

Structure, Function, and Ecology in the Goatfishes (Family Mullidae)¹

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ABSTRACT: The Mullidae differ from other percoid families in a number of structural features. The most notable of these is a pair of highly developed hyoid barbels used in feeding. Many of the other goatfish specializations seem to be associated in one way or another with the use made of these barbels. Structural peculiarities of the Mullidae are described and their functional and ecological implications suggested where possible. The hypothesis is made that the goatfishes have evolved a distinctive ecological niche for themselves based on their use of the barbels in hunting.

MOST OF THE 50 OR SO families of percoid fishes are separated from one another by minor structural features (Regan 1913). The goatfishes (Family Mullidae) differ drastically from this general pattern. They have developed a structural peculiarity unique among percoids, the hyoid barbels, and a number of other specializations, several of which appear to be functionally or structurally associated with the barbels. The adaptations of the Mullidae seem to have been rather successful, for goatfishes are represented circumtropically in inshore areas, often by large numbers of individuals. Within the family, there appears to have been a minor adaptive radiation based on the exploitation of the barbels for various types of feeding because the principal differences between the six otherwise quite similar genera of the family are in dentition.

A pair of well-developed barbels is present in all adult goatfishes. The two members of each pair are independently movable and bear numerous sense organs (Sato 1937). When a goatfish is not feeding, the barbels are folded back under the rims of the chin and gill covers. In feeding, the barbels are lowered to touch the bottom under the fish. Probably all goatfishes use their barbels to detect food items on or slightly below the surface of the substrate (Figure 1). When an area with such items is located, different goatfishes adopt various methods for obtaining the prey. Some, such as

Upeneus tragula, shown in Figure 2, use their barbels as an excavating device (see also the comments of Hiatt and Strasburg [1960:84] concerning *Parupeneus cyclostomus*). In Hawaii *Parupeneus cyclostomus* (formerly *P. chryserydros*) pokes its barbels into holes and crevices in hard substrates to dislodge small animals (Hobson 1974). *Mulloides flavolineatus* (*Mulloidichthys samoensis* auctorum) may back off from an item discovered by the barbels (Figure 1) and "blow" away sand to uncover it (pers. obs.); the same species may also burrow into the sand with its snout to retrieve a food item (Hobson, pers. comm.). *Mullus surmuletus* on occasion ploughs up the mud with its snout in feeding and apparently expels water from its mouth while doing so (LoBianco 1907). These feeding methods are only used by half-grown and adult goatfishes, for all mullids so far as known have pelagic eggs, larvae, and juveniles (Caldwell 1962).

Because of the use that goatfishes make of their barbels and functionally associated characters, the interrelationship between structure, function, and ecology in the Mullidae is particularly close and is stressed here. On the other hand, the distinctiveness of the family seems to have obscured evidence for relationship between the Mullidae and other percoids, and an attempt to determine these relationships has not been very successful. In the present paper the various peculiarities of the goatfishes are described beginning with the barbels. These peculiarities are compared with similar developments elsewhere in teleosts and where possible are interpreted in terms of

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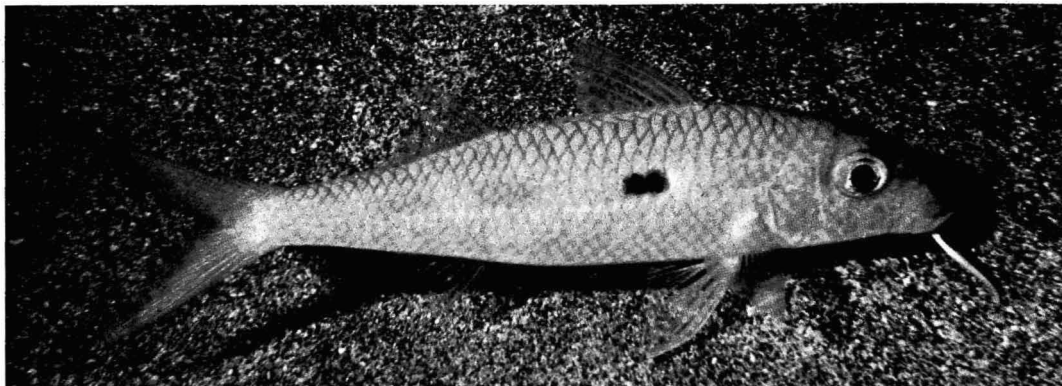


FIGURE 1. *Mulloides flavolineatus* probing for food (Kona, Hawaii). Photograph by E. S. Hobson.

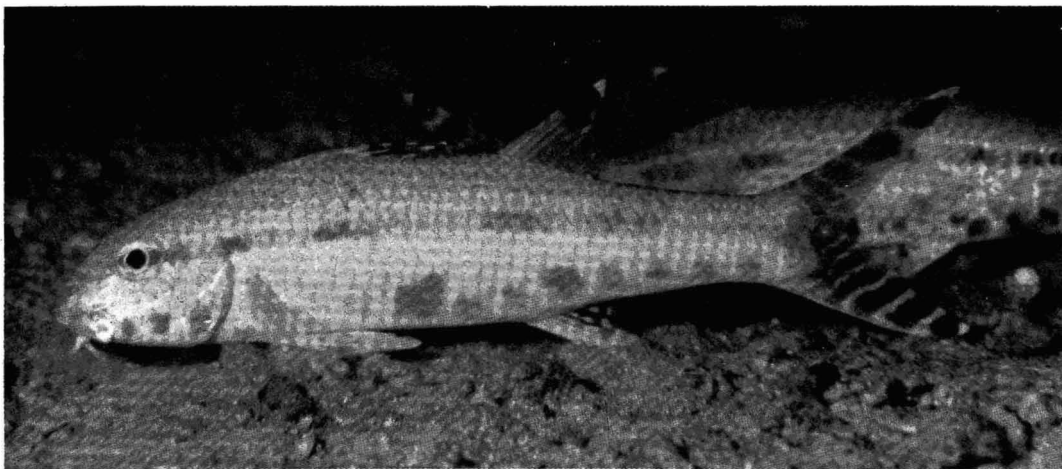


FIGURE 2. *Upeneus tragula* using its barbels as an excavating tool (Ujung off Pandang, Sulawesi, formerly Makassar, Celebes). Photograph by J. E. Randall.

function. Comments on mullid genera, family relationships, and ecology conclude the paper.

The material on which the article is based consists of partly dissected and whole specimens of all six mullid genera in the University of Michigan collections.

The scientific names used in the paper are those suggested by Randall (pers. comm., March 4, 1984). The name changes of concern here are as follows: *Parupeneus chryserydros* is placed in the synonymy of *P. cyclostomus* and *Upeneus arge* in that of *U. taeniopterus*; *Mulloides* is considered a valid generic name, replacing the more widely used substitute *Mulloidichthys*. The question of whether the genus

Parupeneus should be synonymized with the closely related *Pseudupeneus* is left open.

THE BARBEL APPARATUS

There are two mechanically separate components to barbel manipulation in goatfishes (Figure 3 *A, B*). One has to do with the movements of the barbels (*A, A₁*, and *A₂*) relative to the hyoid bars with which they articulate. Each of the two barbels has its own musculature that controls such movements, thus enabling the two to move independently. The second mechanical component (*B, B₁*, and

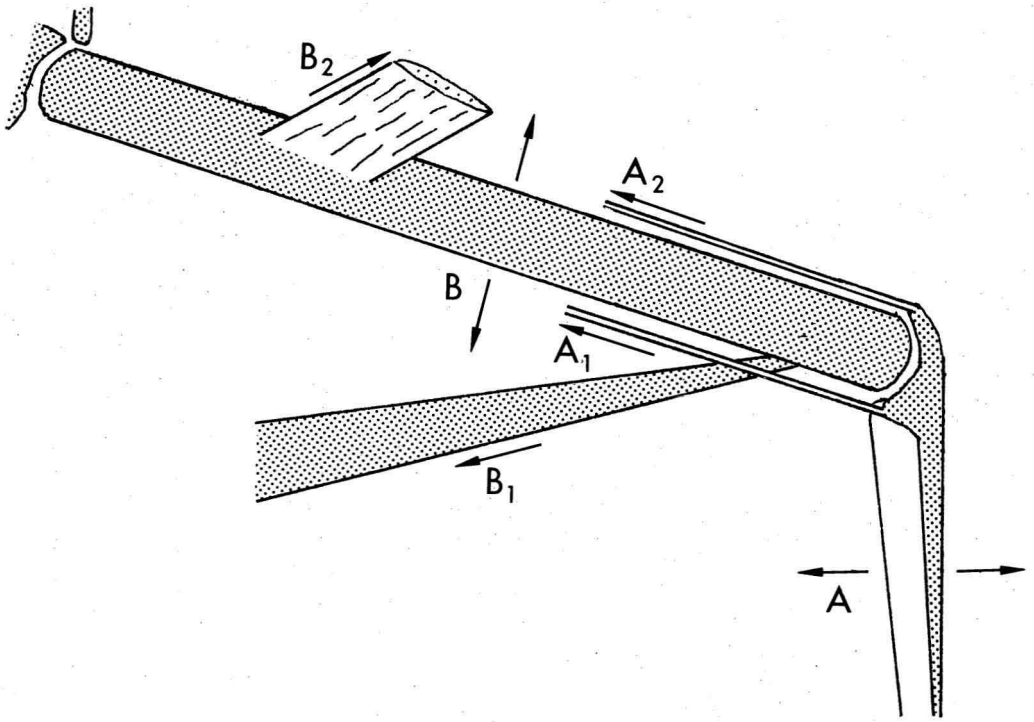


FIGURE 3. Diagram to illustrate goatfish barbel mechanics. Lateral view from right side. Stippled areas represent bone. Arrows indicate direction of movement. *A*, barbel with the ligaments that (*A*₁) retract and (*A*₂) lower it. *B*, hyoid bar with the urohyal (*B*₁) that lowers and the *M. protractor hyoideus* (*B*₂) that raises it.

*B*₂) causes the lowering and raising of the anterior ends of the pair of hyoid bars relative to the head of the fish.

The barbel itself consists of a fleshy, sensory part that encloses a long, tapering, distally flexible branchiostegal ray. A large nerve enters the base of the fleshy part and innervates the numerous sense organs on the surface of the barbel. The modified branchiostegal ray (LoBianco 1907) provides a strengthening support for the barbel. It originates in a cap of fibro-cartilage which forms a socket over the tip of a forward projection from the anterior ceratohyal of the hyoid bar (Figure 4). Two ligaments insert on the cap of fibro-cartilage at the base of the barbel, one above the ceratohyal projection and one below. These ligaments lead back into musculature originating along the hyoid bar (not shown in Figure 3). Contraction of the muscle to the upper ligament (Figure 3*A*₂) lowers the barbel

whereas contraction of the muscle to the lower ligament (*A*₁) retracts the barbel. The muscles to both ligaments appear to be modified parts of the hyohyoideus system (Winterbottom 1974*a*).

The second component of the barbel apparatus governs the movement of the anterior ends of the hyoid bars. Generally in teleosts the hyoid bars are movable at both ends. Anteriorly they are connected to the symphyseal area of the chin by musculature (the *M. protractor hyoideus* of Winterbottom 1974*a*; the *M. geniohyoideus* of Osse 1969); posteriorly to the inner surface of the suspensorium by the intercalation of a movable interhyal bone. In the Mullidae the freedom of movement of the anterior ends of the hyoid of the hyoid bars has been increased and that of their posterior ends reduced to rotation in a firm socket.

The structural changes associated with the

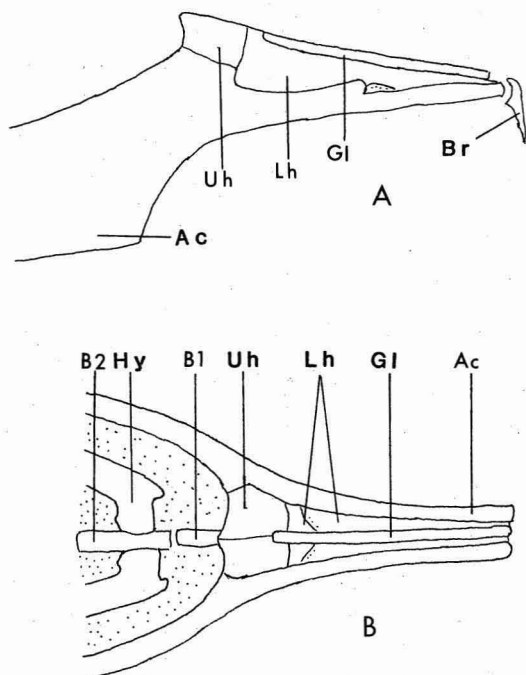


FIGURE 4. Bones associated with the forward end of the hyoid apparatus in *Pseudupeneus maculatus*. *A*, lateral and *B*, dorsal view. Only the basal part of the branchiostegal ray is shown. *Ac*, anterior ceratohyal; *B1*, first basibranchial; *B2*, second basibranchial; *Br*, branchiostegal; *GI*, glossohyal; *Hy*, first hypobranchial; *Lh*, lower hypohyal; and *Uh*, upper hypohyal.

hyoid bar movements of goatfishes are as follows. The posterior end of each hyoid bar is restricted to a socket formed primarily by a semicircular, medianly projecting flange on the inner surface of the interopercle (Figures 3, 5). In front of this flange, the posterior end of the bar is propped from above by the interhyal bone. Anteriorly, the forward end of the pair of hyoid bars is connected with the chin only by flexible membrane. The protractor hyoideus muscle that is usually in this area has moved its posterior attachment well back along the shaft of the hyoid bar (Figure 3*B*₂). It still serves to raise the hyoid bar, but the posterior displacement of its attachment permits considerably greater movement of the anterior ends of the bars than in other teleosts. The cause of such lowering is, as usual, contraction of the sternohyoideus muscles acting via the urohyal bone (Figure 3*B*₁).

Teleosts have evolved ventrally directed projections of various types, usually or always equipped with sense organs. Such projections range from barbels on the chin to extensions of the pectoral rays. However, sensory probes developed in association with branchiostegal rays are rare and occur, to my knowledge, only in the Mullidae and in the beryciform genus *Polymixia*. That the hyoid barbels in these two taxa have evolved independently is clear from a number of structural differences between them. Furthermore, the barbel apparatus of the Mullidae is much more specialized than that of *Polymixia*.

In *Polymixia* three modified branchiostegal rays support the barbel rather than the one ray in the Mullidae (Starks 1904). In *Polymixia* the hyoid bar has the usual movable attachment at both ends rather than the modifications described above in the Mullidae. There is also a considerable difference between the two taxa in the basal articulation of the barbel and in the bones at the anterior end of the hyoid bar.

In *Polymixia* the hypohyal bones hold their usual position, one under the other, at the anterior end of the hyoid bar, and the three branchiostegal rays supporting the barbel have simply moved forward to an articulation with the under surface of the lower hypohyal (Starks 1904: fig. 4). In the larval goatfish *Mullus surmuletus* the branchiostegal rays have their normal serial arrangement (LoBianco 1907), but during growth the anterior branchiostegal moves forward along the hyoid bar and becomes widely separated from the other branchiostegal rays. This forward movement of the anterior branchiostegal ray is apparently accompanied by the development of a forward projection from the lower part of the anterior ceratohyal, because in the adult goatfish, this projection extends anterior to the two hypohyals which themselves have become horizontally aligned (Figure 4; see also Starks 1904: fig. 5). The result of these changes is that in goatfishes the barbel articulation has moved forward to about the level of the tip of the glossohyal (concealed under the membrane of the floor of the mouth) and forward of the hypohyals (Figure 4).

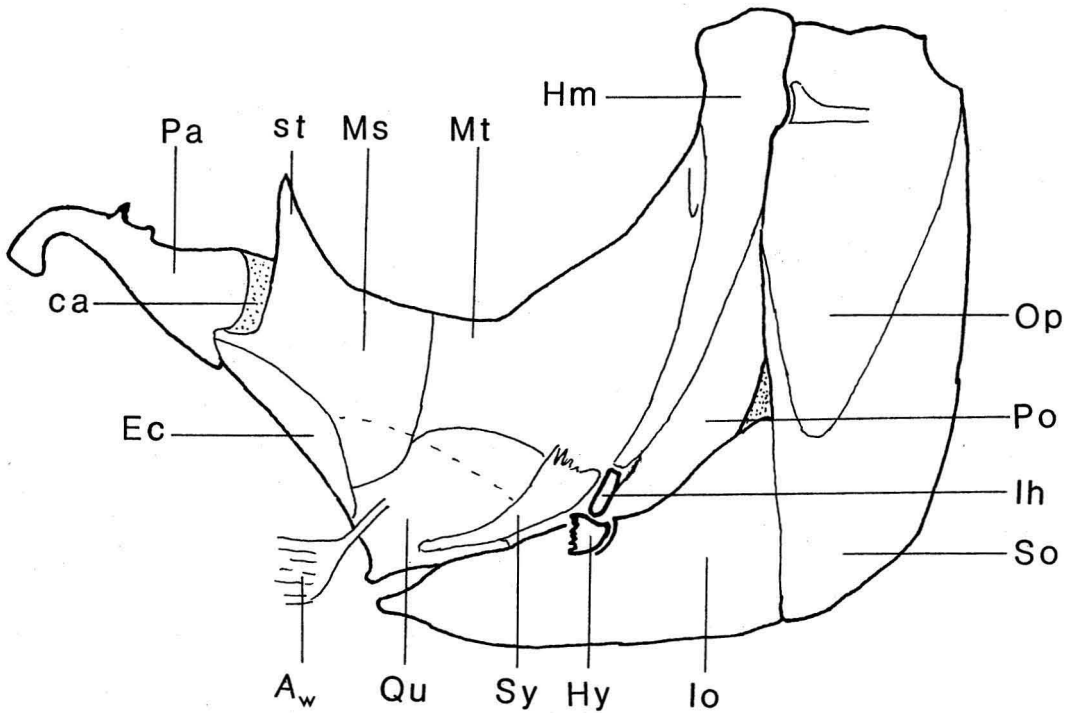


FIGURE 5. Internal view of the suspensorium of *Mullus barbatus* with the posterior end of the hyoid bar and the interhyal included. *A_w*, part of the *A_w* section of the *M. adductor mandibulae*; *ca*, cartilage; *Ec*, ectopterygoid; *Hm*, hyomandibular; *Hy*, posterior part of the hyoid bar; *Ih*, interhyal; *Io*, interopercle; *Ms*, mesopterygoid; *Mt*, metapterygoid; *Op*, opercle; *Pa*, palatine; *Po*, preopercle; *Qu*, quadrate; *So*, subopercle; *st*, strut on the mesopterygoid that abuts against the back of the lateral ethmoid; and *Sy*, symplectic.

There are two points to be made about the forward articulation of the barbel in goatfishes. First, the greater the distance of the articulation from the fulcrum at the posterior end of the hyoid bar, the greater the amount the barbel will be lowered when the bar itself is rotated through a given angle. Presumably, then, the extent to which the hyoid bar can move the barbel downward has been increased by the forward displacement of the barbel articulation. The second point concerns the possible structural relationship between the anterior elongation of the hyoid bar and the lengthening of the preorbital part of the head that appears to have occurred in the Mullidae. In goatfishes the snout region above the mouth has apparently become extended as have the hyoid bars below the mouth, and the possibility seems high that the two features are related.

THE LENGTHENING OF THE SNOUT REGION

The snout length in various goatfishes is quite different, ranging from short and blunt in *Mullus* to considerably extended in *Parupeneus* and *Pseudupeneus*. Nevertheless two osteological features present in all goatfishes suggest that the preorbital part of the head has been lengthened in the mullid ancestral stock. One is in the superficial circumorbital series of bones. Usually in teleosts, the anteriormost member of the series, the lacrimal, articulates with the lateral ethmoid in front of the orbit, and the infraorbital bone behind it is well separated from the lateral ethmoid. In the Mullidae, the lacrimal seems to have shifted forward, for it has only a slight contact with the lateral ethmoid, whereas the infraorbital behind it has the main contact with the lateral ethmoid (Smith and Bailey 1962).

The other apparently forward shift in the anterior head structures occurs in the suspensorium. Normally, the anteriormost bone in the suspensorium, the palatine, provides the only articulation between the forward part of the suspensorium and the skull. As with the circumorbital series, in the Mullidae a bone behind the palatine, the mesopterygoid, has developed an articulation with the skull (Figure 5).

The apparent forward dislocation of the lacrimal and palatine bones in the Mullidae is almost exactly duplicated in another very different group of percoids, the Pentacerotidae (*Quinquarius* examined). Some pentacerotids, like mullids, also have barbels, but those of the pentacerotids are on the chin, not the hyoid bars.

In *Quinquarius* the anterior (palatine) part of the suspensorium appears to have a normal, firm attachment to the rest of the suspensorium, and the whole compound structure seems to move as a single unit. In the Mullidae, however, the upper part of the palatine is joined to the mesopterygoid strut behind it by a flexible area of cartilage (Figure 5), providing a joint between the anterior and posterior components of the suspensorium. Such a joint is common in percoids. Furthermore, in the Mullidae the *M. adductor arcus palatini*, or a more or less separate section of it, extends forward along the inner surface of the palatine. I have not seen such a forward extension elsewhere. It may have to do with the expulsion of a jet of water from the mouth in these fishes.

OTHER STRUCTURES ASSOCIATED WITH THE MOUTH

In addition to the goatfish specializations already discussed, there are a number of other peculiarities associated with the mouth that range in distribution from one which is widely held among percoid fishes to at least one feature that appears to be entirely restricted to the Mullidae.

Adult goatfishes feed on benthic animals and their mouths open forward and downward. Some of the specializations in the snout

region appear to be related to their bottom feeding.

The lacrimal bone, as in many bottom-feeding percoids, (e.g., the lutjanoid-sparoid-haemuloid series, Johnson 1980), is extended downward so as to overlap a large part of the maxillary shaft. Also, as in the same and other percoid groups, the originally movable nasal bone has in goatfishes a rigid posterior attachment to the skull. LoBianco (1907) suggests that in *Mullus* this increased rigidity of the anterior part of the skull is associated with the habit in this genus of ploughing up the bottom with its snout.

Goatfishes have gone one step further along this same line of development than many fishes with rigidly attached nasal bones. They have lost the usual ethmoid-maxillary ligament and have functionally replaced it with a ligament that passes anteriorly from the lateral border of the nasal bone over the palatine prong to an attachment on the forward rim of the maxillary (Figure 6A). This same substitution of ligaments occurs elsewhere in percoids in such fishes as the pentacerotid *Quinquarius* and in lethrinids (pers. obs.; see also Johnson 1980).

In goatfishes the premaxillae protrude in a more or less downward direction, and a number of specializations seem to be associated with this. The anterior face of the vomer has a raised, median, cartilaginous ridge (Starks 1926) over which the ascending premaxillary processes slide. There is a similar ridge in, for example, *Menticirrhus*, a sciaenid with a downwardly projecting mouth opening. In goatfishes the shaft of the maxilla is about equally deep throughout, the primordial ligament does not pass across it to an attachment on its outer rim, and the palatine prong extends down over the maxilla and has a more or less expanded tip (Figure 6A). These features are all present in the sparoid genus *Lethrinus*.

Other peculiarities associated with the mouth of goatfishes cannot readily, if at all, be functionally associated with the downward protrusion of the premaxillae. The most distinctive of these is what will here be called a supramaxillary scale (Figure 6A). Like the supramaxillary bone of many lower percoids this specialized scale, present in all Mullidae,

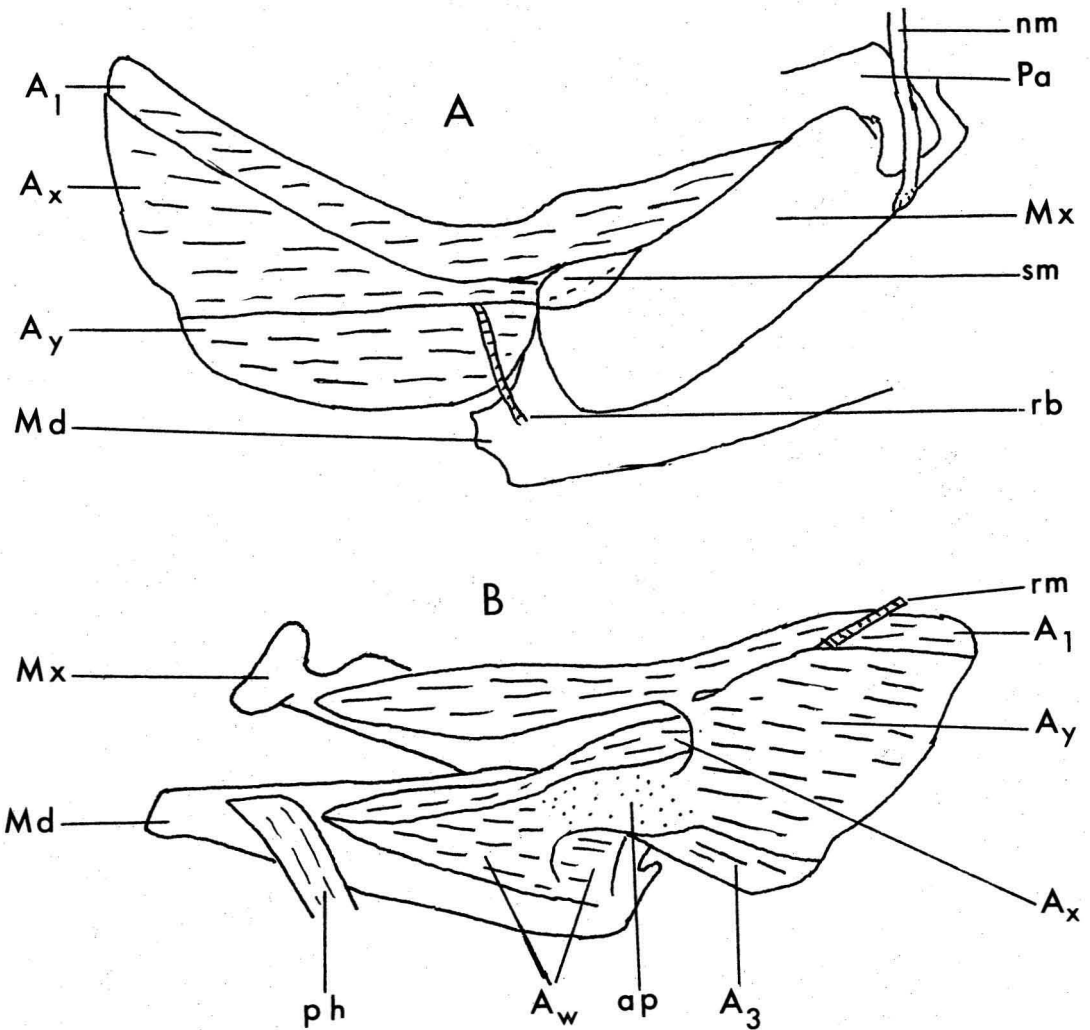


FIGURE 6. The adductor mandibulae muscle and topographically associated features in *Upeneus moluccensis*. A, external and B, internal view. A₁, A₃, and A_w, three of the sections of the M. adductor mandibulae; A_x and A_y, the two parts of the usual A₂ section; ap, aponeurosis; Md, mandible; Mx, maxilla; nm, nasal-maxillary ligament; Pa, palatine; ph, upper end of the M. protractor hyoideus; rb, lower branch of the ramus mandibularis nerve; rm, ramus mandibularis; and sm, supramaxillary scale.

extends upward from the distal end of the maxillary bone. It frequently takes on some of the characteristics of the distal end of the maxillary bone (e.g., sculpturing). Furthermore, it may underlie other, more normally developed scales. It differs from the supramaxillary bone in that its base overlaps the maxilla rather than riding on its upper rim. Furthermore, in *Upeneus parvus*, which has a

particularly large supramaxillary scale, there are circuli around its anterior surface.

Usually in goatfishes there are a number of scales on the maxilla, but in some species of *Upeneus* only the supramaxillary scale appears to be present. I do not know of a scale of this type elsewhere, but in a number of percoids with a scaleless maxilla there is a cartilagelike upward extension along the dorsal rim of the

distal end of the maxilla (e.g., in the sciaenid *Menticirrhus*).

The configuration of the adductor mandibulae muscle, though inadequately investigated in percoids up to now, can be a good systematic character (see, for example, Johnson 1980); it certainly is within the Mullidae. As in so many small-mouthed higher teleosts (see, for example, Winterbottom 1974b) the *M. adductor mandibulae* of all goatfishes is complex (Figure 6). In *Upeneus moluccensis*, which seems to represent the basal goatfish condition in this feature, there are five more or less separate sections of this muscle passing between the suspensorium and the jaws. The uppermost section in external view (Figure 6A) is undoubtedly an extended maxillaris (A_1) component. It originates on the posterior part of the suspensorium and passes forward to an insertion on the inner surface of the maxilla just behind the proximal head of that bone. The usual A_2 component of the *M. adductor mandibulae* appears to be represented by two sections (Figure 6 A_x, A_y). The upper of the two in external view passes forward to an insertion along the inside of the mandible above A_w (Figure 6B). The lower of the A_2 sections in external view almost completely underlies the upper. It passes forward into the aponeurosis with A_w and then is continued forward by A_w on the inside of the mandible. The mandibular ramus of nerve *V* passes forward medial to A_1 and the upper section of A_2 , then forward into the mandible between the two sections of A_2 , sometimes, as in Figure 6A, with a branch that passes down across the base of the lower section of A_2 . A_3 is the usual small muscle visible only in internal view. In addition, A_w , normally limited to the mandible, has a part attached by ligament to the inner surface of the quadrate bone of the suspensorium (Figure 5).

Pseudupeneus (see Smith and Bailey 1962) and *Parupeneus* differ notably from other goatfishes in that most or all of the A_1 section of the adductor mandibulae is attached to the under surface of the infraorbital bones. Such an attachment also occurs in the percoid genus *Lutjanus* (Smith and Bailey 1962) and certain other members of the Lutjanidae

(Johnson 1980), but I do not know of such an attachment elsewhere.

THE SPHENOTIC PROJECTION

Goatfishes all have one peculiarity in the bony postorbital rim. In percoids with more or less cylindrical heads (e.g., *Perca*, Osse 1969), the *M. levator arcus palatini* originates on the under surface of the postorbital part of the skull. In fishes with high, compressed heads this muscle usually originates on the posteroventral surface of a lateral projection from the sphenotic which, with the frontal bone above it, forms a continuous rim around the posterodorsal part of the eye. In goatfishes there is a gap, crossed externally by the dermosphenotic, between the sphenotic projection and the frontal border of the orbit above it. In some goatfishes (e.g., *Mullus*, *Mulloides*, *Upeneichthys*) the *M. dilatator operculi* passes forward through this gap to an attachment on the inner surface of the orbital wall. A similar gap in the postorbital rim occurs in some sparoid fishes (e.g., *Calamus*, *Archosargus*) but by no means all. The functional significance of this gap is unclear, and its systematic significance, if any, has been too little investigated to determine.

STRUCTURES ASSOCIATED WITH THE FINS

Goatfishes always have two, well-separated dorsal fins. They also have a single, minute anal spine and a well-developed scaly process in the axil of the pelvic fin. These features, held in common with other percoids, may or may not have value as indicators of relationship.

In two other features associated with the fins, the goatfishes are highly peculiar. The scapula of the pectoral girdle contains either two or three foramina (Starks 1930). Most other teleosts have only one (Starks, 1930, records two in cirrhitids) through which a major nerve passes (see, for example, Freyhofer 1963). Examination of the scapular foramina of goatfishes indicates that the anterior-most corresponds to that of other fishes, and that the other one or two transmit nothing. Their significance is unclear.

Goatfishes have 13 instead of the usual 15 branched caudal rays of percoids. A reduction in branched ray count occurs sporadically elsewhere in higher teleosts, for example in anabantoids and *Scatophagus*. More notable is the pattern of fusion in the caudal skeleton. Externally the caudal fin of goatfishes is essentially symmetrical but the caudal skeleton is more than usually asymmetrical (see figures in Monod 1968). The hypurals to the upper caudal lobe are fused to one another and to the urostyle, but the hypurals to the lower lobe remain separate from one another and from the urostyle. I have not seen this type of fusion in the caudal skeleton elsewhere.

The reasons behind the differential fusion in the upper and lower caudal lobes of goatfishes can only be a matter for speculation. However, the following possibility seems worth suggesting. Goatfishes have the forked tails of strong swimmers, which they undoubtedly are. Both lobes of the caudal fin are swung from side to side during rapid locomotion, and the fusion in the parts of the caudal skeleton associated with the upper caudal lobe may increase the strength of the tail beat. However, during hunting (Figure 1) or feeding (Figure 2) it is necessary to adjust the head precisely with reference to the bottom. The relative flexibility of the lower caudal lobe may be used for this purpose by enabling differential movements between the upper and lower caudal lobes during slow forward movements or for lowering or raising the head during feeding.

COMMENTS ON GENERA

Dentition is the principal character used for differentiating goatfish genera (see, for example, Lachner 1960). Certain rectifications in descriptions of this feature may be noted here.

Upeneus has the most extensive dentition among goatfishes and one that is of a generalized percoid type. The genus is said to have teeth on the jaws, vomer, and palatines (e.g., Lachner 1954). Though there are normally teeth on the vomer, they may be few. In a specimen of *U. sundaicus* I cannot find any at

all. The teeth on the palatines, on the other hand, are always well represented. Furthermore, the palatine patch seems always to be continued back on to the ectopterygoid to a greater or lesser extent.

Mullus is usually described as lacking teeth in the upper jaw. This, as Caldwell (1962) notes, is only true of adults. The vomer of *Mullus* is expanded into a broad, medially grooved plate bearing pebblelike teeth. Though the palatines are sometimes said to provide part of the patch of teeth on the roof of the mouth (e.g., Lachner 1960), they are toothless and quite separate from the vomer.

Lachner (1960:3) states that *Pseudupeneus* differs from *Parupeneus* in the presence on the upper jaw of a second, outer row of one to several teeth. These may be somewhat reverted and tusklike. What apparently happens here is that the teeth in the single row of juveniles develop irregularly as the fish grows, for I can find no second row of teeth in available specimens smaller than 164 mm in standard length. Specimens available seem to have a single row of teeth in the lower jaw, not two or more as stated by Lachner (1960).

Two other aspects of differentiation between goatfish genera deserve comment.

Upeneichthys, by comparison with other genera, appears to have emphasized perception by the lateralis system, as the old name *porosus* applied to one of the species indicates. In *U. lineatus* the whole snout region is covered by a series of moderately large pores and lacks the embedded scales of other goatfish genera.

Parupeneus and *Pseudupeneus*, two closely related genera (or subgenera), differ more radically from other goatfishes and appear to be the most specialized genera in the family. The following specializations may all be associated with their relatively elongate snouts. In addition to the attachment of the A_1 section of *M. adductor mandibulae* to the infraorbital bones noted above, they have the epaxial body musculature extending farther forward over the top of the head than in other goatfishes (except possibly for some species of *Upeneus*) and have lost the superficial connection between the preopercular and temporal lateralis canals present in other mullids.

FAMILY RELATIONSHIPS

The systematic position of the Mullidae among percoid families is obscure. As already noted, several goatfish specializations appear to be unique among percoids. One of these, the increase in the number of scapular foramina, seems to offer no indication of relationship. Two others suggest something about mullid ancestry by implication. Morphologically, the hyoid barbels have no counterpart, rudimentary or well-developed, elsewhere among percoids, but their position and the use made of them suggest that they originated in a bottom-feeding fish. The supramaxillary scale again seems to have no counterpart elsewhere, but its position suggests a substitute development for the supramaxillary bone of many lower percoids and lower teleosts generally. If this interpretation is correct, two implications are at least worth considering: that goatfishes evolved from a stock that (1) had lost its supramaxillary bone and (2) had scales on the maxilla.

Other goatfish specializations, or even suites of them, seem to have evolved independently in other percoid groups. This is true of the attachment of the A_1 section of the M. adductor mandibulae to the infraorbital bones in certain mullids and lutjanids. It also appears to be true of the several similarities in the anterior part of the head between mullids and the pentacerotid genus *Quinquarius*: the articulations of both the first infraorbital and the mesopterygoid with the lateral ethmoid, and the loss of the ethmoid-maxillary ligament.

Two suggestions concerning mullid relationships have been made. One is with the Lutjanidae by Regan (1913) and the other with the Sparidae by Boulenger (1904). There are far more similarities between goatfishes and the sparoid fishes than between mullids and lutjanids. These similarities are listed below for what they are worth, but to me they do not furnish very convincing evidence of relationship. The possibility of their independent development in two different bottom-feeding percoid groups seems strong. A caveat in this regard is that some of the more notable similarities do not occur between goatfishes

and all sparoids, or even with the most generalized sparoids, but rather with now one segment and now another of the sparoid group (Johnson 1980). To start with the least diagnostic, the features held in common are:

1. a well-developed scaly process in the axil of the pelvic fin;
2. 24 vertebrae;
3. two widely separated nostrils on each side of the head with the posterior one a valved slit near the orbit as in such sparids as *Calamus*;
4. the lacrimal bone broadly overlapping the maxilla;
5. the ethmoid-maxillary ligament functionally replaced by a ligament from the nasal bone to the maxilla as in many sparoids;
6. the maxillary blade of about equal width for most of its length and overlapped anteriorly by a palatine prong that tends to be expanded at its tip as in the lethrinid sparoids;
7. a gap between the sphenotic projection and the frontal border of the orbit above it as in such sparoid genera as *Calamus*; and
8. the distally expanded symplectic.

There are of course numerous differences between the mullids and the sparoids. Perhaps particularly significant among these, so far as possible relationships are concerned, are two characters of the Mullidae that might be expected in a related group but which do not occur in sparoids, namely the two well-separated dorsal fins and the squamation of the maxilla. To me, a real relationship between mullids and sparoids seems far from established, but I am unable to suggest a more convincing relative for the Mullidae.

STRUCTURE AND ECOLOGY

The structural peculiarities of goatfishes seem to be reflected at several points in their ecology, or vice versa. Goatfishes appear to have evolved a particular feeding niche for themselves. This niche depends on a specialized method of hunting, not on the exploita-

tion of any particular food source. To judge from reports of goatfish stomach contents (see, for example, Hiatt and Strasburg 1960, Hobson 1974), mullids eat a wide variety of small to medium-sized animals. No goatfish species appears to be a food specialist. (In this regard the gill rakers and pharyngeal dentition of all goatfishes seem to be of normal, percoid type.)

The highly developed hyoid barbels seem to provide the base from which goatfishes have evolved their ecological peculiarities. Many fishes have sensory probes by means of which they locate food on or in the bottom. The goatfish barbel apparatus, however, has evolved beyond analogous structures in other fishes in a number of respects. The hyoid barbels of the Mullidae are relatively long, strong, and highly movable. They can be and are used as an excavating device (Figure 2) or for harassing and dislodging prey from holes and crevices in hard substrates. Indeed, other fishes often take advantage of these mullid barbel activities. Hobson (1974:962) notes that in Hawaii *Parupeneus chryserydros* (now *P. cyclostomus*) is frequently followed around by the jack, *Caranx melampygus*, "probably as a tactic to capture prey driven from cover as the foraging goatfish disturb the substratum," and Randall has a photograph of a jack investigating the possibilities of *Mulloid* foraging in the West Indies.

Equally or more important is the goatfish ability to raise or lower the barbel apparatus (Figure 3) while the fish maintains a horizontal position above the substrate (Figures 1, 2). Though members of the relatively specialized *Parupeneus* forage in reef areas, the more generalized *Upeneus*, *Mullus*, and *Mulloid* feed over sand or mud. Sandy or muddy bottoms may occur as pockets in hard substrates but are more frequently present as broad, unprotected areas. There appear to be two aspects of the relationship between the goatfish barbel apparatus and feeding in such areas. One has to do with escape from predators. Goatfishes do not have effective spines; they do not bury themselves in the substrate; and they are often far from holes in which they can take refuge. To escape, they simply swim off into open water, a system that

depends on rapid acceleration and sustained speed among other things. The horizontal position of the body above the substrate while hunting or excavating appears to be advantageous here. In moving off, goatfishes do not have first to leave the substrate or to shift from a head-down body position (except when they are actually feeding rather than hunting).

The same horizontal position of the body above the substrate while locating food also appears advantageous as a method of hunting over wide areas with occasional sampling of the bottom for food. Indeed, one goatfish uses, at least on occasion, a roving method of hunting in which the barbels are not used at all. Hiatt and Strasburg (1960:87) state regarding *Upeneus arge* (now *U. taeniopterus*): "It does not probe the sand with its barbels as do other goatfishes but rather seeks out benthic crustaceans living exposed on the bottom. Perhaps because it does not probe, it seems swifter than other goatfishes." However, *U. taeniopterus* has well-developed barbels which it probably uses at least on occasion, as *U. tragula* (Figure 2) certainly does.

To summarize briefly, goatfish feeding over sand or mud seems to combine attributes of roving predators such as the bonefish (*Albula*) and the pompano (*Trachinotus*) with some of those of excavators such as ophichthid eels and flatfishes.

As noted in the introduction, there appears to have been a minor adaptive radiation within the Mullidae. Morphological differences between genera, together with what is known of their ecology, indicate variations in feeding methods. The relatively extensive dentition of *Upeneus* suggests a generalized carnivore from which the genera *Mullus* on the one hand and *Parupeneus* and *Pseudupeneus* on the other have become specialized in two different directions. In *Mullus* the absence of teeth in the adult upper jaw suggests a suction feeder, and its habit of ploughing up the mud is in line with such a feeding method. At the other extreme, the strong jaw teeth near the end of a relatively long snout in *Parupeneus* and *Pseudupeneus* suggest that their teeth are used for immediately seizing active prey that might otherwise escape or be eaten by other fishes. That at least

some of the prey of these two mullid genera are relatively large, active animals is indicated by the higher proportion of fishes in the stomachs of *Parupeneus chryserydros* (now *P. cyclostomus*) than in the stomachs of any of the Hawaiian goatfishes Hobson (1974) investigated.

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