Zeiforms as Primitive Plectognath Fishes

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ABSTRACT

Since 1850 acanthurids have been regarded as the nearest relatives of some or all tetraodontiform fishes. New evidence suggests that acanthurid similarities with all tetraodontiforms or with balistoids only are not significant taxonomically. Zeoids uniquely share a number of derived features with tetraodontiforms, however. The reasons for this new proposal are most easily appreciated when acanthurids and zeoids are compared with the cladistically primitive triacanthoid tetraodontiforms rather than with balistoids.

INTRODUCTION

Tetraodontiforms were first recognized as a natural group by Cuvier (1817) under the name Plectognathes. Since then questions have arisen about the group's monophyly and its relationships to other fishes. This history was summarized by Tyler (1980) in a comprehensive monograph on tetraodontiform skeletal anatomy and taxonomy. No simple diagnosis of this group has been widely accepted, but there is a consensus, nonetheless, that the tetraodontiforms are monophyletic. Proposals concerning their relationship to other fishes have been of two sorts: the nearest relatives of the tetraodontiforms are (1) all perciforms or (2) some subgroup of perciforms. Both proposals imply that the Perciformes is in some sense definable; for the present I am extremely skeptical that this is so except by listing its included taxa. In this paper, I will present evidence that the sister group of the Tetraodontiformes lies outside the presently recognized perciform assemblage.

The notion that the plectognaths have perciform affinities is an outgrowth of a proposal by Dareste (1872) that balistoid fishes are most closely aligned with acanthuroids (taken here to include siganids). The proposal was formulated in this way because Dareste (1850) thought that balistoids were not especially close to four other groups (familles) of tetraodontiforms which he identified as including (1) *Diodon* and *Tetraodon*; (2) *Triodon*; (3) *Orthagoriscus* (the *Orthogoriscus* of

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Schneider, and a synonym of *Mola*), and (4) *Ostracion* (more or less equivalent to Tyler's Ostracioidea). Dareste's 1872 analysis not only formed a basis for subsequent proposals of acanthurid-tetraodontiform relationships but, to the best of my knowledge, never was critically evaluated in an effort to determine whether a suitable basis for such a relationship had in fact been provided. In any case, the idea gained in popularity because many subsequent authors from Regan's (1902) time to the present searched for and "found" confirmation.

What specifically was found is a similarity in general appearance, and in a few particulars, between acanthurids and balistids. When triacanthid and triacanthodid fishes are considered as parts of a monophyletic Tetraodontiformes, those resemblances appear to be spurious. This is because cladistically, triacanthoid fishes not only are the sister group of all other plectognaths and are morphologically more primitive than the others when compared with non-plectognath acanthopterygians, but show no particular similarity to acanthurids. An analysis of Dareste's (1872) original comparisons between balistids and acanthurids illustrates the problem. Dareste made the following major claims of decisive similarity (followed by my comments).

1. The jaws are very small and the maxillaries and premaxillaries are immovably joined together (not true of triacanthoids).

2. The skull is narrow and elongated and descends obliquely downward to the vertebral column behind the orbit, one result of which is that the pterotic is situated very low on the skull (true also of some other laterally compressed fishes such as zeoids and chaetodontids).

3. The supraoccipital juts between the frontals and forms a high crest (true also of zeoids and many percoids).

4. The ethmoid is very elongate, widely separating the frontals and palatines (not true of some acanthurids but true of some zeoids).

5. The parasphenoid and ethmoid have bony laminae which together form a bony partition anteriorly between the right and left nasal cavities (not true of triacanthoids or some acanthurids).

6. The vomer is very small and edentulous (the vomer is rather large in triacanthoids although edentulous).

7. The palatines are equally small, edentulous and are movably articulated with the ethmoid and maxillaries (the palatines are firmly united with the ectopterygoids in acanthurids, and are movably joined to these bones in many other fishes).

8. The bones of the temporal (otic) region are not united at all points except by membrane (cartilage) (not true of acanthurids, *Triacanthus,* or most other plectognaths, but true of triacanthodids, some Beryciformes, and such other acanthopterygians as zeoids).

9. Interopercle rodlike and detached without strong ligamentous attachment to the preopercle (not true of acanthurids, and not rodlike in triacanthoids, but loosely attached to the preopercle in both triacanthoids and zeoids).

10. Hyoid bar very small and with fewer parts than in other fishes (equally small in other laterally compressed fishes with small mouths such as chaetodontids, and number of parts the same as in other fishes).

11. The urohyal is very large, forming two long branches that unite in a right angle (the broadly triangular urohyal so described is found also in zeoids, chaetodontids, pomacanthids, and other representatives of the old Squamipennes).

12. The pectoral fin radials are formed as large plaques (this is a feature common to numerous acanthopterygians).

13. The coracoid bone in the shoulder girdle is very large (not true of triacanthoids).

14. The pelvis is very elongated and the right and left halves are more or less joined (the great length of the triacanthoid pelvis is due to an extreme development of a process posterior to the fin origin; in acanthurids and balistoids pelvic girdle length is attained entirely by bone anterior to the fin origin and this is also the case in the stromateoid genus, *Peprilus*).

15. There are only 20 to 22 vertebrae and the parapophyses of the abdominal vertebrae bear very small ribs (many acanthopterygians have a low vertebral count: caproids, for example, have only 22. Other tetraodontiforms have as many as 30. The ribs pose a special problem, discussed below, but acanthurids

and tetraodontiforms primitively appear to have both normal pleural and epipleural ribs).

Although Regan (1902) found various differences between tetraodontiforms and acanthurids, he, in effect, accepted the above characterizations by Dareste when he wrote "there can be no question as to the close relationship of the less specialized (Plectognathi) to the Acanthuridae. . . ." In 1947, Breder and Clark remarked on the proposed relationship "which no one has seen fit to contest" and, with a minor variation, that acceptance persists today. The minor variation is to assert only that triacanthoids are intermediate between perciforms and other tetraodontiforms (Gosline, 1971) rather than to single out the Acanthuroidea.

Zeiform fishes, however, have at least 11 synapomorphies with tetraodontiforms when the triacanthoids are included in the analysis. But of these 11 characters, seven unite all zeiforms with tetraodontiforms, and the remaining four unite noncaproid zeiforms with them. If this proposed relationship is correct, the zeiforms are therefore not monophyletic. In the discussion that follows, the term zeoid refers only to the fishes presently included in the nominal families Zeidae, Parazenidae, Zeniontidae, Grammicolepidae, Macrurocyttidae, and Oreosomatidae, and the term caproid refers only to the species of *Antigonia* and *Capros*.

ACKNOWLEDGMENTS

ANATOMICAL ABBREVIATIONS

ACC CART, accessory cartilage
ALP, alveolar process
AP, ascending process

ARP, articular process
CB, ceratobranchial
DR, distal radial
$E_{1,2,3,4}$, epibranchial
$EP_{1,2,3}$, epural
FRB, fin ray base
$HYP_{1,2,3,4,5}$, hypural
IAC, interarcual cartilage
LIG, ligament
MES CART, mesial cartilage
MR, middle radial
MX, maxilla
$NPU_{2,3}$, spine or crest
OSS, perichondral ossification
PAL ANT, POST, antopalatine, anterior and posterior
$PB_{1,2,3,4}$, infrapharyngobranchial
$PB_{1,2,3,4}$, infrapharyngobranchial toothplate
PHYP, parhypural
PMX, premaxilla
PMX P, postmaxillary process of premaxilla
PR, posterior radial
PRIN R, principal caudal fin ray
PROC R, procurrent caudal fin ray
$PU_{1,2,3}$, preural centrum
ROST CART, rostral cartilage
SIL BUCKLER, silhouette of buckler
STEG, stegural
$U_{1,2}$, ural centrum
$UN_{1,2}$, uroneural

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History
UMMZ, University of Michigan, Museum of Zoology
USNM, National Museum of Natural History

CHARACTER ANALYSIS

SACCULAR OTOLITH (SAGITTA): Nolf (in press) illustrated this otolith in zeiforms, tetraodontiforms, and acanthurids, among many other teleosts. In *Capros* and *Antigonia* the sagitta is higher than long (the reverse of most teleosts) and indented or constricted anteroposteriorly at the level of the sulcus (approximately the dorsoventral midpoint). In *Capros*, in which the anteroposterior indentations are large, the otolith is dumbbell-shaped in outline. In zeoids, a sagitta of this shape is shown by Nolf for an oreosomatid and grammicolepid; in *Zeus* the ventral part of the sagitta below the sulcar region is much wider than the dorsal part and in a macrurocyttid and parazenid the entire otolith is of a very
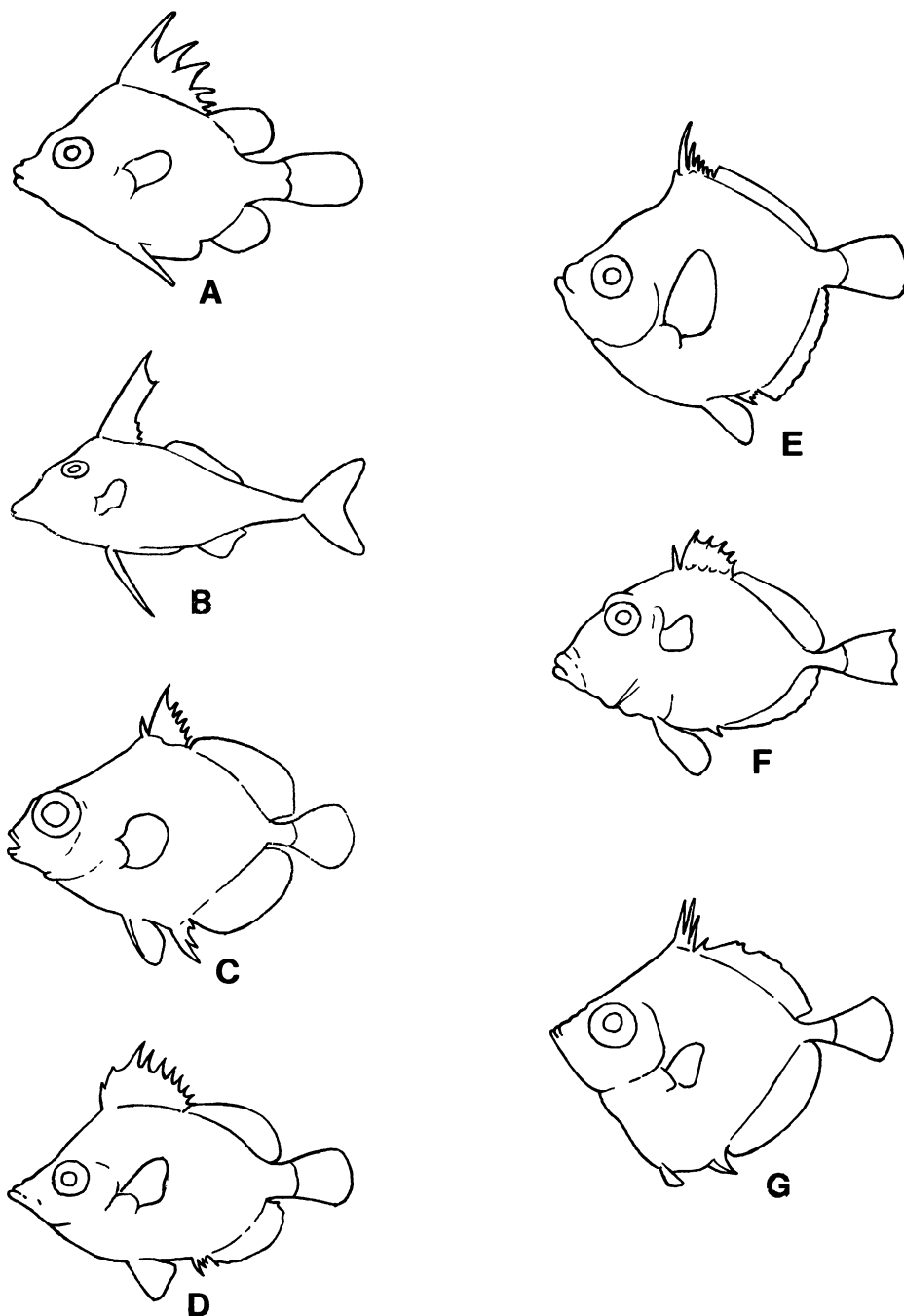
FIG. 1. Body and fin form in some triacanthoids, caproids, and zeoids. A, *Parahollardia lineata* (Langley). B, *Pseudotrianthus strigilifer* (Cantor). C, *Neocyttus rhomboidalis* Gilchrist. D, *Capros aper* (Linnaeus). E, *Antigonia*. F, *Cyttopsis roseus* (Lowe). G, *Xenolepidichthys dalgleishi* Gilchrist.

irregular shape that does not even approximately approach the clamshell-shaped sagitta of most euteleosts. Among tetraodontiforms,

except for *Mola* which has a sagitta unique in teleosts, this otolith is as described for caproids and zeoids with respect to both the
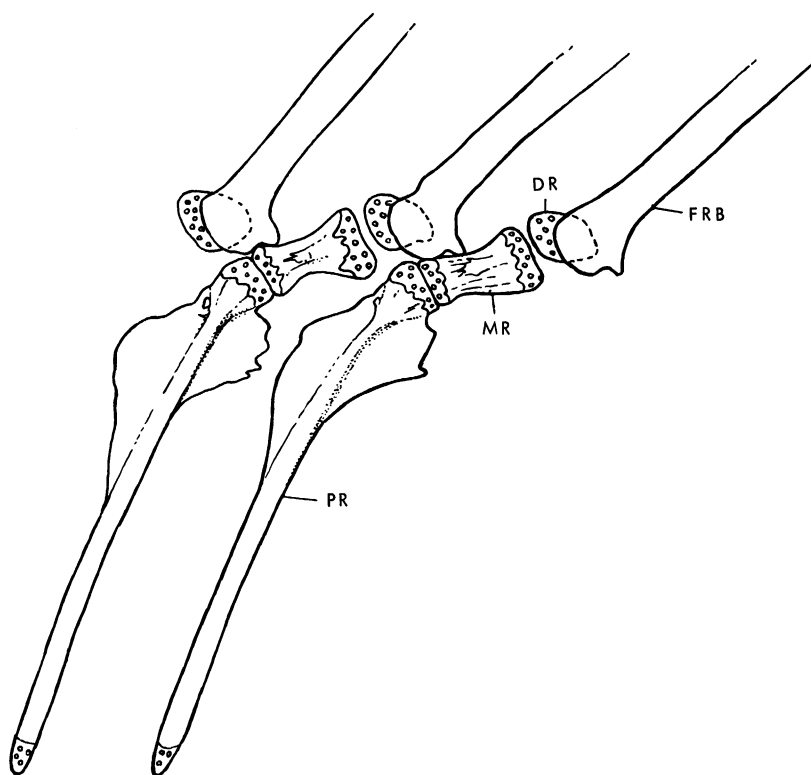
FIG. 2.   *Gephyroberyx darwini* (Johnson), UMMZ 180097. Dorsal fin radials. Shown are bases of rays 9 to 11, of a total of 13 soft rays. Anal radials like those of dorsal. This same condition was found in *Hoplostethus mediterraneus* (Cuvier and Valenciennes), AMNH 49718.

height-length ratio and anteroposterior indentations. A triacanthodid illustrated by Nolf resembles *Capros,* the oreosomatid and grammicolepid; one balistid and an ostraciid resemble *Antigonia*; and another balistid and a tetraodontid resemble *Zeus.* The acanthurid sagitta, on the other hand, is of a very primitive ctenosquamate type, being clamshell-shaped and having a distinct sulcus which includes a short section that enters the anterior margin (the ostium) to form a rostrum and excissura and a longer, downcurved posterior section (the cauda) that ends well short of the posterior margin. Sagittae that are higher than long are illustrated also for some "beryciforms" (*Rondeletia, Gibberichthys, Anoplogaster, Diretmus*) and one gobioid (a trypauchenid) but they all lack the medial constriction at the sulcus. One sagitta is illustrated showing the constriction (*Xiphias*) but it is longer than high.

Although rigorous shape analysis of otoliths is difficult to attain, the combination of a high sagitta with deep anteroposterior constriction supports an alignment of zeiforms and tetraodontiforms and rejects a relationship of either to acanthurids.

SPINOUS DORSAL AND ANAL FINS: All zeiforms have a small spinous dorsal and anal fin that is distinctly separated by a notch or membrane discontinuity from the dorsal and anal soft rays only (the grammicolepid, *Daramattus,* lacks a separate spinous dorsal). Tetraodontiforms lack anal spines but the dorsal spines of triacanthoids are very similar to those of zeiforms. In balistoids and *Triodon* the dorsal spines are well separated from the dorsal rays. Acanthuroids have the dorsal and anal spines continuous with the succeeding soft rays, the two slightly differentiated in siganids and grading together imperceptibly in acanthurids.
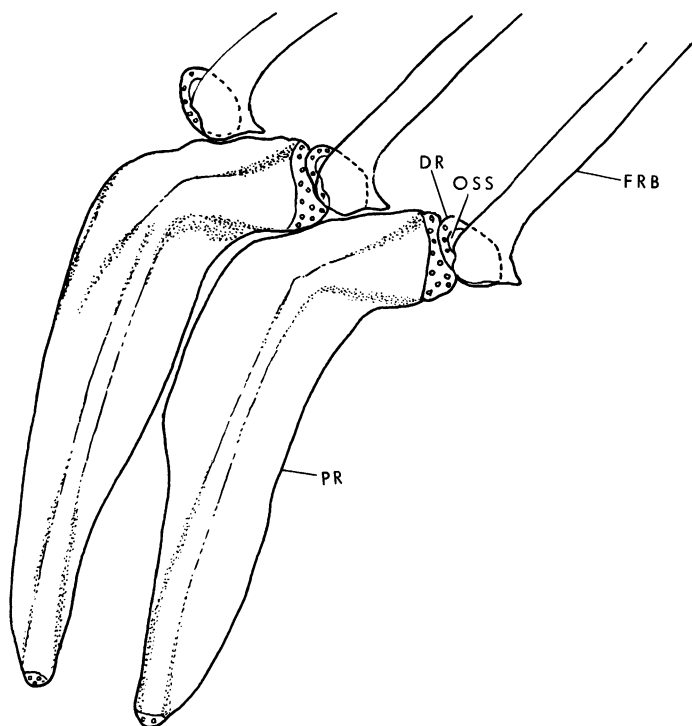
FIG. 3. *Zebrasoma veliferum* (Block), AMNH 38121. Dorsal fin radials. Shown are bases of rays 21 to 23, of a total of 30 soft rays. Anal radials like those of dorsal.

The most generalized condition of those mentioned above is the type of spinous dorsal in zeiforms. *Capros,* in particular, has conditions of the dorsal and anal spines that can be found in various "beryciforms" and "percoids." All other conditions appear to be derived: the zeiform anal spines and balistoid and *Triodon* dorsal spines separated by a gap from the corresponding soft rays, the absence of anal spines in tetraodontiforms, and the continuous and similarly sized spines and rays in the acanthuroid dorsal and anal fins. Dorsal and anal fin structure, therefore, offers no support for an acanthuroid-tetraodontiform linkage.

Indecisive as this kind of evidence seems, however, there is some indication of a community of derived features in body and fin form among zeiforms and triacanthoids (fig. 1). The dorsal spines in both are robust and occupy an area nearly equal to that of the soft dorsal. In both groups, the caudal fin is primitively rounded but emarginate in acanthu-

roids (see Tyler, 1980, fig. 3, for primitive triacanthoid condition). Zeoids and triacanthoids are also similar in having spinules or denticulations present on fin spines and some zeoids further resemble triacanthoids in having a large, locking pelvic spine. How important the latter similarity might be is difficult to assess because there is yet no sound theory of relationships for the nominal families of zeoids, and fin conditions very much like those just described may also be found in monocentrid beryciforms. At present the most that we might conclude is that this kind of evidence is at least consistent with a sister-group relationship between zeiforms and tetraodontiforms.

DORSAL AND ANAL FIN RADIALS: Bridge (1896) was the first to survey the structure of the dorsal and anal fin radials of teleosts. He noted that primitively each fin ray is supported by three elements: a long proximal radial that is situated between the neural or hemal spines but extends away from the ver-
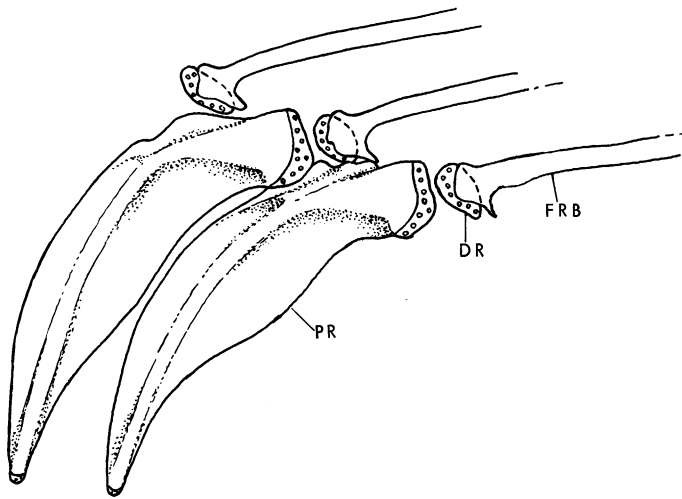
FIG. 4. *Siganus spinus* (Linnaeus), AMNH 29387. Dorsal fin radials. Shown are bases of rays 5 to 7, of a total of 10 soft rays. Anal radials like those of dorsal.

tebral column nearly to the dorsal or ventral midline, and a middle radial of hourglass shape that extends between the proximal radial and the small nodular distal radial between the paired fin-ray bases (fig. 2). Proximal and distal radials are almost always present in teleosts but mesial radials are missing in many cases. Most specializations in fin supports (e.g., fin spines or modified fin ray bases) are associated with the biradial condition. Among euteleosts a triradial condition exists in most, if not all, salmoniforms and primitive ctenosquamates. In fact, more primitive acanthomorphs (fig. 2) are triradial than biradial and the triradial condition exists even among some fishes traditionally aligned as perciforms (e.g., centropomids, enoplosids, kurtids, sphyraenids, and all gobioids). Zeiforms and tetraodontiforms, and acanthuroids as well, are always biradial, however. But the zeiform-tetraodontiform radials are of an unusual kind. In acanthuroids (figs. 3, 4) the proximal radials are bent backward at their tips, the bent section occupying a position comparable with that of the mesial radial in more primitive conditions. This is not to imply that the middle radial is fused in or undifferentiated from the cartilaginous anlagen, although this must certainly be the case in such fishes as clupeoids where a transition from tri-to-biradial elements exists within a single fin. Rather, in acanthuroids there is simply no indication that the fin-ray support was ever triradial in its development; it is of a derived acanthopterygian type found in many perciforms such as lutjanids and chaetodontids. In zeiforms (figs. 5–8) and tetraodontiforms (figs. 9, 10) the tip of the proximal radial is not bent backward but is upright and anteroposteriorly symmetrical; the distal radial, rather than being functionally associated with a preceding proximal radial, is itself anteroposteriorly symmetrical and is associated equally with a proximal radial both fore and aft of its position. Dorsal and anal fin radials of this sort are not unique to zeiforms and tetraodontiforms, however. Bridge (1896) noted their presence in flatfishes (*Pleuronectes platessa*), but the condition must be secondary for flatfishes because the sister group of other pleuronectiforms, *Psettodes,* has radials of the more general perciform type (fig. 11). A condition similar to this also occurs in some apomorph groups of gobiesocids but the distal radials remain associated with their metamerically appropriate proximal radials (fig. 12A). The more symmetrical condition may also be found in some of the ceratioid anglerfishes (e.g., *Melanocoetus*) but, within the batrachoidiform-lophiiform clade, a complete transformation series back to a primitive triradial condition
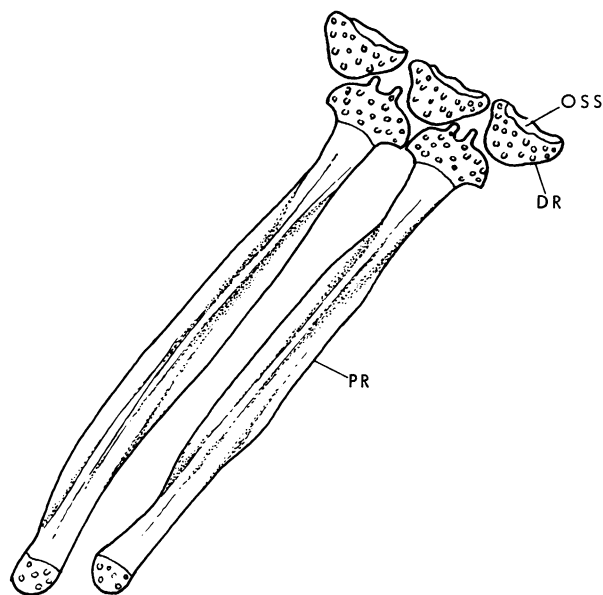
FIG. 5. *Capros aper* (Linnaeus), AMNH 482. Dorsal fin radials. Shown are bases of rays 13 to 15, of a total of 22 soft rays. Anal radials like those of dorsal.

(fig. 12B–E) can be traced [*Melanocoetus* (symmetrical, biradial), *Antennarius* (slightly asymmetrical, biradial), *Lophiomus, Lophius* (asymmetrical, biradial as in acanthuroids), *Porichthys, Batrachoides, Opsanus* (asymmetrical, triradial as in primitive euteleosts)]. In the beryciforms *Anoplogaster* (fig. 13) and *Monocentrus* (fig. 14) some radials are symmetrical and biradial and others are only slightly asymmetrical and biradial or triradial. A symmetrical condition occurs also in *Platax,* whereas other more generalized ephippids have some asymmetric and triradial radials (fig. 15).

These data seem clearly to relate zeiforms to tetraodontiforms but to rule out either as a close relative of ephippids, batrachoidiform-lophiiforms, or pleuronectiforms because of the secondary nature of radial symmetry in the latter, and to rule out acanthuroids where a type of primitive asymmetry is characteristic. But these data do not rule out the possibility that the zeiforms and tetraodontiforms together might be related to *Anoplogaster* or *Monocentrus* or to some group that includes both, or to some ephippids (see discussion of ephippids, below).

FIRST DORSAL FIN RADIAL: In many acanthopterygians the first dorsal fin radial, associated with a strong spine, may be enlarged and close to the occipital region of the skull. Primitively this radial is separated from the occipital region by two or three predorsal bones. In acanthuroids primitively all but one of the predorsal bones are absent (Tyler, 1970) and the first radial either is semi-erect or inclines forward to a position close behind the occiput (fig. 16); it is enlarged distally where it supports a small anterior and a larger posterior spine. This radial is also braced laterally by a flange that extends ventrally from the spine articulation, gradually decreasing in width. The ventral (proximal) end of the radial is slender and inserts in front of the first neural arch just above the first vertebral centrum. In *Naso lituratus* (AMNH 45017) the ventral part of a median anterior flange on this radial penetrates between the exoccipital bones of the skull. In zeiforms and triacanthoids (figs. 17–20) the anterior vertebrae are short and crowded and the first one has its neural arches spread widely apart, bent sharply forward, and firmly united with the occiput along the exoccipital and epioccipital
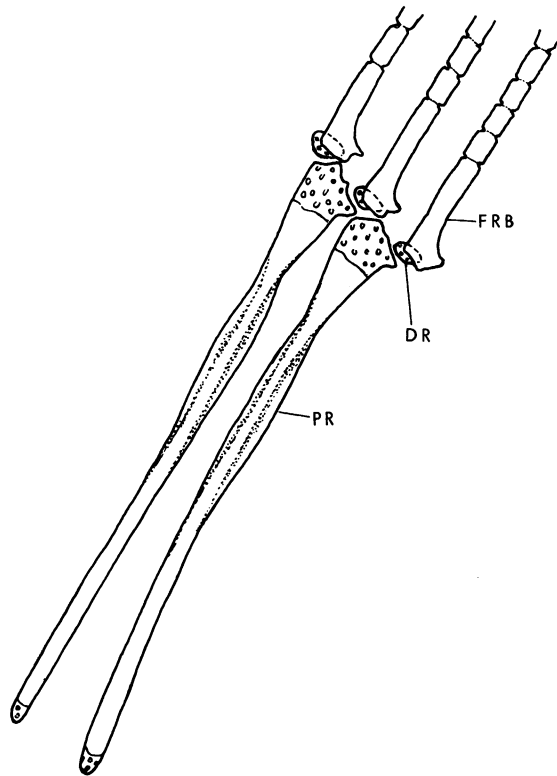
FIG. 6. *Antigonia capros* Lowe, AMNH 29461. Dorsal fin radials. Shown are bases of rays 11 to 13, of a total of 35 soft rays. Anal radials like those of dorsal.

bones. These occipital bones are also separated in the midline. The first dorsal fin radial, which inclines backward, is a robust columnar bone along its entire length and inserts ventrally between the neural arches of the first vertebra and is clasped by the occipital bones. In balistoids this condition is exaggerated; the radials of the spinous dorsal form a single plate that is movably articulated with the skull and what remains of the ventral end of the first radial is a blunt prong of bone that extends from the plate ventrally into a well-defined hole between the epioccipitals. In monacanthid balistoids the radial plate is firmly sutured to the skull. In other tetraodontiforms the radial plate is reduced in size, withdrawn posteriorly from the skull, or absent.

POSTTEMPORAL: The posttemporal of most teleosts is movably attached anterodorsally to the epioccipital and by means of a slender

bony stay or ligament (the ventral arm) anteroventrally to the intercalar or exoccipital when the intercalar is absent. Posteroventrally it joins the supracleithrum. In some fishes the ventral arm to the exoccipital is absent. In acanthuroids the posttemporal is not movable, is irregularly teardrop-shaped, with the slender dorsal part joined by dense ligament with an epioccipital process and the anteroventral part by a suture to the pterotic just in front of its facet for the supracleithrum. The posttemporal of chaetodontids is almost exactly like that of acanthuroids. In caproids the posttemporal attachments are, again, similar but unlike acanthuroids the dorsalmost part of the bone in *Capros* is a broad spatulate part that is molded to the contours of the occipital region. In zeoids, triacanthoids, and balistoids, however, the posttemporal is more firmly anchored to the occipital region, although in small specimens
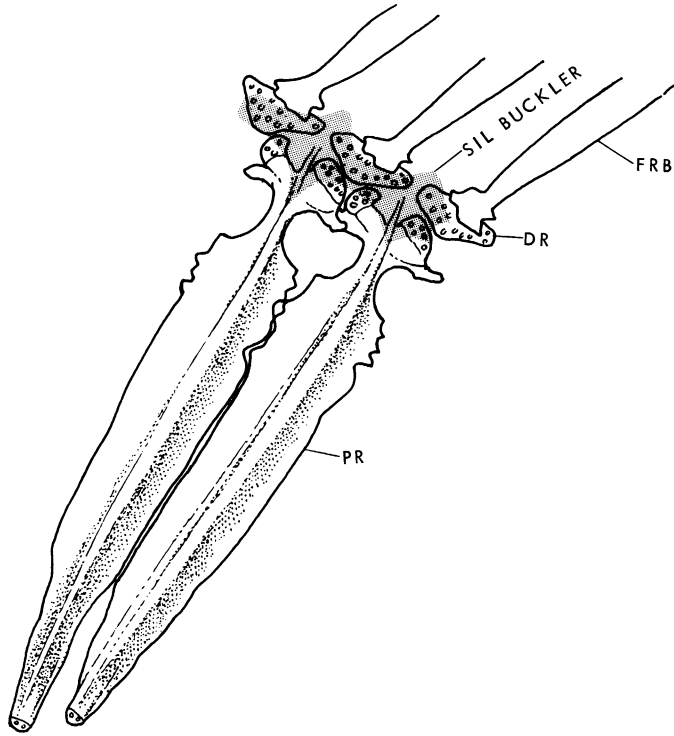
FIG. 7. *Xenolepidichthys dalgleishi* Gilchrist, AMNH 29455. Dorsal fin radials. Shown are bases of rays 15 to 17, of a total of 27 soft rays. Shaded overlay represents outline of superficial bony plates continuous with the lateral ridge on the proximal radial. The fore and aft pair of cartilages on the distal tip of the proximal radial occur also in *Cyttopsis roseus* (Lowe), AMNH 29460.
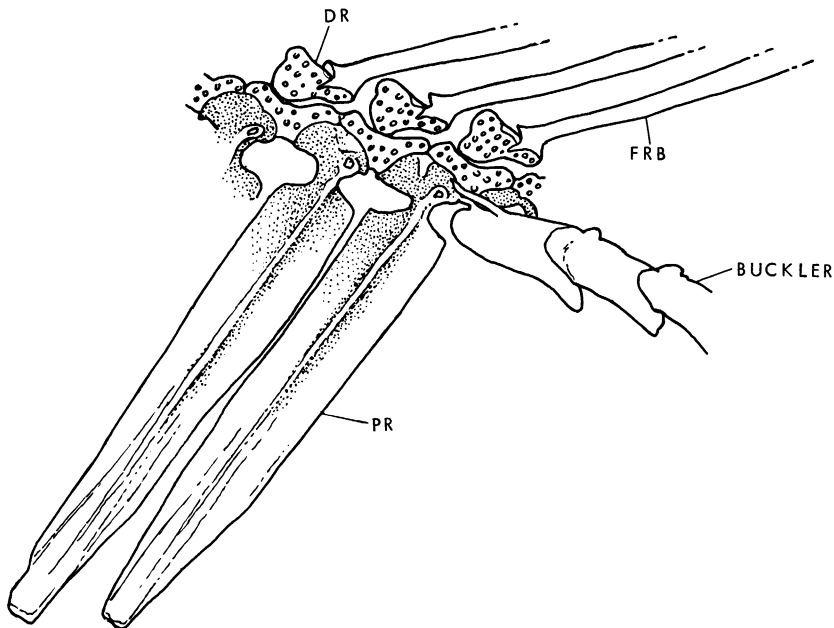
FIG. 8. *Zenion hololepis*, AMNH 29463. Dorsal fin radials. Shown is a more derived state of the cartilages illustrated in figure 7 in which the paired cartilages of each radial have fused and the fore and aft cartilages of adjoining radials have fused. Superficial bony plates cut off at bases to show their point of attachment to the end of the ridge on the proximal radial; two bony plates and part of a third are shown in position to the right of the proximal radials.
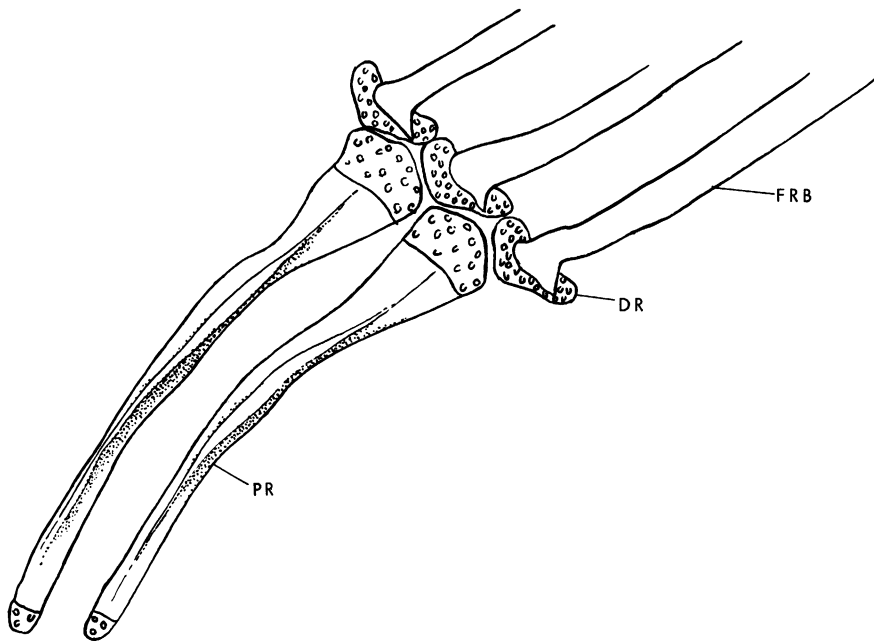
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FIG. 9. *Hollardia hollardia* Poey, USNM 187811. Dorsal fin radials. Shown are bases of rays 10 to 12, of a total of 18 soft rays. Anal radials like those of dorsal.
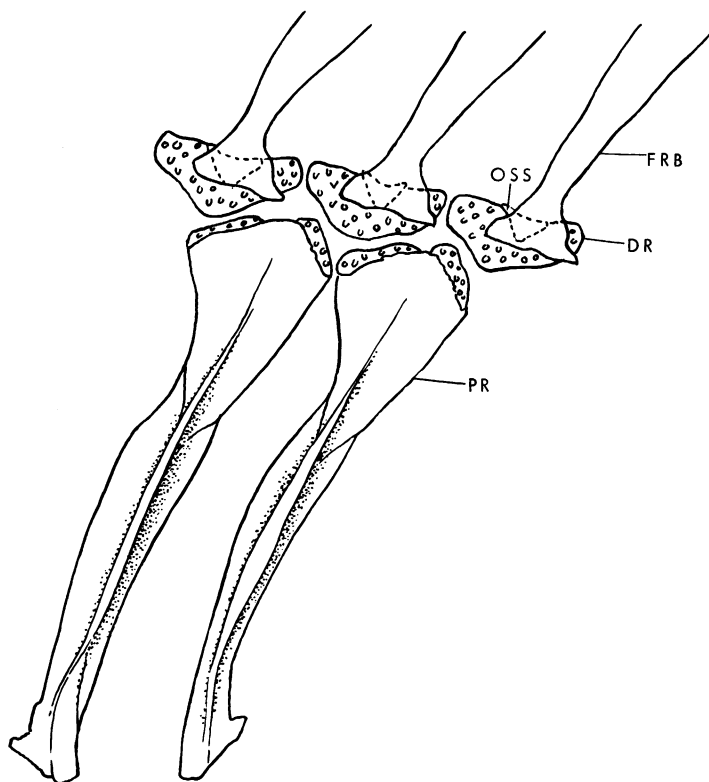

FIG. 10. *Triacanthodes ethiops* Alcock, USNM 93491. Dorsal fin radials. Shown are bases of rays 9 to 11, of a total of 15 soft rays. Note fore and aft pair of cartilages on the distal tip of the proximal radial, and compare with figure 7. Anal radial like dorsal radials of *Hollardia,* figure 9.
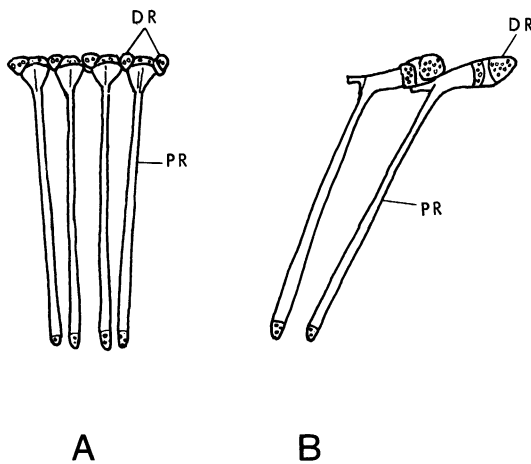
FIG. 11. Pleuronectiform dorsal fin radials, diagrammatic. A, *Scapthalmus aquosus* (Mitchill), AMNH 40585. B, *Psettodes erumei* (Block and Schneider), UMMZ 142008.

of zeoids and triacanthoids the dorsal part of the bone is joined to the skull by ligament rather than suture; in larger specimens the posttemporal is completely incorporated into

the skull wall, forming an integral part of the occipital contour. In spite of some differences in the modes of articulation with the occipital region, a reduced and structurally integrated posttemporal may be a synapomorphy of acanthuroids, chaetodontoids and the zeiform-tetraodontiform assemblage.

PHARYNGOBRANCHIALS AND PARASPHE-
NOID: All zeiforms (figs. 21–23), tetraodontiforms (fig. 24), and acanthuroids (fig. 25) share a modified pharyngobranchial dentition in which the toothpatches are wider than long. In the anteroposterior direction the toothpatches are restricted to from one to a few rows of teeth; they appear comblike in lateral view. In ventral view the toothpatches are comma-shaped, the convex side facing forward, and are either at right angles to the long axis of the skull or slope backward laterally. The second to fourth pharyngobranchials that bear these teeth are correspondingly foreshortened anteroposteriorly. Only zeoids (figs. 22, 23), balistids (fig. 24C), and a few of the more derived ostracioids and tetraodontoids lack a fourth pharyngobran-
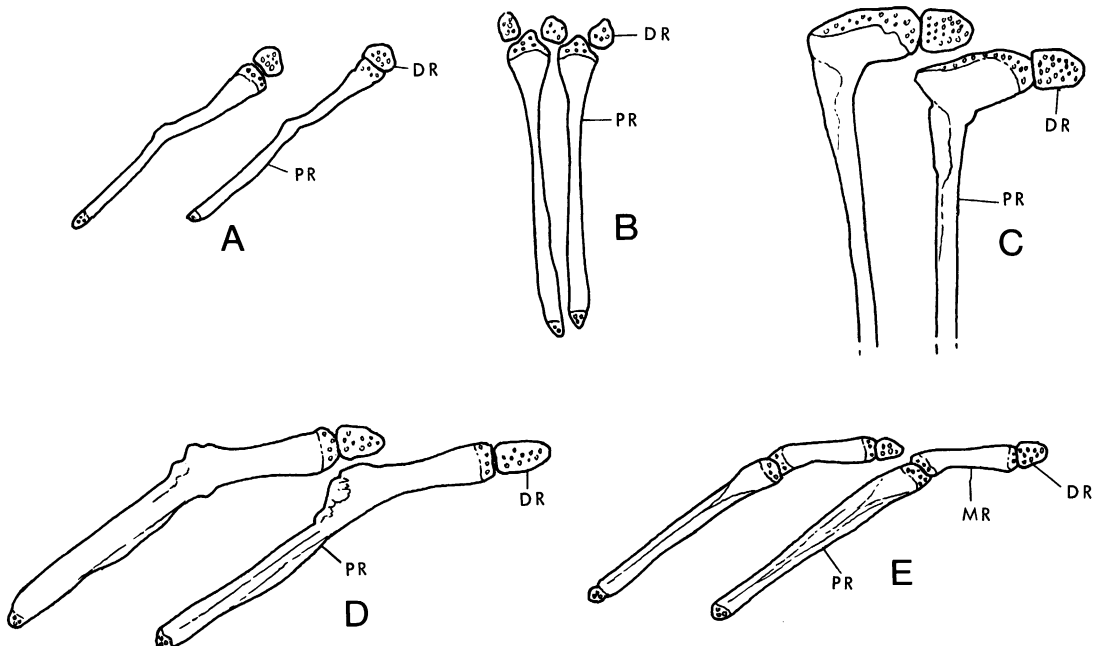

FIG. 12. Dorsal fin radials, diagrammatic. A, *Gobiesox funebris* Gilbert, AMNH 5557. B, *Melanocoetus jolmsoni* Gunther, AMNH 29780. C, *Antennarius nummifer* (Cuvier), AMNH 38127. D, *Lophiomus setigerus* (Vahl), AMNH 26752. E, *Porichthys plectrodon* Jordan and Gilbert, AMNH 19563.
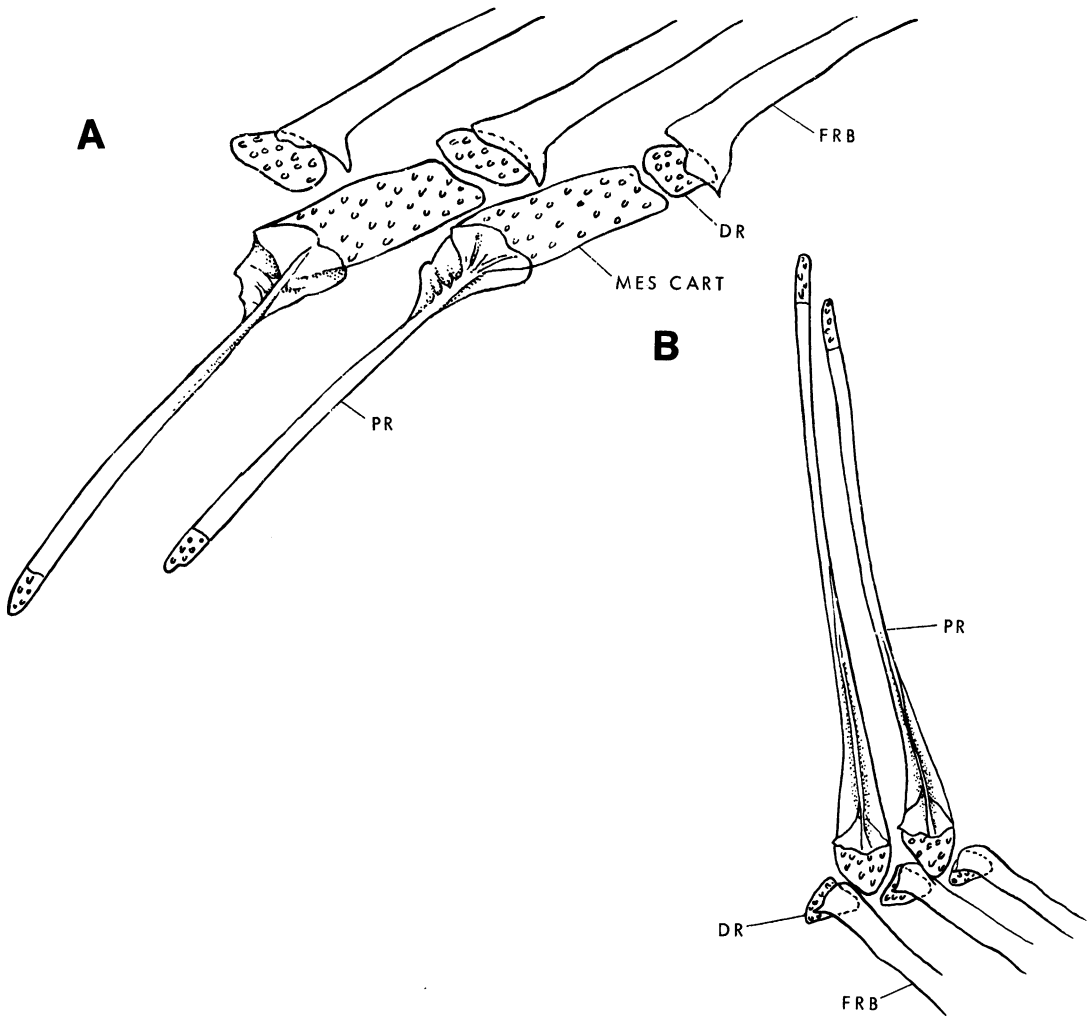
FIG. 13. *Anoplogaster cornuta* (Cuvier and Valenciennes), AMNH 49670. A, dorsal fin radials, including bases of dorsal rays 14 to 16 out of a total of 19 soft rays. B, anal radials, including bases of anal rays 5 to 7 out of a total of nine soft rays. The structure in A is similar to that of *Antennarius*, figure 12C.

chial toothplate. In general the pharyngo-branchial teeth are robust and conical in zeiforms and tetraodontiforms, and filiform in acanthuroids. Comma-shaped toothpatches of filiform teeth occur also in chaetodontids (fig. 26A), pomacanthids, scatophagids (fig. 26B), zanclids, and ephippids. In the latter fishes and in acanthurids the posterior pharyngobranchials are supported from a parasphenoidal apophysis that arises just posterior to the lateral commissure in the prootic; the apophysis has a median base, frequently continuous with the midventral parasphenoidal ridge, but in many cases divided distally into a pair of knobs or flanges. A few acanthuroids, such as siganids and *Xesurus*, and *Zanclus,* lack a distinct apophysis. The more or less general presence of a parasphenoidal apophysis in these fishes corresponds with the presence on the dorsomedial part of the third pharyngobranchial of a ledge that presumably serves as a site of insertion for
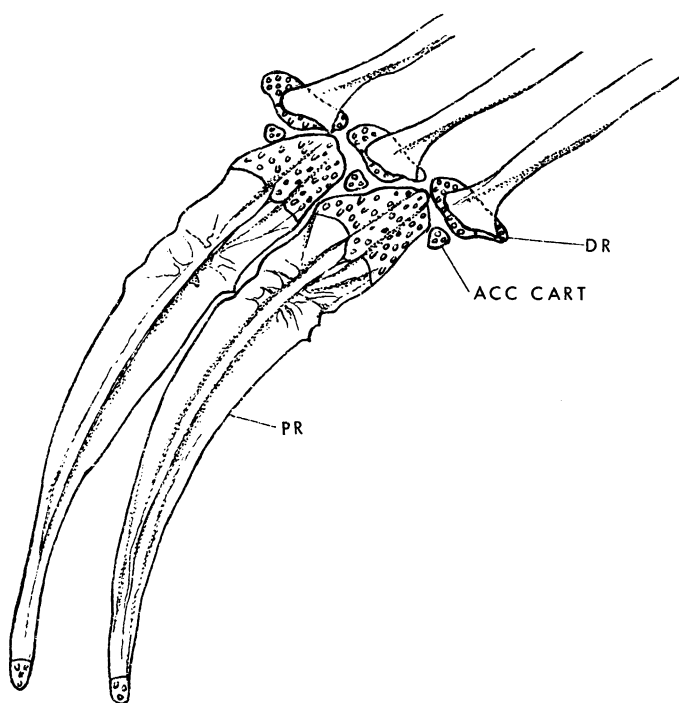
FIG. 14. *Monocentris gloriamaris* (DeVis), AMNH 38197. Dorsal fin radials supporting the bases of rays 6 to 8 out of a total of 11 soft rays. The anteriormost fin ray of soft anal showing middle radial represented by two small ossifications in the cartilaginous tip of the proximal radial.

the obliquus dorsalis muscle. In caproids and triacanthoids there is neither a parasphenoidal apophysis nor a definite ledge on the third pharyngobranchial; the parasphenoid, however, is modified at the level of that bone's connection with the prootic commissure into a distinctly forked shape. The diverging posterior forks of the parasphenoid pass backward onto the basioccipital; at the point of divergence, the forks of the parasphenoid are bridged by a bony arch that defines a posterior opening into the posterior myodome. This parasphenoidal structure is present also in grammicolepids, but in other zeoids the myodomal opening is reduced to a vestige (*Cyttopsis*) or is wanting although the bone remains forked. In non-triacanthoid tetraodontiforms an opening to the myodome is also lacking but some of them (balistids, ostracioids, and *Triodon*) possess a parasphenoidal apophysis of acanthuroid type that projects downward between the third pha-

ryngobranchials; here also the bone retains the two forks that underlie the basioccipital.

In these characters, the filiform teeth and primitively present parasphenoidal apophysis appear to unite a group including acanthuroids, chaetodontids, pomacanthids, scatophagids, zanclids and ephippids, whereas the presence of a specialized opening from the parasphenoid into the posterior myodome unites zeiforms and tetraodontiforms. The absence of the latter character thus defines some zeoids and non-triacanthoid tetraodontiforms and the presence of a parasphenoidal apophysis might be a defining character of the more derived groups of tetraodontiforms. In addition if in all these fishes the presence of comma-shaped toothpatches is a true character conflict rather than a synapomorphy, then these derived toothpatches would constitute a defining character of both the acanthuroid assemblage and the group including zeiforms and tetraodonti-
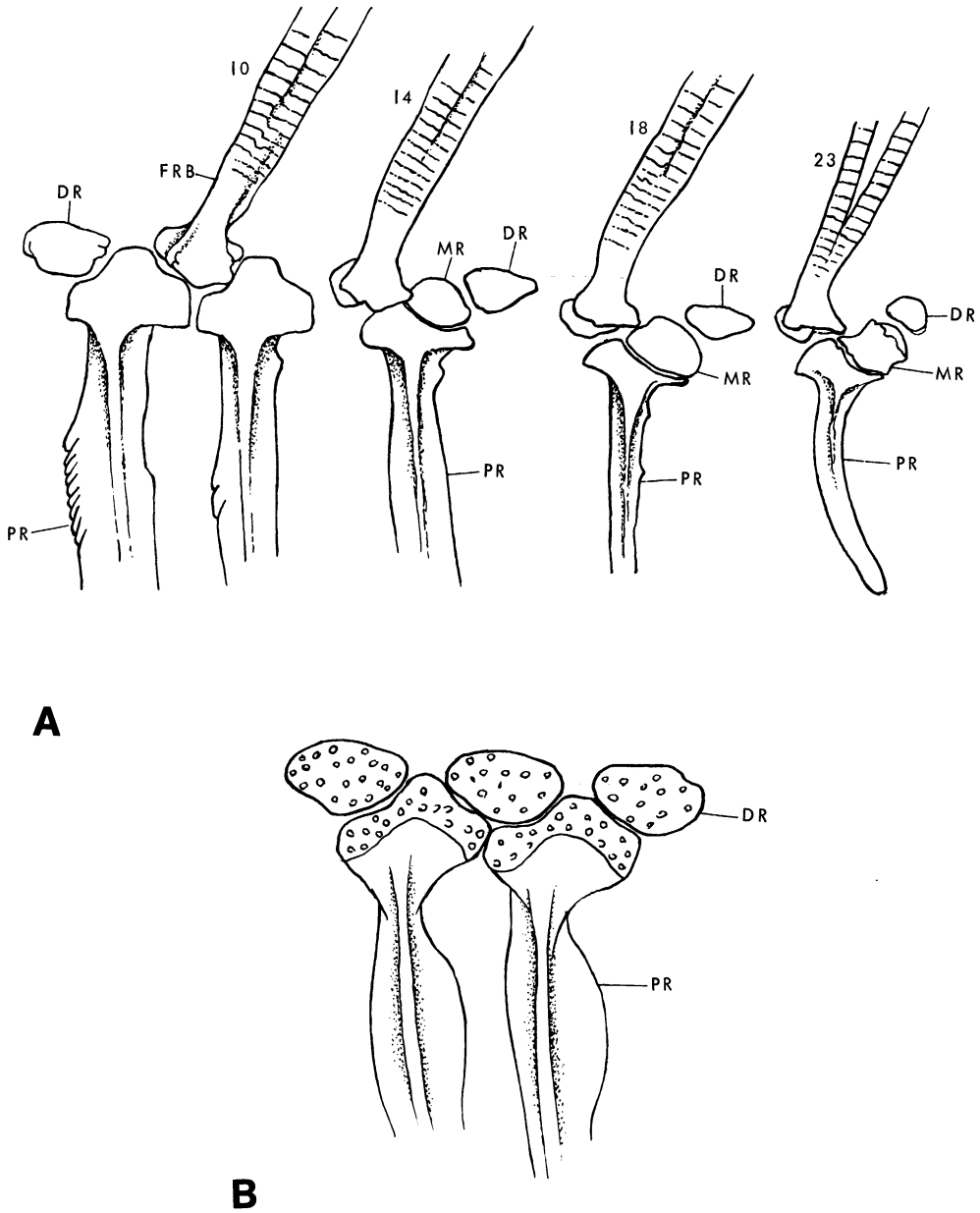
FIG. 15. Ephippid dorsal fin radials. A, *Chaetodipterus faber* (Bronssonet), AMNH 21556, showing front to back transition from a symmetrical, biradial condition to a completely asymmetrical, triradial one. B, *Platax orbicularis* (Forskal), AMNH 38102.

forms (see, below, a discussion of acanthuroid relationships).

INTEROPERCLE: In acanthuroids, the interopercular bone is short and subtriangular, with the narrow end connected by ligaments to the angular of the lower jaw and the broader end to the subopercle and anteroventral corner of the opercle. In zeiforms and triacanthoids the interopercle is long and blade-like, the posterior end slightly wider than the

FIRST PROXIMAL RADIAL

A

FIRST PROXIMAL RADIAL

B

FIG. 16. Acanthuroids, radiographs of skeleton. A, *Acanthurus bahianus* Castelnau, AMNH 25873. B, *Siganus fuscescens* (Bloch and Schneider), AMNH 34874.
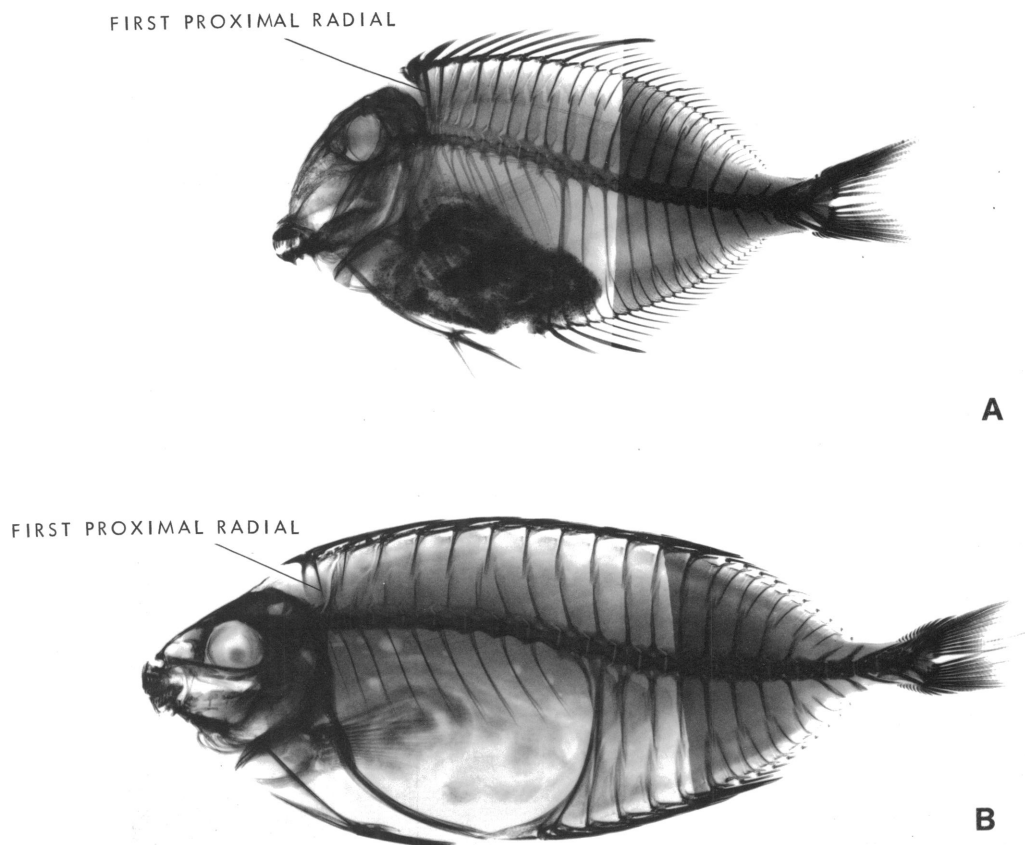
anterior end except in a few zeoids in which the two ends are narrow (i.e., the bone is feather-shaped). In balistoids and ostracioids the bone is simple and rodlike, whereas in *Triodon* and the tetraodontoids it is slender, rodlike, and bears a ventral prong posteriorly in *Triodon* and at the midpoint in the other taxa.

In acanthuroids and caproids the interopercle has normal ligamentous connections with the angular, preopercle, posterior end of the hyoid bar, and the posterior opercular bones. In zeoids and tetraodontiforms, the interopercle is firmly attached only at its anterior and posterior ends (with the angular and subopercle, respectively).

These data specify a relationship between all zeiforms and tetraodontiforms, but a closer relationship between zeoids and tetraodontiforms than between either and the caproids.

UPPER JAW BONES: In all zeiforms and all but long-snouted triacanthoids the premaxillary ascending process is very long in relationship to the alveolar process, has the articular process fully integrated into its lower half (except in *Capros*), and the combined ascending-articular complex separated from the alveolar process by a distinct neck (figs. 27–29). In *Capros* (fig. 27B) the articular process is almost as long as the ascending process with which it is united. The exceptional tria-

FIRST PROXIMAL RADIAL
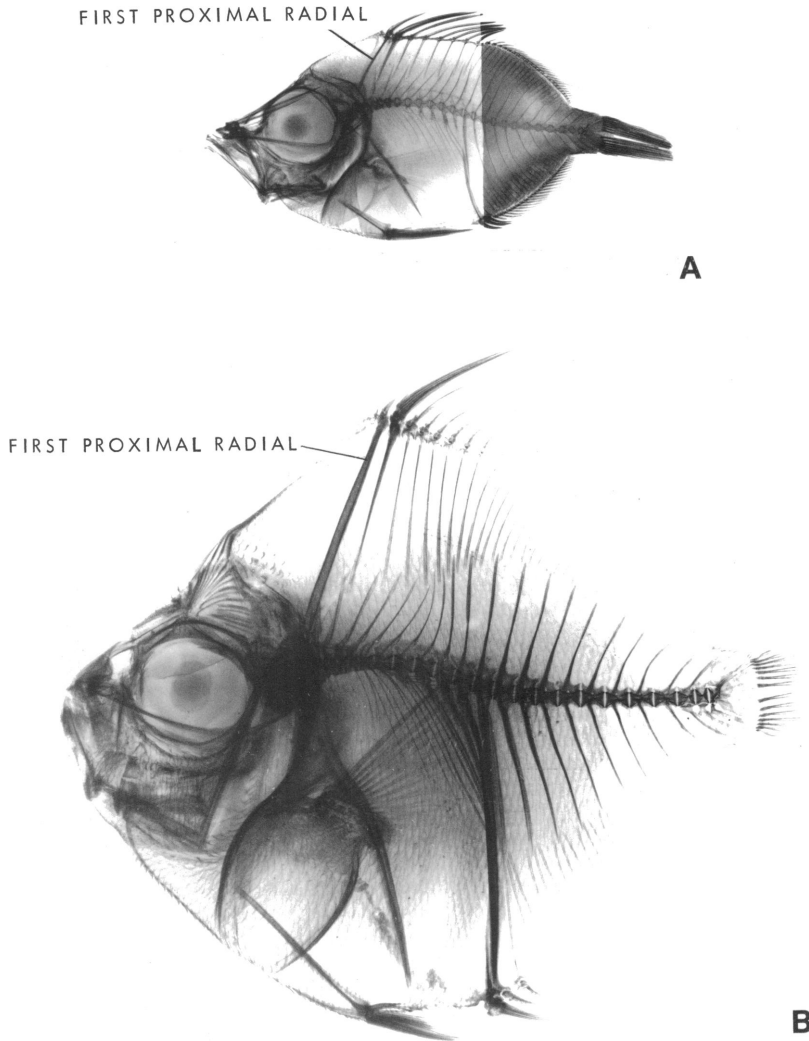
A

FIRST PROXIMAL RADIAL

B

FIG. 17. Caproids, radiographs of skeleton. A, *Capros aper* (Linnaeus), AMNH 51498. B, *Antigonia combatia* Berry and Rathjen, AMNH 2946.

canthoids are genera such as *Macrorhamphosodes* and *Halimochirurgus* in which the tiny jaw bones are situated at the tip of a long, tubelike snout made up of the palatoquadrate and vomer. All zeiforms and the short-snouted triacanthoids have an elongate rostral cartilage near the distal tip of the ascending process. All zeiforms examined, except the grammicolepid, *Xenolepidichthys* (fig. 28C), have a pronglike postmaxillary process. This process is not known in any triacanthoid. The derived character described here refers only to the long ascending process and its elongate rostral cartilage and the very restricted alveolar process. The feature of a distinct neck between the alveolar process and an integrated ascending-articular process is approached by the conditions in such beryciform groups as anomalopids, monocentrids and holocentrids, among others. The zeiform-tetraodontiform pattern differs from this more primitive condition in having a nar-
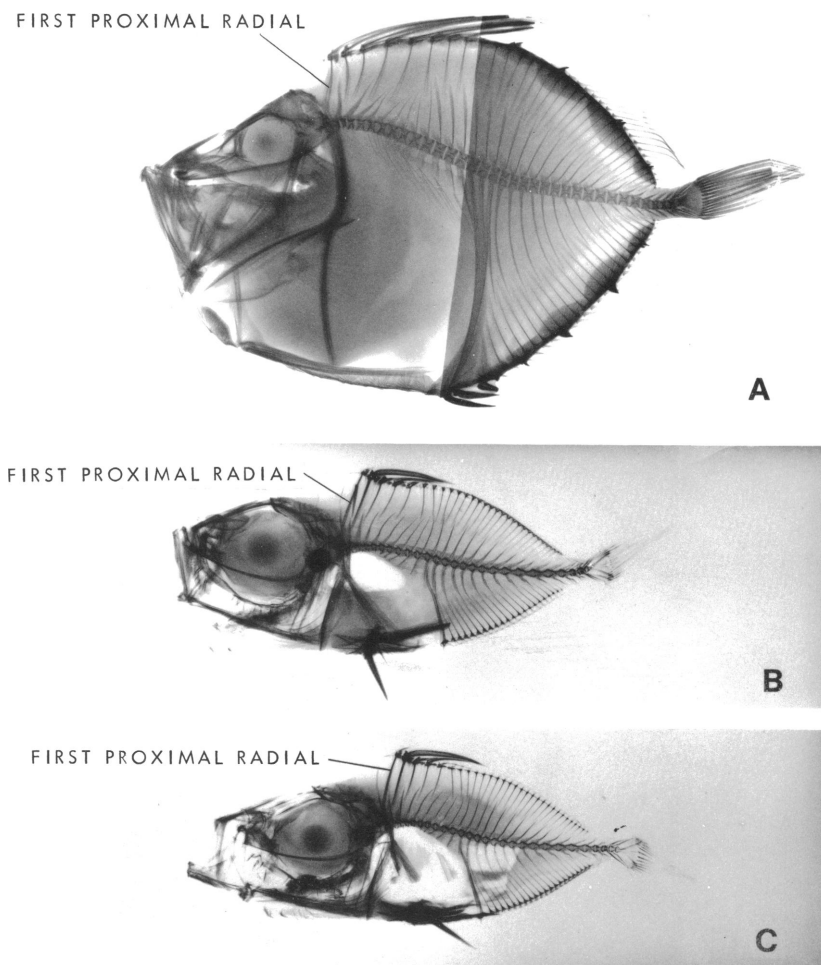
FIG. 18. Zeoids, radiographs of skeleton. A, *Zenopsis conchifera* (Lowe), AMNH 29457. B, C, *Zenion hololepis* (Goode and Bean), AMNH 29463.

rower neck and only a remnant of the primitive notch between the ascending and articular processes (in *Antigonia, Zeus,* and *Cyttopsis*; the notch is absent in other zeiforms and in the triacanthoids). In balistoids and ostracioids the premaxillary is reduced to a small triangular bone without clear demarcation among ascending, articular, and alveolar parts; in *Triodon* and tetraodontoids the premaxillary forms a parrot-like beak.

In acanthuroids (fig. 30) the premaxillary develops much as it does in balistoids and ostracioids and among the group including butterflyfishes, scats, and moorish idols a pre-

maxillary reduction approaching that of acanthuroids is typical. The premaxillary also forms a parrot-like beak in some acanthuroids. In acanthuroids, in the non-triacanthoid tetraodontiforms, and in some chaetodontids and pomacanthids the maxillary is greatly reduced and joined to the premaxillary so that the two upper jaw bones can act only in concert.

Data concerning the upper jaw, therefore, specify a relationship among zeiforms and tetraodontiforms, among all non-triacanthoid tetraodontiforms, and among acanthuroids, chaetodontids, pomacanthids, and
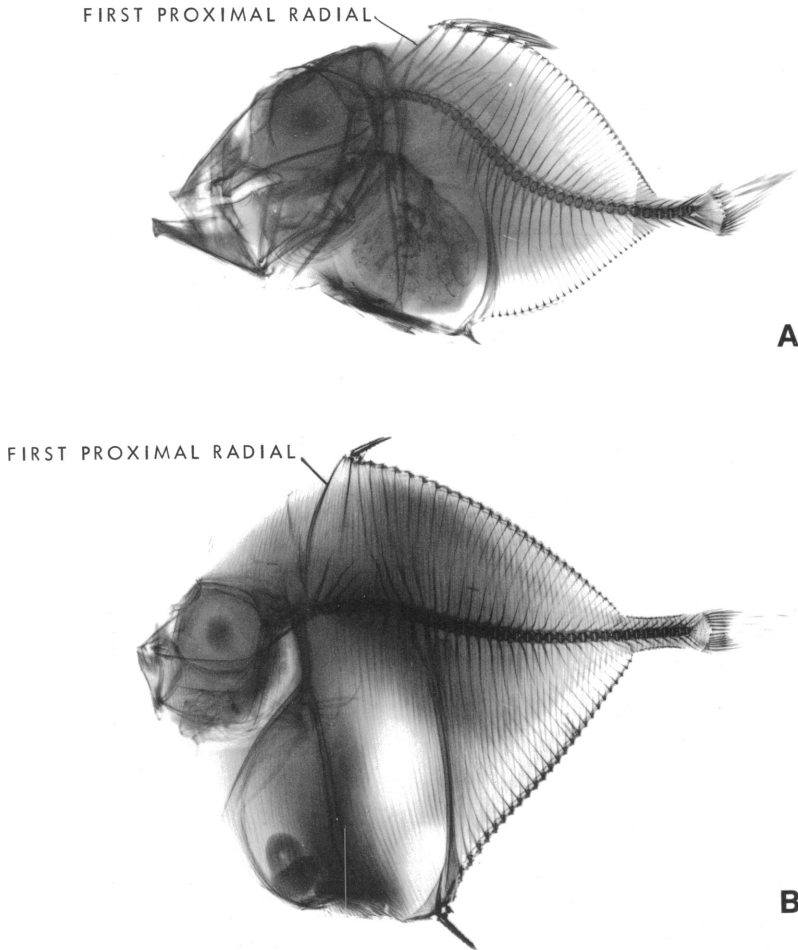
FIG. 19. Zeoids, radiographs of skeleton. A, *Cyttopsis roseus* (Lowe), AMNH 55116. B, *Xenolepi-dichthys dalgleishi* Gilchrist, AMNH 29455.

similar fishes (and see, below, a discussion of acanthuroid relationships).

CAUDAL FIN: Acanthuroids primitively have 17 principal rays, 15 branched, and numerous procurrent rays above and below in the primitive percomorph arrangement. Caproids have 12 or 14 principal rays (10 or 12 branched) and one to four procurrent rays above and below. Zeoids have 13 to 15 principal rays (11 to 13 branched) and one to four procurrent rays. Tetraodontiforms have 12 or fewer principal rays (10 or fewer branched) and, among living species, procurrent rays above (eight) and below (six) only in *Triodon*. Two fossil forms also have procurrent rays

(*Zignoichthys* with two or three rays and *Protobalistum* with one above and below). Known fossil species have the characteristic number of principal rays (12), however. Though fin ray number in general is hardly an impressive sort of evidence, it is at least consistent with an alignment of zeiforms and tetraodontiforms that excludes acanthuroids.

CAUDAL SKELETON: Zeoids share with tetraodontiforms in the possession of a full neural spine on the second preural centrum (figs. 31, 32). Caproids have either a low crest (*Capros*) (fig. 33C) or a leaf-shaped crest (*Antigonia*) (fig. 33A) on this centrum. Acanthuroids have a low crest with a strong posterior
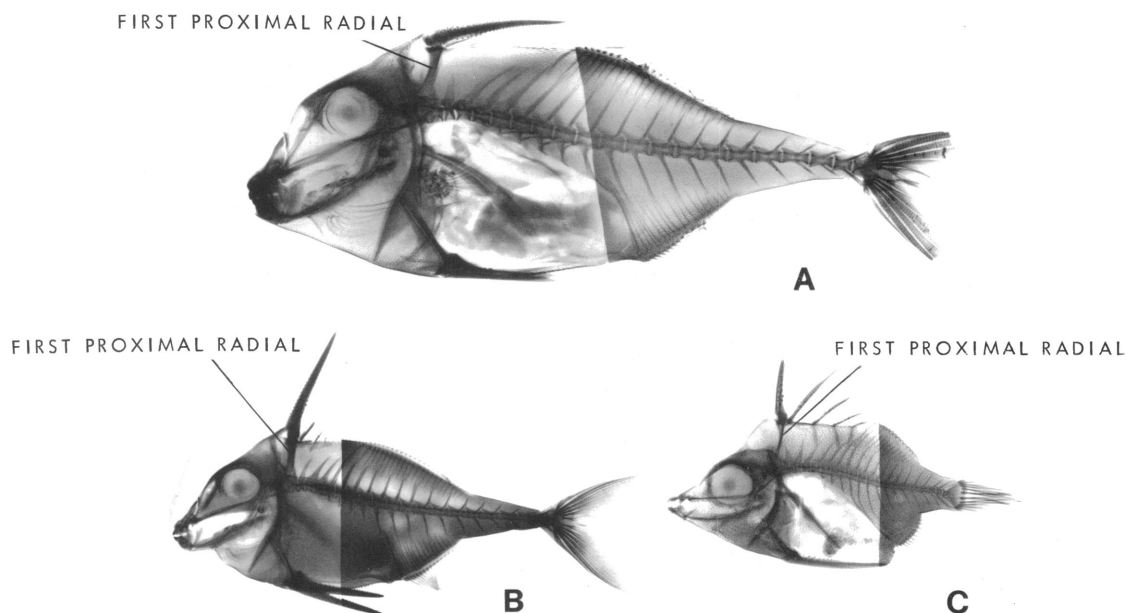
FIG. 20.   Triacanthoids, radiographs of skeleton. A, *Triacanthus biaculeatus* (Bloch), AMNH 15883. B, *Tripodichthys augustifrons* (Hollard), AMNH 32989. C, *Triacanthodes anomalus* (Schlegel), AMNH 55115.

process that extends over the uroneural on the terminal half-centrum (fig. 34). In order to understand why these data reject a theory of relationship of acanthuroids with either zeiforms or tetraodontiforms it is necessary to review a more fundamental problem concerning teleostean caudal skeleton anatomy.

Rosen (1973) argued against the idea that *Elops* possesses a caudal anatomy primitive for all living teleosts on the grounds that elopids have only a half neural spine on the second preural centrum (NPU$_2$). The importance of this observation is that other tailed elopomorphs (megalopids and albulids) have a full spine on PU$_2$, as do clupeomorphs and primitive euteleosteans and the sister group of all the foregoing, the osteoglossomorphs. Among euteleosteans a full spine is present in ostariophysans, esocoids, argentinoids and salmonoids[2] and it is only in neoteleosteans (figs. 35, 36) that this spine undergoes a re-

duction until, at the ctenosquamate level, it is primitively represented as a low crest. A full spine on PU$_2$ has been secondarily redeveloped in a number of ctenosquamate groups, such as troutperch, cods and labyrinth fishes, probably by more than one mechanism.

In its reduced state, the neural spine and arch on PU$_2$ (NPU$_2$) assumes a variety of shapes and sizes and relationships to the first uroneural. In a primitive ctenosquamate, such as a myctophid, the PU$_2$ crest is a low, irregular structure overlain by the stegural process of the first uroneural. This stegural process, which is a membrane-bone extension forward of the dorsal edge of the uroneural, extends between the PU$_2$ crest and the first epural, in some cases nearly contacting the neural spine on PU$_3$ (salmonoids). Among acanthomorph ctenosquamates this stegural is always smaller, not extending beyond the hind margin of the PU$_2$ crest; in this state the first epural can now, and often does, extend forward above the tip of the stegural as far forward as the dorsal margin of the PU$_2$ crest

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[2] The osmeroid and stomioid conditions will be discussed in a forthcoming paper.
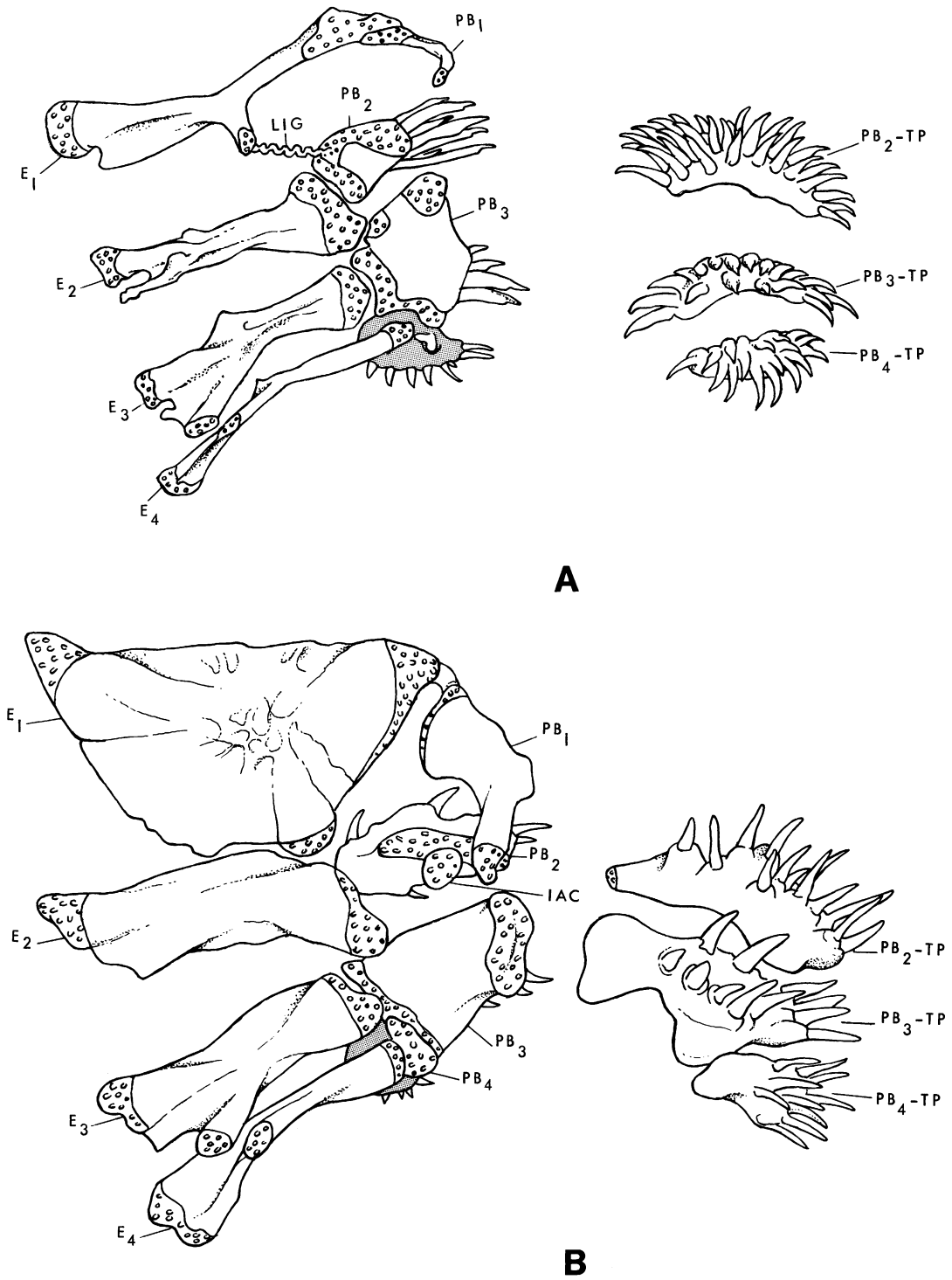
FIG. 21. Dorsal gill arches. A, *Capros aper* (Linnaeus), AMNH 55117. B, *Antigonia capros* Lowe, AMNH 29461.
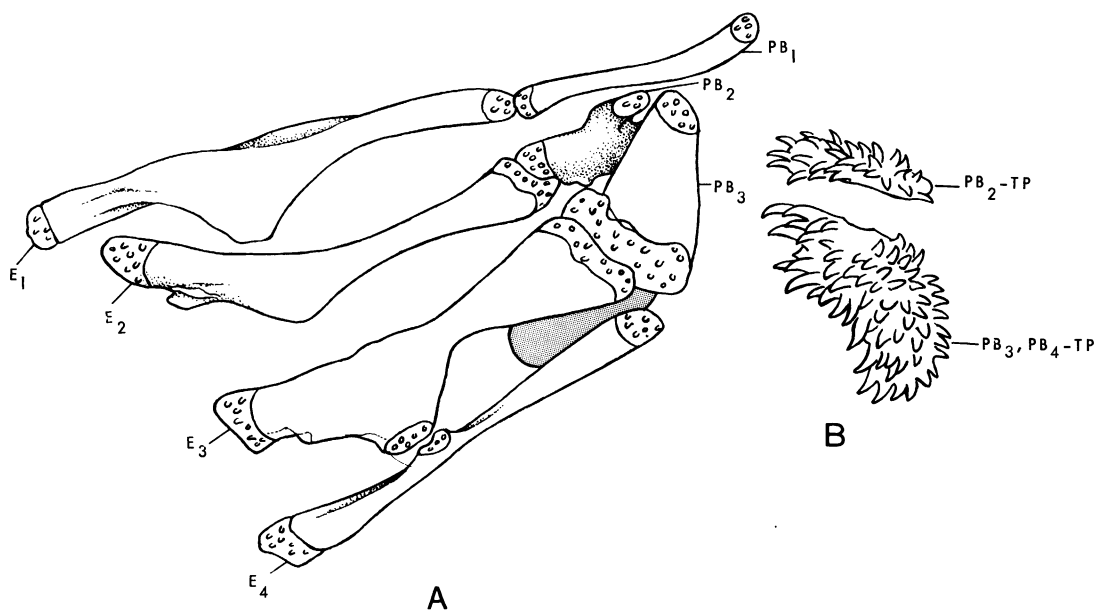
FIG. 22.   Dorsal gill arches of *Zenion hololepis* (Goode and Bean), AMNH 29463. A, dorsal view, left arches. B, ventral view, left pharyngobranchial toothplates.
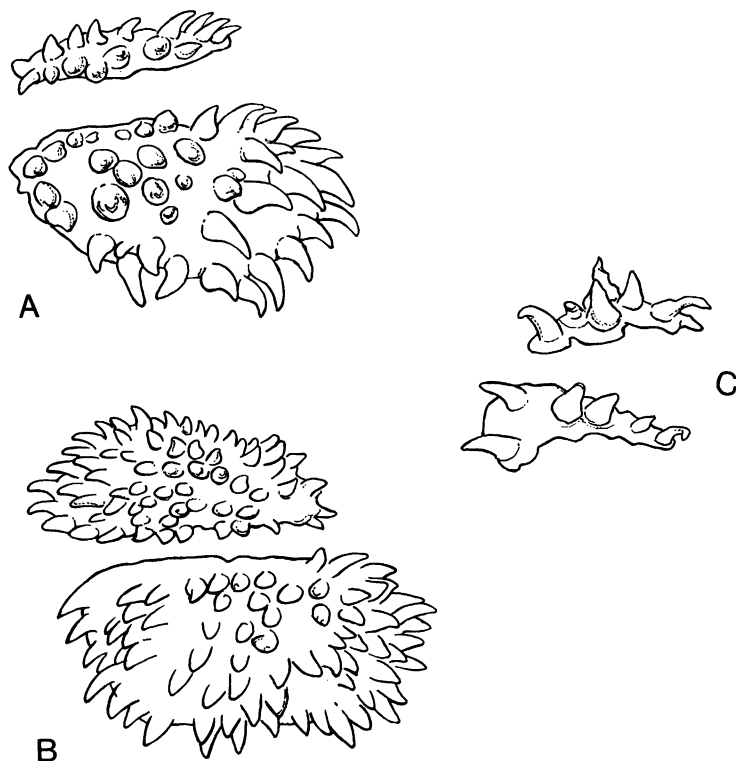
FIG. 23.   Ventral view of left pharyngobranchial toothplates in zeoids. A, *Parazen pacificus* Kamohara, AMNH 29459. B, *Cyttopsis roseus* (Lowe), AMNH 29460. C, *Xenolepidichthys dalgleishi* Gilchrist, AMNH 29455.
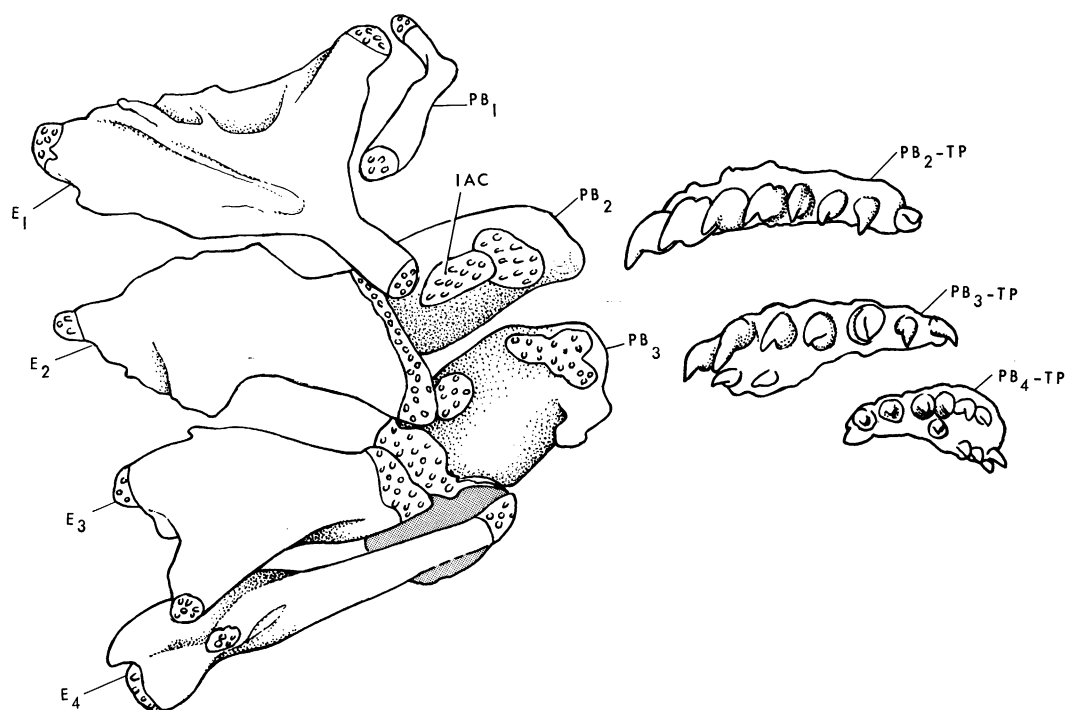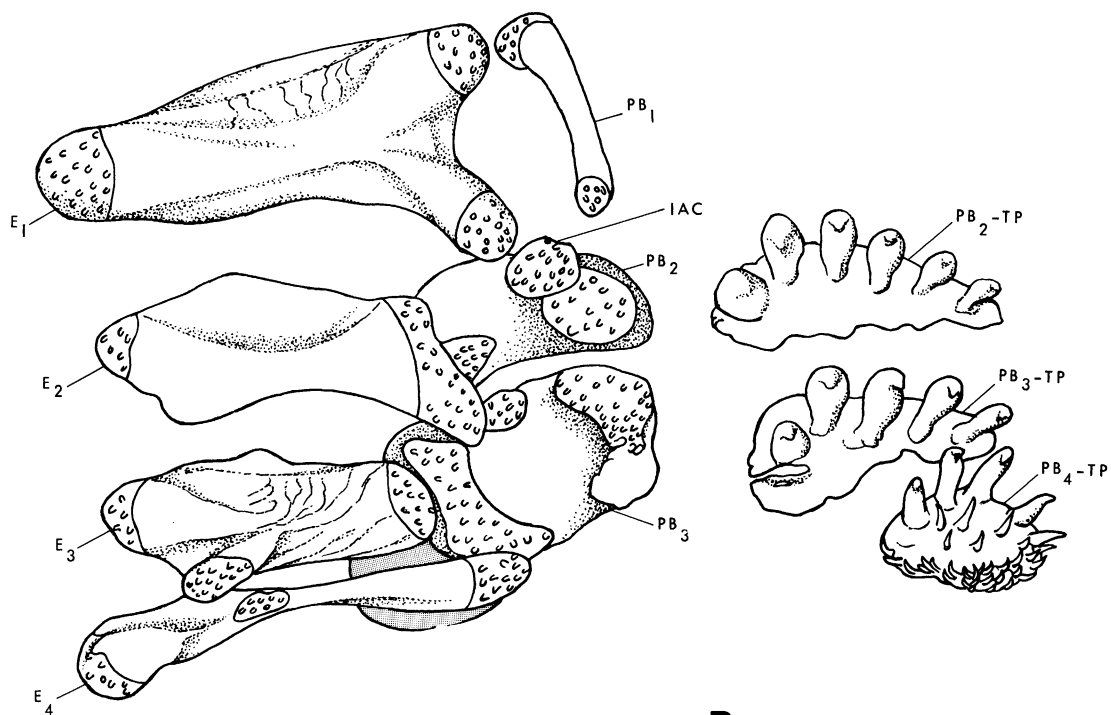
FIG. 24A, B. Dorsal gill arches. A, *Triacanthodes ethiops* Alcock, NSNM 93491. B, *Hollardia hollardia* Poey, USNM 187811 (see following page for fig. 24C).
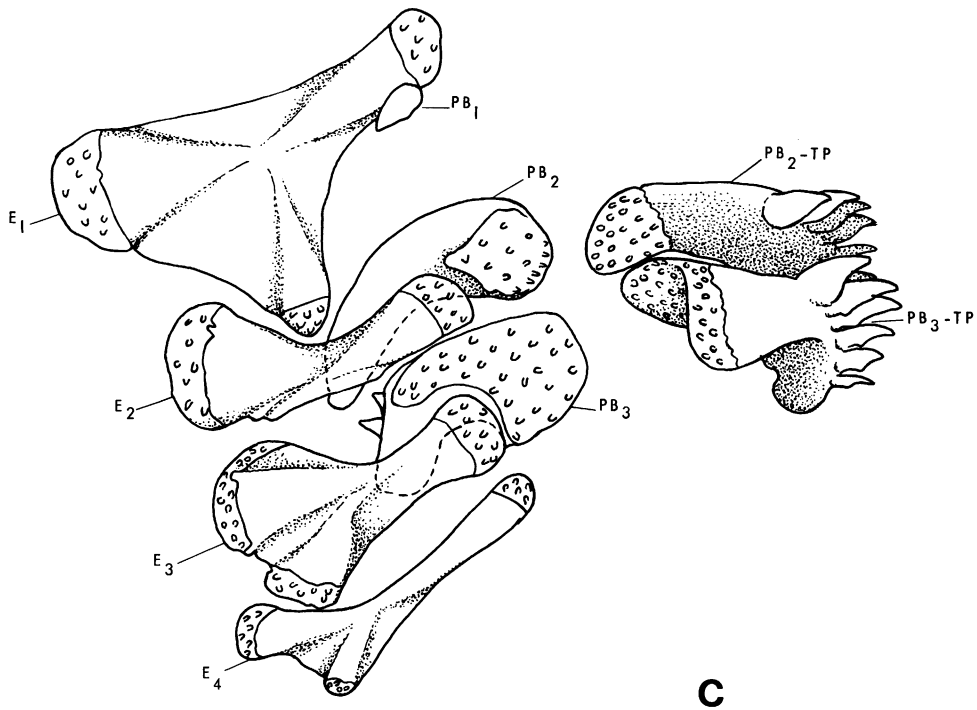
FIG. 24C.   Dorsal gill arches. *Balistes capriscus* Gmelin, AMNH 22008 (see preceding page for figure 24A and B).

(figs. 35H–Q). A still more derived condition, as seen in holocentrids and pomatomids (Rosen 1964, fig. 23D), for example, is to have the stegural reduced to a low peak or irregular flange and a posterior process on the PU_2 crest extending posteriorly over the uroneural. The most derived condition, characteristic of most of the perchlike fishes, is to be without a well-developed stegural and to have the posterior process of the PU_2 crest extending along the dorsal margin of the first uroneural as far back as the ventral tip of the second epural (fig. 37I). The differences among these varying conditions can be viewed as a function of where the tip of the stegural meets the crest of PU_2 or its posterior process in relation to underlying centra. In the mycto-phid condition (I) the stegural separates NPU_2 from the first epural (fig. 35G). In the prim-itive acanthomorph condition (II) NPU_2 overrides the stegural and underlies the prox-imal end of the first epural (figs. 37B–K). In the holocentrid, NPU_2 and the stegural abut

roughly over the intervertebral joint between PU_2 and the terminal centrum ($PU_1 + U_1$ or $PU_1 + U_1 + U_2$) (fig. 37A) (condition III), and in the perchlike fishes (condition IV) NPU_2 overrides the first uroneural and ends well back over the terminal centrum ($PU_1 + U_1 + U_2$) (figs. 37D–I). Conditions I to IV are also reflected, but less precisely, in the extent to which the anterior epurals override the crest on PU_2: in I, not at all; in II and III the first epural lies over the posterior or dor-sal part of the crest; and in IV the first two epurals may lie over the crest and its posterior process and the first epural may extend as far forward as the anterior margin of the crest near the base of the neural spine on PU_3.

Condition II may be found among many groups (fig. 36A–Q) that are considered in some current classifications as members of the Perciformes: kurtids, gobioids, stromat-eoids, scombroids, scorpaenoids (fig. 36D), and blennioids. It is also characteristic of ath-erinomorphs, veliferids, stephanoberyci-

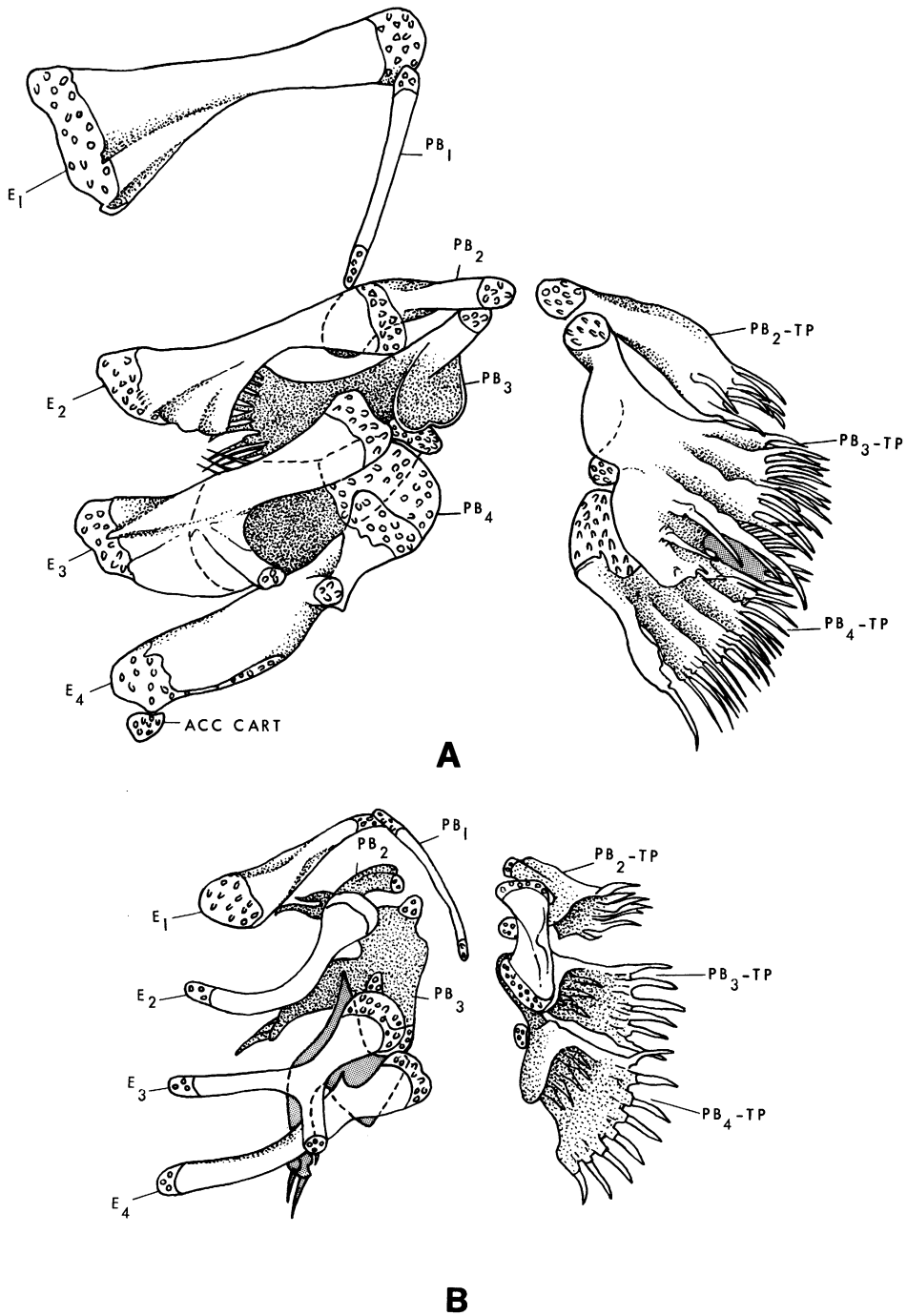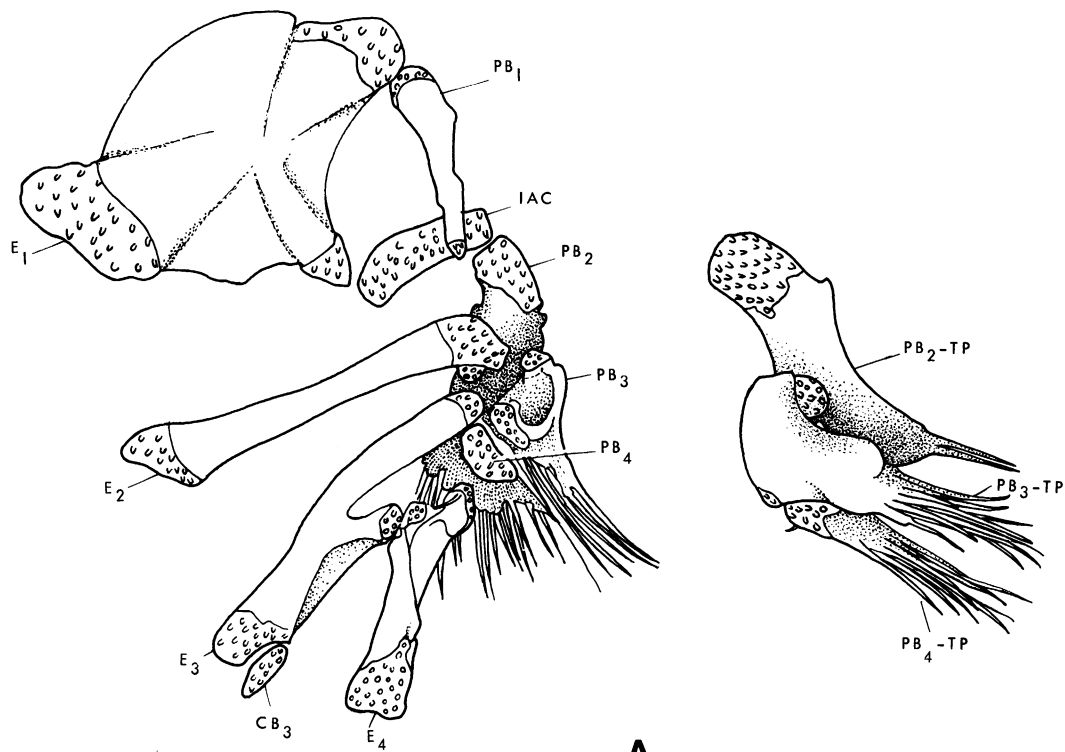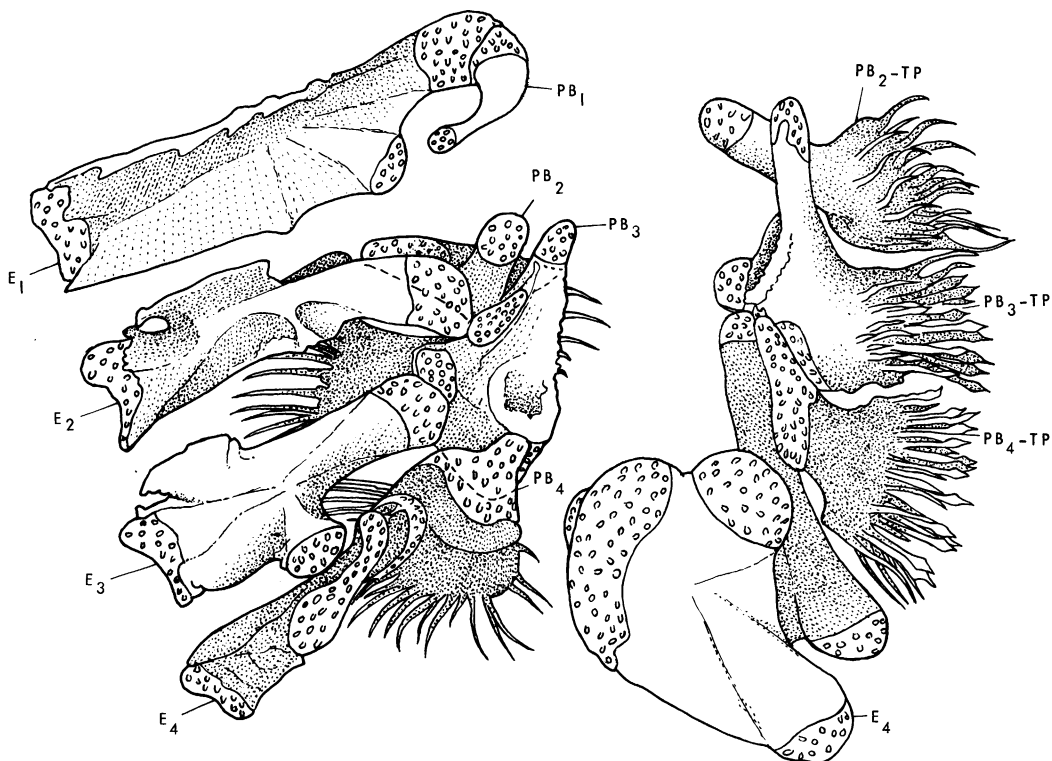FIG. 25. Dorsal gill arches. A, *Acanthurus chirurgus* (Bloch), AMNH 21806. B, *Siganus* sp., AMNH 27474.

forms, and beryciforms other than holocen-
trids (the latter showing a more derived

condition [III] occurring in scatophagids, po-
macanthids, chaetodontids, zanclids, some

FIG. 26.   Dorsal gill arches. A, *Chaetodon xanthurus* Bleeker, AMNH 38110. B, *Scatophagus argus* (Linnaeus), AMNH 20329.

ephippids, moronids, coryphaenids, rachycentrids, and pomatomids). In relation to the present problem, caproids have condition II and acanthuroids, condition IV, indicating the presence in the latter of a very low stegural and long posterior process from the crest of PU_2, and a large stegural and no posterior process in caproids. The conclusion to be reached from these observations is that acanthuroids belong to an apomorph perchlike group of acanthopterygians that does not include caproids and, by extension, zeoids, and that the Perciformes as presently formulated is not monophyletic.

The question that remains is whether the derived similarity between zeoids and tetraodontiforms in having a full spine rather than a low crest on PU_2 is significant. Are the ontogenies of zeoid and tetraodontiform PU_2 spines the same or different? A full spine on PU_2 in a ctenosquamate can, in theory, be achieved by at least three means: (1) fusion of the first epural to the crest on PU_2; (2) secondary elongation of the crest on PU_2; and (3) replacement of PU_2 with PU_3 by dropping out the PU_2 segment during development (fig. 31B, 33B). It is my view that, in the existing absence of detailed ontogenetic data, one can say only that the presence of three epurals in zeiforms rules out the first explanation for them. Nevertheless, the occurrence of a full spine and a greatly reduced first uroneural without a stegural in zeiforms and triacanthoids is consistent with a proposed sister-group relationship and is treated as a synapomorphous feature subject, like all synapomorphies, to reinterpretation with additional data.

HYOID APPARATUS: Zeoids and tetraodontiforms share a hyoid apparatus in which the posterior ceratohyal is greatly foreshortened, the anterior ceratohyal has an ossified posteroventral expansion that extends below the posterior ceratohyal, and the bases of the posterior four branchiostegals are clustered together along the posterior ossified edge of the anterior ceratohyal. The first two of these clustered branchiostegals insert directly on the posteroventral expansion of the anterior ceratohyal and the third and fourth rays generally insert just above the first and second where the anterior and posterior ceratohyals are joined by cartilage. The branchiostegals
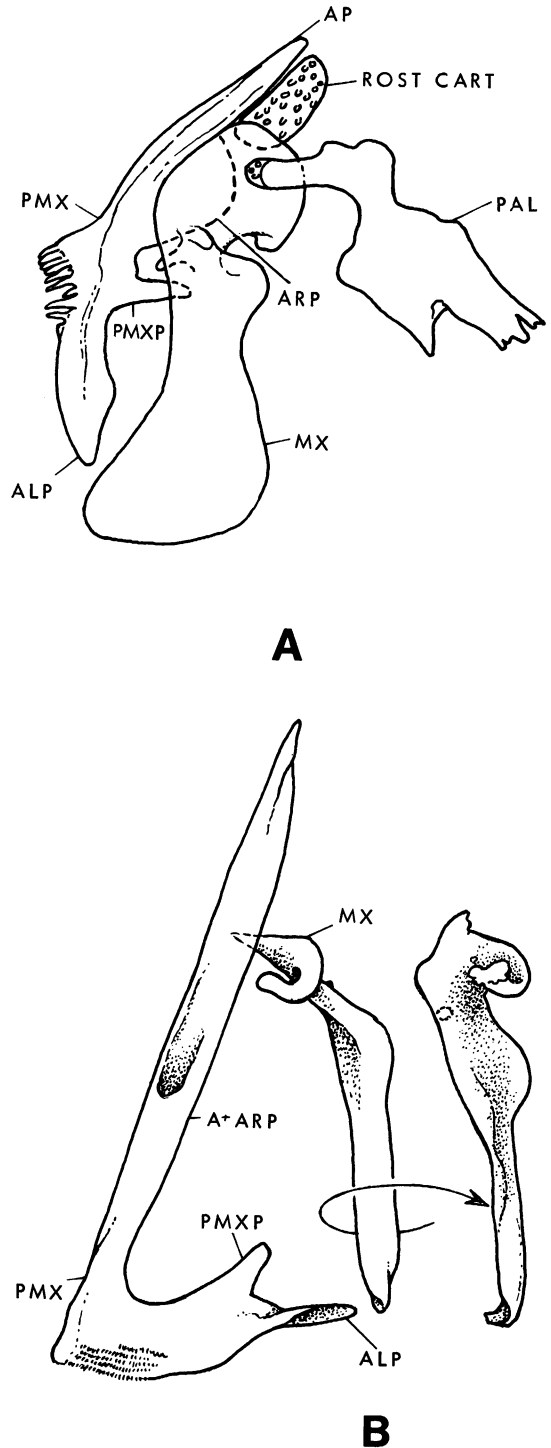

A

B

FIG. 27. Upper jaw bones. A, *Antigonia capros* Lowe, AMNH 29461. B, *Capros aper* (Linnaeus), AMNH 482.
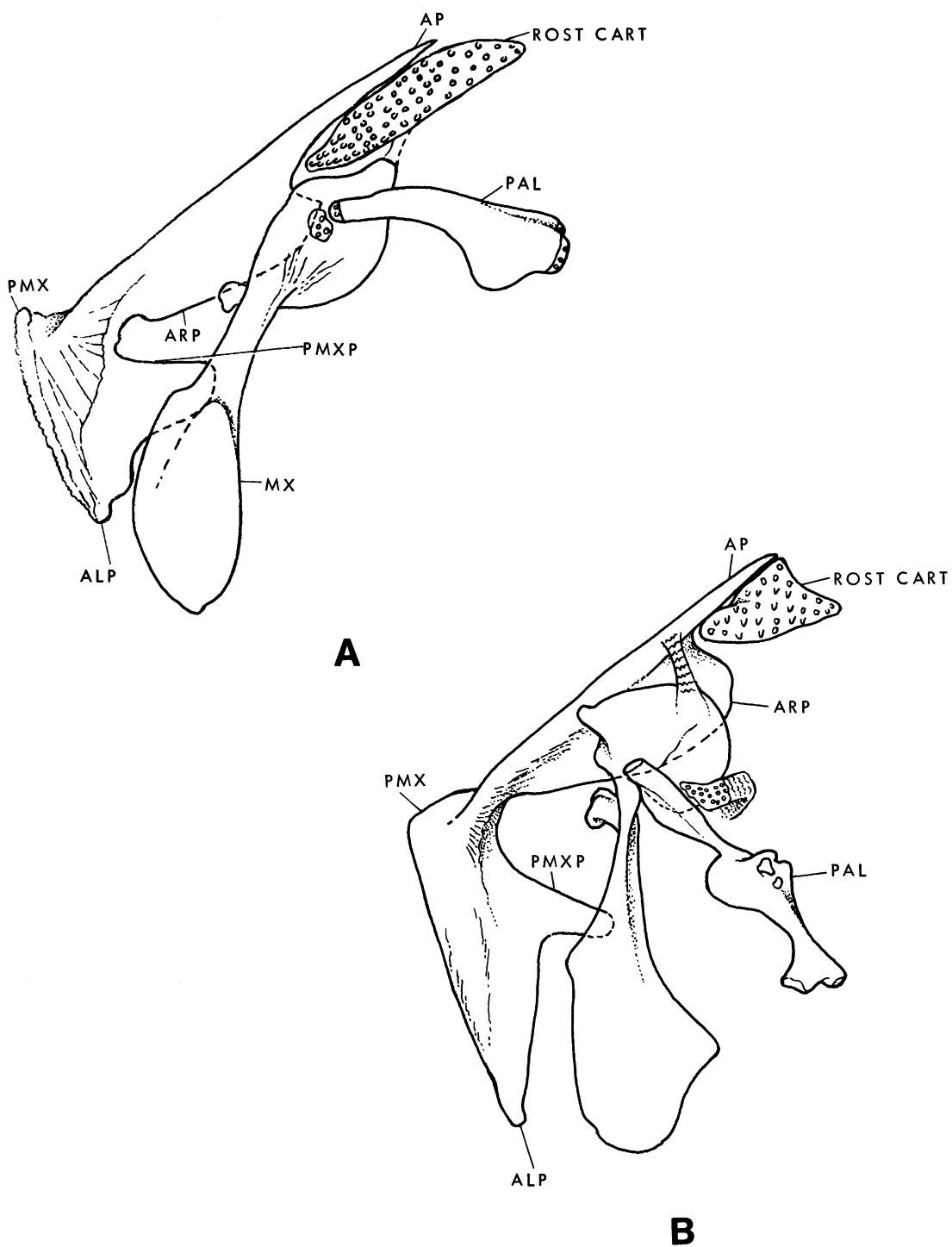
FIG. 28A, B.   Upper jaw bones. A, *Cyttopsis roseus* (Lowe), AMNH 29460. B, *Zenion hololepis* (Goode and Bean), AMNH 29463.

C
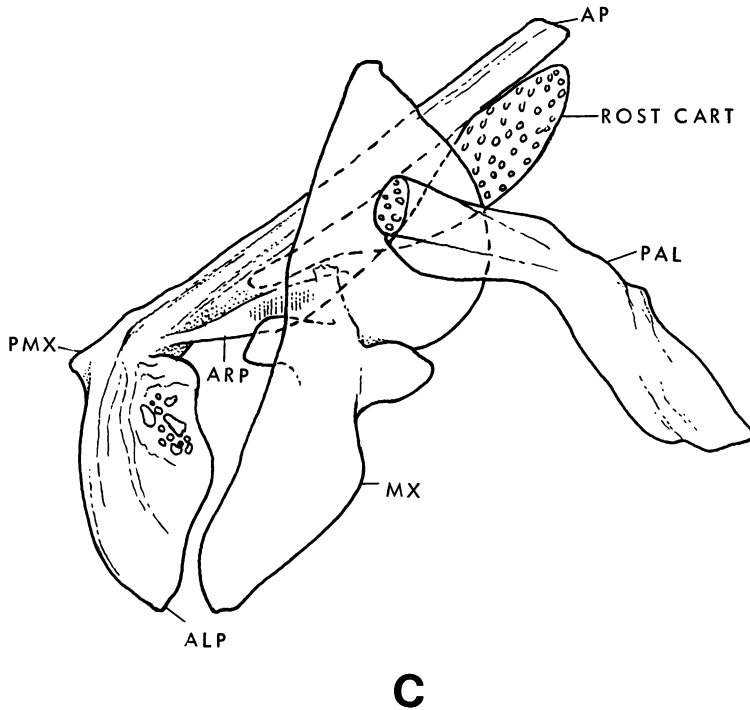
FIG. 28C.   Upper jaw bones. *Xenolepidichthys dalgleishi* Gilchrist, AMNH 29455.

are only little arched and extend sharply backward rather than downward, the result being that the shaft of at least the fourth branchiostegal overlaps the ventrolateral surface of the posterior ceratohyal. Zeoids have three anterior branchiostegals (rarely four, in zeniontids where a fourth ray is present on one side only), tetraodontiforms generally no more than two (a specimen of *Triacanthodes ethiops* has three well-developed anterior rays on the right side and two on the left).

Caproids and acanthuroids have a more generalized hyoid apparatus in which the anterior and posterior ceratohyals are equal in height and the posterior four branchiostegals are distributed on both bones, projecting first in a predominantly ventral direction, then curving backward along the margin of the opercular flap. Caproids have two anterior branchiostegals and acanthuroids usually have one (some specimens of *Naso* may have none; Tyler, 1970). Among other acanthuroid-like fishes examined, chaetodontids have

from one to three anterior rays, but *Platax, Pomacanthus,* and *Scatophagus* have two.

Another feature present in some zeoids, the so-called beryciform foramen, which also occurs in various primitive teleosts, has been used to argue that zeiforms are much too primitive to align with some perciform groups. The foramen does not occur in acanthuroids (although siganids have a notch which is a remnant of it) or the chaetodontids examined. It is also absent in *Capros* and the zeoid *Zenion* where a siganid-like notch is present. It is present, however, in *Antigonia,* other zeoids studied, *Platax,* and in *Pomacanthus* and *Scatophagus* where the foramen is defined dorsally by cartilage rather than bone.

These data imply a relationship between zeoids and tetraodontiforms, and another between acanthuroids and chaetodontids. This trait is discussed further, below, under acanthuroid relationships.
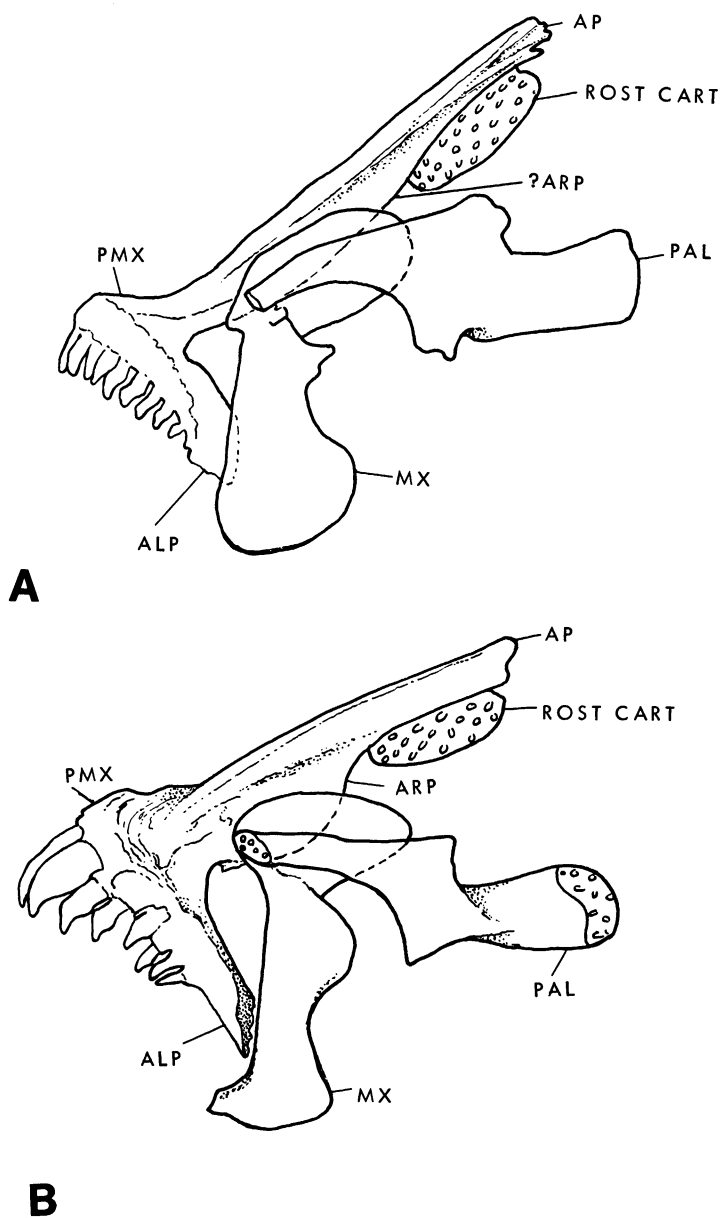
FIG. 29.   Upper jaw bones. A, *Triacanthodes ethiops* Alcock, USNM 93491. B, *Hollardia hollardia* Poey, USNM 187811.

SYNAPOMORPHY SCHEME

Of the 20 characters included in the character-state tree illustrated in figure 38, eight are discussed above. Most of the additional characters are either sufficiently unproblematical so that no extended discussion of them is warranted or they are dealt with in detail by Tyler (1980). Justification for proposing the following scheme must involve recognition that caproids and zeoids are
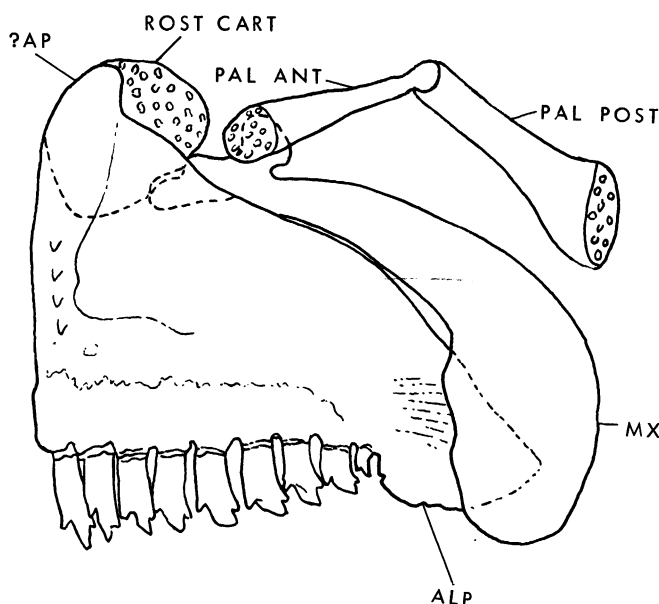
FIG. 30. *Siganus spinus* (Linnaeus), AMNH 29387, upper jaw bones.

monophyletic and that triacanthoids are part of a monophyletic Tetraodontiformes. The latter relationship is supported by six characters (12 to 17), as given, below. The caproid fishes share derived posterior pelvic processes that are sutured together in the midline and flare out laterally into winglike plates, a similar feature occurs also in holocentrids but its condition is judged to be independent since holocentrids lack the features that acanthurids and chaetodontids share with zeiforms-tetraodontiforms (see fig. 36 and pp. 19–27) as well as the seven features uniting caproids with zeoids-tetraodontiforms. The zeoid fishes share a unique combination of characters: no fourth pharyngobranchial or toothplate; no uncinate process on the first epibranchial; dorsal, anal, and pectoral fin rays unbranched; bases of dorsal and anal fins flanked by spines, spiniferous bony plates, or by anacanthous bony plates. Caproids, zeoids and tetraodontiforms (but not acanthuroids) share:

1. Saccular otolith (sagitta) higher than long and constricted fore and aft in the region of the sulcus.
2. Dorsal and anal fin radials symmetrical, consisting of distal radials equidistant between upright proximal radials (this will be a synapomorphy of a larger group if either monocentrids or ephippids are the immediate outgroup).
3. Radial supporting first dorsal fin spine robust, columnar, inserted ventrally between the neural arches of the first vertebrae and the occipital bones of the skull to which they are firmly united.
4. Parasphenoid with a tunnel-like opening to the posterior myodome.
5. Interoperculum elongate, bladelike or feather-shaped.
6. Premaxillary ascending and articular processes elongate and intimately united above a distinct neck that separates them from a very short alveolar process.
7. Caudal fin with 15 or fewer principal rays.
8. Caudal skeleton with a full spine on the second preural centrum and a greatly reduced first uroneural with no stegural.
9. Greatest depth of caudal peduncle less than 13 percent of standard length.
10. Hyoid apparatus with the posterior ceratohyal very short and shallower than the adjoining part of the anterior centohyal; the bases of the four posterior
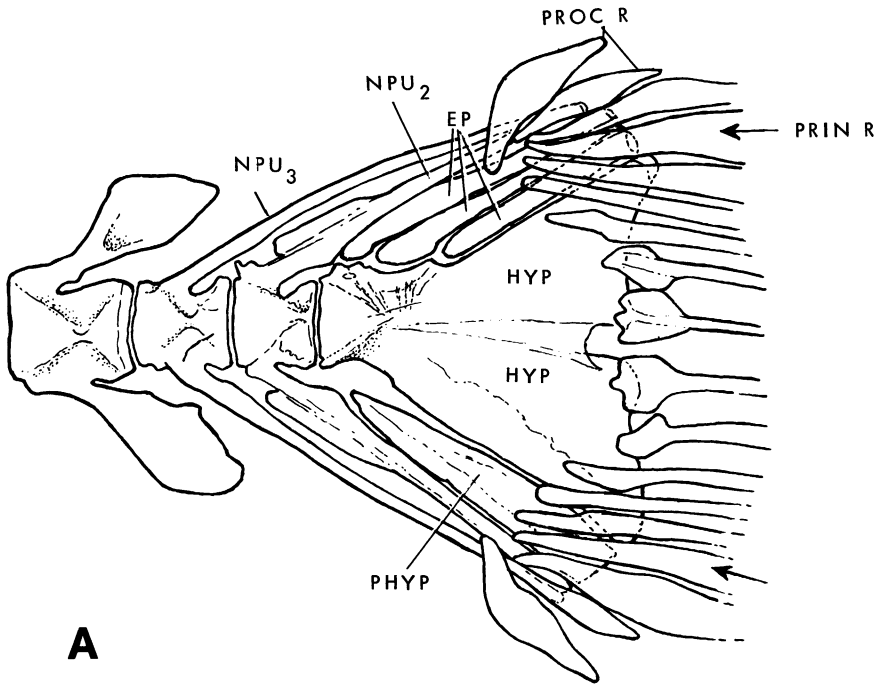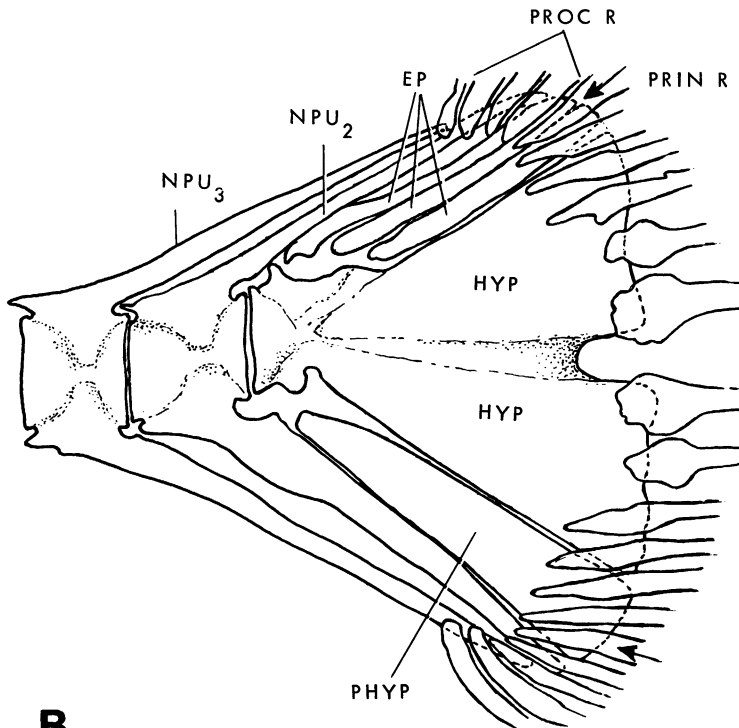
FIG. 31A, B.   Caudal skeletons. A, *Zenion hololepis* (Goode and Bean), AMNH 29463. B, *Cyttopsis roseus* (Lowe), AMNH 29460.
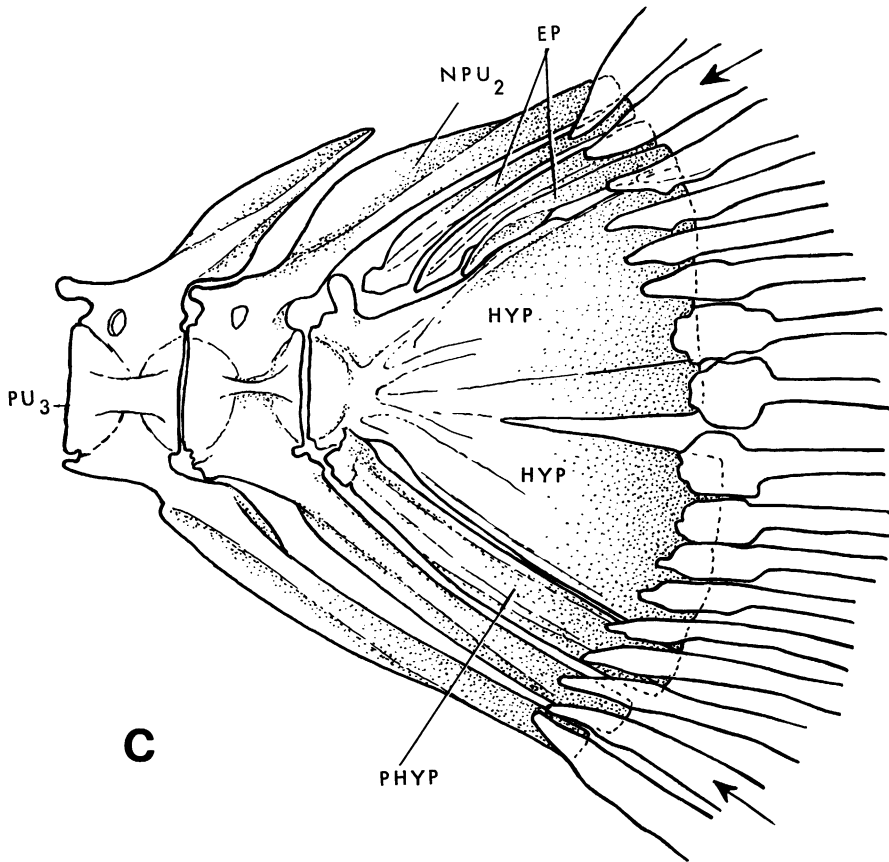
FIG. 31C.   Caudal skeleton. *Xenolepidichthys dalgleishi* Gilchrist, AMNH 29455.

branchiostegals clustered on the postero-ventral margin of the ossified anterior ceratohyal.

11. Interoperculum long and very slender, acinaciform, and only loosely bound to the preoperculum by connective tissue.

Within the Tetraodontiformes triacanthoids share with other members:

12. No anal spines.
13. Caudal fin with 12 or fewer principal rays.
14. No infraorbitals.
15. No parietals.
16. Small, slitlike gill opening just anterior to the pectoral fin base.
17. Pelvic girdles closely joined along their lengths and pelvic fin rays reduced or absent.

Balistoid tetraodontiforms share with ostra-cioids, *Triodon,* and tetraodontoids:

18. Interoperculum rodlike.
19. Pelvic girdle, when present, laterally compressed, shaftlike, and pelvic spine reduced or absent.

Ostracioids, *Triodon,* and tetraodontoids share:

20. Dorsal fins and radials remote from occipital region of skull.

CHARACTER CONFLICTS

Within the last group defined by character 20 there are a number of characters that produce conflicting alignments. *Triodon* is linked to tetraodontoids by the presence of beaklike
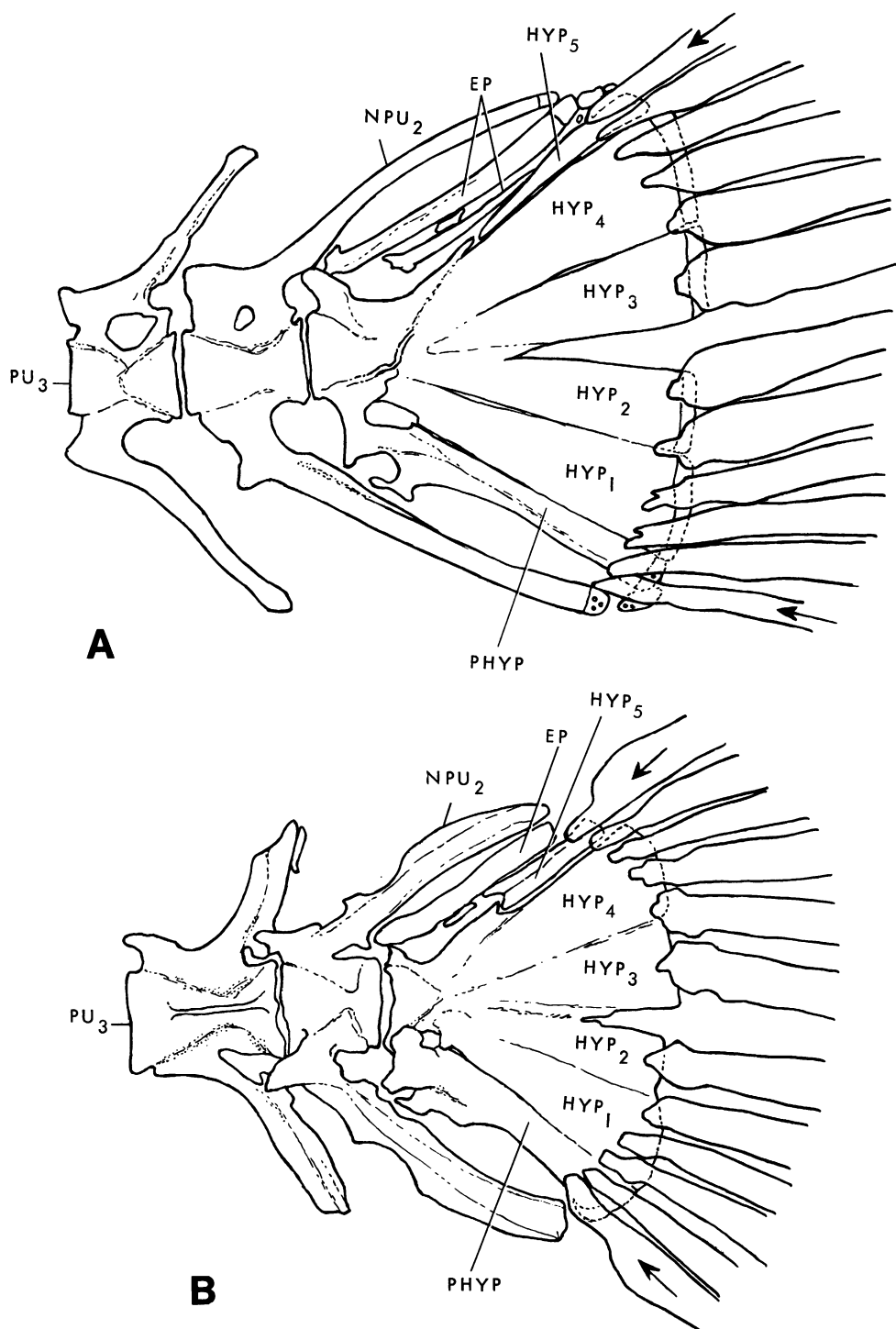
FIG. 32.   Caudal skeletons. A, *Hollardia hollardia* Poey, USNM 187811. B, *Triacanthodes ethiops* Alcock, USNM 93491.
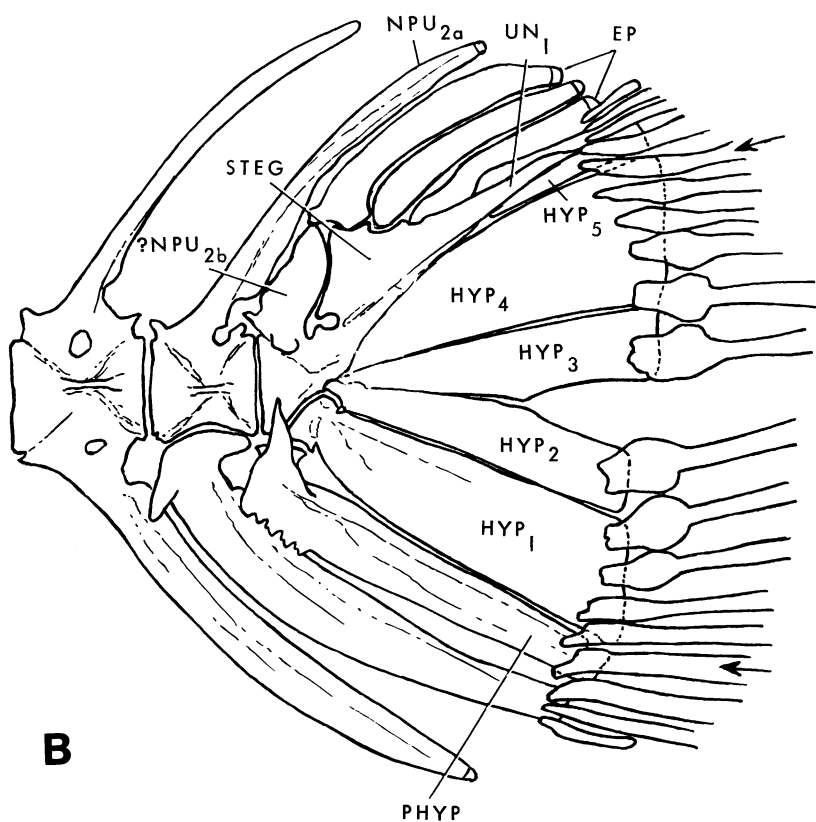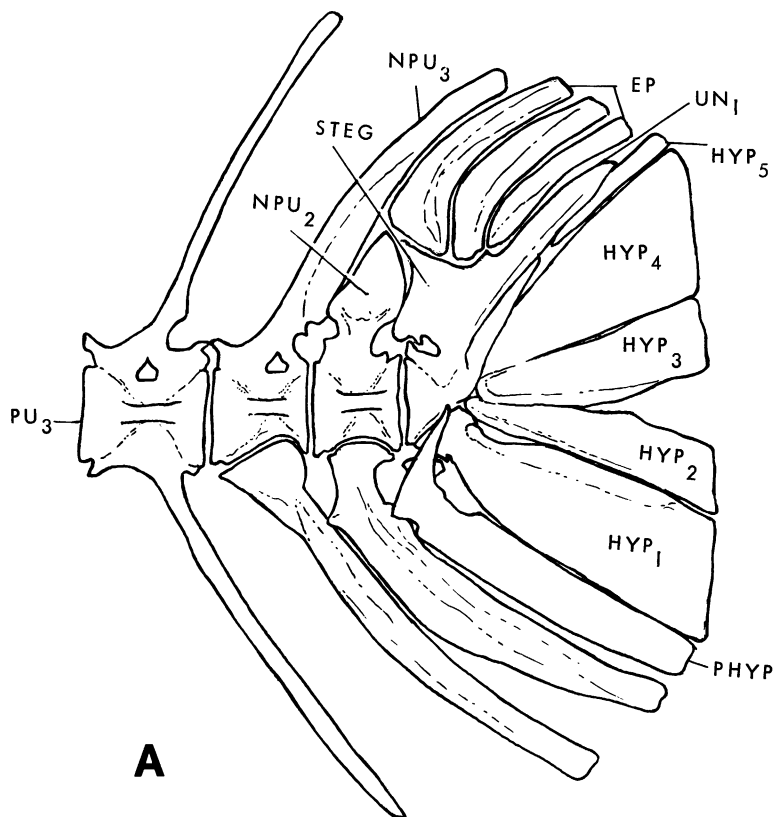
FIG. 33A, B. See following page for caption.
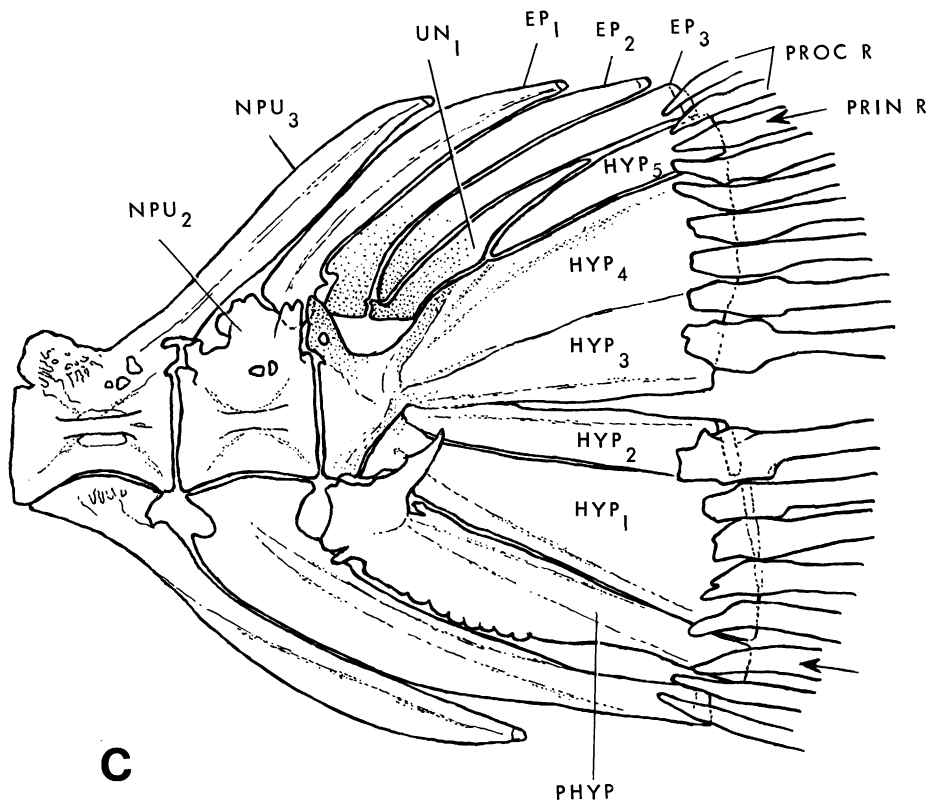
FIG. 33C.   Caudal skeletons. A, *Antigonia capros* Lowe, AMNH 29461. B, same as A, but showing a specimen with the PU₂ crest and PU₃ spine displaced posteriorly by one metamere. C, *Capros aper* Linnaeus, AMNH 482 (see preceding page for figure 33A and B).

jaws and a ventral spur on the interoperculum, and by the loss of the posttemporal bone. The absence of a pelvic girdle, hypural fusion and general reduction of the caudal skeleton, absence of an uncinate process on the first epibranchial bone, and the complete absence of ribs (pleural and epipleural) link ostracioids and tetraodontoids.

Five other character conflicts occur at various levels within this synapomorphy scheme, but neither these nor the foregoing will yield a more parsimonious cladogram than that shown in figure 38.

PLEURAL RIBS: Pleural ribs occur, and are well developed in *Capros, Antigonia,* and *Triodon.* They are present but less strongly developed in the balistoid *Pseudaluteres nasicornis* (Tyler, 1980, fig. 114). Agassiz (1842) illustrated two specimens of the Oligocene triacanthid *Acanthopleurus serratus,* showing

what appear to be pleural ribs on the abdominal vertebrae. Colin Patterson kindly checked all triacanthid fossils in the British Museum of Natural History, including the specimens on which Agassiz's figures were based, and informed me that none of the specimens shows any indication that such ribs were present. Assuming the correctness of the present theory of relationships (fig. 38), pleural ribs were either lost several times (in zeoids, triacanthoids, balistoids except for *Pseudaluteres,* and in ostracioids and tetraodontoids or their common ancestor if they are sister groups. Alternatively, ribs would have had to have been developed twice, in *Pseudaluteres* and *Triodon.*

PROCURRENT CAUDAL FIN RAYS: Dorsal and ventral procurrent rays (indicated by lower case Roman numerals before and after the principal ray counts of unbranched and
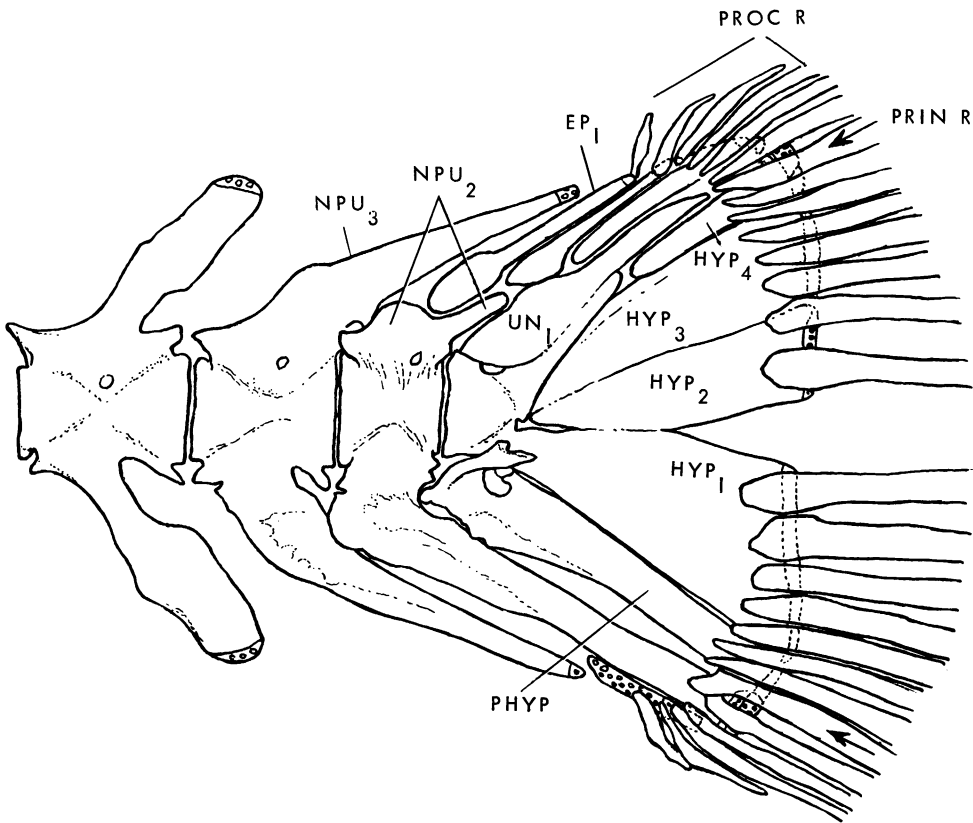
FIG. 34. *Zebrasoma veliferum* (Bloch), AMNH 38121, caudal skeleton.

branched rays in the upper and lower fin lobes) occur in *Capros* (i 1,6-6,1 i), *Antigonia* (iv 1,5-5,1 iv or iv 1,5-5,1 iii), zeoids such as *Zeus* (i 6-7 i: there are no branched rays in this taxon), *Cyttopsis* (iv 1,5-6,1 iv), *Zenion* (iii 1,5-6,1 ii), *Xenolepidichthys* (i 1,6-7,1 i), and in *Triodon* (viii 1,5-5,1 vi), among living species. Among fossil tetraodontiforms a presumed triacanthoid, the Eocene *Protacanthodes ombonii* has a procurrent ray above and below a principal count of 1,5-5,1, and the Eocene eoplectine *Zignoichthys oblongus* [which would stand between zeoids and tetraodontiforms in the cladogram because its presumed nearest ally, the Eocene *Eoplectus bloti,* has a primitive pelvic girdle and fin with a spine and four large branched rays (see character 20, above)] has two or three procurrent rays above and below a principal count of 1,5-5,1. Summarized, these data mean that procurrent rays are entirely absent

only in balistoids, ostracioids, and tetraodontoids (minus *Triodon*), if the fossils are assigned correctly; these small rays would, therefore, have had to have been lost independently in modern triacanthoids and one, two, or three times in other plectognaths depending on how the relationships of balistoids, ostracioids, *Triodon,* and tetraodontoids are resolved.

BRANCHIOSTEGAL ALIGNMENT: As noted above *Capros* and *Antigonia* have a primitive acanthopterygian arrangement of the four posterior branchiostegals on both the posterior ceratohyal and the posterior part of the anterior ceratohyal. Zeoids and most plectognaths, including triacanthoids, have a derived arrangement of all four rays articulating with the posteroventral corner of the anterior ceratohyal. A seemingly primitive alignment of these rays occurs in *Triodon,* however, and, to some degree, also in molid tetraodontoids
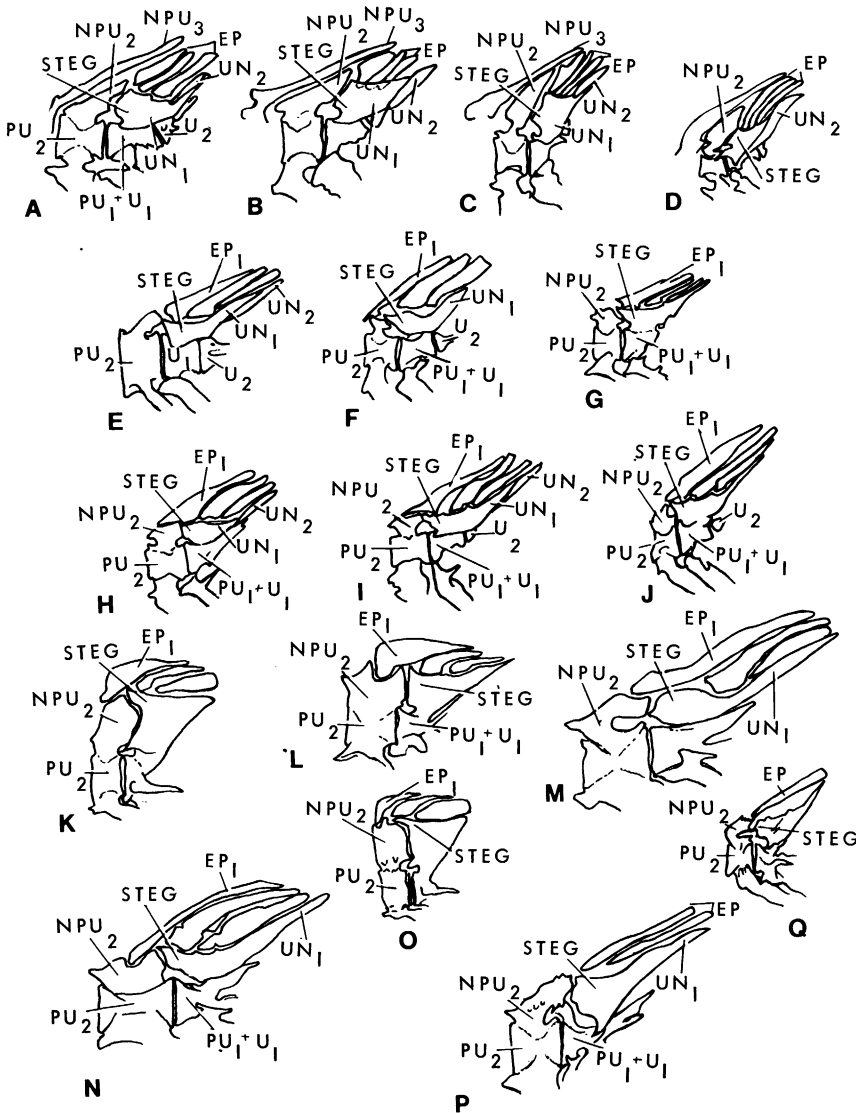
FIG. 35. Epural-uroneural complex of caudal skeleton. A, *Aulopus filamentosus* (after Rosen, 1973); B, *Chlorophthalmus agassizi* (after Rosen, 1973); C, *Scopelosaurus smithi* (after Rosen, 1973); D, *Nematonotus bottae* (after Rosen and Patterson, 1969); E, *Velifer africanus* (after Rosen, 1973); F, *Anoplogaster cornuta* (after Rosen, 1962); G, *Myctophum affine* (after Rosen, 1964); H, *Centraberyx affinis* (after Zehren, 1975); I, *Paratrachichthys* sp. (after Zehren, 1975); J, *Diretmus argenteus* (after Zehren, 1975); K, *Hemirhamphus brasiliensis* (after Monod, 1968); L, *Hyporhamphus* sp. (after Monod, 1968); M, *Zenarchopterus dispar* (after Monod, 1968); N, *Grecarchopterus novae-guineae* (after Monod, 1968); O, *Fodiator acutus* (after Monod, 1968); P, *Menidia menidia* (after Monod, 1968); Q, *Melanotaenia nigrans* (after Monod, 1968).

and in the tetraodontid *Xenopterus neritus* (Tyler, 1980, figs. 186, 277, 310, 321) and the occasional monacanthid balistoid with a reduction in hyoid ossification (e.g., *Psilo-cephalus barbatus,* Tyler, 1980, fig. 126). In each of these apparently exceptional cases the bases of the last four branchiostegals still show indications of clustering and, at least in the
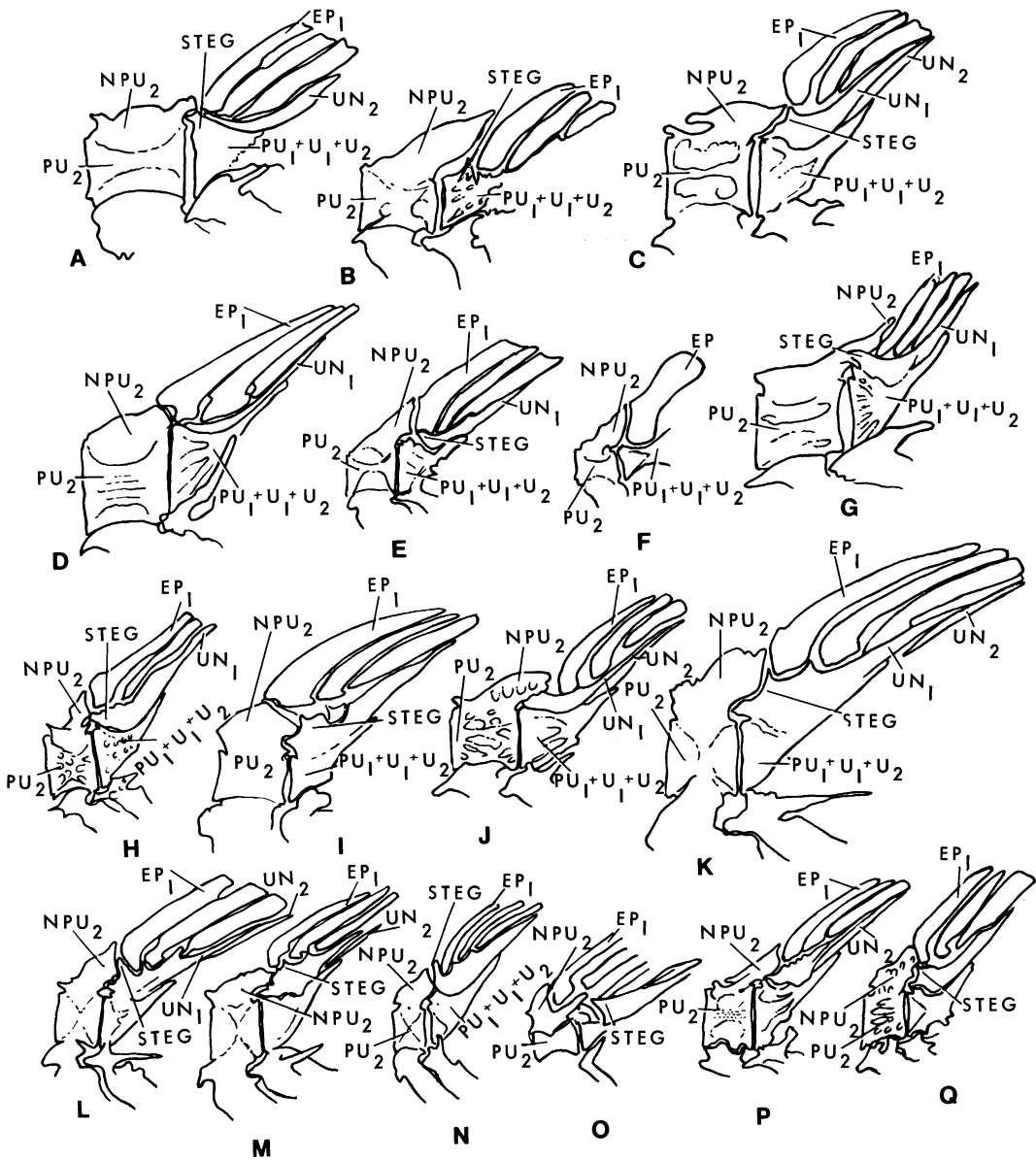
FIG. 36. Epural-uroneural complex of caudal skeleton. A, *Uranoscopus scaber*; B, *Blennius sanguinolentus*; C, *Pomatomus saltator*; D, *Scorpaena senegalensis*; E, *Amblyapistus taenianotus*; F, *Bathygobius soporator*; G, *Rachycentron canadum*; H, *Peprilus alepidotus*; I, *Toxotes* sp.; J, *Dicentrarchus punctatus*; K, *Pomacanthus paru* (AMNH 38130); L, *Centropyge vrolicki* (AMNH 38117); M, *Chaetodon xanthurus* (AMNH 38110); N, *Zanclus canescens* (after Tyler, 1970); O, *Selenotoca* sp. (AMNH 55117); P, *Ephippus hippei* (after Monod, 1968); Q, *Scatophagus argus* (AMNH 55118). A–J and P all after Monod (1968).

cases of *Triodon* and the molids, retention of the derived angle of attachment and curvature. In other words, these conditions appear to be further transformations of the basic zeoid-triacanthoid conditions rather than primitive states.

VERTEBRAL NUMBER: As noted already *Capros* and *Antigonia* have 22 vertebrae and
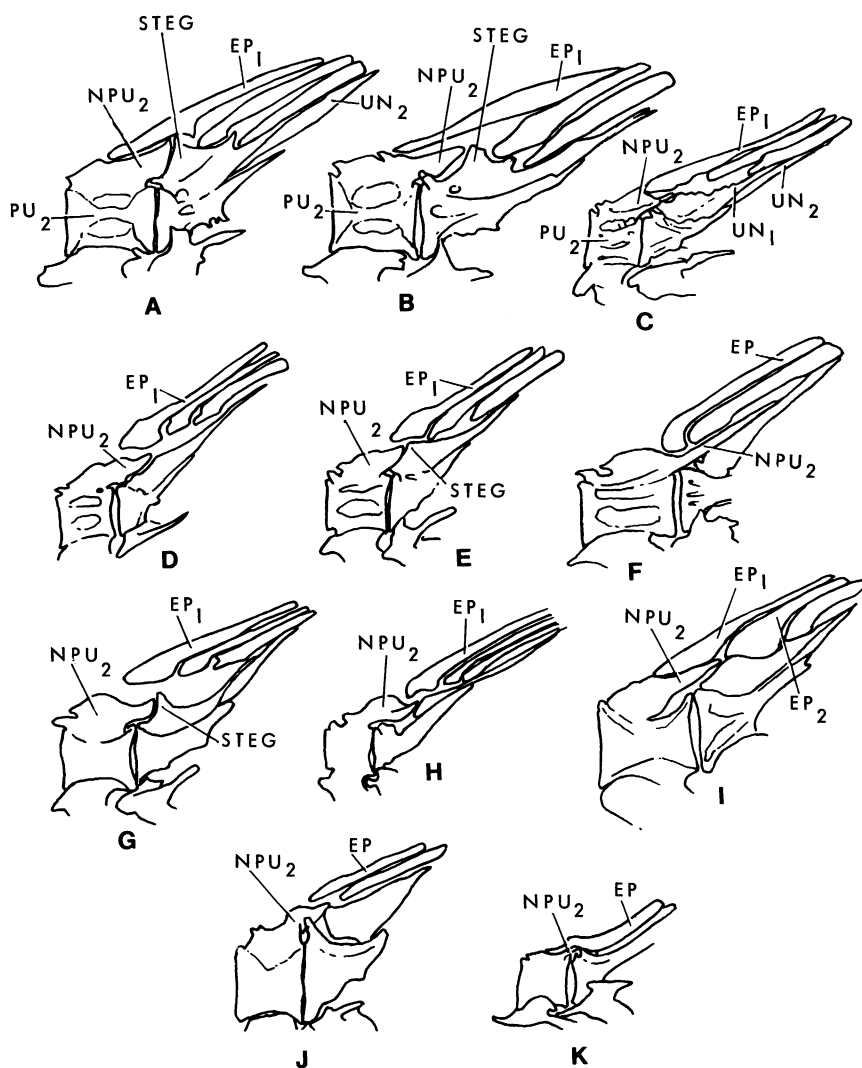
FIG. 37. Epural-uroneural complex of caudal skeleton. A, *Holocentrus ascensionis*; B, *Myripristis murdjan*; C, *Gaterin mediterraneus*; D, *Epinephelus aeneus*; E, *Mycteroperca rubra*; F, *Mugil cephalus*; G, *Parakuhlia macrophthalma*; H, *Apogon orbicularis*; I, *Sphyraena* sp.; J, *Ammodytes* sp.; K, *Scomber scombrus*. All after Monod (1968).

tetraodontiforms a range of 16 to 30 (with a modal range of 17 to 20). Zeoid counts range between 25 and 46. The question of which of these counts is primitive is moot since a precisely allocated sister group for establishing an outgroup polarity base is not known. But if, for example, monocentrids, with about 26 vertebrae, are their sister group, suggesting a gradual transformation of vertebral number from 26 to 22 to 20 or less, then the high count of some zeoids would be judged secondarily increased and, thus, a derived defining character of those fishes.

PELVIC FIN RAY NUMBER: The problem here is similar to that encountered for vertebrae: *Capros* and *Antigonia* each have a spine and five branched rays in the pelvic, the Eocene *Eoplectus*, a spine and four rays, triacanthoids, a spine and two, one or no rays, and the remaining plectognaths have either a

FIG. 38. Character-state tree of caproids, zeoids, and tetraodontiforms for which acanthurids plus chaetodontids are used as an outgroup to establish character polarity. Numbers refer to numbered characters in the synapomorphy scheme in text. Evidence that acanthurids and chaetodontids might be the immediate outgroup is indicated by their infrapharyngobranchial dentition and posttemporal.

remnant of a spine or no fin elements at all, but some zeoids have five rays and others as many as nine. The high count has been used to argue that zeoids are primitive fishes, perhaps allied to some beryciform (Regan, 1910, p. 482). But to reason that the high number is plesiomorphous it is necessary to assume that the high number is present in the cladistically most plesiomorph species of zeoid, and that the low number in *Capros* and *Antigonia* is derived for "zeiforms." Without a precisely allocated sister group of zeiforms and tetraodontiforms, or good theory of zeoid interrelationships, there is yet no reason to argue thus. For the present it is certainly more parsimonious to accept that some zeoids might have a secondarily increased pelvic ray number.

ACANTHUROID RELATIONSHIPS

If acanthuroids are not the sister group of tetraodontiforms, with what groups might they be allied? Since an answer to this question is not the main object of this paper, the comments are brief and offered primarily as a suggestion for future research.

In the older classifications a number of groups of laterally compressed, deep-bodied fishes with small mouths were included in two suborders, the Cirrhitoidei and the Squamipennes. The former included, among others, fishes now grouped as the Caproidae, Ephippidae, and Monodactylidae, and the latter included, among others, the Scatophagidae, Chaetodontidae, Pomacanthidae, part of the presently recognized Ephippidae

(the zanclids), and acanthurids. Siganids were placed in their own adjoining suborder, the Amphacanthini. See, for example, Jordan (1923, pp. 203–208). Principal elements of this arrangement are maintained in all modern classifications.

Without any other obvious clues on how to proceed, members of these groups were selected for comparison representing, among the non-acanthuroid taxa, the genera *Monodactylus, Chaetodon, Pomacanthus, Scatophagus, Selenotoca, Chaetodipterus, Platax,* and *Drepane.* Each of the species represented has 23 or 24 vertebrae, usually 10 + 13 or 14, but one, *Drepane,* has 9 + 15; two or three predorsal bones; a spine and five pelvic rays; anal spines numbering three (or four, in *Scatophagus* and *Selenotoca*), and branched caudal rays 15 (or 14 in the two aforementioned genera). If siganids are primitive acanthuroids, then acanthuroids are unexceptional with respect to the above features. Acanthurids, however, lack predorsal bones, or have but one (Tyler, 1970), and, like the two scatophagids, have 14 (or fewer) branched caudal rays.

In all the foregoing genera, except for *Monodactylus,* the first two dorsal spines are on a single compound pterygiophore, as in acanthuroids and there are only one or two slender branchiostegals on the narrow anterior part of the anterior ceratohyal. In *Monodactylus* there are three such branchiostegals and the first two dorsal spines are on separate, unspecialized pterygiophores both primitive features for acanthopterygians. Monodactylids, therefore, appear to be ruled out as relevant to the immediate problem.

Among the remaining genera, all but scatophagids have a similarly derived pharyngobranchial dentition consisting of narrow rows of very slender teeth on the second to fourth infrapharyngobranchial toothplates. Scatophagids also have long, slender teeth but they have a primitive bunched arrangement except on the third pharyngobranchial of *Scatophagus.* This detail might, therefore, indicate that the search for an acanthuroid ally should be narrowed down to *Chaetodon, Pomacanthus,* and the ephippids.

Of the three groups, only *Chaetodon* and *Pomacanthus* share with acanthuroids an extreme foreshortening of the premaxillary alveolar process as well as an overall reduction in the relative size of the upper jaw bones. More than one kind of upper jaw arrangement occurs in ephippids, as commented on below, but at least in *Chaetodipterus* and *Platax,* which are exceedingly alike in many internal details, both the maxilla and premaxilla have a relatively primitive form.

This leaves only *Chaetodon* and *Pomacanthus* for comparison with acanthuroids, and the structure of the hyoid bar suggests an obvious choice between the two. In *Pomacanthus* the anterior ceratohyal has a large "foramen" bounded above by a bar of cartilage. This was termed the "beryciform foramen" by McAllister (1968) in the belief that this hyoid feature of acanthopterygians is uniquely different from a similar "foramen" that is a primitive feature of all major groups of teleosts, living and fossil. McAllister presented no convincing reason for this belief, however, and I see no need to retain the adjectival modifier "beryciform." A second point is that the opening is not a foramen; nothing passes through it. It is merely a region of slight or absent ossification, primitively adjoining a groove for the lateral traverse of the hyoidean artery along the outside of the hyoid bar. Among the various fishes just considered such a "foramen," which is better termed a fontanel, occurs also in *Monodactylus, Scatophagus, Selenotoca,* and the ephippids. Only a remnant of it, in the form of a depression on the dorsal surface of the anterior ceratohyal, occurs in siganids. In acanthurids and *Chaetodon,* however, there is no sign of it and the anterior ceratohyal is highly modified. The anterior ceratohyal is exceedingly short in relation to its depth, joins the posterior ceratohyal along an oblique suture, has half or more of its dorsal surface covered by the dorsal hypohyal and is distinctly triangular (i.e., three-sided, rather than the primitive four-sided). A suggested relationship between chaetodontids and acanthurids is not new, as noted by Tyler (1970), but if the hyoid anatomy is significant it would place acanthurids closer to chaetodontids than siganids. Tyler (1970) reviewed the joint status of teuthidids (=siganids) and acanthurids and formed no compelling reasons to asso-

ciate them very closely in comparisons that also included chaetodontids and zanclids.

Whether acanthurids are the immediate sister group of chaetodontids, as I suspect is very likely, or are related to a larger group that includes chaetodontids, it seems probable that they will come to rest somewhere among some components of the old Squamipennes. Finally, because a hyoid bar of a form similar to that just described occurs also in some zeoids (Starks, 1898, pl. 34, fig. 5) and tetraodontiforms (Tyler, 1980, several species) the possibility of demonstrating some higher level relationship among all of these fishes remains a distinct possibility. An argument against such a possibility is that *Capros* and the triacanthoids have a somewhat more primitive anterior ceratohyal in which a dorsal notch is present, representing the remains of a ceratohyal fontanel from which the dorsal bridge of bone or cartilage has disappeared. The chaetodontid/acanthurid type of ceratohyal occurs only among more apomorph groups of tetraodontiforms where it appears, therefore, to be secondary.

A NOTE ON EPHIPPIDS,
ZEIFORMS, AND TETRAODONTIFORMS

Earlier we said that there is a similarity between ephippids and zeiforms/tetraodontiforms in the anatomy of the dorsal and anal fin radials, and suggested that a relationship of some sort might be implied. The Ephippidae is complex, however. Considering just the three taxa examined here, *Chaetodipterus, Platax,* and *Drepane,* they can be grouped in two distinct ways. The first includes *Chaetodipterus* and *Platax,* which are very similar in upper jaw anatomy, and the second includes *Platax* and *Drepane,* which are similar in the structure of the dorsal and anal fin radials. *Chaetodipterus* differs from the other genera in having less symmetrical radials. Its anteriormost radials supporting soft rays are entirely symmetrical, including a straight proximal element that is expanded distally into an equilateral triangle of bone; the distal radial, in the form of an inverted, subtriangular bone or cartilage, lies exactly between the triangular heads of adjoining proximal radials. In more posterior radials, however, the peak of the triangular tip of the proximal

radial can be seen as a separate element suturally joined to a widened base; this tip is the middle radial. Still more posteriorly the mesial radial is jointed to the proximal radial by cartilage, not by suture, and, in the posterior part of the fin, this intermediate element increasingly assumes an asymmetrical relation with the proximal element by posterior displacement. The radials supporting the last few fin rays show a relatively primitive triradial condition in which the middle radial is broadly hourglass-shaped and sharply offset from the proximal radial. The distal radial in these last few rays also is asymmetrical and primitively nodular. All radials supporting dorsal and anal fin soft rays in *Platax* and *Drepane* are symmetrical, resembling only the anterior ones in *Chaetodipterus. Drepane* differs from the other two genera in having a more derived upper jaw in which the greatly elongated ascending and articular premaxillary processes are closely joined and separated by a distinct neck from the much shorter alveolar arm; the maxilla is also enlarged, considerably more massive than the premaxilla, and has an enlarged, spatulate palatine process posteriorly and a slightly less wide but very high articular process that covers and extends noticeably dorsal to the combined articular/ascending premaxillary process. In *Chaetodipterus* and *Platax* the premaxillary processes are low, distinct from one another, and not separated by a neck from the much longer alveolar arm, as in the more generalized acanthopterygian jaws; the maxilla is slightly smaller than the premaxilla and has a simpler, more primitive articulation with the latter. If the ephippids are not a monophyletic group, the similarities between *Drepane* and zeiforms-tetraodontiforms in upper jaw structure and dorsal and anal fin radial symmetry might indicate a sister-group status. Caudal anatomy does not conflict with this interpretation since in *Drepane* there is a relationship between the stegural, epurals, and crest on PU_2 similar to that of caproids (condition II, see, above, pp. 19–27), whereas *Chaetodipterus* and *Platax* have the more derived condition III. In general the upper jaw and caudal skeleton anatomy of *Chaetodipterus* and *Platax* resemble those features in pomacanthids.

CLASSIFICATION

There obviously still is much uncertainty about the relationships of acanthuroids, monodactylids, scatophagids, chaetodontids, pomacanthids, and ephippids. Future work may show that chaetodontids should be placed with acanthuroids, some ephippids with pomacanthids, *Drepane* with zeiforms, tetraodontiforms, and so on. But more comprehensive and detailed study is needed. For the present, the only proposals of which I feel reasonably confident are:

1. There is a group that includes caproids, zeoids and tetraodontiforms defined by eight synapomorphies.
2. Within that group, a subgroup including zeoids and tetraodontiforms is defined by five synapomorphies.
3. The tetraodontiforms themselves can be defined as monophyletic by six synapomorphies.

Since this scheme indicates that the term Zeiformes no longer describes a monophyletic group, the simplest solution for representing those three taxonomic proposals not requiring either the creation of new names or the elevation in rank of old ones is to include the zeiforms within the Tetraodontiformes.

ORDER TETRAODONTIFORMES
    Series 1
        Family Caproidae
    Series 2
      Division Zeomorphi (Zeiformes of Heemstra, 1980)
        Family Grammicolepidae
        Family Parazenidae
        Family Zeniontidae
        Family Zeidae
        Family Oreosomatidae
      Division Plectognathi
        Suborder Triacanthoidei (Triacanthoideo and Triacanthoidea of Tyler, 1980)
          Family Triacanthodidae
          Family Triacanthidae
        Suborder Tetraodontoidei
          Superfamily Balistoidea (Balistoideo of Tyler, 1980)
            Family Balistidae
            Family Monacanthidae
          Superfamily Tetraodontoidea (Ostracioidea Tetraodontoidei of Tyler, 1980)
            Family Aracanidae
            Family Ostraciidae
            Family Triodontidae
            Family Diodontidae
            Family Molidae

Within this scheme the interrelationships of the families of zeomorphs and the Tetraodontoidea are presently unresolved although the latter group is under study by J. Tyler and R. Winterbottom (MS). Tetraodontoidea, as used here, would include the ostraciids, triodontids, tetraodontids, and molids.

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NOTE ADDED IN PROOF

Mok and Shen (1983), reviewed the problem of interrelationships of many of the taxa discussed here, namely, the members of the old Squami-pennes, and the tetraodontiforms, but they did not examine any "zeiform" fishes. Our conclusions differ in some ways and agree in others. In general, theirs is an exemplary review in which many taxa and characters were examined, and their most significant contribution is their demonstration that there exists a substantial basis for aligning the tetraodontiforms, as defined here to include the "zeiforms," with some members of the old Squami-pennes. Two of their most interesting discoveries, which, in various ways associate the pentacerotids, chaetodontids, pomacanthids, scatophagids, and acanthuroids with tetraodontiforms are that "their pelvic spine and pelvic bone are interlocked" through a pelvic foramen and that "the supratemporal canal [is] posteriorly directed" and "extends posteriorly through a non-bony canal." They also propose a sister-group relationship between acan-

thuroids and tetraodontiforms on the basis of two features of the ribs and epipleural ribs which, in my view, is ambiguous at best for many of the reasons discussed above (p. 36). For example, two of these features are: "pleural ribs associated with the first or second vertebra," "epipleural ribs absent on the first vertebra." The realities are that acanthuroids generally have the first pleural on the second, and tetraodontiforms, in the two special cases where ribs exist at all, on the first, and triacanthoids have no epipleurals on the first three vertebrae, whereas acanthuroids generally have them on the first vertebra, as do some other squamipennian fishes. To Mok and Shen this demonstrates a significant "trend," but to me it says that the ribs, when they occur as cartilage structures in one monacanthid, and as bony ones in the much argued-about Triodon, are all secondary features added on in development.

Their work is detailed and painstaking and should be reviewed thoroughly by all ichthyologists concerned with these general problems.