The Evolution of Some Structural Systems with Reference to the Interrelationships of Modern Lower Teleostean Fish Groups

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Abstract Five morphological character complexes are surveyed as a primary basis for the consideration of lower teleostean relationships. The first two of these—the caudal skeleton and the connection between the swim bladder and the ear—are reviewed from the literature. The accounts of the other three are based on an examination of modern lower teleosts. The main results from these three complexes are as follows:

(1) The postcleithrum of osteoglossiform fishes is the single anocleithrum inherited from ancestral forms. Other modern teleosts may have two additional postcleithra which seem to be scale derivatives. The iniomous (myctophiform) genus *Aulopus* appears to have three postcleithra, as do various modern lower teleosts, but more advanced forms have a maximum of two.

(2) In the evolution of structures associated with pectoral fin movements two major series of changes seem to have occurred. One of these has to do with the anteriormost pectoral ray and differentiates modern lower teleosts from their "holostean" ancestors. The other is a series of individually minor changes associated with the loss of the meso-coracoid arch in the iniomous fishes and higher teleosts.

(3) Of the various types of premaxillary movements that have evolved in lower teleosts, two have led to widely adopted protrusion systems. The acanthopterygian system of most higher teleosts, represented in an incipient stage in the iniomous genus *Aulopus*, provides a firm bite against protruded premaxillaries. A primary component seems to be the strong palatine strut that extends over a proximal part of the maxillary, with exclusion of the maxillary from the gape a secondary but almost constant feature. The second highly successful protrusion system, that of the cyprinoid ostariophysines, seems to have evolved in association with a suction system of feeding. A key element in the development of the cyprinoid system appears to be the downward and forward pull on the distal end of the premaxillary caused by a lip-like structure around the corner of the mouth.

With regard to interrelationships the conclusions reached are as follows. The elopiform, salmoniform, clupeiform, gonorynchiform, and ostariophysine fishes form a series of related groups that are clearly delimited from the osteoglossiform fishes on one side and from the iniomous-acanthopterygian teleosts on the other. The elopiform fishes represent an early offshoot from this central lower teleostean stock. The clupeiform, gonorynchiform, and ostariophysine fishes, like the iniomous-acanthopterygian series, all seem to have evolved in different ways from a basal type of lower teleost which is here considered to be salmoniform. Among these salmoniform derivatives, the gonorynchiform and ostariophysine series seem to be closest to one another.

Contents

Introduction

This paper originated in an attempt to determine the relationships of the ostariophysine

fishes (the catfishes, characins, gymnotids, cyprinids, and their allies) to other lower teleosts. Extensive work on Mesozoic forms of other lower teleostean groups in the last few years has led to a greatly increased knowledge of their early history. In the absence of a known fossil history that indicates anything about ostariophysine ancestry, the relationships of this group can only be investigated through its modern representatives. Five morphological complexes that seemed to be possible indicators of ostariophysine ancestry were surveyed in modern lower teleostean groups. As it turns out, the surveys suggest more about lower teleostean relationships than about ostariophysine derivation. The emphasis of the paper has been shifted accordingly.

Two of the character complexes surveyed, the caudal skeleton and the connection between the swim bladder and the ear, are reviewed and summarized from the literature. For the other three, new information is added. Two of these are pectoral features: the postcleithra, and certain structures at the fin base. The third has to do with aspects of the gape, particularly the evolution of premaxillary protrusion mechanisms.

The fish groups under consideration may be divided among six series: osteoglossiform, elopiform, clupeiform, gonorynchiform, ostariophysine, and higher teleostean. No particular taxonomic level is intended by any of these names, and no formal classification is suggested in the paper. For present purposes higher teleosts are considered to begin with the iniomous genus *Aulopus* among modern fishes.

The caudal skeleton

The caudal skeleton has received a great deal of recent attention, for it has proved to be of considerable value in interpreting teleostean relationships. This structural complex is often well preserved in fossil material. As a result, it has been possible to trace the history of the caudal skeleton of most lower teleostean groups well back in time. A brief review of certain aspects of this structural complex follows.

The caudal skeletons of modern teleostean fishes appear to be derived from a type con-taining the following structures:

Two separate ural centra that are independent of other skeletal elements except for neural arches.

Neural arches on all of the centra except the last.

Several (usually about 7) pairs of free, strut-like uroneurals, the anteriormost pair extending forward over the second pre-ural centrum.

Three epurals.

No modern fish has a caudal skeleton with all of the above components. However, they are present in a number of fossil forms, e.g., *Leptolepis coryphaenoides*, the Jurassic type species of its genus (see, for example, fig. 33B in Patterson and Rosen, 1977).

The relatively large, variable number of **uroneurals** is continued into the basal members of the osteoglossiform series, e.g., the fossil genera *Eohiodon* and *Lycoptera* and the modern *Hiodon* (Taverne, 1977a). In all other modern teleostean groups, the basal pattern is two relatively long anterior uroneurals and, usually, one short posterior uroneural (Patterson and Rosen, 1977). Further reduction in uroneural number has occurred in both the osteoglossiform series (Taverne, 1967) and in other teleostean groups, but the reduction appears to have followed a different pathway in the osteoglossiform series from that followed by other modern fishes. The osteoglossiform caudal skeleton will not be considered further.

The inherited construction of two separate, autogenous **ural centra** in the adult fish is known from at least one basal member of all modern lower teleostean groups except the ostariophysines, i.e., from the fork-tailed elopiform fishes (Forey, 1973a), the fossil *Erichalcis* among clupeiform fishes (Forey, 1975), various salmoniform fishes (Rosen, 1974), and the fossil *Parachanos* among the gonorynchiform fishes (Taverne, 1974b). However, in most modern lower and all higher teleosts the first ural centrum fuses with adjacent elements. Usually it fuses with the preural centrum ahead of it, but in two groups ural centrum 1 fuses first with the base of one or two of the lower hypurals. In the Lower Cretaceous *Notelops*, assigned by Taverne (1974a, 1976a) to the salmoniform fishes and

by Forey (1977) to a salmoniform-like group of *incertae sedis* position, ural centrum 1 is fused with the base of the two lower hypurals, as it is in the related fossil Pachyrhizodontidae (Forey, 1977; Taverne, 1976b). In the clupeiform fishes ural centrum 1 first fuses with hypural 2. Furthermore, there is a general tendency for hypural 1 to lose its basal articulation, though hypural 1, like hypural 2, becomes fused basally with ural centrum 1 in at least some specimens of *Denticeps* (Monod, 1968: fig. 263). This peculiarity of fusion pattern appears to be a constant, distinctive feature of modern clupeiform fishes (Greenwood, 1968) and is only absent, so far as known, from the Cretaceous genus *Erichalcis*. Forey (1975) with regard to *Erichalcis* and Monod (1968) in reference to *Denticeps* have called attention to similarities in the caudal skeletons of the clupeiform and salmoniform fishes.

The remainder of this section deals with the problem of relationships raised by the ostariophysine caudal skeleton. In all known ostariophysines there is considerable fusion of parts. The most generalized ostariophysine caudal skeleton, i.e., that with the least consolidation of components, appears to be represented in such characins as *Brycon* (Weitzman, 1962). Here preural centrum 1 and the ural centra are represented by a single unit to which the anterior uroneural, the base of hypural 2, and the parahypural are also fused; there are three epurals. The *Brycon* pattern of fusion appears to be most closely approached by *Gonorynchus* (Monod, 1968: fig. 442) among gonorynchiform fishes and *Spratelloides* (Monod, 1968: fig. 261) among clupeiform fishes. In these three genera and in most of the fishes of the groups to which they belong the most striking feature is the fusion of the base of the first uroneural with the preural centrum to form what Monod (1968) has termed a "pleurostylar" type of caudal skeleton. In most salmoniform fishes and lower acanthopterygians (Patterson, 1968b), by contrast, the anterior uroneural is expanded basally but free from the centrum complex and forms a "stegural" type of caudal skeleton.

It appears, to me at least, that the similarities in the caudal skeletons of clupeiform, gonorynchiform, and ostariophysine fishes have been developed independently in the three groups (see also Forey, 1975: 167). In the more generalized clupeiform fishes the first fusion in the caudal skeleton is between ural centrum 1 and hypural 2, as noted above, but in the gonorynchiform fishes, as in most other non-clupeiform groups, the first fusion is between ural centrum 1 and the pre-ural centrum ahead of it. The latter pathway of fusion seems to have been followed by the ostariophysines, to judge from the figure of the caudal skeleton of a juvenile catfish provided by Lundberg and Baskin (1969: fig. 2A) and from the general alignment of the caudal skeleton in adult ostariophysines. From the caudal skeleton of gonorynchiform fishes, that of some ostariophysines differs in the primitive number of three epurals whereas in all known gonorynchiform fishes, recent and fossil, the epurals are reduced to two or fewer.

There seem to be three possible explanations for the similarites in the caudal skeletons of clupeiform, gonorynchiform, and ostariophysine fishes. One is that they arose independently by pure chance. A second is that the potentiality for the similar developments is the result of a common genetic inheritance in the three stocks. The third is that the similarities arose through convergence in association with a similar selection pressure exerted on early members of all three groups.

The connection between the swim bladder and the ear

The chain of Weberian ossicles between the swim bladder and the fluid surrounding the ear is the most notable specialization of the ostariophysine fishes. Osteoglossiform and clupeiform fishes have also developed a highly complex otophysic connection, but in these groups extensions of the swim bladder are in direct contact with the fluid around the otic organs. In the megalopid fishes a much simpler direct connection between the swim bladder and the ear occurs (Greenwood, 1970), and in higher teleosts a simple connection has evolved repeatedly.

The osteoglossiform, clupeiform, and ostariophysine fishes have not only developed far more complex otophysic connections than

other fish groups but in addition all three have evolved what appear to be adjuncts to the otophysic system. These adjuncts consist of openings in the skull where the perilymphatic fluid surrounding the ear is not enclosed by cranial bones. Such openings occur in various places, for example, the areas where only membrane separates the perilymph from invaginations of the lateral line canal system in clupeiform (Greenwood, 1968) and osteoglossiform (Kapoor, 1964) fishes, the fontanel separating the frontals in many ostariophysine fishes, and the paravertebral sacs of cyprinids (Sagemehl, 1891).

Because of the high development of the otophysic connection and associated structures in the osteoglossiform, clupeiform, and ostariophysine fishes the possibility that two of these three groups have evolved from a single stock has often been considered. Sagemehl (1885), for example, believed on a priori grounds that the Weberian apparatus must have evolved as a modification of some pre-existing otophysic connection of a direct type. One structural problem with this thesis is that all known direct otophysic connections are paired, with two forward projections from the swim bladder entering the skull separately, whereas the two halves of the Weberian apparatus abut anteriorly against a median sinus impar. Rosen and Greenwood (1970) have shown how the Weberian apparatus might have arisen from structures in a fish without a previous otophysic connection, or, at least, without a connection of the usual bilateral type. Though they postulate an origin of the Weberian apparatus from gonorynchiform structures, it seems that structures of at least some other lower teleosts would provide equally good sources. The similarities between the otophysic connections of osteoglossiform and clupeiform fishes have frequently been noted, for example, by Greenwood (1973) and Taverne (1973). However, other structural features such as those of the caudal skeleton noted above strongly suggest that these two groups are only distantly related and have evolved their otophysic connections independently. It therefore seems best to question the use of the otophysic connections in ostariophysine, clupeiform and osteoglossiform fishes as evidence regarding establishment of the interrelationships.

The postcleithra

The postcleithra associated with the pectoral girdle have received only sporadic attention. From the point of view of ichthyological investigation they suffer from several disadvantages: their inconstancy, their small size and frequent loss in skeletons or dissections, and their occasional similarity to scales, with which they have sometimes been confused. Here, only a brief general survey of the postcleithra in modern lower teleostean groups is undertaken.

One postcleithral unit, the **anocleithrum**, has been traced back as a pectoral girdle component to the earliest bony fishes (Jarvik, 1944; see also Jessen, 1968, and Gosline, 1977). In *Amia* (see, for example, Jessen, 1972) the anocleithrum extends posteriorly from the upper part of the cleithrum; it underlies the posteroventral part of the supracleithrum and to some extent the posterior border of the upper end of the cleithrum. The anocleithrum is the only postcleithral bone in lower actinopterygians, *Amia*, and osteoglossiform fishes (Taverne, 1977a, 1978).

The basal number of postcleithra in modern lower teleosts other than the osteoglossiform fishes is three. Three postcleithra are present in elopoids (Forey, 1973a), characins (see, for example, Weitzman, 1962), certain salmoniform fishes—*Argentina* (Chapman, 1942a), *Nansenia* (Chapman, 1948), and salmonids (Norden, 1961), in at least one clupeiform fish (*Clupanodon*, see below), and apparently in the iniomous genus *Aulopus* (see below). Reduction in postcleithral number has occurred repeatedly, but no additional postcleithral elements appear to have evolved in teleosts.

Where three postcleithra are present (Fig. 1) the uppermost is located in the area of junction between the supracleithrum and cleithrum and appears to be an anocleithrum. Usually it underlies the supracleithrum and, to some extent, the posterior border of the upper part of the cleithrum (Fig. 1A). In the clupeiform *Clupanodon* (Fig. 1D), however, the anocleithrum appears to have moved around the posterior border of the cleithrum to an
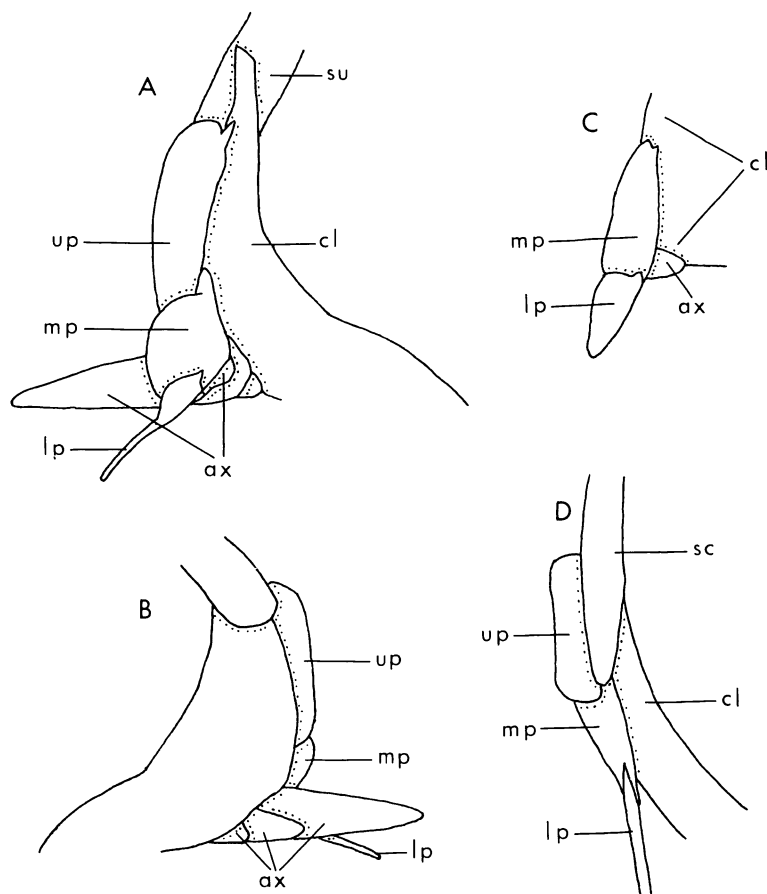
Fig. 1. Postcleithra and associated structures: *Elops saurus*, left side, A, internal
view, and B, external view; C, the two lower postcleithra and axillary scale of
Stenodus leucichthys, left side, internal view; and D, postcleithra of *Clupanodon
punctatus*, right side, external view. ax, axillary scale; cl, cleithrum; lp, lower
postcleithrum; mp, middle postcleithrum; sc and su, supracleithrum; and up,
upper postcleithrum.

overlapping position. Its principal membra-
nous attachment in *Clupanodon* is with the
lower surface of the supracleithrum, as it is
in *Aulopus*.

The three postcleithra may form a single
series of overlapping ossifications, as in the
elopoids *Elops* and *Albula*, the salmoniform
genera *Argentina*, *Microstoma* and *Salmo*, the
characin *Brycon meeki*, the clupeid *Clupanodon*,
and the iniomous *Aulopus*; or the three post-
cleithra may have an interspace between the
uppermost and the lower two, as in the elopoid
Megalops, the salmonid *Stenodus*, or the
characins *Ichthyoelephas* (Roberts, 1973) and
Brycon guatemalensis (personal observation).

Whether in one or two series, the upper two
postcleithra are laminar bones that extend
under the posterior border of the cleithrum
(except *Clupanodon* and *Aulopus*); the lower-
most postcleithrum, however, is membranously
attached above to the under surface of the
middle postcleithrum and is usually, in part
at least, a curved, terete, spine-like unit that
extends ventrally and medially behind the
pectoral fin base (Fig. 1A).

The two lower of the three postcleithra seem
to have arisen from scales in the ancestral
stock of modern teleosts other than the osteo-
glossiform fishes. Before evidence regarding
the squamous origin of the lower postcleithra

is presented, it is necessary to note Weitzman's (1967a: 513) statement regarding osmerids: "Postcleithra are unossified in all species examined but present as two elongate cartilages extending ventrally from the posterior border of the cleithrum." Such cartilages could not be scale derivatives, but I have not been able to find them.

In *Elops* (Fig. 1A, B) the squamation along the upper side of the pectoral base seems to have undergone two types of specialization. Certain of the scales have become incorporated into the superficial axillary process that extends back above the pectoral base. Two other scales have, I think, become the two lower postcleithra. The anterior elements of the axillary process and the two lower post-cleithra are similar, adjacent, overlapping units that extend forward under the posterior border of the cleithrum. This has led Taverne (1974a: 48) to consider scales of the axillary process of *Elops* as postcleithra. In salmonids the axillary process is little developed, but in *Salmo*, as in *Stenodus* (Fig. 1C), a scale that appears to be the equivalent of the basal scale of the axillary process of *Elops* is wedged between the middle of the three postcleithra and the cleithrum. In *Stenodus* Norden (1961) has considered this scale to be a postcleithrum, probably because the small lowermost post-cleithrum (Fig. 1C) was missing in the specimen he described and figured. In the characin *Brycon* the basal scales of the axillary process are again wedged between the cleithrum and the middle postcleithrum, in this genus excluding most of the central postcleithrum from contact with the cleithrum. With the increasing specialization of the postcleithra in the course of teleostean evolution the difficulty of distinguishing them from scales diminishes.

If the condition of the postcleithra and of the pectoral **axillary process** in *Elops* can be considered ancestral for modern non-osteo-glossiform teleosts, then both structural units have been lost or modified repeatedly. Only two of the changes in the axillary process will be noted. In certain characins, e.g., *Poecilobrycon* (Weitzman, 1964) and far more strikingly in catfishes, the elopoid axillary process has been functionally and morphologically replaced by a posterior projection of

the cleithrum over the pectoral base. This appears to be a common development in fishes. In the gonorynchiform genus *Chanos* the axillary process has become modified in a very different, apparently unique way. Here, the highly developed axillary process is supported below by a backward projection from the scapula (Starks, 1930: fig. 3).

In each of the major groups of modern teleostean fishes the postcleithra seem to have undergone loss. They are absent in, for example, the mormyrids among the osteoglosso-morph series, the eels among elopomorphs, the engraulids among clupeomorphs, and the catfishes among ostariophysines. Postcleithra are absent in all modern gonorynchiform fishes.

In the majority of teleosts, however, the postcleithra are not completely lost but undergo reduction in number, with specialization in the remaining units. The question arises of which of the three original postcleithra of non-osteoglossiform teleosts are represented in the reduced number. This question seems to have different answers in different groups. In *Etrumeus* (Chapman, 1944a), a clupeoid fish with two postcleithra, the lowermost, spine-like postcleithrum of *Clupanodon* (Fig. 1D) appears to have fused with the middle, laminar postcleithrum, with the uppermost anocleith-rum represented as a separate element. In cyprinids there is only a single postcleithrum, but which of the three postcleithra of chara-cins it represents is unclear. Finally, in the iniomous genus *Aulopus*, as in the basal acan-thopterygians, there are two, straight, more or less vertically aligned postcleithra (Goody, 1969: fig. 91). In addition, between the top of the upper of the two postcleithra and the supracleithrum that overlaps it there is a small flat plate firmly attached to the under surface of the supracleithrum. This plate seems to be the old anocleithrum. Presumably it is this upper, anocleithral element that is lost in the basal acanthopterygians.

Structures associated with pectoral fin movements

In the course of teleostean evolution the pectoral fin moves from its essentially ventral position on the body in such "holosteans"

as *Amia* to a location well up on the sides in higher teleosts. Accompanying this shift in position, the part of the **scapulocoracoid border** with which the pectoral fin supports (actinosts) articulate changes from nearly horizontal in *Amia* (Jessen, 1972: fig. 3), through more or less L-shaped in lower teleosts, to approximately vertical in higher teleosts. In the course of this change two series of structural developments occur, each of which seems to correspond to a shift in the nature of pectoral fin movements. One series concerns features associated with the anteriormost ray and takes place in the evolutionary series between "holosteans" and *Elops*. The other comprises a number of individually minor developments that accompany the loss of the mesocoracoid arch in iniomous and higher teleosts.

In the "holosteans" *Amia* and *Lepisosteus* all of the pectoral rays articulate basally with a series of movable endoskeletal elements that extend between the base of the pectoral fin and the scapulocoracoid part of the pectoral girdle (Jessen, 1972). These elements together form a flat plate-like structure that articulates basally along the more or less horizontally oriented scapulocoracoid rim. The movable nature of the separate endoskeletal units at the base of the fin indicates that the pectoral fins of *Amia* and *Lepisosteus* are capable of a certain amount of swiveling around a more or less central axis, though the relatively short endoskeletal unit at the base of the first ray of *Amia* (Fig. 2B) suggests that the axis is eccentric. There are only two muscle masses involved in the pectoral fin movements of *Amia* and *Lepisosteus*, the M. adductor above inserting on the basal part of the dorsal half-rays and the M. abductor below inserting on the ventral half-rays (Jessen, 1972). In *Amia* there are two features in the anterior part of the pectoral musculature that foreshadow conditions in the lower telests. One is the incipient separation of the muscle fibers to the anteriormost ray from the rest of the muscle masses. The other is that the M. abductor extends up around the front of the first ray to an insertion that is partly on the base of the splint that extends along the upper half of this ray (personal observation). The
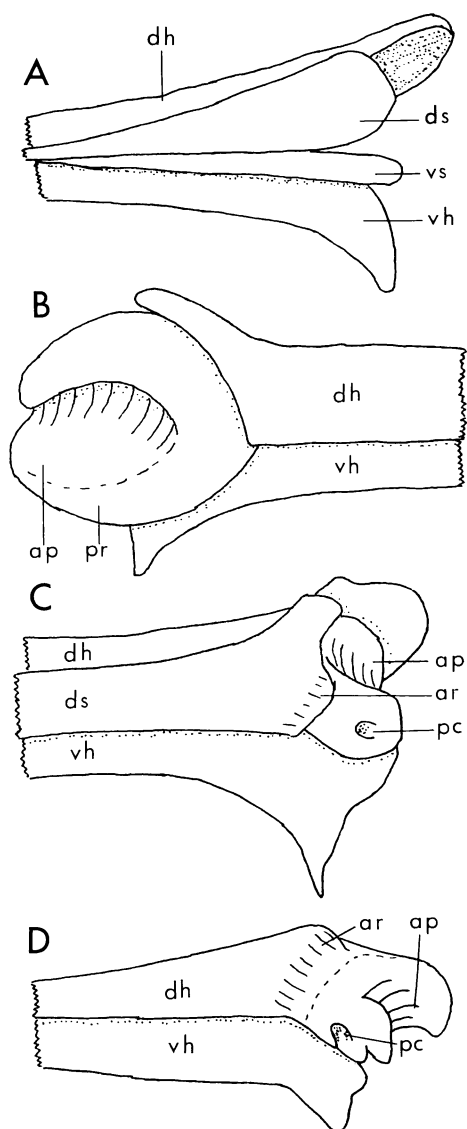

Fig. 2. Base of anterior ray, right pectoral fin: A, *Amia*, lateral view; B, *Amia*, anteromedial view, including propterygial unit (based on Jessen, 1972: pl. 1, fig. 3); C, *Elops*, lateral view; and D, *Micropterus*, superolateral view, with the approximate limit of the propterygial unit indicated by a dashed line. ap, Area of propterygium that articulates with the scapulocoracoid plate; ar, area of insertion of the **M. arrector ventralis**; dh, dorsal half-ray; ds, dorsal splint; pc, propterygial canal; pr, propterygium; vh, ventral half-ray; and vs, ventral splint.
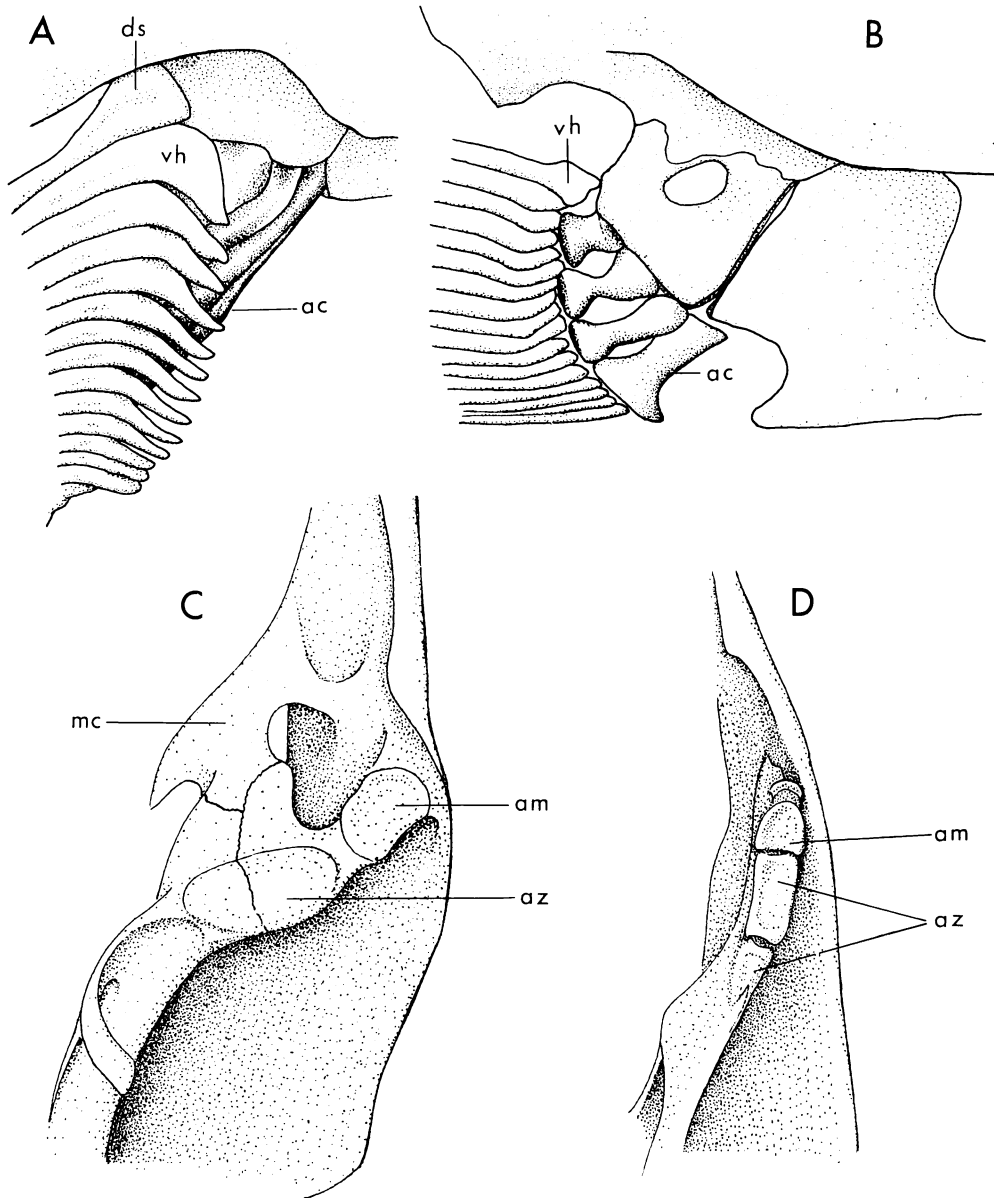
Fig. 3. Right pectoral fin base, lateral view, of A, *Elops*, and B, *Micropterus*. Posterior view of right scapulocoracoid arch to show the articular areas of the anterior pectoral ray and of the actinosts in C, *Elops*, and D, *Micropterus*. ac, Actinost (the lowermost of the four actinosts is labeled); am, articular area for the marginal (anterior) pectoral ray; az, articular area for actinosts; ds, dorsal splint; mc, mesocoracoid arch; and vh, ventral half-ray.

first pectoral ray in *Amia* and *Lepisosteus* consists, like the other pectoral rays, of two nearly symmetrical halves. It differs from the other rays in having one to several splint-like processes attached to the anterior surface of each half ray in *Lepisosteus* and a single

such process at the base of each half ray in *Amia*. The dorsal member of the pair in *Amia* is considerably larger than the ventral splint (Fig. 2A).

In *Elops* a whole series of changes has taken place in the structures described above for

Amia and *Lepisosteus*, all of them directly or indirectly related to the anterior pectoral ray. There is no longer a movable articulation between the anterior ray and the endoskeletal unit between it and the scapulocoracoid plate. Rather, this endoskeletal unit has become firmly wedged into the base of the anterior pectoral ray. The only movable articulation at the base of the anterior pectoral ray in modern teleosts is between its base and the scapula (Fig. 2C, D). The other pectoral rays, however, retain their movable articulations with the endoskeletal elements, the actinosts. Because of the movable actinosts, which are usually progressively longer toward the rear of the fin, the posterior part of the fin base can be swiveled upward or downward relative to the anterior ray base. In other words, the axis of rotation has been shifted from a more or less central location in the pectoral fin of *Amia* and *Lepisosteus* to its anterior border in *Elops*.

The anterior pectoral ray of *Elops*, via its endoskeletal addition, articulates with a nearly vertical part of the scapulocoracoid rim, whereas the remaining endoskeletal units at the pectoral base (the actinosts) continue to articulate with a more or less horizontal part of the rim (Fig. 3A, C) as in *Amia* and *Lepisosteus*. The somewhat elongate, saddle-like articular facet under the base of the first pectoral ray of *Elops* more or less restricts the first ray to a fore and aft plane of movement. (It is difficult to force the first pectoral ray of *Elops* upward or downward in preserved specimens.)

The partial rotation in alignment of the anterior ray base of *Elops* relative to the other pectoral rays is associated with certain asymmetrical developments in the first ray. In this genus as in other teleosts, the anterior part of the M. abductor has developed into a completely separate muscle (Fig. 4A), the **M. arrector ventralis**, which extends forward along the external side of the pectoral girdle from an insertion that is entirely on the first ray. This muscle appears to be the principal agent in erecting the pectoral fin in *Elops*. Its insertion is not, however, on the ventral half of the first ray to which it properly belongs. Rather, it crosses over the front of
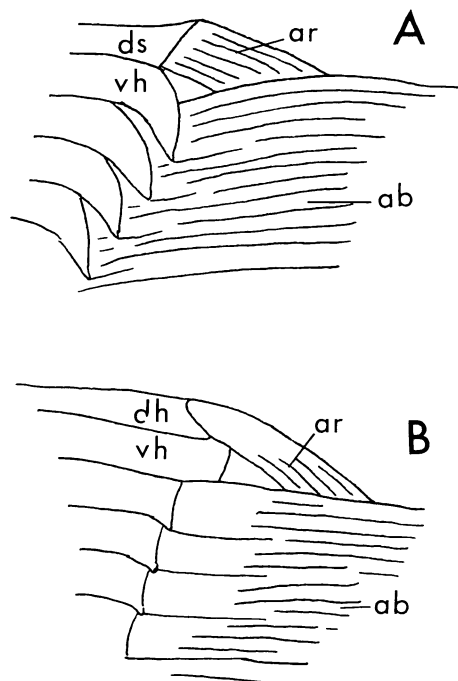

Fig. 4. Diagram of musculature to the outside of the anterior pectoral rays, right side, in A, *Elops*, and B, *Micropterus*. ab, M. abductor; ar, M. arrector ventralis; dh, dorsal half-ray; ds, dorsal splint; and vh, ventral half-ray.

the fin to an effective insertion on the dorsal half of the first ray. In *Elops* this dorsal half-ray is represented by two tightly united components, the half-ray itself and a splint along its anterior surface (Fig. 2C). The M. arrector ventralis inserts on the base of the splint in elopoids (on the base of the dorsal half-ray in modern teleosts other than elopoids). This splint undoubtedly represents the dorsal element in the pair of splints in *Amia*; the ventral member of the pair is gone in modern teleosts, and the dorsal member as well in modern teleosts other than elopoids.

All of the modifications associated with the first pectoral ray of *Elops* mentioned above appear to be specializations for erecting the leading edge of the pectoral fin against pressures that could only be caused by water flowing past the body. If this analysis is correct, the specializations of the first pectoral ray are functionally associated with the increased forward propulsion made possible by

the improvements in early teleostean caudal structure (Patterson, 1968a; Nybelin, 1974). They suggest that in *Elops* the pectorals are used primarily to alter the course of the forward trajectory, much as in sharks, sturgeons, and swordfishes, except that in *Elops* the pectorals are depressible.

In the retention of a splint along the dorsal half of the first ray the elopoids appear to be primitive among modern teleosts (Gosline, 1965; Jessen, 1972; Forey, 1973a). A similar splint is figured in the illustrations of several fossil teleosts, e.g., *Wenzia congolensis* (Taverne, 1975b: fig. 2), *Leptolepis coryphaenoides* and *Allothrissops mesogaster* (Taverne, 1975a: figs. 1 and 2). In the modern *Exocoetus* there is also a splint tightly applied to the base of the first ray but it is of different origin (see below).

With regard to the flexibility of the first ray, the catfishes have restricted its plane of movement even more than in *Elops*. In siluroids the complete restriction of the first ray (spine) to fore and aft movements is accompanied by an elongation of the actinost swivel mechanism supporting the more posterior rays (see, for example, Starks, 1930: fig. 12). Most lower teleostean groups, however, have an anterior ray that is more, not less, flexible than that of *Elops*. This is indicated in osteoglossiform and salmoniform fishes by structural modifications of two different types. In modern osteoglossiform fishes it is suggested by the shorter articular facet for the first ray and by the spread of both the origin and the insertion of the M. arrector ventralis. This spreading occurs in *Hiodon* (personal observation); in the mormyrid genus *Gnathonemus* (Grenholm, 1923) the M. arrector ventralis is divided into two laterally separate components, as it appears to be in the figures of *Osteoglossum* and *Pantodon* provided by Greenwood and Thomson (1960). Among salmoniform fishes, at least some modern forms have very flexible pectorals (Wassnetzoff, 1922). Here the flexibility appears to be associated with the retention of considerable cartilage in the parts of the pectoral girdle associated with fin movement.

A final set of specializations in the lower teleostean pectoral girdle to be noted here occurs in certain clupeiform and ostariophysine fishes. In the clupeiform genus *Chirocentrus* and in the characin *Rhaphiodon* the various units supporting the pectoral rays other than the first have become united into a single elongate plate (Starks, 1930). This specialization has evolved independently in the two groups, but the potentiality for its development suggests a probably remote common ancestor.

All higher teleosts starting with the iniomous fishes have lost the **mesocoracoid arch** (Wassnetzoff, 1922). This arch, present in most lower teleosts but frequently lost (Starks, 1930), has been inherited from the "holostean" stage of evolution (Jessen, 1972). The mesocoracoid arch appears to function as a supporting strut between the vertical and horizontal components of the pectoral girdle in those fishes that have a horizontally aligned axis for the pectoral base. The loss of the mesocoracoid arch in higher teleosts appears to be associated with an upward shift in the whole fin base. As a result of this shift, the depressed pectoral is folded against the sides of the fish and its base has a nearly vertical axis (Fig. 3D), rather than the horizontal axis of *Amia* or the L-shaped axis of *Elops*. In higher teleosts the horizontal component of the scapulocoracoid axis and the mesocoracoid strut supporting it are gone.

With the change from a horizontal to a vertical alignment of the actinosts, there has been a shift in the direction of movement of all but the anteriormost fin ray. In *Elops* erection of the depressed fin consists of pulling the first ray laterally across its basal articulation, but all of the other pectoral rays swing out along their basal articulations (Fig. 3A). In higher teleosts all of the fin rays move out laterally across their basal articulations (Fig. 3B). Conversely, depression of the erect fin in *Elops* consists primarily of folding the fin rays back in along the actinost rims whereas it is primarily a movement at right angles to the actinost rims in higher teleosts. This shift from longitudinal to right-angle movement of the posterior pectoral rays involves some changes in muscle structure and function. The recurved tips of the ventral halves of the pectoral ray bases on which the M.

abductor of *Elops* inserts (Figs. 3A, 4A) are greatly reduced in higher teleosts (Figs. 3B, 4B), and the M. abductor itself is divided into separate slips that insert on the individual ray bases. As Wassnetzoff (1922) noted, higher teleosts can and do move one part of the pectoral forward while moving another part backward.

In higher teleosts the work of erecting the depressed pectoral appears to be distributed more evenly between the various pectoral rays than in *Elops*, where it is concentrated on the anteriormost ray. Accompanying the reduced importance of the first ray in higher teleosts, there is a gradual diminution in the size of both the first ray and its M. arrector ventralis. In the iniomous genus *Aulopus* the anterior (now upper) pectoral ray is still a full-sized ray, as it is in lower teleosts, but generally in higher teleosts it is reduced, and in some, e.g., the gobioid fishes (Grenholm, 1923), the marginal ray and its M. arrector ventralis have disappeared completely.

The presumably indirect functional relationship between the size of the marginal ray and the presence or absence of a mesocoracoid arch is well illustrated by the various "flying" fishes. In *Exocoetus*, which belongs to a group without a mesocoracoid arch, the marginal ray is a short splint rigidly attached to the ray behind (personal observation). In *Pantodon* (Greenwood and Thomson, 1960) and *Gasteropelecus* (Weitzman, 1954), both of which have a mesocoracoid, the marginal ray is large.

The pectoral modifications in *Elops*, as noted above, suggest adaptations for changing course in a fish that is moving through open water at considerable speed. As Wassnetzoff (1922) pointed out, the loss of the mesocoracoid arch seems to indicate the adoption of a quite different mode of life. In *Aulopus* and acanthopterygians the loss of the mesocoracoid is associated with an upward shift in the pectoral base and by structural features that seem to provide greater flexibility of movement in the individual fin rays. These developments are often associated with a forward movement of the pelvic bases, and the two pairs of fins are frequently used in conjunction (Harris, 1953). To me these various

changes in the paired fins of *Aulopus* and higher teleosts suggest a shift from a free-swimming, open-water mode of life to one in which the primary paired fin adaptations are for maneuvering in close quarters, i.e., for abrupt stopping, holding position in the water, backing, and turning at zero speed. Inasmuch as maneuvering in close quarters is primarily useful in the proximity of fixed objects, there is not much effective difference between the functional hypothesis suggested here and that of Wassnetzoff (1922), who associated the loss of the mesocoracoid with the adoption of a benthic mode of life. Most benthic fishes are maneuvers, though some, like the elopoid *Albula*, seem to be free-swimming forms.

One reason for adopting a slight shift in Wassnetzoff's hypothesis lies in the extinct ctenothrissiform fishes. This group, generally considered to be ancestral to at least one section of the whole acanthopterygian series (Patterson, 1964; Gaudant, 1978), lacks a mesocoracoid. The ctenothrissiform fishes, as reconstructed, do not look like strongly swimming fishes, but neither do they look like strictly benthic forms. Possibly the ctenothrissiform fishes lived at the backs of caves foraging at night in nearby midwater areas as modern species of the beryciform genus *Myripristis* do (Hobson, 1974).

Aspects of mouth structure

Only features associated directly or indirectly with the border of the gape are considered here. An account of the morphological evolution of the acanthopterygian type of premaxillary protrusion is followed by a discussion of certain aspects of the gape in small-mouthed lower teleosts.

The development of **premaxillary protrusion** has been one of the major themes of teleostean structural evolution. Although the ability to project the jaw away from the skull has developed many times, a particular system of premaxillary projection appears to be basic to modern teleosts at and above the iniomous (*Aulopus*) level of classification. This method of upper jaw protrusion, here called the **acanthopterygian system** following Alexander (1967a), has been modified in various ways in

higher teleosts (see, for example, van Dobben, 1935). Its distinctive functional attribute, as Alexander (1967a) demonstrated, is the provision of a firm bite at various stages of premaxillary projection.

Lowering and raising of the mandible against an upper jaw in which the maxillaries and premaxillaries are rigidly attached to the cranium seems to have been the only jaw movement in most early actinopterygian fishes (Schaeffer and Rosen, 1961). Additional jaw movements have evolved repeatedly, beginning with the sturgeons at the chondrostean level. So far as the main line of actinopterygian evolution is concerned, a dominant functional problem has been to combine the advantages obtained from upper jaw projection with the retention of a firm bite. The problem arises because all movements in the upper jaw carry its movable components away from their support.

If the central actinopterygian stock has combined the evolution of upper jaw movements with the retention of a firm bite, extreme types in which either the bite or the protrusion greatly predominate have repeatedly evolved. At one extreme, represented primarily among predaceous forms, overriding requirements of a strong bite have often led to the secondary loss of inherited upper jaw movements. Thus, in eels the premaxillaries are completely fused with the skull (Norman, 1926). The opposite extreme is represented in many microphagous fishes that suck the food into the mouth rather than biting it. Here, various types of jaw protrusion have developed that carry the premaxillaries away from any contact with the skull. Examples are the sturgeons, *Phractolaemus* (Thys van den Audenaerde, 1961), and *Gonorynchus* (Ridewood, 1905). Both of these extremes of upper jaw development are evolutionary cul-de-sacs.

From the original fixed actinopterygian upper jaw, fishes at the "holostean" level of structural development have evolved a movable maxillary that swings down over the corner of the mouth when the mandible is lowered. In such fishes, e.g., *Amia*, a compromise between firm bite and upper jaw movement is attained by concentrating all of

the movement in the maxillary and most of the bite on the fixed premaxillary. This same general type of compromise occurs frequently in lower teleosts, e.g., eels and many characins. In higher teleosts, and to some extent in cyprinoids, the compromise between a firm bite and upper jaw movement is attained in a different way, namely by the development of a protrusile premaxillary that maintains an indirect contact with the skull at all stages of protrusion (Alexander, 1966, 1967a). It is the morphological evolution of this type of protrusion that concerns us here.

Elops (Fig. 5A) differs from *Amia* in that a slight amount of movement occurs in the premaxillary in addition to that in the maxillary. This slight premaxillary movement has two components that foreshadow the premaxillary protrusion of higher teleosts. First, although the motion of the maxillary causes that in the premaxillary, the nature of the motion in the two bones is somewhat different. This is true of most, though by no means all, teleosts. Second, the maxillary has a double articulation. In addition to that between the proximal end of the maxillary and the skull inherited from the "holostean" grade of evolution, teleosts have a second maxillary articulation with the anterior (autopalatine) end of the suspensorium. This palatine-maxillary articulation is an almost constant feature of teleosts (Griffith and Patterson, 1963) that has been secondarily lost in only a few forms, e.g., *Gymnarchus* (Taverne, 1972) and some eels (Robins and Robins, 1971).

In *Elops* the anteromedial rim of the premaxillary bone has a hinge-like articulation with the somewhat overhanging anterolateral rim of the rostral region of the skull (Fig. 5A). Distally, the premaxillary extends along the anterior surface of the maxillary, to which it is membranously attached.

The proximal part of the maxillary has two primarily sliding articulations, though a certain amount of rotation of the maxillary relative to these articulations also occurs. Medially, the inner surface of the somewhat flattened maxillary head (Fig. 5A) abuts against a cartilaginous area on the lateral surface of the cranium. Somewhat more distally, the inner surface of a raised area on the maxillary
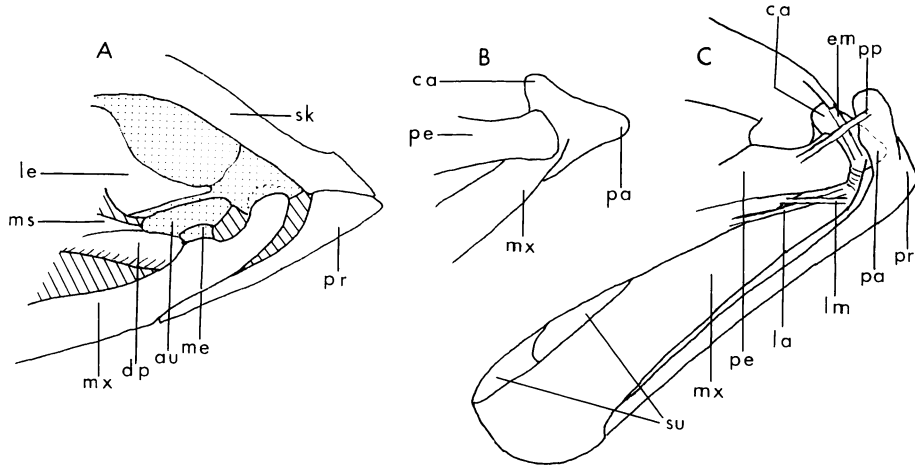
Fig. 5. Upper jaw structure, right side, external view, of A, *Elops saurus*, juvenile, 130 mm in standard length, and B, C, *Aulopus filamentosus*, adult. In A, hatching represents interspaces and stippled areas, cartilage. In B, the proximal head of the maxillary has been rotated somewhat more toward the premaxillary protrusion condition than in C. Membranous tissue between the palatine and the maxillary is indicated by parallel lines in C. au, Autopalatine; ca, cranial articular head of maxillary; dp, dermopalatine; em, ethmoid-maxillary ligament; la, primordial ligament; le, lateral ethmoid; lm, ligament from lacrimal to maxillary; me, meniscus between maxillary and autopalatine; ms, mesopterygoid; mx, maxillary; pa, premaxillary articular head of maxillary; pe, palatine; pp, palatine-premaxillary ligament; pr, premaxillary; sk, cranial roofing bones; and su, supramaxillary.

articulates, via a meniscus (Fig. 5A), with the anterolateral surface of an anterior (autopalatine) area of the suspensorium. The distal end of the long maxillary overlaps the mandible, to which it is attached by a strong membrane.

The anterior (autopalatine) end of the suspensorium is cartilaginous (at least in half-grown *Elops*). It extends forward to between the maxillary articulation externally and a cartilaginous area of the skull internally. The articular area between the autopalatine and the skull is horizontally elongate and permits the anterior end of the suspensorium to slide upward and outward over the cranial surface.

There are two major ligaments in the proximal part of the upper jaw apparatus (see, for example, Gosline, 1969: fig. 4B). One extends from the anteroventral surface of the maxillary to the skull. The other is from the superficial surface of the palatine across the maxillary to an attachment on the upper rim of the premaxillary. These ligaments, plus the hinge-like articulation of the premaxillary with the skull, seem to be the

principal means of preventing dislocation of the proximal end of the upper jaw during movements of its component elements.

Opening of the mouth in *Elops* seems to involve synchronous movements resulting in expansion of the gape in two directions, vertical and lateral (Vrba, 1968). The vertical movement is brought about by lowering the mandible, which causes the distal end of the maxillary to swing downward and forward. This in turn causes a certain amount of sliding and rotation of the proximal part of the maxillary relative to its two articulations. The downward and forward swinging of the distal end of the maxillary also forces the distal end of the premaxillary slightly *forward* ahead of it. The diagonally oriented hinge-abutment between the premaxillary and the skull prevents forward movement of the proximal end of the premaxillary and translates the forward force exerted on the proximal end into an outward and forward rolling of the toothed (alveolar) premaxillary surface. The palatine-premaxillary ligament is probably an additional cause of outward rolling in the
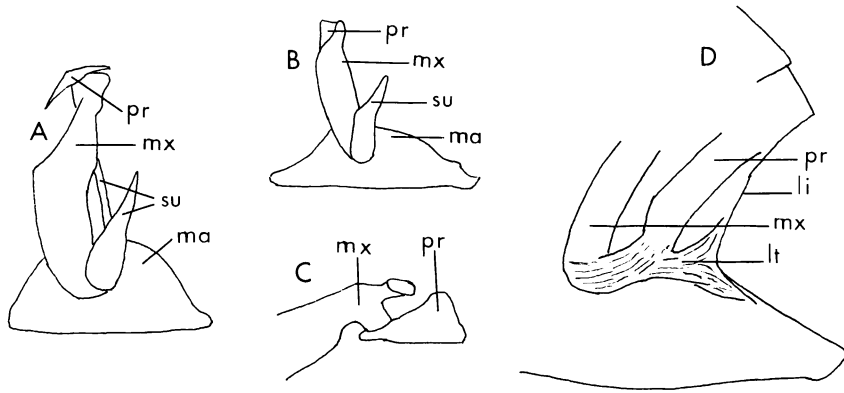
Fig. 6. Mouth parts of A, *Opisthonema oglinum*, left side, lateral view; B, *Coregonus nigripinnis*, left side, lateral view, and C, maxillary and premaxillary from the rear; and D, *Carassius auratus*, right side, lateral view, with some of the skin at the corner of the mouth removed to show the ligamentous tissue. li, Lip; lt, ligamentous tissue extending back from lip; ma, mandible; mx, maxillary; pr, premaxillary; and su, supramaxillary.

premaxillary when the maxillary is lowered.

Lateral expansion of the mouth is brought about by spreading apart, i.e., widening the distance between, the areas of mandibular articulation on the suspensoria of the two sides of the head. One result of such lateral expansion of the gape is to spread apart the distal ends of the two maxillaries. Such a maxillary movement would force the forward end of the bone away from its autopalatine articulation were it not for a synchronous movement in the anterior end of the suspensorium: as the mandibular articulation areas of the suspensorium swing wide the anterior, autopalatine ends slide outward over their cranial articulations. Because of this outward (and somewhat upward) movement of the forward ends of the suspensorium these continue to intervene between the skull and the maxillary at all stages of mouth opening. These autopalatine wedges thus serve in *Elops* to strengthen the bite regardless of the size of the mouth opening when the prey is seized.

A number of lower teleosts have what may be called a clupeid type of upper jaw construction dealt with more fully below. Fishes with this type of jaw construction have small, weakly-toothed mouths with short premaxillaries and abruptly curved maxillaries. They have movable premaxillaries, but the cause of the movement is different from that in *Elops*.

In the long-jawed *Elops* the anterior end of the **premaxillary** articulates with the rostrum well anterior to the proximal end of the maxillary (Fig. 5A), and the two bones are in contact with one another only along the distal part of the premaxillary. In fishes with a mouth of the clupeid type (Kirchhoff, 1958) the border of the anterior part of the upper jaw extends almost transversely across the snout. The premaxillary directly overlaps the anterior end of the maxillary (Fig. 6A), and the maxillary has a sharp angle between a large posterior longitudinally-aligned superficial limb and a short, transversely-aligned anterior part that carries it in behind the premaxillary to its articulation with the skull. Because of the angle, the short proximal limb of the maxillary rotates relative to its cranial articulation when the distal end of the maxillary is lowered. (The same phenomenon occurs when, in changing an automobile tire, the long arm of an L-shaped lug wrench is lowered to rotate the short arm and the wheel lug.) In fishes with the clupeid type of upper jaw, it is the twisting of the proximal limb of the maxillary, not the lowering of the distal limb as in *Elops*, that is the direct cause of premaxillary movement (Fig. 5A).

In *Clupea*, as in *Elops*, the movements of the premaxillary and of the maxillary are somewhat different. The premaxillary of