

Jaw Structures and Movements in Higher Teleostean Fishes

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Abstract All of the diverse jaw structures in higher teleosts appear to be modifications of a single basal type and are treated as such. Only some of the principal variants are discussed. Though the two jaws act as a coordinated unit during feeding, their movements are different. The upper and lower jaws are discussed separately. In the upper jaw the principal concern is with the various types of premaxillary protrusion and with the secondary development in some groups of a rocking premaxilla. For the lower jaw most of the account is devoted to the repeated differentiation of movements in its anterior and posterior sections. The paper concludes with comments on the jaw apparatus as a functional unit and its evolution in higher teleosts.

Higher teleosts show a great diversity in what they eat and how they feed. What they eat is most directly reflected in dentition, but how they eat is at least in large part associated with jaw construction and jaw movements. Any comparative study of jaw structures and movements is complicated by a number of factors. The first is that many, perhaps most, higher teleosts move their jaws in at least qualitatively different fashion depending on the nature and position of the items they are eating (Liem, 1979). Second, the effect of contracting certain muscles with jaw attachments remains questionable. This is most notably true of the "geniohyoideus" (Osse, 1969; the protractor hyoidei of Winterbottom, 1974a) and the A_1 section of the adductor mandibulae. Third, there is the great diversity of jaw structures to cope with. Fortunately, all of the variants appear to represent modifications from a type of mouth that is still approximately represented in such modern fishes as the percoids *Doederleinia* (see Gosline, 1986) and *Perca* (see Osse, 1969) and the scorpaeniform genera *Sebastes* (see Alexander, 1967a) and *Helicolenus* (see de la Hoz and Dyer, 1984). This mouth type provides a base with which the various modifications can be compared.

The upper jaw

In higher teleosts the two bones of the upper jaw—the toothless maxilla behind and the generally toothed premaxilla in front—are movably associated with the skull and rarely united to one another. The different kinds of upper jaw all

seem to be modifications of a type associated with a particular (acanthopteran) system of premaxillary protrusion (Alexander, 1967a; Gosline, 1981). The diagnostic feature of this protrusion system, which provides a firm bite with protruded premaxillae, is an inner maxillary process that moves forward as a wedge between the extended premaxillae and the skull. This maxillary blocking system is present in nearly all higher teleosts, even some of those, e.g., *Scomber*, that have secondarily lost the ability to protrude the premaxillae.

The nature of the movements in the toothed limb of the upper jaw almost always depend on the relationship between the premaxillae and the skull. The medial part of the toothed limb usually has a posterodorsal projection, the ascending process (Fig. 1), that via an underlying rostral cartilage rides over or abuts against the front of the skull. Movements of the premaxillae are basically of two types with intermediate conditions. If the ascending processes are short, the premaxillae generally rock around or over the front of the skull as the mouth opens. If the ascending processes are long (Figs. 1, 2) they slide forward over the skull providing a more or less unidirectional protrusion.

The acanthopteran protrusion system apparently evolved in some fish with an upper jaw construction like that of *Aulopus* in which the premaxillae are still primarily of the original rocking type (Gosline, 1980). In the majority of percoids and higher teleosts protrusion is more or less well developed, and those forms without protrusion seem to have secondarily lost it.

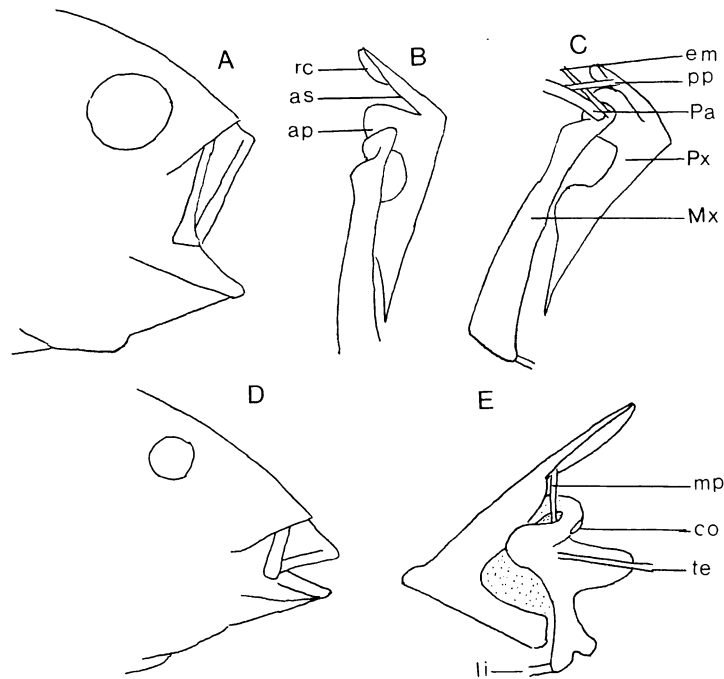


Fig. 1. *Rhomboplites* (Lutjanidae): A, side view of head with the mouth open; B, right upper jaw bones with the mouth open and C, with the mouth closed. *Orthopristis* (Haemulidae): D, side view of head with the mouth open; E, medial view of right upper jaw bones. ap, articular process of the premaxilla; as, ascending process of the premaxilla; co, condyle for the articulation between the maxilla and the skull; em, ethmoid-maxillary ligament; li, ligament from the inner surface of the distal end of the maxilla to the outer surface of the mandible; mp, anterior maxillary-premaxillary ligament; Mx, maxilla; Pa, palatine; pp, palatine-premaxillary ligament; Px, premaxilla; rc, rostral cartilage; te, tendon from the A₁ section of the adductor mandibulae muscle.

The basal type of protrusion in these higher teleosts appears to be one in which moderately well-developed ascending processes are separate from slightly more lateral articular processes (Fig. 1B, C). The mechanism of protrusion in such fishes has received much attention and need not be described again in detail (Van Dobben, 1935; Alexander, 1967a; Gosline, 1981; Dutta and Chen, 1983; De la Hoz and Dyer, 1984). Two separate premaxillary processes, indicating this basal system, are present in a wide range of higher teleostean taxa: various lower percoids, e.g., *Rhomboplites* (Fig. 1A–C), the northern blennioid *Ronquilus*, the southern blennioid *Tripterygion*, the gobioid *Eleotris*, and in various Scorpaeniformes (*Sebastes*), Batrachiformes (*Batrachoides*) and Lophiiformes (*Lophius*).

This basal protrusion system seems to have

evolved in, and mostly occurs among, broad-headed fishes that eat larger, free-swimming animals. In such fishes a moderate amount of premaxillary protrusion is accompanied by a highly-developed suction into the oral-opercular cavities caused by rapid lateral as well as vertical expansion of these cavities (Osse, 1969). The lateral expansion is also a cause, via expansion of the distal ends of the maxillae, of premaxillary protrusion and the insertion of the maxillary block behind the premaxillae (Alexander, 1967a). However, in large-mouthed fishes, e.g., the scorpaenids *Sebastes* (see Alexander, 1967a) and *Helicolenus* (see De la Hoz and Dyer, 1984), forward movement of the distal end of the maxilla as the mandible is lowered can also bring about protrusion. It seems probable that forward movement of the distal end of the maxilla becomes at least the

principal cause of protrusion not only in the more narrow-headed of the fishes with separate ascending and articular premaxillary processes, e.g., *Tripterygion*, but also in all those forms with premaxillary protrusion that have the two premaxillary processes united.

The great majority of the other fishes to be discussed here have the ascending and articular premaxillary processes united into a single compound structure. As compared with these, the forms with the two processes separate have certain limitations. First, they seem capable of only a moderate amount of protrusion. Second, they appear to have a rather imprecise occlusion (Gosline, 1981). On the other hand they have developed one adaptation that does not occur in fishes in which the articular process is united to a well-developed ascending process. This has to do with the combination of moderate protrusion and the formation of a rounded mouth opening.

A rounded gape is advantageous not only for elimination of lateral escape hatches for prey but more notably in the development of suction into the oral cavity (Alexander, 1967b; Liem and Osse, 1975). In higher teleosts without well-developed ascending premaxillary processes, a rounded gape can be approximated by simply swinging the maxilla and toothed limb of the premaxilla forward over the side of the lower jaw as in lower teleosts. Here, the proximal end of the premaxilla simply rocks over the anterior end of the skull. However, a forward plane of protrusion by a well-developed ascending process is never combined with a forward swinging of its distal end if the two premaxillary processes are united (as in Fig. 1D, E). Here, the ascending process and the toothed limb remain at the same angle to one another whether the mouth is closed or open. When such fishes approximate a rounded opening to the gape it is by some secondary means, such as the membrane across the corner of the open mouth in *Pterophyllum* (see Alexander, 1967a). Most of the fishes with two separate premaxillary processes have, by contrast, developed a flexible area at the base of the ascending process that permits the toothed limb of the premaxilla to swing forward relative to the base of the forwardly moving ascending process (Fig. 1B, C) and across the corner of the gape when the mouth opens. This flexible area, often developed into a definite joint, is easily demonstrated by observing the change in position

of the articular process relative to the ascending process as the distal end of the premaxilla is manipulated forward.

The change from a premaxilla in which the ascending and articular processes are separate to one in which they are firmly united has occurred many times in higher teleosts. The shift from one type to another and its effect on upper jaw movements can be exemplified by a comparison between the lutjanoid fishes (processes separate except in *Aphareus* and probably *Randallichthys*) and the haemuloids (processes united).

In lutjanoids the amount of premaxillary protrusion is never more than moderate and is completely suppressed in *Aphareus* and *Randallichthys* (see Johnson, 1980). Aside from the forms without protrusion, the species investigated have either a flexible area at the base of the ascending premaxillary process (Fig. 1B, C) or, in the Caesionidae, a definite hinge in that area (Johnson, 1980).

Most of the haemuloids have long ascending premaxillary processes with the articular processes forming shoulders along their sides (Fig. 1E). However, the range in the length of the ascending processes and in the amount of premaxillary protrusion is very great. At one extreme, in *Xenocys*, the ascending premaxillary processes are short, protrusion is minimal, and the toothed limb of the premaxilla simply rocks forward to provide about the same sort of rounded mouth opening as in the lutjanid *Rhomboplites*. In haemuloids with longer ascending processes there is no premaxillary rocking, and, as noted, the toothed limb of the premaxilla remains at a fixed angle to the ascending process. Though this fixed relationship between the ascending premaxillary process and the toothed limb diminishes the approximation to a rounded mouth opening (Fig. 1D), it enables the development of a second method of premaxillary protrusion. In lutjanoids with two separate premaxillary processes protrusion is entirely caused by twisting of the maxillary head (Alexander, 1967a). In most haemuloids, to judge by the ligament from the inner maxillary process to the ascending premaxillary process (mp of Fig. 1E; see also Gosline, 1981), maxillary twisting is still used as a means of protrusion, but a second method has been added. This is an anteroventral force exerted on the distal end of the toothed premaxillary limb when the mouth is opened by the forward swinging of the maxilla behind it (see Fig. 1E). (In many

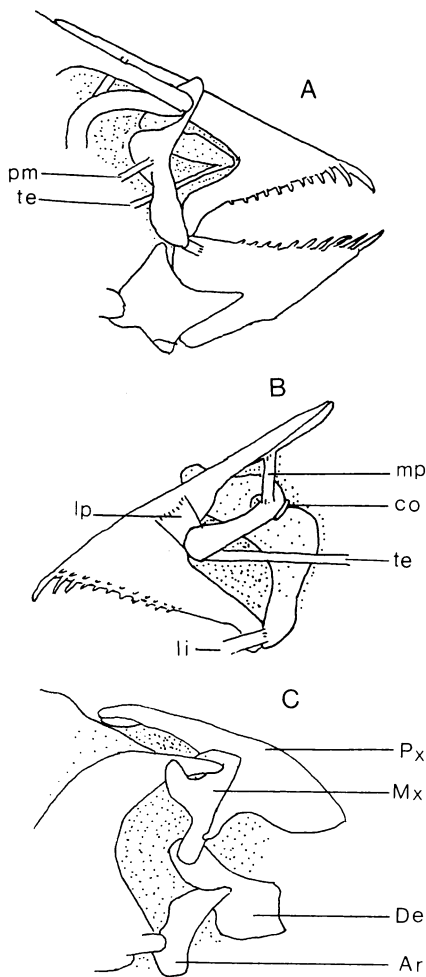


Fig. 2. *Coris gaimardi*: A, jaws, lateral view, and B, upper jaw, medial view. *Scarus (oviceps?)*: C, jaw bones with the mouth widely open, drawn mostly from a skeleton. Ar, articular-angular and retroarticular; De, dentary; lp, anterior ligamentous sheet between the maxilla and the premaxilla; mp, upper anterior ligament between the maxilla and premaxilla; and pm, a ligament from the base of the palatine area of the suspensorium to the outer surface of the maxilla. Other lettering as in Fig. 1.

fishes, e.g., *Chaetodon*, the maxillary component of this protrusion method has been eliminated by a direct ligamentous attachment between the distal end of the premaxilla and the lower jaw.) In the haemuloid family Inermiidae, members of which have very long ascending premaxillary pro-

cesses and extensive protrusion, forward swinging of the maxilla has become the only method of protrusion (Johnson, 1980). Here, the maxillary-premaxillary ligament (mp) is gone, and the only function of premaxillary twisting seems to be to provide a blocking system behind the protruded premaxilla.

An extensive premaxillary protrusion such as that of the Inermiidae has developed repeatedly in distantly related higher teleosts: the Zeidae (see Hofer, 1938), Nandidae (see Liem, 1970), Gerreidae (see Schaeffer and Rosen, 1961), Ammodytidae (see Kayser, 1962), Callionymidae (see Kayser, 1962), the cichlid genus *Pterophyllum* (see Alexander, 1967a), and *Epibulus* among labrids (Van Dobben, 1935). Though many of these fishes have their own upper jaw peculiarities, all have in common a very long ascending premaxillary process that slides over the skull and an articular process that is either reduced to a narrow shelf along the ascending process or absent completely. These examples of extreme protrusion have been extensively investigated, and only one problem that does not seem to have been discussed may be mentioned here, namely the innervation and vascularization of such premaxillae. *Epibulus* is unique among these fishes in that it has developed a method for protruding the lower as well as the upper jaw.

A long ascending premaxillary process does not necessarily indicate extensive protrusion. Indeed, there are a number of higher teleosts such as most labrids (Rognes, 1973; Van Hasselt, 1979) and chaetodontids (Motta, 1985) that have quite long ascending premaxillary processes but relatively slight premaxillary protrusion. These fishes have specialized teeth at the tips of the jaws that seem to be used primarily for plucking out small sedentary animals or for nipping off parts of such animals. This type of feeding has led repeatedly to the development of long-snouted forms: *Aulichthys* in the Gasterosteiformes, the labrid *Gomphosus*, the chaetodontid *Forcipiger*, and the triacanthoid *Trixipichthys*.

In most labrids the strongly developed ascending premaxillary processes (Fig. 2A, B) provide some, but not much, protrusion. Rather they seem to serve primarily as a prop for the specialized teeth at the anterior tip of the upper jaw. In the genus *Anampses* such teeth are the only ones present in the jaw. A bite against a firm object by such

teeth will force the tips of the ascending processes downward against the skull while tending to raise the anterior toothed areas up away from the skull. Raising of the front of the premaxillae is minimized in various ways. There are ligaments extending up to the premaxillae posteriorly from the palatine (Figs. 1C: pp, 2A) and anteriorly from the head of the maxilla (Fig. 2B: 1p). Probably more important are two strong bindings, one between the distal ends of the maxilla and premaxilla and another that extends over the anterior parts of the ascending processes from the upper rim of one external maxillary process to that of the other side. The maxillae in turn are prevented from upward displacement by the overlapping palatine prongs, by a sheath of ligamentous tissue that extends medially from the palatine prong to the outer maxillary head, and by a ligament (Fig. 2A: pm) from low on the suspensorium to the maxilla. All of these bindings permit a certain amount of fore-and-aft sliding of the ascending premaxillary processes but prevent their upward displacement.

The type of upper jaw discussed above, i.e., in small-mouthed forms with specialized anterior teeth and rather long ascending premaxillary processes with moderate to slight protrusion, has evolved repeatedly in higher teleosts. Sometimes it has developed directly from a basal type of premaxilla with separate ascending and articular processes as in the blenny series *Tripterygion-Labrisomus*, and sometimes it has evolved from a premaxilla of a primarily rocking type, as in the percid series *Ehippus-Drepane*. Conversely, a premaxilla with a long ascending process has in some instances developed into one of a rocking type as in the tetraodontiform series *Triacanthodes-Balistes*.

Within the labroid series the upper jaw type discussed above has evolved in two directions. In one, represented by *Lachnolaimus* and *Epibulus*, premaxillary protrusion has become very extensive. The other development has led to the upper jaw represented in *Scarus*.

In the family Scaridae the jaws have become more or less beak-like with sharp outer cutting edges. In *Cryptotomus*, the most generalized of scarid genera at least in so far as the retention of separate teeth is concerned, the upper jaw structure is very much like that of the labrids discussed above. However, in the specialized genus *Scarus* (see Lubosch, 1923; Van Dobben, 1935) the jaws

are far more complex (Fig. 2C). The lower jaw has a well-developed internal joint (see below), and in the upper jaw the premaxilla, in addition to undergoing a certain amount of protrusion, rocks upward from its posterior abutment against the skull as the mouth opens. Apparently the upward component of movement in the premaxilla is caused by the upward rocking of the posterior end of the dentary (Fig. 2C; not of the articular-angular as indicated in Van Dobben's fig. 50). A similar upward movement in the anterior rim of the upper jaw when the mouth opens, though caused differently, occurs in such fishes as the Oplegnathidae, the genus *Secutor* in the Leiognathidae (see Weber and de Beaufort, 1931: fig. 69), and in the acanthuroid *Zanclus* (see Gosline, 1986: fig. 3).

In *Scarus*, *Oplegnathus*, *Secutor*, acanthuroids, and in the tetraodontoids discussed below, lowering of the premaxilla is presumably nearly synchronous with raising of the mandible. In this respect these fishes differ from forms with the basal type of acanthopteran protrusion in which the lower jaw is raised against the protruded premaxillae. Two features seem to be involved in this change from differential to synchronous closure of the two jaws. One is a tighter binding between the distal end of the maxilla and the mandible. The other has to do with the A₁ section of the adductor mandibulae muscle. All that can be said about the latter from the observation of preserved specimens is that A₁ is differently inserted on the maxilla in labrids (Fig. 2A, B: te) and scarids than it is in more basal higher teleosts (Fig. 1E). A₁ has again quite different maxillary attachments in acanthuroids (Gosline, 1986: fig. 3) and in most tetraodontiform fishes (Winterbottom, 1974b).

Among tetraodontiform fishes other than the basal Triacanthoidei (Tyler, 1980), there has been a quite drastic simplification in upper jaw structure. Premaxillary protrusion has not only been lost but the premaxilla and maxilla have become firmly united to one another. So long as the premaxilla and maxilla have topographically different fulcra, as they have in all of the fishes previously discussed, there must be some independence of movement in the two bones. In all of the Tetraodontoidei the sliding articulation between the maxilla and the skull has been lost. Furthermore only one of the two usual anterior

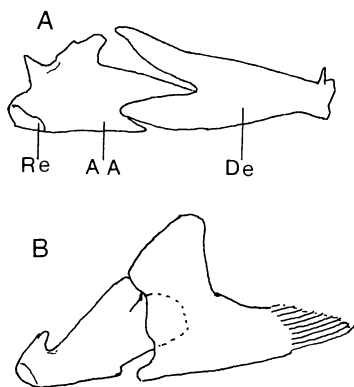


Fig. 3. External view of the lower jaw of A, *Epinephelus* and B, *Holacanthus*. AA, articular-angular; De, dentary; Re, retroarticular.

upper jaw articulations has been retained. In the superfamily Balistoidea of the suborder Tetraodontoidei the single articulation is between the

premaxilla and the skull, with that between the palatine and the maxilla playing at best a supplementary role. On the other hand, in the superfamily Tetraodontoidea it is the palatine that acts as a fulcrum for the maxilla and upper jaw; the skull-premaxillary articulation has been lost.

The lower jaw

There are three bones in each half of the lower jaw of higher teleosts (Fig. 3), the dentary, articular-angular (or angulo-articular), and retroarticular (Nelson, 1973). These three bones may be divided into two functional units. It is with the development of a movable association between these two units that the present account is primarily concerned. The anterior of these is the dentary, which, directly or indirectly, bears whatever teeth are present in the lower jaw. Posteriorly, the small retroarticular is always firmly united to the articular-angular, and the two bones together,

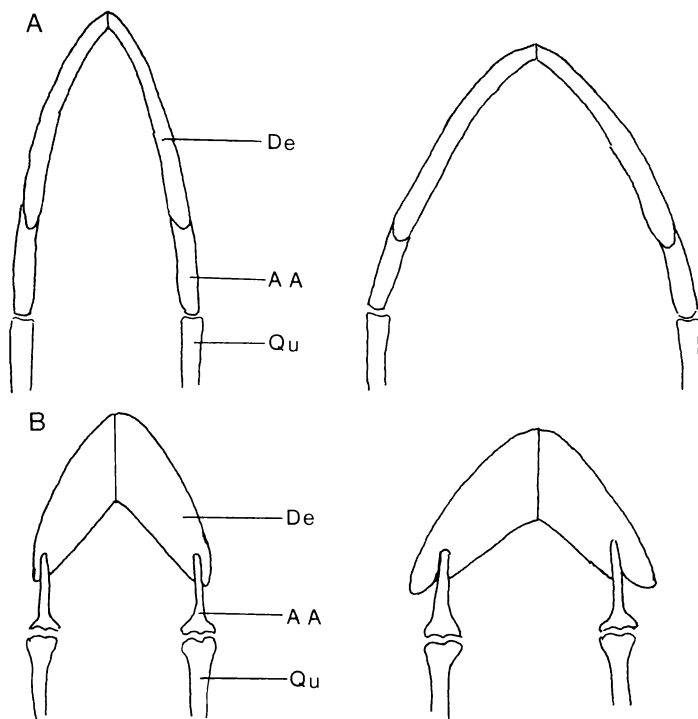


Fig. 4. Diagrams to indicate the nature of the movements in the lower jaw when the lower ends of the suspensoria swing apart (right half of each figure). A, *Epinephelus*; B, the labrid *Tautoga*. Viewed from below; the retroarticular is not indicated. AA, articular-angular; De, dentary; Qu, quadrate.

via their ligaments and muscular attachments, provide the means for lowering and raising the jaw.

There are two main kinds of movement in the lower jaw. The first and principal type is the vertical lowering and raising of the front of the jaw. The second is associated with the lateral expansion and contraction of the oral cavity (Fig. 4). When the mouth expands laterally, the lower ends of the suspensoria, including their mandibular articulations, spread apart. The posterior ends of the mandible spread with them. In fishes in which the articular-angular and dentary are firmly united, e.g., *Epinephelus* (Fig. 4A), such expansion involves a spread of the symphyseal hinge between the two halves of the jaw in front, and, posteriorly, a change in the angle between each half of the lower jaw and the suspensorium, i.e., a slight lateral movement of the articular-angular across the face of its quadrate articulation. (A very slight amount of twisting also seems to be involved here, but is not further discussed.)

In *Epinephelus* (Fig. 3A), as in most long-jawed higher teleosts, the dentary and articular-angular are firmly attached to each other, and each half of the lower jaw moves as a single structural unit. However, even here the area of firm attachment between the two bones is limited to the junction between the upper surface of the lower posterior extension of the dentary and the lower surface of the forward projection of the articular-angular and may provide enough flexibility to diminish jaw breakage. In *Epinephelus* lateral spreading in the posterior parts of the lower jaw is accommodated in front by a vertical symphyseal hinge and posteriorly by what amounts to a ball-and-socket-like, or more specifically a saddle-like articulation between the articular-angular and the quadrate. This type of articulation permits not only vertical movements of the mandible but also some lateral movement of the articular-angular across its quadrate articulation.

In various unrelated, mostly short-jawed higher teleosts there has been an increase in the flexibility between the dentary and the posterior part of the lower jaw. This increased flexibility may permit either twisting or vertical movement of the dentary relative to the articular-angular, or both.

The development of a twisting type of movement between the dentary and the rest of the jaw is notably developed in short-jawed labrids (Fig.

4B, see also Van Hasselt, 1979). Here, the lateral expansion of the mouth cavity is much less than in *Epinephelus*, but such expansion as there is causes very different lower jaw movements. The twisting that occurs within the labrid lower jaw has two structural causes. First, the symphyseal hinge line between the two halves of the lower jaw is oblique (see Fig. 2A), not vertical. As a result, the posterior parts of the dentary do not simply spread apart but rather the upper rims of the dentary fold outward and forward relative to the oblique hinge line (Fig. 4B, right side). Second, the articulation between the articular-angular and the quadrate has become horizontally elongate and somewhat double-faceted (indicated in Fig. 4B). This articulation permits neither lateral movement nor twisting of the articular-angular relative to the quadrate. The result of these two structural features is that when the lower parts of the suspensoria spread apart, the upper rims of the dentaries fold out over the forward ends of the articular-angulars (Fig. 4B, right side).

Though this twisting of the axis of the dentary relative to that of the articular-angular seems particularly notable in short-jawed labrids, it probably occurs to some extent in many fishes with an oblique symphyseal hinge between the two dentaries, e.g., in the sparid *Lagodon*. Nor is it a distinctive lower jaw feature. On the one hand, long-jawed labrids such as *Lachnolaimus*, *Cheilio*, and *Gomphosus* have reverted to the type of jaw in which the articular-angular and dentary are firmly united. On the other, a twisting movement within the lower jaw similar to that of labrids occurs in such scarids as *Sparisoma* but has given rise to the vertical movement of the dentary relative to the articular-angular in *Scarus*.

A lower jaw in which the dentary rocks vertically over the articular-angular has evolved repeatedly in higher teleosts. It occurs, for example, in the anabantoid genus *Helostoma* (see Liem, 1967), the Pomacanthidae, *Scarus* and in the acanthurids and siganids. Examples of increasing development in this feature, though drawn from unrelated fish groups, are discussed below.

In the pomacanthid fishes the dentaries are movably attached to the articular-angulars and there is a specialized area of abutment between the upper parts of the two bones (Fig. 3B). However, it appears that the lower part of the dentary can, at least to some extent, slide back and forth over

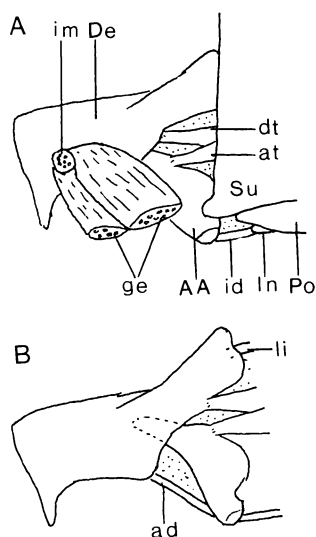


Fig. 5. *Acanthurus*: A, inner view of lower jaw; B, same with the suspensorium, the protractor hyoidei and the inframandibularis muscle removed. AA, articular-angular; ad, ligament between the articular-angular and dentary; at, tendon from adductor mandibulae to articular-angular; De, dentary; dt, tendon from adductor mandibulae to dentary; ge, protractor hyoidei muscle (two forward attachments); id, ligament from interopercle to retroarticular; im, inframandibular muscle; In, interopercle; li, ligament between maxilla and dentary; Po, preopercle; Su, suspensorium.

the lower part of the articular-angular thus providing the possibility of up-and-down movement of the dentary relative to its dorsal fulcrum. The musculature to the lower jaw of pomacanthids is of quite normal, basal percoid type (Gosline, 1986). The nature of the slight flexibility within the lower jaw of pomacanthids suggests a simple shock-absorber function.

Considerably greater movability of the dentary occurs in *Acanthurus* (Figs. 5A, B). Here the dentary rocks over the tip of the articular-angular. Apparently, in lowering the mandible there is a synchronization of movements in the two functional components of the lower jaw because the ligament from the interopercle to the retroarticular is functionally continued forward from the retroarticular to the ventral edge of the dentary (Fig. 5B). However, there are two separate means for raising the two components of the mandible. In

Acanthurus the A_w section of the adductor mandibulae muscle is absent (though a small, posteriorly-displaced remnant of this section is present in the related *Zanclus*). There are two tendons extending forward to the inside of the lower jaw (Fig. 5A, B) from separate subdivisions of A_2 . The lower of these is attached to the articular-angular, and the upper to the dentary above its fulcrum on the articular-angular. (In *Naso*, which has far less, if any, independent movement of the dentary, there is only a single tendon from a single, undivided A_2 ; however, this tendon divides into two parts anteriorly.) Thus, the upward movements of the dentary and articular-angular of *Acanthurus* are under separate control and are not necessarily synchronous. Apparently the fish can rock the dentary upward relative to the articular-angular. Whether it can also rock the dentary downward separately depends on whether the protractor hyoidei (Winterbottom, 1974a) can be used to accomplish this. There is a pair of large attachment areas for this muscle on the inside of the dentary (Fig. 5A), but whether its contraction moves the hyoid bars forward or the dentaries backward or both has been a source of disagreement (see Osse, 1969) that cannot be resolved by observation of preserved specimens.

A maximum development of independent movement in the dentaries occurs in the genus *Scarus* (Fig. 2C). Here the dentary can be rocked upward or downward over the articular-angular. The very complex lower jaw musculature enabling such movement has been described by Lubosch (1923, 1929). Suffice it to say here that there are muscles to the dentary both above and below its fulcrum on the articular-angular. (In *Scarus*, and apparently in *Acanthurus*, the lower jaw seems to operate on the same principle and for the same reason as the mechanized scoop-shovel used for removing piles of dirt or snow from the ground.)

Though increased flexibility within the lower jaw has developed many times in unrelated groups, it does appear to be limited to certain categories of fishes. Negatively, it does not occur in long-jawed forms. The short-jawed fishes with separate vertical movements of the dentary are generally forms that use a scraping, browsing, or grazing method of feeding. In such groups the teeth are specialized in one way or another. Often a joint in the lower jaw is combined with flexible teeth, as in *Helostoma* and *Ctenochaetus*. Some-

times, however, the principle of flexibility within the jaw seems to have moved forward to the area between the dentary and the dentition. Thus, in *Mugil* and salariine blennies the dentary and articular-angular are firmly attached to one another but the teeth have lost their insertion on the dentary. (My erroneous citation of salariine blennies as fishes with a hinge within the lower jaw [1986: p. 710] was based on the examination of specimens of *Entomacrodus* with broken jaws.)

The two jaws as a single functional unit

Though the movements within the two jaws are quite different, they act together in biting and in opening and closing the mouth. Certain aspects of their combined function may be noted.

First, certain structural features cause movements in both jaws. In the basal higher teleostean adductor mandibulae configuration (Gosline, 1986) the A_1 section has forward attachments on both the maxilla and the mandible. Again, the ligament from the distal end of the maxilla to the mandible (li of Fig. 1C, E) causes a forward swinging of the maxilla when the mandible is lowered. Furthermore, in such fishes as *Scarus* (see above) the tighter binding between the maxilla and the dentary may cause a return movement of the maxilla when the mandible is raised.

At a more general level, there is during feeding a forward movement of both jaws. Premaxillary protrusion in the upper jaw has received most attention. However, there is usually some forward movement of the lower jaw as the premaxilla is being protruded, either as a result of raising the head (Tchernavin, 1948) or because, when it opens, the lower jaw swings somewhat forward as well as downward around a ventrally located articulation with the quadrate (Motta, 1985). It may be that in at least some fishes the premaxillary protrusion in the upper jaw merely compensates for forward movements in the mandible.

Evolution of the jaw apparatus in higher teleosts

The various higher teleostean jaw structures seem to represent a diversification in many directions from a single original kind of mouth construction. This basal type, though it seems to have originated among lower teleosts near *Aulopus* (see Gosline, 1980), is approximated today in such fishes as

Perca (see Osse, 1969). It seems to be adapted for the capture of relatively large, free-swimming animals, which is accomplished by a combination of forward swimming, suction into the mouth cavity, and a bite by the jaws, the upper with a particular (acanthopteran) type of premaxillary protrusion. The creation of a suction into the mouth by means of horizontal as well as vertical expansion of the oral-opercular cavities is probably the most important feeding movement, and the relatively slight premaxillary protrusion, with its adaptation for the development of a rounded gape (see above), may perhaps be viewed as a forward extension of the suction apparatus.

The most diagnostic feature of the basal type of higher teleostean mouth seems to be the presence of separate ascending and articular processes on the premaxilla. This type of premaxilla is present in a wide range of higher teleostean taxa. Though it occurs mostly in large-mouthed forms, it seems to be particularly associated with the lateral expansion of the oral cavity presumably found in broad-headed fishes. Among such fishes the basal type of premaxilla is present in some forms with quite small mouths, e.g., *Podotheucus acipenserinus*.

Most of the more specialized higher teleosts shows a reduction, though rarely a complete loss, of lateral expansion on the oral cavity. This change generally, though by no means always, indicates a reduction in emphasis on suction in the feeding process and its replacement in importance by the jaw bite. The alteration in relative importance of the two components of the feeding process is accompanied by a number of structural features. One is the loss of separate ascending and articular premaxillary processes. Another is the usual loss of teeth on the vomer and palate in the mouth (Gosline, 1985).

The increased emphasis on the jaw bite appears to have opened up to higher teleosts a number of food sources unavailable to fishes primarily dependent on suction feeding. These include various kinds of sedentary animals and plants. In order to feed on these, different higher teleosts have evolved various specializations in both of the jaws and in teeth, which they use for nipping, plucking, browsing, or grazing. Some of the specialized jaw types evolved have been discussed in preceding sections of the paper.

There are, of course, many other types of jaw specialization in higher teleostean fishes, for

example, those among oceanic and freshwater forms. If those among inshore marine fishes have been emphasized here, it is partly because higher teleosts appear to show most variation, or, if you will, have succeeded best, in this particular environment.

Here, only two minor points regarding specializations are noted. Sometimes a high degree of specialization in jaw structures characterizes a group of fishes, e.g., the Ammodytidae (see Kayser, 1962) or, presumably, the Pegasidae (see Pietsch, 1984). At other times a highly specialized jaw apparatus occurs in only one or a few members within a family, e.g., *Epibulus* in the Labridae or *Scarus* in the Scaridae.

Finally, because the two jaws act as a single functional unit specializations in one jaw are usually paralleled in the other, for example, jaw length or dentition. This is not always so. The acanthurids and siganids have quite similar lower jaws but very different upper jaw structure (Starks, 1907) and the same is true of balistoids and tetraodontoids (see above). The nature of the movements in the two jaws has evolved over quite different pathways, as previously discussed, and change in the jaw musculature (Gosline, 1986) has again evolved semi-independently.

Material examined

The specimens on which the paper is primarily based are listed below in approximately phylogenetic order except for genera, which are alphabetically arranged. All of the material is in the University of Michigan fish collections. Catalog numbers followed by an "s" indicate skeletons.

Myctophiformes

Aulopidae: *Aulopus japonicus*, 186637, Japan.

Gasterosteiformes

Aulorhynchidae: *Aulichthys japonicus*, 198384, Japan.

Perciformes

Percoidei

Serranidae: *Epinephelus fulvus*, 17304-s, Bermuda.

Lutjanidae: *Aphareus furcatus*, 182891, Japan;
Rhomboplites aurorubens, 174040, Mexico.

Haemulidae: *Orthopristis chrysoptera*, 199057, Texas; *Xenocys jessiae*, 190976, Galapagos Is.

Inermiidae: *Emmelichthys atlanticus*, 174143, Mexico.

Sparidae: *Lagodon rhomboides*, 155275, Louisiana.

Gerreidae: *Diapterus plumieri*, 199580, Honduras.
Leiognathidae: *Secutor insidiator*, 191456, Thailand.

Ephippidae: *Drepane punctata*, 116754, Java;
Ephippus orbis, 191417, Thailand.

Oplegnathidae: *Oplegnathus fasciatus*, 185129, Japan.

Pomacanthidae: *Holacanthus bermudensis*, 17406-s, Bermuda; *H. passer*, 190304, Costa Rica.

Chaetodontidae: *Chaetodon sedentarius*, 174046, Mexico; *Forcipiger longirostris*, 198010, Mariana Is.

Scombroidei

Scombridae: *Scomber scombrus*, 201402, Netherlands.

Blennioidei

Tripterygiidae: *Tripterygion etheostoma*, 212789, Japan.

Clinidae: *Labrisomus nuchipinnis*, 175947, Bermuda.

Bathymasteridae: *Ronquilus jordani*, 93896, Washington.

Gobioidei

Eleotridae: *Eleotris picta*, 172082, Mexico.

Labroidei

Labridae: *Cheilio inermis*, 100524, Philippine Is.; *Coris gaimardi*, 185593, Madagascar, also 177365-s, Tahiti; *Gomphosus caeruleus*, 185596, Madagascar; *Lachnolaimus maximus*, 154881, Florida; *Tautoga onitis*, 181666-s, Rhode Island.

Acanthuroidei

Acanthuridae: *Acanthurus bahianus*, 172603, Puerto Rico; *Ctenochaetus striatus*, 197945, Mariana Is.; *Naso unicornis*, 198274, Mariana Is.

Zanclidae: *Zanclus canescens*, 197941, Mariana Is.

Scorpaeniformes

Scorpaenidae: *Sebastes maliger*, 94241, Washington.

Agonidae: *Podothecus acipenserinus*, 182254, Alaska.

Tetraodontiformes

Triacanthoidei

Triacanthodidae: *Triacanthodes anomalus*, 183507, Japan.

Tetraodontoidei

Balistidae: *Rhinecanthus aculeatus*, 197857, Mariana Is.

Tetraodontidae: *Lagocephalus spadiceus*, 183366, Japan.

Batrachiformes

Batrachidae: *Batrachoides surinamensis*, 203485, Brazil.

Lophiiformes

Lophiidae: *Lophius litulon*, 204157, Korea.

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真骨魚類の高位群の顎の構造と機能

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全ての真骨魚類の高位群の顎の構造は、一つの基本型の変形したもののようであるので、その様にここでは取り扱う。ここで論ずるのは幾つかの主な型のみである。上下の顎は摂食の際は協調した一つの単位として働くが、各々の動きは異なっている。上顎の場合は前上顎骨が伸出する際のさまざまな型と、幾つかの魚類群で二次的に発達した可動式前上顎骨を主に取り上げた。下顎の場合はその前部と後部の動きの、繰り返し行われた特化に重点を置いた。機能単位としての顎の構造と真骨魚類の高位群の進化の問題にも言及した。