

Fig. 7. Diagram of certain mouth parts of A, *Opisthonema oglinum*; B, *Aulopus filamentosus*; and C, *Carassius auratus*. In A and B, the effect of rotating the proximal end of the maxillary is indicated by the orientation of the oval (pm); a similar initial effect would occur in C, in which the proximal end of the maxillary is not shown. dm, Distal part of maxillary; ke, kinethmoid; li, lip; ma, mandible; pm, proximal end of maxillary; pr, premaxillary; sk, cranium.

*Clupea* does not roll directly with the proximal limb of the maxillary. The median end of the premaxillary overlaps the rostrum to which it is membranously attached and, because of this, the rotating proximal limb of the maxillary does not carry the premaxillary with it but rather slides over the under surface of the premaxillary. Since the proximal limb of the maxillary is flattish rather than round in cross section, its rotation has the effect of forcing the lower, dental border of the premaxillary forward and outward (Fig. 6A).

In *Elops* the premaxillary is moved by forward pressure on its distal end. In *Clupea* pressure is exerted on a proximal part of the premaxillary, and lowering of the maxillary has no effect on its distal end. In both genera, the result is to rock the dental surface of the premaxillary forward and outward. So long as there is pressure on only one area of the premaxillary a rocking movement ensues, at least in lower teleosts. The evolution of the acanthopterygian type of premaxillary protrusion depends on the development of two pressures on the premaxillary, one at either end of the bone. The force that moves the distal end of the premaxillary in acanthopterygian protrusion is that of *Elops*. The force exerted near the proximal end is brought about by a modification of the twisting of the proximal limb of the maxillary that occurs in *Clupea*.

The structural modifications involved in the clupeid type of upper jaw construction seem

to have carried it beyond the point of possible ancestry for acanthopterygian jaw protrusion. A more moderate series of developments is present in certain of the salmoniform osmerids. Here, the large-toothed *Osmerus* has an upper jaw structure very much like that of *Elops*. In the relatively small-toothed *Spirinchus* (Weitzman, 1967a, 1974), however, the premaxillary, though long enough to have its distal end forced forward by lowering of the maxillary, also seems to be affected proximally by rotation of the proximal end of the maxillary directly behind it. In *Spirinchus* both maxillary forces on the premaxillary seem to work together. However, the resulting premaxillary movement is still rotation because the lower teleostean type of membranous attachment between the median part of the premaxillary and the dorsal surface of the rostral area of the skull prevents protrusion.

The basic difference between protrusion and the premaxillary rotation of *Clupea*, osmerids, etc., is in the nature of the movement in the proximal part of the premaxillary. In *Clupea*, etc., the dental surface of the premaxillary rocks forward and outward around the membranous attachment between the premaxillary and the skull (Fig. 7A). In acanthopterygian protrusion the whole proximal part of the premaxillary moves forward relative to the skull (Fig. 7B). Several morphological changes are involved. First, there is the replacement of the membranous attachment between the premaxillary and the skull by a flexible area

of skin. The change from rotation to protrusion also involves the development of a sliding articulation between the premaxillary and the skull, usually accompanied by the development of an ascending premaxillary process. Again, premaxillary protrusion requires a shift in the insertion of the palatine-premaxillary ligament from the lateral position on the premaxillary it holds in *Elops* to a point well forward on the premaxillary in higher teleosts (Fig. 5C). Finally, the fact that acanthopterygians can close the mandible against premaxillaries in various stages of protrusion precludes the possibility of a precise bite between the jaws, i.e., the bite of the mandible will be against different levels of the premaxillary depending on the amount of horizontal extension of the premaxillary when the mouth is closed. In *Aulopus* the broad bands of jaw teeth provide a grasping bite at various stages of premaxillary protrusion, but the precise shearing bite of such forms as the parrotfishes and tetraodontiform fishes has only been attained by considerable modification in the basic acanthopterygian protrusion system.

A crucial aspect of the evolution of the acanthopterygian type of jaw protrusion remains to be dealt with, namely the mechanism for maintaining a firm bite at all stages of premaxillary extension. Alexander (1967a) has demonstrated that acanthopterygians can and do raise their mandibles, i.e., bite, against protruded premaxillaries. A key element in the supporting system for protruded premaxillaries appears to be the strong **palatine prong** that extends forward over a proximal area of the maxillary. This strut, developed in most, though by no means all, acanthopterygians, replaces the palatine prop against the inner surface of the maxillaries in lower teleosts (see, for example, Gosline, et al., 1966).

In *Aulopus* (Fig. 5B, C), as in such lower teleosts as *Clupea*, the maxillary extends well forward between the premaxillary and the skull, and twisting of the maxillary head causes premaxillary movement. The proximal end of the maxillary in *Aulopus* seems comparable to a two-headed hammer. So long as the axis between the two heads remains

parallel to the side of the skull the premaxillary is retracted (Fig. 5C), but a twisting of this axis enlarges the size of the wedge between the skull and the premaxillary (Fig. 5B), forcing the premaxillary away from the cranium.

There seem to be two ways of changing the axis between the two maxillary heads. One, present in many lower teleosts, is lowering the distal end of the maxillary, but since the curvature of the maxillary of *Aulopus* is much less than in *Clupea*, this method of forcing the premaxillary forward seems to be less effective in *Aulopus* than in *Clupea*. In *Aulopus*, this inherited method of moving the premaxillary is combined with another that depends in large part on the presence of a strong palatine strut over the maxillary. Lateral expansion of the mouth during feeding has the effect of forcing the lateral end of the maxillary outward and hence of bowing the whole arched maxillary outward and upward. Near the anterior end of the maxillary the overlapping palatine prong (Fig. 5B) prevents this upward displacement, forcing the proximal head of the maxillary to slide downward over its articulation with the cranium, the taper of which is such as to force the articular head of the maxillary anteroventrally. However, anteroventral movement of the whole anterior end of the maxillary is prevented by ligaments that extend forward to an attachment on its anterodorsal surface (Fig. 5C). As a result, the cranial articular head of the maxillary slides anteroventrally under these ligaments, rotating the maxillary and shifting the axis between its two articular heads from parallel with the skull to a right angle.

This is the same motion that is imparted by lowering the distal end of maxillary, and, in premaxillary protrusion, the two systems of maxillary rotation are synchronized. However, they act differently in the retraction of the protruded premaxillaries. This difference arises because the fish only narrows its oral cavity after the mandible has been raised (Alexander, 1967a). So long as the two halves of the mandible remain spread apart the maxillaries are propped into position by the mandibular rami forcing them outward distally and the palatine prongs forcing them

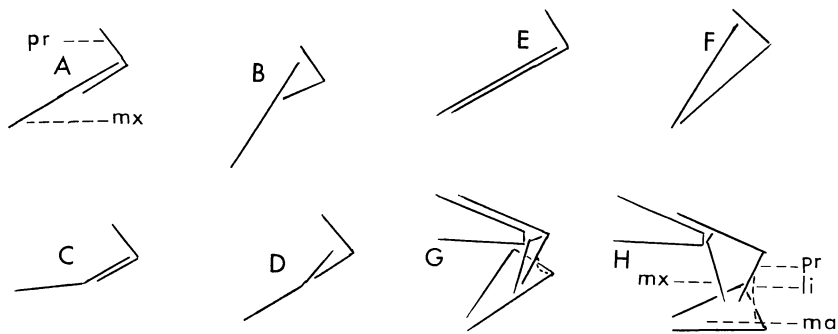


Fig. 8. Diagrammatic representations, with the premaxillaries retracted on the left and protruded on the right of each pair: A, B, short premaxillary, straight maxillary; C, D, short premaxillary, curved maxillary border; E, F, long premaxillary; and G, H, long premaxillary with a long ascending process. In H, as the distal end of the maxillary swings forward its proximal end swings up (actually medially) as a block against the protruded premaxillary. li, Lip; ma, mandible; mx, maxillary; pr, premaxillary.

downward proximally. Only when the lateral force under the distal ends of the maxillaries is released by a narrowing of the mouth cavity can the maxillaries be untwisted and the premaxillaries retracted. The amount of premaxillary retraction will depend directly on how much the two halves of the mandible have moved together. Until this closure occurs the mandible has a firm bite against protruded premaxillaries that are forced away from the skull by the twisted maxillary wedges.

*Aulopus* shows a rather undeveloped stage of acanthopterygian protrusion. It has the strong palatine prong that appears to be a prerequisite of the system, but of the numerous structural features that usually accompany acanthopterygian protrusion *Aulopus* has only one, namely the **exclusion of the maxillary from the gape** by the premaxillary. There seems to be a close correspondence between the development of acanthopterygian protrusion and a lengthening of the distal end of the premaxillary. In no modern fishes and in relatively few fossil forms that seem to have had acanthopterygian premaxillary protrusion is the maxillary included in the gape. There appears to be a good functional reason for this.

Consider first a theoretical fish with the acanthopterygian type of jaw protrusion and a premaxillary that extends only a short way along the front of a maxillary with a straight

anterior border (Fig. 8A, B). When the proximal part of such a premaxillary is protruded an angle will be created between the part of the gape bordered by the premaxillary and that part bordered by the maxillary (Fig. 8B). Such an angle is disadvantageous from the point of view of either biting prey or of sucking it into the mouth. A theoretically more practical configuration, and one that seems to have been present in ctenothrissiform fishes (Patterson, 1964), is that in which a relatively short, protrusile premaxillary extends in front of part of a maxillary with a strongly convex anterior border (Fig. 8C, D). With this configuration premaxillary protrusion can be combined with some lowering of the distal end of the maxillary to provide a straight upper jaw margin (Fig. 8D). It is, however, only at a certain stage of maxillary lowering that a straight border can be attained, whereas with a premaxillary that extends the full length of the gape its border is straight at all stages of mouth opening (Fig. 8E, F). An additional theoretical advantage of a premaxillary that excludes the maxillary from the gape is that the same amount of twisting in the maxillary will result in greater effective jaw protrusion than if the premaxillary is shorter; however, this theoretical advantage may be offset by the fact that a long premaxillary is more susceptible to breakage than a shorter one.

In *Aulopus* the amount of premaxillary protrusion possible appears to be relatively slight, and the genus does not possess the fold in the skin between the upper jaw and the top of the head that is usually a good indicator of protrusibility. The skin in this area in *Aulopus* seems especially distensible but is not infolded. Another feature usually associated with acanthopterygian jaw protrusion that is poorly represented in *Aulopus* is the development of ascending processes that extend up and back over the anterior part of the cranium from the proximal parts of the premaxillaries. These aid in guiding the course of premaxillary protrusion. In acanthopterygians that have become specialized in the direction of extensive premaxillary protrusion the ascending processes extend well up over the skull when the jaw is retracted (Fig. 8G). Such forms have largely or completely dispensed with maxillary rotation as a means of forcing the premaxillary forward during protrusion. Rather, the membranous attachment of the distal end of the premaxillary has been shifted from the maxillary to a separate direct insertion on the mandible. Lowering of the mandible pulls the premaxillary downward (Fig. 8H), and the long ascending premaxillary processes translate this downward pull into protrusion. In such fishes, twisting of the maxillary loses its propulsive function but retains its role as a blocking system that can lock the premaxillary at any stage of protrusion. This system, though only one of many types of acanthopterygian premaxillary specialization, seems to be the evolutionary endpoint of the particular protrusion process represented in its initial stage by *Aulopus*.

Among modern lower teleostean groups the salmoniform series shows the greatest variation in jaw bite. Though the salmoniform fishes include such small-mouthed forms as *Macropinna* (see Chapman, 1942b) with no premaxillaries and no jaw teeth, they have never developed the extensive premaxillary protrusion of several gonorynchiform fishes and the cyprinoid ostariophysines; the closest approach to premaxillary protrusion in salmoniform fishes appears to be in *Polyipnus* (Weitzman, 1974). The salmoniform fishes also appear to have lost the parasphenoid

bite of more primitive teleosts, e.g., elopoids, though many have a post-jaw bite between the tongue and the roof of the mouth (Rosen, 1974). The premaxillary varies from absent to a long bone that effectively excludes the maxillary from the gape in some galaxioids (McDowall, 1969). Premaxillary dentition ranges from absent to long, sagitate fangs in the stomioid genus *Astronesthes* (Weitzman, 1967b). Among predaceous forms there are two rather different types of upper jaw development. In one, represented by *Salmo*, the premaxillaries are firmly attached to the skull, and most of the upper jaw movement is in the maxillaries. This is the type of upper jaw structure represented in such varied predaceous fishes as the "holostean" *Amia*, many osteoglossiform fishes, the eels in the elopiform series, apparently in *Pellonula* among clupeiform fishes (Taverne, 1977b), and in catfishes among ostariophysines. A second type of predaceous salmoniform upper jaw appears to be represented in *Astronesthes* in which the premaxillary moves directly with the maxillary. A similar united premaxillary-maxillary movement occurs in the clupeiform *Chirocentrus*, and in such ostariophysines as the characin *Ichthyoborus*. In these predaceous forms the autopalatine structure varies considerably and is usually cartilaginous.

For reasons specified below, the modern clupeiform, gonorynchiform, and ostariophysine fishes all seem to have evolved from small-mouthed ancestors, whatever the subsequent diversification. However, they differ from each other in jaw structure. Before these differences are discussed, certain general aspects of mouth structure in small-mouthed fishes may be noted.

Most teleosts use some combination of two basically different feeding mechanisms: one is the jaw bite, and the other is the development of a negative pressure in the oral and opercular cavities as the mouth is opened. Whether the fish emphasizes the bite or suction depends in part on the size of the items eaten. Though some small-mouthed forms, e.g., the serrasalmonine characins, have a powerful bite by means of which they shear pieces from large objects, most feed on relatively small items and emphasize a suction method of capture.

It is these that are of concern here.

As Alexander (1967b) has pointed out, a major criterion of effectiveness in the suction method of feeding, as in a pipette, is a round, level-bordered mouth that is small relative to the suction-pump behind it. The evolution of such a mouth from the long-jawed ancestral gape involves in part a blunting of the sharp snout but more importantly the closing off of the lateral extensions of the gape. In most small-mouthed lower teleosts both jaws participate in closing off the corners of the gape as it opens (Fig. 6A, B). As the mandible is lowered, the distal part of the maxillary swings downward and forward from above and a steeply rising mandibular border (coronoid process) rolls forward from below.

The steeply rising mandibular border is a widespread feature among small-mouthed lower teleosts. It occurs in such varied salmoniform fishes as *Coregonus* (Fig. 6B), *Hypomesus*, and *Opisthoproctus*, in various clupeids (Fig. 6A), in the gonorynchiform genus *Chanos*, and, among ostariophysines, in the gymnotid genus *Eigenmannia*. The contribution of the lower jaw to the rim of the gape seems to be diminished in lower teleosts such as cyprinids (Figs. 6D, 7C) which protrude the whole upper jaw forward over the mandible when the mouth opens.

So far as the upper jaw in small-mouthed forms is concerned, the simplest structure seems to occur in forms that pick individual small, free-swimming items out of the water, for example the salmoniform *Coregonus nigripinnis* (Fig. 6B, C). In this fish lowering of the maxillary forces the lateral part of the premaxillary forward and outward via an articular facet near its distal end (Fig. 6C). The result is to roll the alveolar border of the premaxillary forward and upward relative to the membranous attachment between its dorsomedial rim and the skull. The premaxillary movement in *Coregonus* is of the same general type as that described above for *Elops*.

From the generalized structural arrangements in *Coregonus*, the clupeiform, gonorynchiform, and ostariophysine fishes have all developed different systems for projecting forward a larger part of the upper jaw border. The system in clupeids involves only a slight

structural modification of the upper jaw of *Coregonus* and results in a relatively slight projection of the border of the gape. In clupeids there has been a proximal shift in the articulation between the maxillary and the premaxillary. As a result of this shift, the maxillary forces the proximal part of the premaxillary out relative to the cranial attachment, forcing the distal end to swing wide ahead of the premaxillary (Fig. 6A; see also Kirchoff, 1958). There is a fold in the skin of the clupeid upper jaw between the distal part of the premaxillary and the maxillary which permits expansion of the distance between these two bones. With the mouth open, the distal end of the premaxillary pulls forward with it the fleshy border of the gape between the tip of the premaxillary and the maxillary, a relatively extensive area that in some clupeids contains a separate bone, the hypomaxillary.

With the clupeiform fishes it is the consistently short premaxillary that suggests a small-mouthed ancestry. The clupeoid type of premaxillary movement, which seems to be an inherent feature of modern clupeiform fishes (*Denticeps*?) and which moves the distal part of the premaxillary away from the premaxillary, appears to be incompatible with either a long premaxillary or a strong bite. When modern clupeiform fishes have a long upper jaw, as in *Chirocentrus* or anchovies, it is the maxillary that is extended, and the premaxillary remains small. Whether the type ancestral to modern forms developed within the series or goes back to the base of the clupeiform fishes seems questionable. In certain aspects of mouth structure, e.g., the parasphenoid and entopterygoid teeth, the Cretaceous forms of *Diplomystus* (Patterson, 1967) seem far less specialized than the presumed small-mouthed ancestor of modern forms.

Other mouth structures in modern clupeiform fishes suggest an ancestry among deep-bodied and/or midwater fishes. Included here are the high sides to the mandible in clupeids and the lower oral valve, a membrane extending between the two halves of the mandible that seems to be a constant feature of the clupeoids but sporadic in the other fishes

examined. Another character that may well point in the same direction is the usually expanded *M. levator arcus palatini* (Forey, 1975). Better evidence for a midwater habit is the presence of abdominal scutes (Aleev, 1969). In all of these structures the modern clupeiform fishes differ from gonorynchiform and ostariophysine fishes.

The modern gonorynchiform fishes, like the modern members of the clupeiform series, have small maxillaries. All are small-mouthed forms and all except *Chanos* have become specialists in upper jaw projection, though their system of premaxillary protrusion differs from that of cyprinoid ostariophysines and from acanthopterygians.

In the ostariophysine fishes the premaxillaries are quite variable in size. In many the premaxillaries are large and more or less effectively exclude the maxillaries from the gape, e.g., in cyprinids, catfishes and in the gymnotid genus *Electrophorus*. The main evidence for a small-mouthed ostariophysine ancestor lies in the palatine, which is either separately movable or entirely free from the rest of the suspensorium. The argument that this type of palatine indicates a small-mouthed ancestry has been presented in a previous paper (Gosline, 1973). Suffice it to say here that a firmly knit strut from the front of the palatine to the quadrate articulation seems to be a functionally important part of the mechanism for lateral expansion of the oral cavity in most large-mouthed lower teleosts. Among small-mouthed forms, a separately movable palatine similar to that of the cyprinoid ostariophysines seems to be present in the gonorynchiform genus *Kneria* (Lenglet, 1974). Salmoniform and clupeiform fishes do not appear to have a palatine that articulates movably with the rest of the suspensorium, but in the salmoniform genus *Argentina* (Chapman, 1942a) the palatine is firmly attached to the skull by membrane, and there appears to be some flexibility in the cartilage that intervenes between the palatine and the more posterior part of the suspensorium. Some clupeoids, e.g., *Opisthonema* (Chapman, 1944b), have a similar more or less flexible cartilaginous area between the palatine and the rest of the suspensorium. In the develop-

ment of a separately movable palatine the ostariophysines (and *Kneria*) have evolved in the opposite direction from *Aulopus* and acanthopterygians, in which a firmly emplaced palatine forms a key component of the premaxillary protrusion mechanism (see above).

The four major ostariophysine groups have evolved in quite different directions so far as structures associated with feeding are concerned (Gosline, 1973). Of the four groups, the cyprinoids have progressed a long way toward dependence on a suction method, e.g., in the replacement of jaw teeth by a pharyngeal bite and in the fleshy rim of the lower jaw that extends between the dentary anteriorly and the raised coronoid process laterally. Their system of premaxillary protrusion resembles that of acanthopterygians in certain respects, notably in the exclusion of the maxillary from the gape and in the ability to raise the mandible against a protruded premaxillary (Alexander, 1966). As in acanthopterygians, the primary impetus for premaxillary protrusion lies in the twisting of the maxillary head, but cyprinoids also have a complex system of kinethmoid (Fig. 7C) rotation (Fiebiger, 1933; Alexander, 1966). This kinethmoid mechanism, however effective in adding to the amount of possible premaxillary protrusion, provides little support to an already weak extension system which, notably in catostomids, acts as a sort of vacuum cleaner extension (Alexander, 1966).

With regard to evolution, it appears that the cyprinoid system of premaxillary protrusion may have developed over a quite different route than that of acanthopterygians. A lip-like structure that extends around the corner of the mouth, absent in *Aulopus*, seems to be a key component of the cyprinoid system.

Among most lower teleosts, as in the iniomous genus *Aulopus* and in the beryciform *Myripristis*, there is a strong membrane extending forward from the inner and posterior surface of the distal end of the maxillary to the outer surface of the mandible. It is this membrane that pulls the distal end of the maxillary forward over the corner of the mouth when the mandible is lowered. This membrane never forms part of the border of the gape, and there is always a shear between

the maxillary (or premaxillary) above and the mandible below however widely the mouth is opened. Cyprinoids have this system, but they also have a fleshy "lip" that extends forward from the distal end of the maxillary across and attached to the end of the premaxillary and forward to the outer surface of the mandible. This lip closes off the corner of the open mouth in cyprinoids. When the mouth is opened this "lip" also has the effect of pulling the premaxillary downward, and in some cyprinoids, e.g., *Carassius*, of pulling the premaxillary downward relative to the maxillary (Fig. 6D). Such a downward pull on the distal end of the maxillary may provide the second force necessary to convert the usual single-pressure premaxillary rotation of lower teleosts to a protrusion system (see above).

The lip-like structure appears to be a constant feature of cyprinoids, though it is lightly constructed in such large-mouthed genera as *Elopichthys* and *Opsariichthys*, genera in which, perhaps coincidentally, the amount of premaxillary protrusion is reduced. A membrane that is at least effectively similar in closing off the corner of the mouth extends between the upper and lower jaws of catfishes. Among other lower teleostean groups the closest approach to the lip-like structure of cyprinoids that I have found occurs in the salmoniform genus *Galaxias*. However, in *Galaxias maculatus* (examined) there is a groove extending back from the rictus between the lips of the upper and lower jaws and there is no premaxillary protrusion. Among higher teleosts the lip-like structure of cyprinoids is present in such varied genera as the cyprinodontoid *Fundulus*, the gadoid *Merluccius*, and the percoid *Pterophyllum*. In *Fundulus* and *Pterophyllum* (Fig. 8G, H) it seems to be the primary force in premaxillary protrusion. So far as I am aware such a structure occurs only where there is a premaxillary attachment and never to a maxillary alone. There is, for example, no such structure in characins.

Whatever the course of its evolution, the premaxillary protrusion system of cyprinoids seems to be an independent development within the ostariophysine series with the resemblances between it and the acanthopterygian

system a result of convergence. In its more basic palatine construction, the ostariophysine mouth features show some resemblance to those of the gonorynchiform genus *Kneria*, but, aside from an ancestrally small gape, none that I can find with the mouth structures of the clupeiform fishes.

#### Relationships of modern lower teleostean fish groups

The basal **iniomous** genus *Aulopus* seems to provide an excellent terminal point for an investigation of the relationships between modern lower teleostean groups. Though *Aulopus* retains some ancient teleostean features, e.g., the fulcral scales at the base of the caudal fin (see, for example, Gosline et al., 1966), it belongs with the higher acanthopterygians rather than with the lower teleosts in a number of characteristics. As discussed above, *Aulopus* seems to be the first modern fish in the teleostean series with an acanthopterygian type of jaw protrusion. It also has paired fin structures (see above) and a caudal skeleton (Patterson, 1968b) of acanthopterygian rather than of lower teleostean type. That *Aulopus* and the iniomous fishes are derived from a salmoniform stock is generally agreed, but they have evolved in a different, acanthopterygian direction from the lower teleostean groups of concern here.

Concepts with regard to these lower groups have undergone much recent change, in large part because of increased knowledge of fossil forms. This is particularly true of the osteoglossiform and salmoniform fishes.

Primarily on the basis of features in the caudal skeleton Patterson and Rosen (1977) have shown, I think conclusively, that the modern **osteoglossiform** fishes are the sole living representatives of an early teleostean assemblage with several to numerous uroneurals in the caudal skeleton. In addition to the reduction in uroneural number, the other modern lower teleostean groups hold in common several advanced features that are not present in the osteoglossiform fishes. One of these is the addition of two postcleithra (see above) to the original anocleithrum. Another is the antorbital-supraorbital pumping system over the nasal cavity (Derschied,

1924; Gosline, 1965). In brief, the other modern lower teleostean groups seem to be derivatives of a common stock that has evolved beyond the osteoglossiform stage of structural development in a number of features.

Of the modern non-osteoglossiform teleosts the basal **elopiform** fishes retain a number of inherited features that have been lost in the others, e.g., the pectoral splint (see above) and the gular plate (see Nybelin, 1956; Gosline, 1965). However, the elopiform series as presently interpreted (Greenwood et al., 1966) also has specializations that seem to exclude it from the direct ancestry of other modern teleostean groups: the leptocephalous larva (see Hulet, 1978), the fusion sequence of the bones in the mandible (Nelson, 1973), the compound neural arch structure in the caudal skeleton (Patterson and Rosen, 1977), and the various modifications of the sensory canal system in the snout (Allis, 1903; Forey, 1973a; McDowell, 1973).

Though unintended, the evidence from the structural complexes investigated here reinforces at one point or another each of the conclusions stated above. The effect is to circumscribe more firmly than ever the four remaining lower teleostean groups, i.e., the salmoniform, clupeiform, gonorynchiform, and ostariophysine series. An obverse effect is to leave these four groups a more compact unit, at least compact in the sense that they all seem to have arisen from the same restricted segment of teleostean evolution. This base level common to the four groups appears to be represented in its most generalized state by certain, mostly small and poorly preserved Upper Jurassic and/or Lower Cretaceous fishes recently reinvestigated in part by Taverne (1975a, etc.), Patterson and Rosen (1977), and Forey (1977).

For purposes of discussion the remaining four modern lower teleostean groups can be divided into two categories: (1) the clupeiform, gonorynchiform, and ostariophysine groups, each more or less definable on the basis of one or more specializations, and (2) the undefinable salmoniform series.

Attempts made up to the present time to characterize and hence delimit the **salmoniform** group, e.g., by Taverne (1974a), seem to rest

on weak grounds (see, for example, Forey, 1977). The salmoniform fishes seem to represent, or to be very close to, the basal, post-elopiform teleostean stock. If one traces the clupeiform or gonorynchiform series back in the fossil record or tries to reconstruct a hypothetical ostariophysine ancestor one approaches a generalized teleost of salmoniform-like construction. The salmoniform fishes seem to retain today a plasticity of evolutionary potential, at least so far as structure is concerned, that is restricted in the other lower teleostean groups within the limits of their specialized developments. In brief, the salmoniform series appears to be what Schaeffer (1965) has termed an experimental group. Today, the salmoniform fishes are best represented in biologically peripheral areas, e.g., the deep sea and cold freshwater regions, where, presumably, they have not been replaced by other, more specialized groups.

Eventually it may be possible to distinguish lineages in the salmoniform series in the same way that the old isospondylous category has now been separated. At present this is not possible, and two different approaches have been taken to the Mesozoic salmoniform-like fishes. Taverne (1974a, etc.) places these in the salmoniform series; Patterson and Rosen (1977) and Forey (1977) allocate them, or many of them, to separate groups of *incertae sedis* status in the teleosts.

Here the concept of the salmoniform series as including those teleosts along the post-elopiform pathway that have not developed the basic specializations of the clupeiform, gonorynchiform, ostariophysine, or iniomous-acanthopterygian groups is provisionally adopted. This provisional decision has at least the advantage of avoiding such circumlocutions of doubtful meaning as speaking of possible derivation from an "*incertae sedis*" group.

In the two specialized lower teleostean series with a relatively well-known fossil record, the clupeiform and gonorynchiform fishes, the features that distinguish the modern members become less well-differentiated in the early forms.

In the **clupeiform** fishes all of the features



of the highly complex otophysic connection of modern members (Greenwood, 1968) disappear as the group is traced back through such fossil forms as *Ornategulum* (Forey, 1973b) and *Spratticeps* (Patterson, 1970b) to *Diplomystus* (Patterson, 1967) and *Erichalcis* (Forey, 1975). The peculiar pattern of ural centrum 1 fusion, discussed above, appears to go farther back in the clupeiform series and is only absent, so far as known, in the Lower Cretaceous (Albian) *Erichalcis*. Another at least equally old, though inconstant, clupeiform specialization is the abdominal scute development (Forey, 1975). Though modern clupeiform fishes are highly distinctive, that is not true of the early forms, as is sufficiently indicated by the composite Cretaceous genus *Clupavus*. It is only recently (Taverne, 1977c; see also Patterson, 1970) that the clupeiform and salmoniform members of this nominal genus have been sorted out.

Though the clupeiform fishes are an early offshoot of the basal teleostean stock, there is nothing to indicate that the fishes from which they arose had not already evolved beyond the elopiform stage of structural development (Patterson and Rosen, 1977). The only question seems to be the nature of the post-elopiform derivation of the clupeiform fishes. With the exception of the parasphenoid teeth of *Diplomystus* (Patterson, 1967), I know of no ancestral features in the clupeiform series that are not also represented in the salmoniform stock.

The modern **gonorynchiform** fishes are all specialized for feeding on small items. The premaxillary is reduced in size as compared to *Elops* and either moves more or less directly with the maxillary as in *Chanos* or is carried completely away from the skull during upper jaw protrusion as in *Kneria*, *Phractolaemus*, or *Gonorynchus*. The gill membranes are attached to the isthmus, and the number of branchiostegal rays is reduced to five or fewer in modern forms. However, the Cretaceous *Dastilbe* had a higher, more normal count of eight branchiostegal rays (da Silva Santos, 1946). Greenwood et al. (1966) associated the gonorynchiform with the salmoniform fishes, and Taverne (1974c) has more recently suggested a derivation from a specific

salmoniform group.

In the absence of a known fossil record that aids in determining the ancestral history of the **ostariophysine** fishes, speculation on their origin and relationships must be based on the modern members of the group. Certain features found in these have led some authors to suggest a very ancient origin for ostariophysines, e.g., Sagemehl (1885), Øravig (1957), and Bertmar (1959). However, it seems more satisfactory to derive the various ostariophysine specializations discussed in this paper from a salmoniform-like prototype than from any earlier teleostean stock.

Rosen and Greenwood (1970) have suggested a direct gonorynchiform ancestry for the ostariophysines. There are certainly resemblances, but these suggest to me related groups, not that one has been derived from the other. The evidence from jaw structure, and the presence of three epurals in the caudal skeleton of many characins support the view of Lenglet (1974) and others of an independent origin for the ostariophysines.

The above conclusions can be summarized by stating that the clupeiform, gonorynchiform, and ostariophysine fishes all seem to have evolved from a basal post-elopiform stock that is here considered to be salmoniform.

According to Patterson and Rosen (1977) the clupeiform fishes are of pre-salmoniform derivation whereas the gonorynchiform and ostariophysine fishes are apparently allocated to the Euteleostei with the salmoniform series. If one judges from the morphology of modern forms, and there is no other basis for the ostariophysines, then, from general trends in the caudal skeleton, the otophysic connection, the mouth, and the pectoral girdle, it seems at least as probable that the clupeiform, gonorynchiform, and ostariophysines were derived from one section of the salmoniform (or pre-salmoniform) stock and the iniomous-acanthopterygian lineage from another. This possibility is presented not as a thesis but as an alternative working hypothesis to suggest that in the present state of knowledge derivations from a salmoniform-like stock can be postulated about equally well in a number of ways.

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#### 原始的眞骨類における若干の構造の進化と類縁関係

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原始的眞骨類の類縁関係を探索するため、尾部骨格、鰾と耳域の関係を文献に基づき検討し、また解剖により次の3点を論じた。すなわち(1)オステオグロスム目魚類の後擬鎖骨 postcleithrum は祖先型より受け継いだ anocleithrum である。他の眞骨類は鱗起源とみられるもう2個の後擬鎖骨を保持していることがある。ハダカイワシ目のヒメ科 *Aulopus* は種々の原始的眞骨類と同様3個の後擬鎖骨を保持しているようであるが、より進歩した型の魚では最高2個までである。(2)胸鱗の運動と関連した構造系の進化において、一連の大きな変化が二つほど起こっているようである。その一つは胸鱗の最前端鱗条と関係があり、これで全骨類型祖先と原始的眞骨類と区別できる。もう一つはハダカイワシ目と高等な眞骨類における中鳥口骨 mesocoracoid の喪失と関連した一連の変化である。

る。(3) 原始的眞骨類において進化をとげた前上顎骨の種々な型の運動のうち、二つの方法が顎の伸出法として広く適用されている。*Aulopus* によって代表される型は、殆どの高等な棘鱗条類において、強く咬むための支えを伸出した前上顎骨に提供している。殆どの高等な眞骨類において、上顎骨の基部の上方に伸びる強大な口蓋骨の突起が存在し、上顎骨は口裂から排除されている。第二の伸出法としてはコイ目にみられる型が成功している。これは口部による吸引摂餌法と関係している。重要なことは、口角をめぐる唇状構造に起因する、前上顎骨の後端での前下方向への引力であるように思われる。

類縁関係に関する結論を述べると以下のようなになる。カライワシ目、サケ目、ニシン目、ネズミギス目、コイ目、ナマズ目魚類は一連の関連群を形成しており、一方ではオステオグロスム目、他方ではハダカイワシ目一棘鱗条類と明確に区別される。カライワシ目は上記関連群の中で最も早期に枝分かれした魚類である。ニシン目、ネズミギス目、コイ目、ナマズ目はハダカイワシ目一棘鱗条類と同様に原始的眞骨類のもととなる型（ここではサケ目と考える）から異った方向に進化したと思われる。これらのサケ目派出群のうち、ネズミギス目とコイ目、ナマズ目が最も近縁であるように思われる。