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A SURVEY OF UPPER JAW MUSCULATURE IN HIGHER
TELEOSTEAN FISHES

BY WILLIAM A. GOSLINE*

ABSTRACT.—*Gosline, W.A. 1993. A survey of upper jaw musculature in higher teleostean fishes. Occ. Pap. Mus. Zool., Univ. Michigan 724: 1–26, 9 figs.* Upper jaw musculature, consisting of one or more muscular attachments to the maxilla, occurs in most higher teleosts. The original type of attachment is via the development of a tendon to the maxilla from an upper section of the lower jaw musculature (*M. adductor mandibulae*). It seems to have evolved in conjunction with the acanthopterygian type of premaxillary protrusion first present at the myctophiform-aulopiform level of teleostean evolution and appears, at least in its original form, to activate a braking system behind the protruded premaxilla. The maxillaris musculature undergoes numerous variations among higher teleosts, most of them repeatedly, but all of them seem to have evolved from the same basal type. This basal configuration and its major categories of variation are described and their presumed functions discussed. A survey of the maxillaris musculature in the various higher teleostean groups, with comments on functionally related features, is then presented.

The objectives of the paper are two. The first is to provide background information as a basis for clarifying confusion. A great deal of descriptive and experimental information is available regarding musculature to the mandible, but that concerning upper jaw musculature is for the most part sporadic and incidental. As a result the parts of the maxillaris system have received inconsistent designation, and variations in the system that have evolved repeatedly have sometimes been considered phylogenetic characters.

The second objective is to determine what aspects, if any, of the maxillaris musculature suggest relationships among higher teleostean fish groups. Because of the repeated development of many of the variations

*Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109-1079

in the maxillaris musculature, this subject must be approached with extreme caution. Nevertheless, suggestions concerning possibilities in this regard are made in the last section of the paper.

Key words: *M. adductor mandibulae*, maxillaris section, maxillary protrusion, teleosts.

INTRODUCTION

In most higher teleosts the cheek musculature to the lower jaw has a direct attachment to the maxilla of the upper jaw. Though a slight contradiction in terms is involved, this part of the cheek musculature is generally known as the maxillaris component of the *M. adductor mandibulae*. The function of this maxillaris component, though not entirely clear (see below), is different from that of the rest of the cheek muscle, and its morphological variations are of a semi-independent nature. It is this maxillaris musculature and structures associated with it in higher teleosts that form the subject of the paper.

The musculature to the maxilla in higher teleosts, like the rest of the cheek muscle, has a basic type of configuration that is present in at least some members of most of the higher teleostean orders (Gosline, 1986) and appears to be an inherited feature throughout. However, this configuration undergoes various modifications at all levels of higher teleostean classification. Some of the principal types of variation and associated structures are the subject of this paper, which has two objectives. The first is to provide background information. In the past the maxillaris muscle has been variously designated and interpreted, mostly because of a lack of such information. The second is to determine to what extent, if any, the maxillaris musculature is useful as an indicator of relationships between higher teleostean groups.

Previous information on the morphology of maxillaris musculature must be extracted from accounts of the whole *M. adductor mandibulae* of which it is a part. The most comprehensive of these are old, e.g., Dietz (1914) and Lubosch (1929). The *M. adductor mandibulae* within groups has been treated most intensively by Howes (1988) for the gadiform fishes, by Johnson (1980) for lutjanoids, and by Yabe (1985) for cottoids.

METHODS AND DESIGNATIONS

The classification followed here is that of Nelson (1984) and Eschmeyer (1990) except that in the group accounts somewhat distantly related groups are sometimes considered together. The names of the muscle sections are conventional (Winterbottom, 1974a) except that Roman typeface has been substituted for the Greek in the subscripts under the parts of the A_1 section.

Unstained preserved specimens were dissected under a binocular microscope. This method is inadequate for very small specimens, which were not used here. Removal, or merely uplifting, of the skin of the cheek and the circumorbital bones will expose the part of the *M. adductor mandibulae* under consideration. Inasmuch as the maxillaris musculature has developed from the A_1 section of the *M. adductor mandibulae* it is important to distinguish this section from the rest of the cheek muscle. From experience (Gosline, 1986; see also Howes, 1988) the most reliable way of doing this is to follow the course of the nerve tract *N. ramus mandibularis V*. In almost all of the higher teleosts examined here (Appendix) and elsewhere this tract extends anteroventrally from its exit from the skull, around the anterior border of the *M. levator arcus palatini*, and then on between the A_1 and A_2 sections of the cheek muscle and forward to the mandible (Fig. 1). Tracing the course of this nerve tract is easier to do from back to front, particularly in those fishes in which the A_1 section has secondarily merged with the rest of the cheek muscle. In such fishes the part of the combined muscle mass above and external to the *N. ramus mandibularis V* is considered to belong to the A_1 section.

The A_1 section of the *M. adductor mandibulae* may become separated into two (or more) parts. This development evolves in various ways. When, but only when, this division results in one part of A_1 to the maxilla and the other to the mandible, the part to the maxilla is here designated A_{1b} (following convention) and the part to the mandible A_{1a} .

BASAL CONFIGURATION AND MAJOR TYPES
OF MODIFICATION

The basal pattern of cheek musculature and its maxillaris component in higher teleostean fishes is briefly redescribed herewith (see also Gosline, 1986). The external part of this pattern is divided into two sections, A_1 above and A_2 below (Fig. 1). The posterior part of

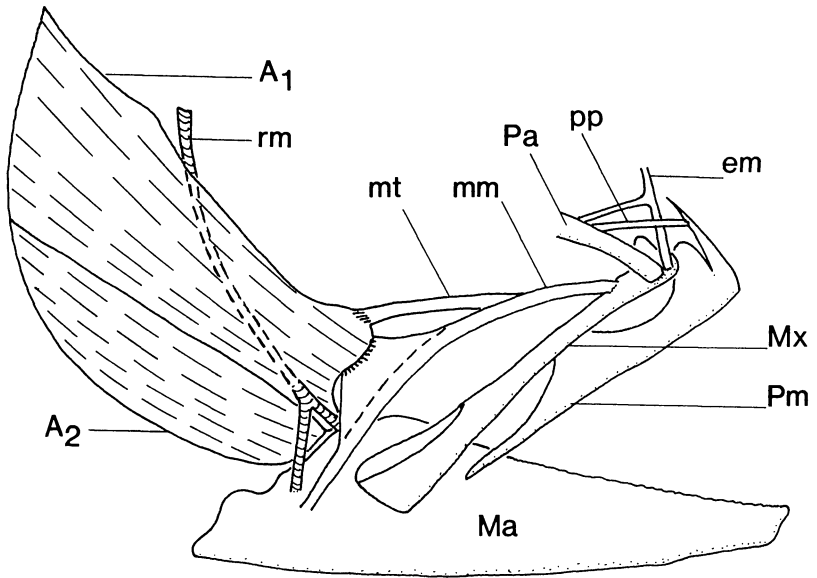


FIG. 1. Jaw structures and cheek musculature of the percid *Lateolabrax japonicus*. Lateral view. A₁, A₂, sections of the M. adductor mandibulae; em, ethmoid-maxillary ligament; Ma, mandible; mm, mandibular-maxillary ligament; mt, maxillaris tendon; Mx, maxilla; Pa, palatine prong; Pm, premaxilla; pp, palatine-premaxillary ligament; and rm, N. ramus mandibularis V.

A₁ somewhat overlaps A₂. Both pass anteriorly, usually by aponeurosis, to the under side of the mandible. A₁ has, in addition, two connections with the maxilla. One is direct, via a tendon, here called the maxillaris tendon, to the inside of a forward part of the maxilla. The other is indirect, via a membrane between the anterior border of A₁ and the mandibular-maxillary ligament, which in turn has an anterior attachment to a forward part of the outside of the maxilla. The N. ramus mandibularis, as noted above, passes forward between A₁ and A₂. Anteriorly it becomes exposed externally and divides into two branches. The larger passes forward to the under side of the mandible. The smaller extends down over the base of A₂ to the outside of the rear of the mandible.

Various modifications of the basal maxillaris configuration (Fig. 1) have evolved again and again in higher teleosts. Only some of the major types are described below. The few constants in the maxillaris muscle are noted herewith: 1) the muscle is always derived from the A₁ section of the M. adductor mandibulae; 2) it is always attached

(except in some synodids) to the maxilla, not the premaxilla, of the upper jaw; and 3) its contraction always pulls the maxilla posteriorly.

Among the various modifications in maxillaris musculature, some are definitely associated with other aspects of mouth structure. Others do not appear to be.

One type of modification is constantly associated with elongation of the preorbital snout. In such forms, e.g. the syngnathiform fishes, the long-nosed gasterosteiform fishes, and *Sphyræna*, much or all of the origin of *M. adductor mandibulae* has become anteriorly displaced. In *Sphyræna* most of the maxillaris muscle originates on the lateral ethmoid (Takahasi, 1925).

A second type of association with other aspects of the mouth is the posterior displacement along the maxillary shaft of the maxillaris attachment in those fishes with restricted forward swinging of the maxilla when the mouth opens. This displacement occurs again and again (see Figs. 4, 5, and 9), sometimes in individual components of a group, e.g. *Bregmaceros* in the gadiforms (Howes, 1988, fig. 22 above), and sometimes throughout whole groups, as in the *Batrachoidiformes*.

Another type of modification in the maxillaris musculature has to do with losses. To my knowledge an A_1 section of the *M. adductor mandibulae* is always present in higher teleosts, though it often merges with A_2 as noted. However, A_1 may lose either its maxillaris or its mandibularis component. The maxillaris component has been lost, for example, in the syngnathiform and scombroid fishes. In these the loss is probably related to the secondary absence of premaxillary protrusion. However, a maxillaris component is also absent in *Trachypterus* and presumably other lampriform fishes, a group with very good upper jaw protrusion.

Other higher teleosts have a good maxillaris musculature but have lost the mandibularis component of A_1 . Among these are such varied forms as the gadiform fishes (Howes, 1988), the atherinid-mugilid group (see Fig. 6), the percoid *Kuhlia*, and the zoarceoid *Zaprora*.

Among fishes with both maxillaris and mandibularis components to A_1 , there are modifications in both the attachment and the origin of the maxillaris part. As to attachment, in the basic maxillaris muscle type (Fig. 1) there are two of these attachments to the anterior part of the maxilla, as noted. That via the mandibular-maxillary ligament goes far back in teleostean history, for example to *Elops* (Winterbottom, 1974a, fig. 1). In early teleostean evolution the membrane between an upper part of the *M. adductor mandibulae* and the mandibular-maxillary ligament probably served primarily to retract the cor-

ner of the mouth when the jaws closed and had little, if anything to do with maxillary movement. However, in higher teleosts the forward part of the ligament with its A_1 attachment often becomes an integral part of the maxillaris muscle system. The direct attachment of A_1 to the inside of the maxilla via the maxillaris tendon is a more recent teleostean development (see below). Often in higher teleosts both the tendon and ligament are replaced by a direct muscle attachment of the maxillaris to the maxilla. This is particularly prevalent in forms in which the maxillaris attachment has moved back along the shaft of the maxilla (see above).

As to the body of the maxillaris musculature, a frequent modification, as already noted, is for the maxillaris part of A_1 to become separate from the mandibular part. In the original separation, as in *Polymixia* (Howes, 1988, fig. 27b), the separate maxillaris part (A_{1b}) extends back above the mandibular part (A_{1a}). However, an independent A_{1b} often shifts its origin relative to the rest of the cheek muscle. Sometimes it moves up to an origin on the bottom of the subocular shelf, as in members of the percoid families Carangidae, Lutjanidae, and Mullidae. More frequently, it passes back to an origin on the suspensorium either internal or external to the upper part of the other cheek musculature. Passage of A_{1b} back and down externally over the cheek occurs, for example, in polynemids (see Fig. 8). Passage down and back behind the rest of the cheek muscle (see Fig. 3) is more frequent and occurs in fishes at all levels of higher teleostean classification from the percopsiform fishes upward. When this happens, A_{1a} often merges with A_2 .

FUNCTION

From morphological topography it is clear that contraction of the maxillaris muscle must pull back on the maxilla. What effect this has on the upper jaw can only be inferred from anatomy, for there appears to be no experimental evidence on the subject beyond a few manipulative experiments by Rognes (1973). None of the extensive experimental work on jaw movements deals with the effect of contracting the maxillaris musculature (Liem, Westneat, pers. comm.).

That the maxillaris musculature is somehow associated with the development of an acanthopterygian type of premaxillary protrusion is suggested by the fact that both appear at about the same time in teleostean evolution, i.e. at the myctophiform-aulopiform level (Gosline, 1986). This particular type of premaxillary protrusion system is

characterized by the ability to hold the protruded premaxillae firmly in place during the initial stages of mouth closure, thus providing a firm bite with protruded premaxillae (Alexander (1967a).

Forward protrusion of the premaxillae occurs as the mouth is opening. Inasmuch as the maxillaris tendon in the basal type of construction (Fig. 1) originates on the A_1 section of the M. adductor mandibulae, a muscle primarily concerned with mouth closure, retraction of the maxillaris tendon is necessarily synchronized with jaw closure and cannot be an active factor in the forward movement of the premaxillae. If only for the lack of other possibilities, then, the maxillaris musculature must be somehow associated with the establishment of a blocking system behind the protruded premaxillae (Alexander, 1967a).

It may be noted further that such a blocking system can only be in effect during the initial stages of mouth closure because when the mouth is completely closed the premaxillae are retracted. That the maxillaris tendon is only retracted during these initial stages is suggested by its origin on A_1 , a section which in *Perca* (Osse, 1969, fig. 28) starts and stops contracting before the rest of the M. adductor mandibulae does. Parenthetically, it may be noted that the division of the M. adductor mandibulae into A_1 and A_2 sections also originates at about the myctophiform-aulopiform level of teleostean evolution.

The mechanism by which a retraction of the maxillaris tendon can presumably block the premaxilla in protruded position is complex and apparently involves only a slight amount of movement in the maxilla. Anterior to the overlapping prong from the palatine the maxilla has an arched, raised condyle that fits into a meniscus which in turn abuts against the dorsolateral surface of the vomer (Fig. 2). The condyle can rotate over its meniscus, which itself can slide over the vomer. When the mouth opens the distal end of the maxilla moves downward and somewhat outward. Because of the overlapping palatine prong, such movements force some shifting of the maxillary condyle and its meniscus relative to the vomer. The maxillary shaft also twists, which indirectly causes premaxillary protrusion (Alexander, 1967a; Gosline, 1981) and rotation of the condyle over its meniscus in a counterclockwise direction. Presumably retraction of the maxillaris tendon pulls the maxillary condyle and its meniscus back over a more expanded area of the vomer, where squeezing of the meniscus prevents untwisting of the condyle. Inasmuch as the inner head of the maxilla has, during premaxillary protrusion, moved out to under the articular head of the premaxilla, prevention of untwisting of the maxillary condyle will block premaxillary retraction.

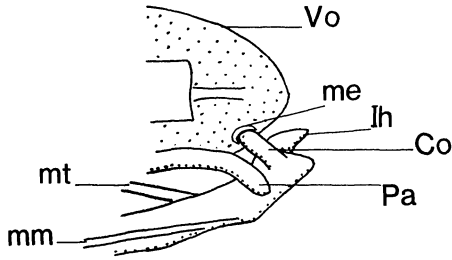


FIG. 2. Association between the maxilla and the skull in *Lateolabrax*. Superior view. Co, articular condyle of maxilla; Ih, inner head of the maxilla; me, meniscus; mm, mandibular-maxillary ligament; mt, maxillaris tendon; Pa, palatine prong; and Vo, vomer.

So long as the maxillaris tendon originates on an undivided A_1 section of the *M. adductor mandibulae* with both maxillaris and mandibular components, retraction of the maxillaris tendon is necessarily synchronized with the initial stages of mouth closure. However, there are two types of maxillaris modification in which this necessary synchronization is lost. Section A_1 may lose its mandibular component, or the maxillaris component of A_1 may become separate from the part to the mandible. When either of these things happen contraction of the maxillaris component becomes potentially independent of mouth closure. Potentially then, blockage of the protruded premaxillae may occur at any stage of premaxillary protrusion, including different stages in the same fish under varying circumstances (see, for example, Liem, 1980, fig. 10). Furthermore in some fishes with separate maxillaris musculature this musculature may take on different functions from that of a blocking system behind protruded premaxillae. Thus, in acanthurids and many tetraodontiform fishes contraction of the maxillaris musculature lowers the front of the upper jaw; in cyprinodonts it seems to cause premaxillary protrusion (Alexander, 1967b); and in mastacembelids the maxillaris musculature appears to have become involved in manipulating the elongated snout (Gosline, 1983, fig. 1).

GROUP ACCOUNTS

In the following accounts it is assumed that the variations in the maxillaris musculature are all ultimately derived from the pattern shown in the basal percoid *Lateolabrax* (Fig. 1). Other basal percoids,

e.g. *Doderleinia* (Gosline, 1986, fig. 1), could have been used equally well to demonstrate this pattern, or, for that matter, the aulopiform genus *Aulopus*. The objective of these accounts is to compare and contrast the different pathways of derivation from this pattern in the major higher teleostean groups. For this reason the forms within each group that show the greatest similarity to this configuration have received primary attention. In some of the larger groups, e.g. the Scorpaeniformes, only such forms have been discussed. Any effort to be comprehensive in such groups would expand the paper far beyond reasonable length.

Aulopiform fishes.—As noted in an earlier paper (Gosline, 1986), *Aulopus* seems to stand at the base of the higher teleostean series so far as the configuration of the M. adductor mandibulae is concerned. This is true of its maxillaris component. In *Aulopus*, as in *Lateolabrax* (Fig. 1) and other higher teleosts, this component develops from a separate A_1 section, with the N. ramus mandibularis passing internal to it to the mandible. Various groups of "lower" teleosts have developed musculature to the maxilla, but it is either of an entirely different type, as in ostariophysan fishes, or the N. ramus mandibularis V passes external to the maxillaris muscle, as in stomiids, neoscopelids, and myctophids.

Among aulopiform fishes the cheek musculature of a species tentatively identified as *Chlorophthalmus nigripinnis* is like that of *Aulopus*. However, in the other aulopiform fishes examined including *Chlorophthalmus agassizi*, the A_1 section has merged with the rest of the cheek muscle to form a single, complex mass. A few of the synodids appear to be unique among higher teleosts in having a direct muscle attachment on the premaxilla.

Percopsiform fishes.—In these fishes the maxillaris (A_{1b}) and mandibularis (A_{1a}) parts of A_1 have become completely, or almost completely (*Percopsis*), separate. A_{1b} extends forward to a direct attachment on the inside of an anterior area on the maxilla. Posteriorly A_{1b} passes down behind the upper part of A_{1a} to which, in *Percopsis*, it is somewhat attached. As already noted, this type of A_{1b} has developed repeatedly in higher teleosts.

In *Amblyopsis* (Fig. 3) the outer cheek musculature below A_{1b} is divided into two sections, A_{1a} above and A_2 below, with the N. ramus mandibularis passing between them. However, in *Percopsis* these two sections have merged, with the N. ramus mandibularis passing into them from the inside. Thus the muscle labeled A_{1a} by Howes (1988, fig. 24) seems to be A_{1a} plus A_2 .

Gadiform fishes.—The cheek musculature of these fishes has been

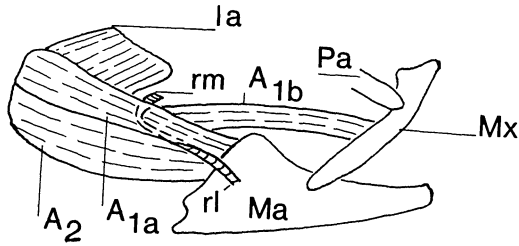


FIG. 3. Cheek musculature in the percopsiform *Amblyopsis spelaea*. A_{1a} , mandibularis part of section A_1 ; A_{1b} , maxillaris part of section A_1 ; A_2 , section of *M. adductor mandibulae*; *la*, *M. levator arcus palatini*; *Ma*, mandible; *Mx*, maxilla; *Pa*, palatine prong; *rl*, lower branch of *N. ramus mandibularis V*; and *rm*, *N. ramus mandibularis V*.

reported *in extenso* by Howes (1988, 1989). Numerous variations are present, but all hold one peculiarity in common, namely the lack of any mandibularis component in the A_1 section. The maxillaris component, by contrast, is highly developed and varied. It is often divided into two, and sometimes into three parts. The question arises whether the original gadiform pattern had a single maxillaris muscle, as in *Trachyrincus* (Howes, 1988, fig. 7), that subsequently divided, or started out with two, as in such genera as *Bathygadus* (*loc. cit.*, fig. 9). Under either interpretation the labelling of a second separate maxillaris muscle raises a problem. If, as here, A_{1a} is used for a mandibular component of A_1 , then that label should not be applied to the second maxillaris part in gadiform fishes. The type of proliferation that occurs in the maxillaris musculature of gadiform fishes is not present elsewhere in teleosts.

Ophidiiform fishes.—The maxillaris musculature in these fishes varies greatly, as it does in other large groups. The only feature held in common by the forms examined and those illustrated by Howes (1988) is a separate A_{1b} part that originates internal to the other components of the cheek musculature, a feature not particularly diagnostic since it occurs in various other groups.

Among the genera examined *Brotula* has a cheek-muscle configuration most like the basal type (Fig. 1). The main difference, aside from the separate A_{1b} , is the replacement of the maxillaris tendon by a tendinous sheath that is attached over the surface of the maxilla posterior to the palatine prong.

Batrachoidiform fishes.—A number of features in all of the batrachoidiform fishes examined are peculiar. One is unique, namely the replacement of the palatine prong by the lateral ethmoid as a fulcrum for movements in the anterior part of the maxilla (Fig. 4).

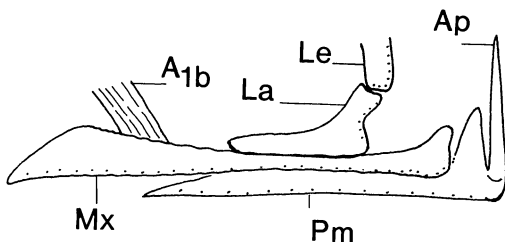


FIG. 4. Upper jaw structures in the batrachoidiform *Batrachoides goldmani*. A_{1b} , maxillaris part of section A_1 ; Ap, ascending process of the premaxilla; La, lacrimal; Le, lateral ethmoid; Mx, maxilla; and Pm, premaxilla.

The palatine prong does not extend over the maxilla. Instead, the lacrimal has become firmly attached along the upper border of the maxilla, and the two bones rock together around the base of the lateral ethmoid.

A number of the peculiarities in the mouth structure of these fishes appear to be associated with the nature of their mouth opening, which seems to be more lateral than vertical. That this is so is indicated on the one hand by the movable articulation at the base of the ascending premaxillary process and, on the other, by the attachment of the maxillaris muscle far back on the maxilla.

This maxillaris muscle (A_{1b}) extends back above and finally behind the rest of the cheek muscle, which it joins posteriorly. That the muscle mass below is in part A_{1a} is indicated by the N. ramus mandibularis, which penetrates from the inside the muscular mass of which the maxillaris muscle forms the upper part.

Lophiiform fishes.—The mouths in these fishes vary from small and subterminal in *Ogcocephalus* to very large and somewhat upturned in *Lophius*. The maxillaris musculature varies similarly. However, the jaw musculature in *Antennarius* is very like that of the basal acanthopterygian type (Fig. 1). From this basal configuration there are three different types of maxillaris muscle modification, all of which recur elsewhere. In one, represented in *Histrion* and *Lophius*, A_1 has expanded downward to cover the whole lower part of the cheek. In a second, represented in *Haliutaea* and *Ogcocephalus*, A_{1b} has become separate from A_{1a} and extends down behind A_{1a} posteriorly. Finally, as usual in fishes with reduced maxillary swinging, the maxillaris attachment has moved back on the shaft of the maxilla. This has happened in various lophiiform fishes, e.g. *Lophius*, *Chaunax*, and *Ogcocephalus*.

Gobiesociform fishes.—The investigation here is limited to *Gobiesox*, one of the few genera in the group with individuals attaining a rela-

tively large size. Here A_{1b} is a small muscle passing medially from the maxillary shaft to the palatine. A_{1a} is very large and completely overlaps A_2 . The N. ramus passes anteroventrally between A_{1a} and A_2 .

Cyprinodontiform fishes.—Because of the difficulty in distinguishing muscle sections of small fishes, only some of the larger cyprinodonts have been examined. In these, a constant feature is the division of A_1 into two separate parts, A_{1a} to the mandible and A_{1b} to a direct attachment along a lateral portion of the maxillary shaft (Fig. 5). Posteriorly A_{1b} covers all or, in *Aplocheilus*, only the lower part of the cheek. A_{1a} may be separate from (Fig. 5) or merged with A_2 .

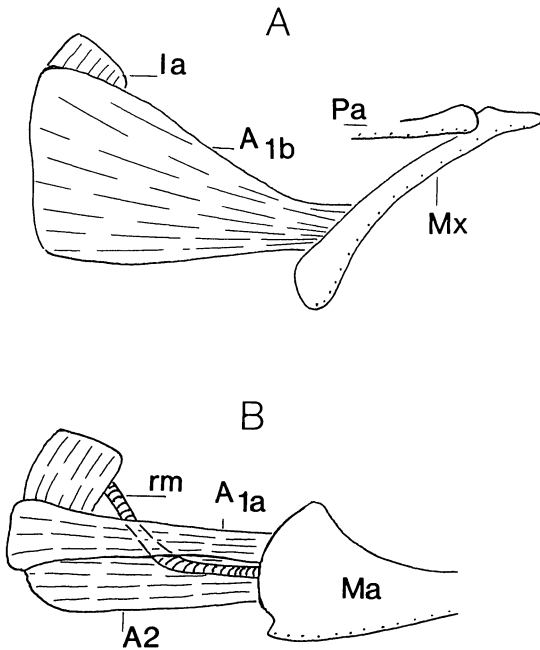


FIG. 5. Cheek musculature in the cyprinodontiform *Anableps dowi*. A, lateral view. B, same with part A_{1b} removed. A_{1a} , mandibular part of section A_1 ; A_{1b} , maxillary part of section A_1 ; A_2 , section of M. adductor mandibulae; la, M. levator arcus palatini; Ma, mandible; Mx, maxilla; Pa, palatine prong; and rm, N. ramus mandibularis V.

Belontiiform fishes.—In none of the members of this group examined is there any musculature to the maxilla. In *Exocoetus* a separate A_1 section is present, but in the others the cheek muscle forms a more or less undifferentiated mass.

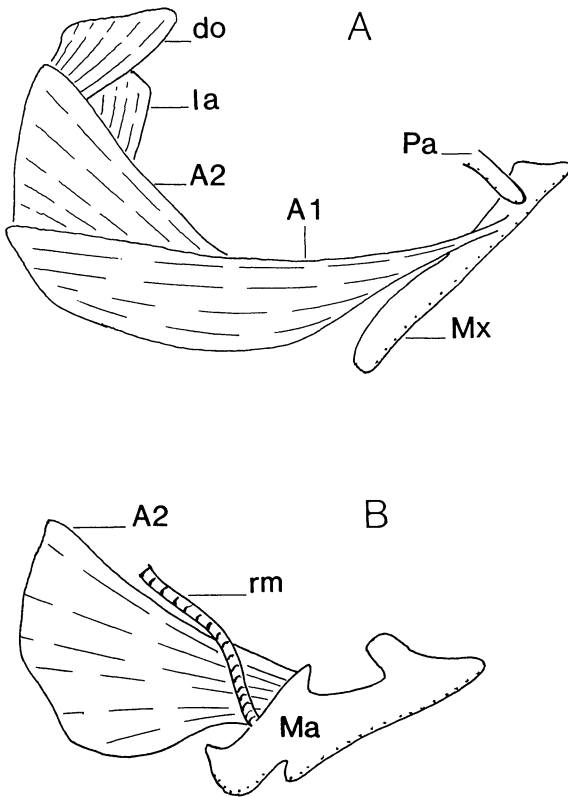


FIG. 6. Cheek musculature in the mugilid *Agonostomus monticola*. A, lateral view. B, same with section A_1 removed. A_1 , A_2 , sections of the M. adductor mandibulae; do, M. dilatator operculi; la, M. levator arcus palatini; Ma, mandible; Mx, maxilla; Pa, palatine prong; and rm, N. ramus mandibularis V.

Atherinid and mugilid fishes.—These two groups are taken up together because of the similarities in their cheek muscle modifications. In both the A_1 section has lost its mandibular connection and extends back and down over the lower part of the cheek (Fig. 6). This type of modification is rare but does occur elsewhere, e.g. in gadiform fishes. To this basal atherinid-mugilid arrangement the atherinids have added a tendon from A_1 to the lacrimal (Alexander, 1967b, fig. 1), a feature represented elsewhere in higher teleosts in the Emmelichthyidae (Johnson, 1980, fig. 18). Within the two families, members with reduced maxillary swinging have moved the A_1 attachment back along the maxillary shaft as usual, e.g. in *Atherinops* and *Liza*.

Zeiform and lampriform fishes.—In upper jaw and maxillaris con-

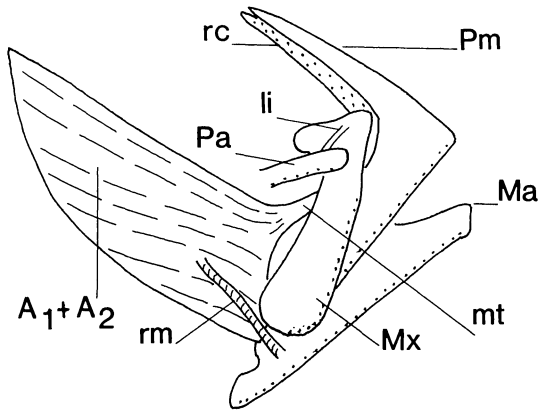


FIG. 7. Cheek musculature and jaw structures of the zeid *Zeus faber*. $A_1 + A_2$, combined sections of the *M. adductor mandibulae*; li, ligament from palatine prong to maxilla; Ma, mandible; mt, maxillaris tendon; Mx, maxilla; Pa, palatine prong; Pm, premaxilla; rc, rostral cartilage; and rm, N. ramus mandibularis V.

struction the fishes usually placed in the Zeiformes fall into two groups: *Antigonia* and *Capros* in the one and *Zeus* and its relatives in the other. In *Antigonia* the cheek musculature (Gosline, 1986) and jaw construction are much like those in the basal acanthopterygian type (Fig. 1). *Capros* shows a somewhat specialized version of these in features associated with its far more extensive premaxillary protrusion, which does not, however, involve forward movement of the proximal heads of the maxillae, as it does in *Zeus*.

Zeus and other zeids examined differ from *Antigonia* and most other acanthopterygians in the nature of their highly developed upper jaw protrusion. When the premaxillae protrude, the maxillary heads move forward with them to a considerable extent. In the course of the forward movement of the maxillary heads, the maxillary shafts slide down from under the palatine prongs, to which they are only attached by an extended ligament (Fig. 7), and the maxillary condyles slide down over a vertical surface on the vomer. There is no ethmoid-maxillary ligament to restrict the forward movement of the maxillary heads.

The peculiar type of upper jaw protrusion in which the maxillae and premaxillae move forward together and the ethmoid-maxillary ligament is lost is more highly developed in lampriform fishes than in *Zeus* and reaches its extreme development in *Stylophorus* (see, for example, Pietsch, 1978). In *Velifer*, considered the most generalized

lampriform genus, the only connection between the M. adductor mandibulae and the maxilla is via an attachment of the front of the A₁ section along the posterior border of the mandibular-maxillary ligament, and in *Trachypterus* even that is lost. In other respects the cheek musculature of these two lampriform genera and *Zeus* are similar, with A₁ and A₂ merging around an anteriorly exposed N. ramus mandibularis. In the two lampriform genera there is no palatine prong, i.e. lateral extension from the anterior end of the palatine, though *Velifer* seems to retain ligamentous tissue extending up from the palatine to the premaxilla.

Beryciform fishes.—In the members of this group examined there seem to be two main types of maxillaris musculature. In one, represented by *Beryx*, *Hoplostethus*, and *Ostichthys*, the A₁ section is undivided and passes anterodorsally into a sheath-like structure with most or all of its attachment on the outer border of the maxilla. In the other, *Polymixia* and *Melamphaes*, the A₁ section is divided into a maxillaris (A_{1b}) and a mandibularis (A_{1a}) part, and the former has a tendon to the inside of the maxilla. Only a few holocentrids, e.g. *Holocentrus sammara*, have well-developed premaxillary protrusion and here the protrusion is of a percoid, not zeid type.

Gasterosteiform fishes.—Gasterosteids are the only available members of this order. In all of the members of this family there is considerable jaw protrusion. The snouts become progressively longer in a series from *Gasterosteus* to *Aulorhynchus*, and the origin of the maxillaris musculature moves forward accordingly (see above), with that of *Aulorhynchus* originating on the front of the lateral ethmoid. In all, the anterior border of the M. adductor mandibulae is attached to the back of a mandibular-maxillary ligament that extends up from the coronoid area of the mandible to the outside of a forward part of the maxilla. In *Gasterosteus* A₁ and A₂ are separate, with the N. ramus mandibularis extending between them, but in *Spinachia* and *Aulorhynchus* the two sections appear to have merged.

Syngnathiform fishes.—These long-snouted fishes have no premaxillary protrusion and, in the forms examined, no maxillaris musculature.

Scorpaeniform fishes.—*Sebastes* shows the basic acanthopterygian pattern (Fig. 1) of adductor musculature and its mandibularis component (Gosline, 1986). As with any large group, this musculature undergoes specializations of various sorts in the different scorpaeniform derivatives. Many parallel those in the perciform fishes, discussed at greater length below. For example, in the scorpaeniform *Hexagrammos* A₂ has an inner lobe extending behind the M. levator arcus

palatini similar to that in the zoarceoid and notothenioid perciform fishes. The various peculiarities of the maxillaris musculature among the cottoid scorpaeniforms have been described and illustrated by Yabe (1985, figs. 33, 34).

Percoid fishes.—All of the members of this large, basal perciform group seem to have certain generalized acanthopterygian mouth features in common. Thus, all seem to have considerable premaxillary protrusion and a maxilla that swings well down when the mouth opens, with the maxillaris muscle attachment far forward along its shaft.

The basal *Lateolabrax* (Fig. 1) configuration of cheek musculature is widely represented (see, for example, Johnson, 1980). Of the various types of modification that occur only two are mentioned here. In one, so often found elsewhere, the maxillaris (A_{1b}) and mandibularis (A_{1a}) parts of the A_1 section have become separate. This occurs, for example, in *Percichthys*, sciaenids, branchiostegids (Marino and Dooley, 1982), and *Opistognathus*. In the other, a maxillaris origin on the base of the subocular shelf has developed three different times in percoids (lutjanids, carangids, and mullids) but not, to my knowledge, elsewhere.

Polynemoid fishes.—The construction of the subterminal mouth in polynemids is unusual in a number of respects. The palatine prong is not in contact with the maxilla and seems to serve primarily as a base for the palatine-premaxillary ligament (Fig. 8). The A_1 section of the *M. adductor mandibulae* is separated into two parts, with the maxillaris (A_{1b}) part extending back across and external to the rest of the more or less vertically aligned cheek muscles (A_{1a} plus A_2).

Labroid fishes.—The *M. adductor mandibulae* in representative members of the major groups of labroid fishes has been dealt with by Stiassny (1981) and that of scarids in an old paper by Lubosch (1923). Numerous papers take up the jaw musculature of individual labroid genera, notably among cichlids. Gosline (1986) pointed out that the most generalized type of *M. adductor mandibulae* among labroids is that of the Embiotocidae, with cheek musculature much like that of *Lateolabrax* (Fig. 1).

Zoarceoid and notothenioid fishes.—In these two groups the general trend in *M. adductor mandibulae* development is toward increased overlap of section A_1 external to A_2 . The latter extends its origin upward and inward around the front of the *M. levator arcus palatini*, where it often forms a more or less separate lobe. At the same time A_1 tends to extend its anterior border and often the whole section ventrally over A_2 and the *N. ramus mandibularis*, except in pholids

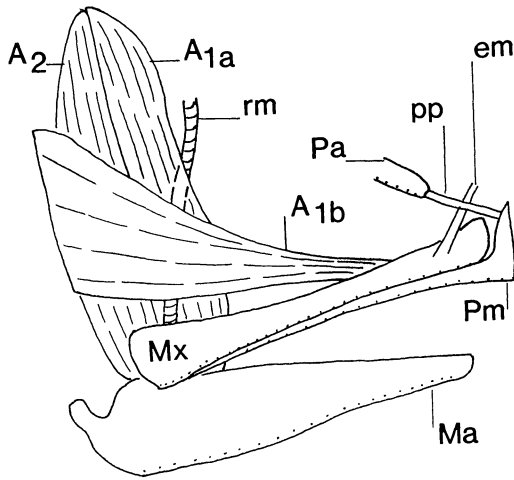


FIG. 8. Cheek musculature and jaw structures of the polynemid *Polydactylus octonemus*. A_{1a}, mandibular part of section A₁; A_{1b}, maxillaris part of section A₁; A₂, section of *M. adductor mandibulae*; em, ethmoid-maxillary ligament; Ma, mandible; Mx, maxilla; Pa, palatine prong; Pm, premaxilla; pp, palatine-premaxillary ligament; and rm, N. ramus mandibularis V.

and a few others. Aside from a few zoarcids A₁ is not separated into two parts.

The type of *M. adductor mandibulae* characteristic of zoarceoids and notothenioids does occur elsewhere, e.g. in the perciform cirrhitids and the scorpaeniform *Hexagrammus*, but differs considerably from that of blennioids, *Parapercis*, and branchiostegids (see below).

Trachinoid fishes.—Of the 11 families assigned to the trachinoid fishes by Pietsch and Zabetian (1990), members of four have been examined. Of these the forms of the Trachinidae, Uranoscopidae, and Percophidae have an undivided A₁ section of the *M. adductor mandibulae* with both a maxillaris and a mandibularis component, the latter extending down over the front of the N. ramus mandibularis. However, in the long-jawed *Bembrops* (Percophidae) the mandibularis component passes forward to the top, rather than the inside, of the lower jaw. The genus *Parapercis* (Pinguipedidae) differs notably from the others in having two separate parts of the A₁ section of a type resembling that found in the blennioids (see below).

Blennioidei and Parapercis.—In these fishes the A₁ section is always divided into two parts, but the parts differ from the usual A_{1b} and A_{1a} in that both have, except in the Blenniidae, mandibularis and

maxillaris connections. In a fish such as *Tripterygion*, only a small portion of the upper A_1 part shows externally. It extends posteriorly internal to the lower part of A_1 and anteriorly gives rise to the maxillaris tendon as well as a mandibular connection. The lower part of A_1 extends down to meet A_2 external to the N. ramus mandibularis. A sheath-like membrane extends up along the front of A_2 , along the anterior border of the lower part of A_1 , and thence to an attachment on the outer surface of the maxilla behind the palatine prong.

The members of the family Blenniidae differ from the others in having direct attachments of both parts of A_1 relatively far back along the maxillary shaft.

As in the Blennioidei, the A_1 section of the cheek musculature of the pinguipedid genus *Parapercis* has two separate sections that do not conform to the usual A_{1a} and A_{1b} types. In *Parapercis*, as in blennioids, both of these A_1 parts have mandibular connections, although, unlike blennioids, only one has a maxillary attachment. In *Parapercis* the maxillaris part of A_1 extends well forward to an attachment on the upper surface of the maxilla slightly behind the palatine prong; anteroventrally its fibers merge with the anterior part of A_2 to the mandible; posteriorly the maxillaris part of A_1 passes into a connective tissue fascia attached to the forward part of a curved crest on the hyomandibula. The other part of the A_1 section in *Parapercis* is exposed on the cheek above A_2 posteriorly, but then passes anteroventrally behind the maxillaris part of A_1 into the mandible above the N. ramus mandibularis V.

Callionymoid fishes.—In the species examined the maxillaris muscle extends down and back over the lower part of the cheek from an attachment on the inside of the maxillary shaft. The N. ramus mandibularis V can be seen externally where it passes over A_2 above the posterior part of A_1 . In *Synchiropus* A_1 has both maxillary and mandibular connections and is undivided.

Gobioid fishes.—In all of these fishes the maxillaris musculature is attached well back on the shaft of the maxilla. In *Eleotris* this attachment is via a sheath-like tendon, but in the others the maxillaris musculature is directly attached to the maxilla.

The A_1 section may or may not be divided into separate maxillaris and mandibularis parts. At one extreme, in *Acanthogobius*, A_1 is undivided and extends anteroventrally down over the N. ramus mandibularis and into the mandible as well as anterodorsally to the maxilla. Generally, however, A_1 is more or less completely divided. Where this occurs, A_{1b} extends posteriorly down behind the upper part of A_{1a} .

Acanthuroid fishes and other groups with beaked jaws.—As in a number of other groups, acanthuroids have jaws adapted to nipping or scraping. In many such groups the jaws have a beak-like appearance, but their construction differs. Probably the most generalized morphotype is that of the percoid family Oplegnathidae, or in such basal tetraodontiform genera as *Triacanthodes*, which retain some premaxillary protrusion and a cheek muscle configuration like that in Fig. 1. From this basal type the labroid scarids have evolved in one direction, with a hinge between the premaxilla and maxilla (van Dobben, 1935), and the acanthurids, siganids, and advanced tetraodontiform fishes in another, with the maxilla and premaxilla quite closely united and moving together. In the latter groups there is no premaxillary protrusion and the upper jaw rocks as a unit around a pivot on the palatine prong (Fig. 9) or ethmoid. Here, backward movement of the distal end of the maxilla rocks the front of the premaxilla down and slightly forward.

In *Siganus* this downward movement of the front of the jaw is brought about by contraction of the maxillaris muscle and its pair of tendons to the internal side of the maxilla. In acanthurids and advanced tetraodontiform fishes the maxillaris musculature is directly attached to a distal part of the maxilla. *Prionurus* (Fig. 9) has the A_1 section divided into two parts, an external A_{1b} to the maxilla and an A_{1a} to the mandible. In other acanthurids, as in some tetraodontiform fishes (Winterbottom, 1974b), the A_{1b} part becomes further subdivided.

Sphyraenoid fishes.—*Sphyraena* has no premaxillary protrusion; the front of the upper jaw rocks upward when the mouth opens. It has a maxillaris muscle that originates on the preorbital (Takahasi, 1925) and apparently partly on the inside of the lacrimal. This anterior origin of the maxillaris muscle is probably associated with the elongation of the preorbital part of the head (see above).

Scombroid fishes.—In the examples of the Scombridae, Gempylidae, and Trichiuridae examined there is no maxillaris musculature. However, a maxillaris muscle attached to the back of a mandibular-maxillary ligament is described and figured by Dietz (1914: 126–127, fig. 14) for *Xiphias gladius*.

Stromateoid fishes.—*Hyperoglyphe* appears to have a small, separate part of A_1 to the maxilla. The other stromateoids examined have an undivided A_1 section that is enclosed anteriorly in a membranous sheath which extends well forward over the maxilla to which it is attached. In *Nomeus* the N. ramus mandibularis is exposed anteriorly between A_1 and A_2 , but in the others A_1 extends down over the ramus.

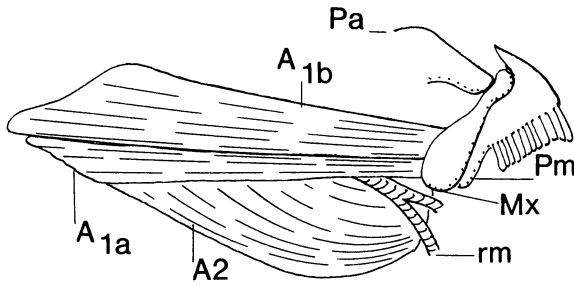


FIG. 9. Cheek musculature and upper jaw of the acanthurid *Prionurus microlepidotus*. A_{1a}, mandibular part of section A₁; A_{1b}, maxillary part of section A₁; A₂, section of M. adductor mandibulae; Mx, maxilla; Pa, palatine prong; Pm, premaxilla; and rm, N. ramus mandibularis V.

Hyperoglyphe also appears to be the only stromateoid examined with premaxillary protrusion. In the others the distal end of the premaxilla merely swings down around the proximal end as a pivot to provide a round mouth opening.

Anabantoid and channoid fishes.—In *Anabas* the A₁ section is separated into a maxillary (A_{1b}) and a mandibularis (A_{1a}) part. Section A_{1b} has the usual maxillary tendon to a forward part of the inner side of the maxilla and the muscle itself passes back horizontally external to A_{1a}. The N. ramus mandibularis is exposed anteriorly between A_{1a} and A₂ and passes down across A₂ to the mandible.

Ctenopoma differs from *Anabas* chiefly in the incomplete separation between A_{1b} and A_{1a}. In *Trichogaster* A_{1b} extends back down over the lower part of the cheek and covers the front of the N. ramus mandibularis.

In *Channa*, as in other fishes with restricted maxillary movement, the attachment of the maxillary muscle is well back along the shaft. The A₁ section is undivided and covers the whole cheek.

Pleuronectiform fishes.—In the more generalized flatfishes, e.g. *Hippoglossoides*, the jaw musculature is much like the basic acanthopterygian pattern (Gosline, 1986) except that the A₁ section is attached to the maxilla via the mandibular-maxillary ligament rather than by its own maxillary tendon. In specialized groups like the Cynoglossidae the M. adductor mandibulae is far more complicated.

Tetraodontiform fishes.—As in the Pleuronectiformes and other large groups the M. adductor mandibulae varies from close to the basal acanthopterygian type in *Triacanthodes* to highly complex (Winterbottom, 1974b).

DISCUSSION

The generally accepted conclusion that a single basal type of jaw construction has been inherited throughout the higher teleostean fishes is supported by the repeated representation of the pattern of cheek muscle shown in Fig. 1 (Gosline, 1986). The upper jaw musculature is a component of this pattern, but its variations are semi-independent.

General conclusions concerning these variations can be briefly summarized. Most of them have developed repeatedly. Some of the modifications in the basic pattern are obviously associated with other aspects of head structure. For others such an association is not apparent. Among the various higher teleostean groups there is no relationship between the amount of modification in the maxillaris musculature and the place of the group in systematic classification, for the maxillaris musculature, like other aspects of jaw construction, has undergone a high degree of specialization at various levels of classification.

A survey such as the one presented above should throw some light on the relationships of groups surveyed even though repeated independent development of similar modifications in maxillaris musculature make any speculations on this matter hazardous. Such indications as the maxillaris musculature and associated features do seem to provide are presented below, but merely as possible leads for investigations along other lines.

Maxillaris musculature provides indications of fish relationships of two main sorts: one derived from similarities, the other from dissimilarities. The indications from similarities can again be divided into two types: those within groups and those between groups.

Within groups there is the possibility that those members closest to the basal type of maxillaris musculature, e.g. *Brotula* in the ophidiiform fishes, are the most generalized in other features. This possibility has been explored to some extent in an earlier paper which deals with the cheek musculature as a whole including its maxillaris component (Gosline, 1986).

As to similarities between larger categories, certain groups show modifications in maxillaris musculature that seem to be derived from one another rather than through independent developments. This is true of the modification type that occurs in atherinids and mugilids, where an undivided A_1 section of the *M. adductor mandibulae* has a single attachment to the maxilla but has lost its mandibular connection and extends back and down external to the rest of the cheek

muscle. To this pattern atherinids have added an A_1 tendon to the lacrimal. Other groups seem to show similar trends of development from the same, not very distant ancestral type. This is true of the notothenioids and zoarceoids and of the acanthuroids and tetraodontiform fishes. The notothenioids and most zoarceoids, also *Bembrops*, have an undivided A_1 section with a maxillaris tendon and the front of the section with an attachment to the mandibular-maxillary ligament that has worked down over the front of the N. ramus mandibularis; they also have an $A_{2,3}$ section with an internal lobe that extends behind the M. levator arcus palatini. Acanthuroids and tetraodontiform fishes have each developed a beak-like upper jaw, the front of which is lowered in part by contraction of the maxillaris musculature. Finally there is the suggestion that one group of fishes shows a further development along a line of modification initiated by another. Thus, the relatively slight forward movement of the proximal head of the maxilla with premaxillary protrusion in zeids has been carried to an extreme among the lampriform fishes, with concomitant reduction and loss of maxillaris musculature.

As to dissimilarities, major differences in maxillaris musculature between groups that have sometimes been placed together and sometimes more or less widely separated support the hypothesis of separation. An instance of this type is the zeids and caproids. These two families have usually been allocated to the Zeiformes, e.g. by Eschmeyer (1990), but Heemstra (in Smith and Heemstra, 1986) removed the Caproidae and placed it among the percoids. The maxillaris musculature supports Heemstra. In older classifications the Pomacanthidae were considered a subfamily of the Chaetodontidae but Burgess (1974) demonstrated a clear separation between the two groups, and cheek-muscle patterns indicate the same thing (Gosline, 1986). In recent classifications (e.g. Eschmeyer, 1990; Pietsch and Zabetian, 1990, fig. 21) the Percophidae and Pinguipedidae are placed next to one another among the trachinoid fishes. However, the maxillaris musculature of the pinguipedid examined (*Parapercis*) is not only different from that of *Bembrops* (Percophidae) but shows specializations characteristic of the blennioid fishes. Finally, two instances may be mentioned in which differences in maxillaris musculature merely add to the list of characters separating groups that have often been united. Such differences (see Group Accounts, above) occur between siganids and acanthurids, usually placed together in the Acanthuroidi, e.g. by Tyler, et al. (1989), but often placed in separate suborders by older authors, e.g. Berg (1940). Again, a maxillaris muscle is pre-

sent in *Xiphias* but absent in scombroids, usually placed together in the Scombroidei (but see Gosline, 1968).

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APPENDIX: SPECIES EXAMINED

Species are listed here in the same order as in the Group Accounts. Within these groups taxa are arranged alphabetically. All fishes listed are in the collections of University of Michigan and the numbers in parentheses refer to lots in those collections. The specimens of *Bembrops* and of *Velifer* have been received through the kind offices of the Smithsonian Oceanographic Sorting Center.

Aulopiform fishes.—Aulopidae: *Aulopus japonicus* (186640). Chlorophthalmidae: *Chlorophthalmus agassizi* (216206); *Chlorophthalmus (nigripinnis?)* (216742). Synodontidae: *Synodus variegatus* (185880).

Percopsiform fishes.—Amblyopsidae: *Amblyopsis spelaea* (157175); *Chologaster agassizi*

(177561). Aphredoderidae: *Aphredoderus sayanus* (210402). Percopsidae: *Percopsis omiscomaycus* (130321).

Ophidiiform fishes.—Bythitidae: *Brosmophycis marginatus* (147431); *Dinematchichthys ilucoeteoides* (185633); *Lucifuga subterraneus* (157157); *Stygicola dentata* (157166). Ophidiidae: *Brotula multibarbata* (185631); *Lepophidium pheromystax* (177299); *Neobythites silvicola* (uncatalogued); *Ophidion holbrookii* (153408); *Otophidium scrippsi* (94690).

Batrachoidiform fishes.—Batrachoididae: *Batrachoides goldmani* (144155); *Halobatrachus didactylus* (218178); *Halophryne trispinosus* (191489); *Opsanus beta* (164996); *Porichthys notatus* (63608); *Thalassophryne maculosa* (186304).

Lophiiform fishes.—Antennariidae: *Antennarius striatus* (178792); *Histrio histrio* (136301). Chaunacidae: *Chaunax fimbriatus* (142773). Lophiidae: *Lophiomus setigerus* (204169); *Lophius litulon* (204157). Ogocephalidae: *Halieutaea stellata* (204150); *Ogocephalus pantostictus* (138762). Oneirodidae: *Oneirodes bulbosus* (211773).

Gobiesociform fishes.—Gobiesocidae: *Gobiesox maeandricus* (162056).

Cyprinodontiform fishes.—Anablepidae: *Anableps dowi* (191725). Aplocheilidae: *Aplocheilus panchax* (187859). Cyprinodontidae: *Fundulus catenatus* (88125); *Orestias mulleri* (179282); *Profundulus guatemalensis* (166701). Goodeidae: *Allophorus robustus* (202424); *Goodea* sp. (201587). Poeciliidae: *Belonesox belizanus* (187749); *Mollienesia sphenops* (143706); *Xiphophorus helleri* (210966).

Beloniform fishes.—Belonidae: *Strongylura marina* (192872). Exocoetidae: *Cheilopogon* sp. (213514); *Exocoetus obtusirostris* (176556); *Parexocoetus brachypterus* (60533). Hemiramphidae: *Arrhamphus brevis* (100333); *Euleptorhamphus viridis* (56659); *Hyporhamphus sajori* (214948); *Zenarchopterus ectuntio* (171811). Scomberesocidae: *Cololabis saira* (71135).

Atherinid and mugilid fishes.—Atherinidae: *Atherinomorus pinguis* (100223); *Atherinops affinis* (131794); *Chirostoma lucius* (167724). Mugilidae: *Agonostomus monticola* (213677); *Liza carinata* (217387); *Mugil cephalus* (162639).

Zeiform and lampriform fishes.—Zeiformes—Caproidae: *Antigonia capros* (117101); *Capros aper* (63068). Zeidae: *Cyttus* sp. (216722); *Zenopsis nebulosa* (213781); *Zeus faber* (213758). Lampriformes—Trachypteridae: *Trachypterus trachypterus* (178220). Veliferidae: *Velifer hypselopterus* (220456).

Beryciform fishes.—Berycidae: *Beryx splendens* (142822). Holocentridae: *Holocentrus sammara* (185639); *Ostichthys japonicus* (204076). Melamphaidae: *Melamphaes bispinosus* (176339). Polymixiidae: *Polymixia japonica* (142823). Trachichthyidae: *Hoplostethus mediterraneus* (142821).

Gasterosteiform fishes.—Gasterosteidae: *Aulorhynchus flavidus* (93909); *Gasterosteus aculeatus* (85670); *Spinachia spinachia* (193303).

Syngnathiform fishes.—Aulostomidae: *Aulostomus chinensis* (198264). Centriscidae: *Macrorhamphosus* sp. (216739); *Notopogon schoteli* (95469). Fistulariidae: *Fistularia serrata* (198398). Syngnathidae: *Syngnathus californiensis* (171865).

Scorpaeniform fishes.—Hexagrammidae: *Hexagrammos decagrammus* (92858). Platycephalidae: *Platycephalus* sp. (183205). Scorpaenidae: *Scorpaena guttata* (176288); *Sebastes inermis* (212669).

Percoid fishes.—Moronidae?: *Lateolabrax japonicus* (182830). Opistognathidae: *Opistognathus maxillosus* (172852). Percichthyidae: *Percichthys vinciguerra* (218460). Sciaenidae: *Cynoscion nebulosus* (218023).

Polynemoid fishes.—Polynemidae: *Eleutheronema tetradactylum* (213325); *Filimanus* sp. (213332); *Galeoides decadactylus* (213358); *Polydactylus octonemus* (154823); *Polynemus multifilis* (171713).

Zoarceoid and notothenioid fishes.—Notothenioidei—Bovichtidae: *Bovichtus chilensis*

(215425); *Cottoyperca gobio* (215354); *Pseudaphritis bursinus* (187421). Nototheniidae: *Eleginops maclovinus* (215372); *Trematomus bernacchii* (184348). Zoarceoides—Bathymasteridae: *Bathymaster caeruleofasciatus* (182117); *Ronquilus jordani* (147454). Pholidae: *Apodichthys flaviceps* (93775). Stichaeidae: *Lumpenella longirostris* (129000). Zaproridae: *Zaprora silenus* (127699). Zoarcidae: *Lycodes diapterus* (202553); *Zoarcas viviparus* (201246).

Trachinoid fishes.—Percophidae: *Bembrops filifera* (220457). Trachinidae: *Trachinus draco* (185126). Uranoscopidae: *Astroscoptes y-graecum* (153439); *Gnathagnus elongatus* (212866); *Ichthyoscopus lebeck* (212882); *Kathetostoma albigutta* (174161); *Uranoscopus japonicus* (142739).

Blennioid fishes and *Parapercis*.—Blennioidei—Blenniidae: *Blennius pholis* (173684); *Hypsoblennius gilberti* (63747); *Istiblennius* sp. (198123). Clinidae: *Clinus* sp. (72624); *Gibbonsia metzi* (63895); *Heterostichus rostratus* (60778). Dactyloscopidae: *Dactyloscopus amnis* (179957). Labrisomidae: *Labrisomus nuchipinnis* (200439); *Mniurpes macrocephalus* (190315). Tripterygiidae: *Tripterygion etheostoma* (212844). Trachinoidei?—Pinguipedidae: *Parapercis sexfasciatus* (176721).

Callionymoid fishes.—Callionymidae: *Callionymus lunatus* (198905); *Calliurichthys japonicus* (142735); *Dactylopus* sp. (219178); *Synchiropus ocellatus* (191491).

Gobioid fishes.—Eleotridae: *Dormitator maculatus* (162016); *Eleotris amblyopsis* (197251); *Gobiomorus maculatus* (164606); *Guavina guavina* (217930). Gobiidae: *Acanthogobius flavimanus* (187539); *Awaous tajasica* (209726); *Gillichthys mirabilis* (141168); *Glossogobius* sp. (218564); *Gobioides broussonetti* (140103); *Gobius kessleri* (185103); *Sicydium multipunctatum* (190780); *Tridentiger obscurus* (142641).

Acanthuroid and other fishes with beaked jaws.—Acanthuroidei—Acanthuridae: *Acanthurus matoides* (100418); *Prionurus microlepidotus* (178985). Siganidae: *Siganus canaliculatus* (213525). Labroidei—Scaridae: *Scarus sordidus* (185950). Percoidei—Oplegnathidae: *Oplegnathus fasciatus* (183106).

Sphyrnaoid fishes.—Sphyrnaidae: *Sphyrna argentea* (63970).

Scombroid fishes.—Gempylidae: *Rexea solandri* (216751). Scombridae: *Rastrelliger kanagurta* (212739); *Scomber japonicus* (93974); *Scomberomorus maculatus* (199143). Trichiuridae: *Trichiurus lepturus* (199144).

Stromateoid fishes.—Ariommidae: *Ariomma regulus* (174105). Centrolophidae: *Hyporoglyphe perciformis* (157106); *Psenopsis anomala* (142818). Nomeidae: *Nomeus gronovii* (87946). Stromateidae: *Pampus argenteus* (215020); *Peprilus alepidotus* (199128).

Anabantoid and channoid fishes.—Anabantoidei—Anabantidae: *Anabas testudineus* (195421); *Ctenopoma kingsleyae* (195014). Belontiidae: *Trichogaster pectoralis* (218103). Channoidei—Channidae: *Channa striata* (217651).

