internal hook which inserts into a socket on the premaxilla. Depression of the lower jaw twists the maxilla on its axis, driving the premaxilla forwards. No specialised ligaments are developed to control the movement.

4. The condition found in the Ostariophysi, of a single median ligament restricting the premaxilla.

Examination of the jaws of *S. acus* seems to indicate that the Syngnathidae are related to fishes of the cyprinodont type (Microcyprini of Regan, Cyprinodontiformes of Berg). *S. acus* is admittedly a highly specialised fish, and the mechanism of protrusion is absent, but certain generalisations can be made which support this relationship.

Despite the fact that the upper jaw is supported by many small ligaments, none of these are well developed, nor are they arranged as the typical perciform crossed ligaments; and there is no median rostral ligament as in the Ostariophysi. The lack of specialised ligaments in the upper jaw indicates closer affinity with the cyprinodont type than with any other type.

The presence of a rudimentary hook on the inside of each maxilla is further indication that the Syngnathidae are close to the cyprinodont type.

The usual systematic procedure is to place the sticklebacks, tube-mouths, and sea-horses in three groups, namely the Gasterosteoidea, Hemibranchii, and Lophobranchii; the last including the Syngnathidae. The three groups are associated in various ways by various authors.

Gregory (1933) includes all three as suborders of the Thoracostei. Regan (1929) associates the hemibranch and lophobranch fish in the order Solenichthyes, and considers the gasterosteoids to be a separate and unallied order—a view which is supported by the work of Starks (1902) on the hemibranch shoulder girdle. Berg (1947) places the Syngnathidae in the Syngnathiformes, allied to the hemibranch fishes (which he terms the Aulostomiformes). Smith (1950) also places the pipefish in a separate order, Lophobranchii, associated with the Aulostomi, but distinct from the gasterosteoids.

The present work indicates that the Syngnathidae (and their allied family, the Solenostomidae), differ markedly from the Hemibranchii in the development of antorbital plates. The view has already been put forward that these are lacrimal and suborbital bones, and the development or loss of these is indicative that there is a deep gap between the Lophobranchii and the Hemibranchii.

It is suggested that these two groups have evolved from the same ancestors, but that the elongate snouts of both are similar due only to parallel evolution; and it is further suggested that due to the retention of the lacrimal and suborbital, the Lophobranchii are more closely allied to the Gasterosteoidea than are the Hemibranchii.

SUMMARY

1. The osteology of the skull of *Syngnathus acus* is described, with particular reference to the snout and jaws.
2. The homology of the antorbital plates is discussed, and evidence put forward that they represent lacrimal and suborbital bones.
3. The anatomy of the cranial muscles is described.
4. Based on the anatomical investigation and observation of the live animals, suggestions are put forward as to the method of feeding in *S. acus*. It is concluded that the animal captures food by a sucking mechanism, and the structure of the skull and muscles is discussed in this light.
5. Possibly phylogenetic affinities of the Syngnathidae and allied groups are put forward. It is suggested that the snouts of the Syngnathidae and the Hemibranchii are similar due only to parallel evolution.

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