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INTRODUCTION

The classification of modern lower teleostean fishes has been erected piecemeal, and the interrelationships of many of the groups remain unknown. That the structure of some of these groups suggests that they are systematically quite isolated from others is hardly a sufficient excuse for neglecting the study of teleostean phylogeny.

There would seem to be several possible ways of investigating lower teleostean relationships. One is a reevaluation of existing literature on the subject, but although this has been attempted repeatedly during the last 30 years, no material advance has resulted. Apparently further knowledge of the fishes themselves is needed.

The new information that might be expected to bear most cogently on teleostean phylogeny is that to be derived from paleontology. However, for primarily technical reasons knowledge of fossil fishes is slow in forthcoming, and the nature of the fossil record is such that many crucial data will probably never be forthcoming at all. Thus a good proportion of teleostean classification will always have to depend upon such information as can be gathered from modern fishes. In any event, the ichthyologist working on existing forms can do much to point out what fishes and what structural features need particular attention if they ever are located among fossils.

In work with modern fishes there are two possible approaches to phylogenetic studies. One is the investigation of individual groups. In broad-based studies of this type, such as that of Makushok (1958) on the northern blennioid fishes, much becomes evident regarding the derivation of the group.

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[1] About half of the work on the caudal skeleton reported below was done in the British Museum (Natural History). The rest of the paper was prepared in the U. S. National Museum. The author wishes to acknowledge his indebtedness to the staffs of these institutions for the facilities, and to the Guggenheim Foundation for the Fellowship, which have made this work possible.

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 142, NO. 3

The other approach, and the one used here, constitutes an attempt to broaden the basis for classification by the evaluation, from a phylogenetic point of view, of hitherto unused or neglected characters. Examples of this type of approach in progress are Svetovidov's studies of the fish brain, Marshall's investigation of the air bladder, and Orton's work on the possible significance of larval characters for teleostean classification. None of these studies will in themselves provide a teleostean phylogeny, but they can contribute data that will bear on such a phylogeny in two ways. First, they can suggest working hypotheses concerning relationships. Second, they can provide general background information concerning the possible usefulness of a particular structure for classification: which parts of a structure are likely to prove constant and which variable; to what extent a feature is correlated with the nature of the environment or with other characters; and what has been the general sequence of evolutionary development in the feature. Once these things are known, a structure can be added with greater confidence to the stock of data bearing on teleostean relationships.

All the structures to be dealt with in the present paper are osteological. They are (I) the caudal skeleton, (II) certain aspects of pelvic structure, (III) the superficial bones of the snout region (except the nasal), and (IV) the development of a protrusile upper jaw mechanism. All these structures are followed in greater or lesser detail from the clupeiform fishes through to the percoids. The paper concludes with a summary showing how the information presented would seem to bear on the individual lower teleostean "orders" and with a discussion of possible groupings of these "orders."

For purposes of the present exposition Berg's (1940) ordinal arrangement and nomenclature are adopted.

Certain general statements about the four structural complexes to be dealt with may be placed here advantageously. The first concerns methodology. It has been found by experience that the members within an order that have been considered "primitive" on other grounds are also usually "primitive" with regard to the four features studied here and are hence of special importance for a study of derivations. Since the objective is an understanding of ordinal relationships this paper deals primarily with these "primitive" members within orders. Conversely, specializations that appear to have taken place within an order, e.g., the protrusile jaw of the cyprinoids, are usually summarily dismissed, however interesting they may be structurally.

Second, all four features show a progressive change from the basal clupeiform fishes to the percoids. Frequently the nature of the change that occurs between the basal members of different orders is of the same type as that occurring between the more "primitive" and more "advanced" members of a single order (though this is by no means always true). Under the circumstances it seems well to point out that the successive levels of organization found in a structure can have evolved in two quite different ways (diagram 1). At the left, four levels of structural organization are represented as having arisen through a single father-son lineage; at the right, these same levels are shown as having developed through parallel changes occurring to different degrees in different lineages. In short, similar or successive levels of structural organization in any one character may or may not be indicative of genetic relationships, depending, among other things, on whether the similarities have been developed by the means indicated at the left or at the right of the diagram.

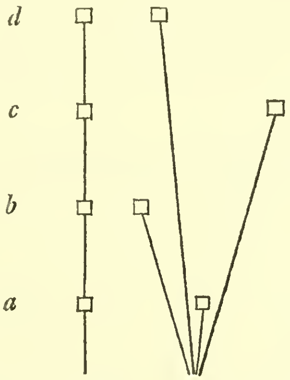

Diagram 1.

I. THE CAUDAL SKELETON

The caudal skeleton of teleostean fishes has been the subject of a number of investigations, but no very coherent picture of the evolution of this structure in teleosts has materialized. There are a number of reasons for this, one being that the forms with a specialized caudal skeleton, e.g., the cods, have received a large proportion of the attention. The resulting impression is one of kaleidoscopic permutations brought about by losses and fusions. If, however, the basal members of the less aberrant groups are compared, as will be done here, a more stable picture emerges.

In a previous paper (Gosline, 1960) the caudal skeletons of isospondylous fishes were discussed. There it was demonstrated that the "primitive" members, e.g., *Elops, Salmo, Hiodon,* and *Esox,* have a large number of features of caudal structure in common, and that this basic type has evolved in various ways within the order. The present paper deals with the caudal skeleton in certain of the orders usually placed between the isospondylous fishes (Clupeiformes) and the percomorph fishes (Perciformes). All the caudal structures to be discussed parallel one of three of the types developed within the isospondylous fishes. By way of background these three types will be redescribed.

Here, as in the earlier paper, the "terminal vertebra" (*TV* of figs.) is defined as the one bearing a laterally flanged lower hypural (*HY1* of figs.); this, in turn, is the lowest of the (typically) three hypurals articulating with the lower lobe of the caudal fin. In the percomorphs, as well as in most of the fishes discussed in this paper, the terminal vertebra forms the posterior end of the vertebral column, but in the lower teleosts there may be one or two separately ossified centra behind it. If so, these are called "postterminal centra" (*PT* of fig. 1). When two are present, as in the elopoid *Pterothrissus* (fig. 1A), hypurals 2 and 3 attach to the anterior (*PT1*) and one or more hypurals of the upper caudal lobe to the posterior (*PT2*).

Basically it is the varying fate of these two postterminal centra that distinguishes the three types of isospondylous skeletons. Usually these centra become incorporated in the terminal vertebrae in advanced forms, but in one group of isospondylous fishes, the osteoglossoids, a different fusion has taken place. There, a typical intervertebral articulation is retained between postterminal centra 1 and 2, and the latter seems to have fused with a large block presumably formed at least in part from the upper hypurals (fig. 1B). Later in the paper this caudal structure will be called Type III.

The other two types incorporate the two postterminal caudal centra into the terminal vertebra through different sequences of fusion. The usual method is to add the anteriormost first. At this point the three lower hypurals all attach to the terminal vertebra, leaving only a few of the upper hypurals articulating with the remaining postterminal centrum. In a second step, the second (posterior) postterminal centrum also fuses with the terminal vertebra (fig. 4A). In this line of development it is notable that the uroneural structure, even as far up

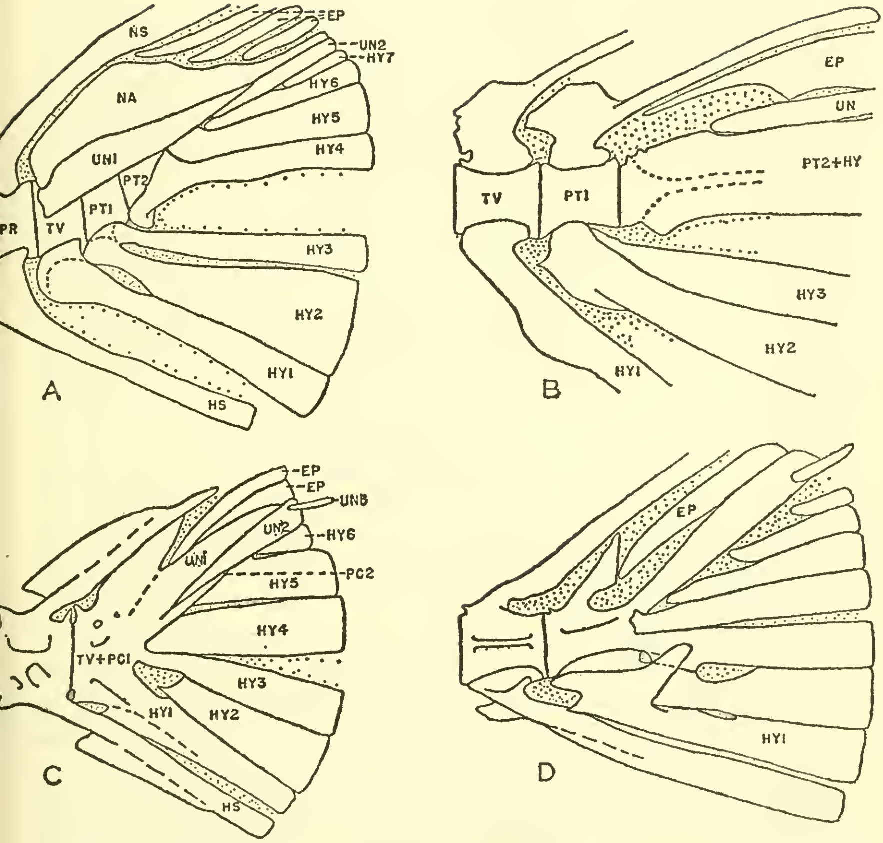

FIG. 1.—A, Caudal skeleton of *Pterothrissus gissu* (Clupeiformes). *EP*, epural; *HS*, hemal spine; *HY*, hypural; *NA*, neural arch; *NS*, neural spine; *PR*, preterminal vertebra; *PT*, postterminal centrum; *TV*, terminal vertebra; *UN*, uroneural.

B, Caudal skeleton of *Pantodon* sp. (Clupeiformes). Lettering as in A.

C, Caudal skeleton of *Brycon moorei* (Cypriniformes). *PC*, postterminal centrum. Other lettering as in A.

D, Caudal skeleton of *Chasmistes* sp. (Cypriniformes). Lettering as in A.

as the Serranidae, may retain its independent identity; consequently it is in this line, which will be called Type I, that a simple urostylar structure most frequently occurs.

A rather different course of evolution seems to have occurred in the herringlike fishes (Clupeidae, Dussumieriidae, Engraulidae), and the caudal structure of these fishes will be called Type II. Here, one or more uroneurals fuse with the terminal vertebra so that the upturned strut, sometimes called urostyle in these fishes, is really a composite structure made up largely of the uroneurals. (This was noted long ago by Regan, 1910). Additionally, there is a difference from Type I in the way the postterminal centra become fused to the terminal vertebra. As a first step, the base of hypural 3 fuses with at least a portion of postterminal centrum 1. As a result, what appears to be the base of hypural 3 interdigitates between the terminal vertebra and the remaining (second) postterminal centrum. Also with the fusion between the base of hypural 3 and the anteriormost postterminal centrum, hypural 2 loses all basal articulation (as in fig. 1C). Later in the evolution of this lineage, postterminal centrum 2 also becomes fused with the uroneural-postterminal centrum complex (as in fig. 1C). At a final stage the uroneurals, terminal vertebra, and postterminal centra may fuse into a single structure without indication of origin (as in figs. 1D and 2A).

Though the basic purpose of this paper is to trace morphological similarities in the caudal skeleton as possible indicators of phylogenetic evolution, a secondary objective is to check certain aspects of the relationship between skeletal structure and fin form. As was noted in the earlier paper, there seems to be an indirect association between tail shape, number of caudal rays, and structure of the caudal skeleton. Since the ostariophysine fishes provide excellent material for investigating certain aspects of this relationship, they will be dealt with first.

Order Cypriniformes.—Among the ostariophysine fishes the caudal skeletons of the basal members—*Brycon* (Characidae, fig. 1C), *Chasmistes* (Catostomidae, fig. 1D), and *Diplomystes* (a catfish, fig. 2A)—show a surprising amount of general similarity. In none of the three is there a separate postterminal centrum. In all, there are the usual three lower hypurals; the terminal vertebra has a well-developed, upright neural arch; and the anterior uroneural and hypural 3 are fused with the terminal vertebra.

In most respects the caudal skeleton of *Brycon* is the most primitive of the three. Thus, in *Brycon* there are three uroneurals and a wedge,

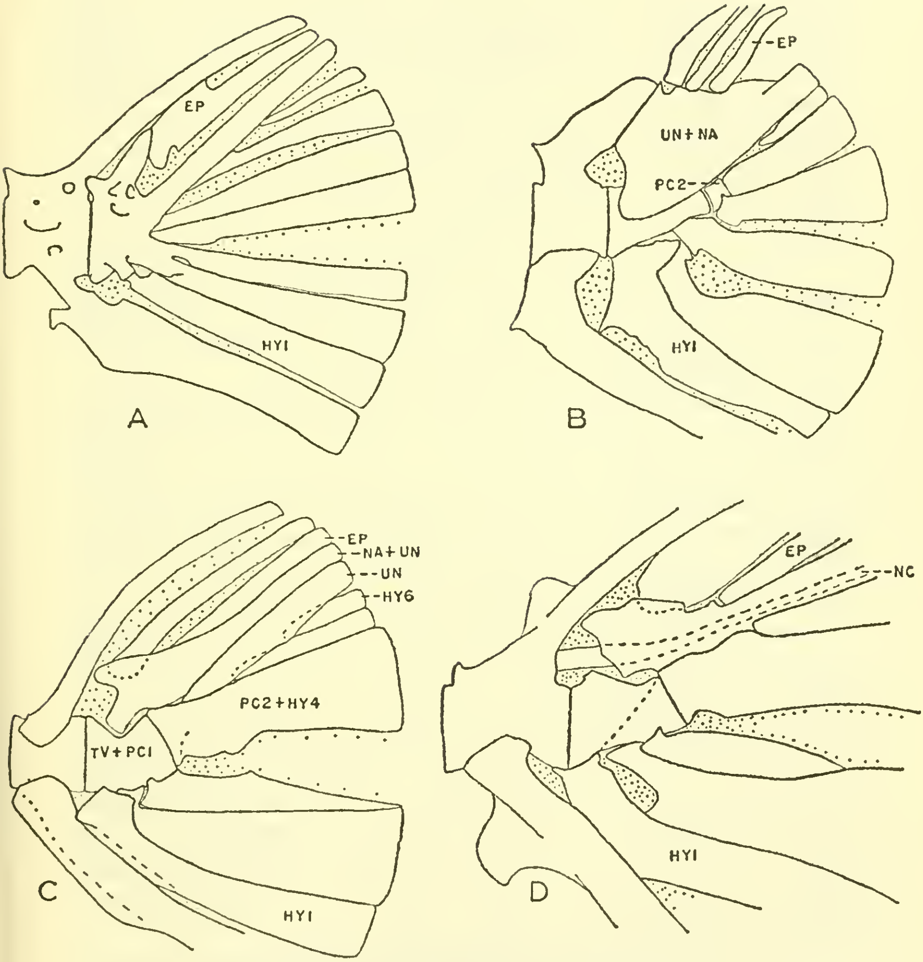

FIG. 2.—A, Caudal skeleton of *Diplomystes* sp. (Cypriniformes). Lettering as in figure 1, A.

B, Caudal skeleton of *Chlorophthalmus agassizi* (Scopeliformes). Lettering as in figure 1, A and C.

C, Caudal skeleton of *Percopsis* sp. (Percopsiformes). Lettering as in figure 1, A and C.

D, Caudal skeleton of *Aphredodorus sayanus* (Percopsiformes). *NC,* nerve cord. Other lettering as in figure 1, A.

undoubtedly representing one or more postterminal centra (*PC2* of fig. 1C), running up below the anterior end of uroneural 2; in the other two genera mentioned above, uroneural 2 has fused with uroneural 1 and the postterminal centra to form a single monolithic structure. In *Brycon* there are two epurals; in the others only one. In one feature, the lack of fusion between hypural 1 and the terminal vertebra, *Chasmistes* seems to represent the primitive condition.

With regard to variations other than those mentioned, hypural 2 seems to show the greatest plasticity. In *Brycon moorei* (fig. 1C) hypural 2 is separate from the hypurals above and below, but in a U. S. National Museum skeleton of *Brycon oligolepis,* hypural 2 fuses basally with hypural 3 for a short distance and distally with hypural 1. In *Chasmistes* there is a basal fusion between hypurals 1 and 2, and in *Diplomystes* between hypurals 2 and 3.

As to possible relationships of the order, the caudal skeleton of *Brycon* bears a striking resemblance to that of the round herring, *Dussumieria* (Gosline, 1960, fig. 7). The upright neural arch of the terminal vertebra of *Brycon, Chasmistes,* and *Diplomystes* is a notable feature of the Clupeoidae in general. The fusion of hypural 3 with the terminal vertebra is found again in *Dussumieria* as is the *Brycon* characteristic of a wedgelike strut running below uroneural 2.

From the basal types of ostariophysine caudal skeletons described above, the various lineages have evolved different peculiarities. Two of the more specialized types of catfish caudal skeletons have been illustrated by Whitehouse (1910, pl. 47, figs. 7, 8). The characins have presumably given rise to the gymnotid eels, many of which have a tail tapering to a fine filament; in these, at least, the caudal skeleton has been lost entirely. In the cyprinoids, by contrast, the caudal skeletons seem to remain relatively constant: those of the catostomids, cyprinids, and even of the round-tailed cobitid *Misgurnus anguillicaudatus,* differ only in minor detail.

In view of this cyprinoid constancy of skeletal structure, the variation in caudal ray count comes as something of a surprise. In all the members of the Cyprinidae examined—*Hypophthalmichthys, Garra, Gobiobotia, Saurogobio, Hemibarbus,* and numerous American forms (but not *Moapa* and *Eremichthys,* which were unavailable)—the branched caudal rays are constantly 17. On the other hand, most of the cyprinoids examined except the Cyprinidae have fewer than 17 branched rays (*Psilorhynchus* was unavailable). In numerous catostomids examined (including *Myxocyprinus* of China) the branched caudal ray count is constantly 16. Among old world relatives of the family Cyprinidae, the caudal count is more variable and may best be shown in tabular form (table 1).

Only one aspect of the data in table 1 will be discussed here. All the fishes listed except *Cobitis* and *Misgurnus* have a caudal outline that varies from emarginate to deeply forked. It is, then, the round-tailed members of the cyprinoid group that have the lowest (and also apparently the most variable) number of caudal rays. (Some attempt was made to determine whether the number of forked caudal rays in *Misgurnus* varied with size, but no such ontogenetic change was found in specimens between 41 and 150 mm. in standard length.)

TABLE 1.—*Branched caudal rays in certain cyprinoid fishes*

Species	*Number of branched rays*						*Region*	*USNM No.*
	12	13	14	15	16	17		
Catostomidae					x[1]			
Cyprinidae						x[2]		
Homalopteridae								
Bhavania australis						2	India	165107
Balitoria brucei						3	Burma	44808
Hemimyzon formosanus					1	4	Formosa	161711
Gyrinocheilidae								
Gyrinocheilus aymonieri					8		China	117718
Cobitidae								
Cobitinae								
Cobitis taenia		1	4				Turkey	143864
Misgurnus anguillicaudatus	1	8	23	3	1		China	85944, 130354
Acanthophthalmus kuhlii			4				Aquarium specimens	
Botiinae								
Botia sp.						9	China	89178, 89179
Nemachilinae								
Nemachilus (*Barbatula*) sp.					9		China	91713
Gastromyzonidae								
Crossostominae								
Glaniopsis hanitschi					2		Borneo	113325
Gastromyzoninae								
Beaufortia pingi				6			China	117718
Gastromyzon borneensis					6		Borneo	113324

[1] All catostomids examined had 16 branched caudal rays; see text.
[2] All cyprinids examined had 17 branched caudal rays; see text.

The question remains as to why the caudal count should vary in the fork-tailed cyprinoids. An attempt was made to get at this problem by comparing the cyprinids (17 branched rays) with the catostomids

(16 branched rays). Preliminary analysis showed that the difference in ray count occurs in the upper caudal lobe (9 branched rays in cyprinids, 8 in suckers). To pinpoint the position of the lost ray an effort was made to relate the rays to the hypural on which they originate. Here the complication was promptly encountered that in both cyprinids and suckers the number of hypurals extending to the upper caudal lobe varies between 3 and 4. In the catostomids examined, almost all had 4 upper hypurals, though the uppermost (fig. 1D) is sometimes quite small; the only exception was in *Erimyzon sucetta,* where, in three specimens examined, the uppermost hypural was missing completely. In the Cyprinidae, on the other hand, the majority of forms examined had only 3 upper hypurals, but *Carassius auratus* (two specimens), *Semotilus corporalis* (two specimens), and *Campostoma anomalum* (one specimen) had 4. Though the number of 3 or 4 seemed to be constant within species in the available material, no relationship between hypural number and the systematic position of the species could be discerned. When an attempt was made to relate certain caudal ray bases with specific hypurals, it was discovered that the number of ray bases articulating with any one hypural varied by plus or minus 2 (compare Makushok, 1958, p. 11), even when members of the same family with the same number of hypurals were compared. Furthermore, it was found that some of the ray bases extended over parts of two hypurals. From all this it was concluded that there is no close correlation between the caudal ray bases and the hypurals in cyprinoid fishes. It was also concluded that for systematic purposes in cyprinoids a difference of one hypural has less significance than the difference of one branched ray. However, the mystery of the disappearing ray in the upper caudal lobe of catostomids remains unsolved.

Order Scopeliformes.—Among the iniomous fishes caudal skeletons of the genera *Aulopus, Synodus, Chlorophthalmus, Solivomer, Lampanyctus, Omosudis, Lestidium,* and *Alepisaurus* have been examined.

Aulopus differs immediately from all the others in the retention of bony fulcral scales in front of the accessory caudal rays above and below. As to the caudal skeleton itself, the basic features of caudal structure shown for *Chlorophthalmus* (fig. 2B) are found throughout these genera. The terminal vertebra and postterminal centrum 1 have fused into an elongate structure; a separate postterminal centrum 2 is frequently visible in lateral view; the anterior uroneurals have a high median crest (probably a neural arch structure) but are never fused with the centra below (except perhaps in *Lampanyctus*).

One of the most frequent variations and one that is apparently of little systematic significance is the loss of postterminal centrum 2; this occurs in the adult *Synodus,* in *Lampanyctus, Omosudis, Lestidium,* and *Alepisaurus.* The loss of this structure in alepisauroids is probably correlated with the rather sharp upturning of the last vertebra as compared with myctophoids. There is also a repeated fusion of hypurals, particularly the three lowermost. The three epurals seem more constant; they are reduced to 1 or 2 only in the synodontids among the material examined. The synodontids also are unique in that the anterior uroneurals are broken up into a number of platelets in the adult (Hollister, 1937b).

Order Anguilliformes.—The caudal skeletons of five eels belonging to three families are illustrated by Whitehouse (1910, pl. 48, figs. 9-13). Though these are obviously specialized, it is tempting to identify the lower, double hypural as the fusion of the hypurals usually numbered 2 and 3. If this is correct, then these eels have one complete postterminal centrum, plus a second fused with the posteriormost hypural plate. The elements labeled n. a. (equals neural arch) in Whitehouse's plate would appear to be uroneurals. Under the explanation offered here, the eel caudal skeleton is merely a specialized offshoot of a basically primitive type.

Miscellaneous orders.—The halosauroids and notacanthoids all have a long, tapering tail with little or no possibility of a caudal skeleton. The same is true of the macruroids. The caudal skeleton of the cods has received a considerable amount of attention (e.g., Barrington, 1937). However, it seems to be far more aberrant than even that of the eels, and its parts cannot easily be homologized with those of any of the fishes dealt with here.

In the Beloniformes, Syngnathiformes (c.f., Whitehouse, 1910, pl. 48, fig. 15), and Gasterosteiformes the caudal skeletons consist of platelike hypurals that obviously represent secondary simplification, leaving little trace of their derivation. They cannot profitably be discussed here.

No caudal skeletons of the Phallostethiformes have been available.

Order Percopsiformes.—The caudal skeleton of "*Columbia*" has been figured by Regan (1911b, p. 295, fig. B); those of *Percopsis* and *Aphredodorus* are illustrated here (figs. 2C and D). In a number of features all are peculiar. The terminal vertebra and 1st postterminal centrum have fused, but in *Percopsis* (fig. 2C) there is a sharp upward bend in this combined element, and in *Aphredodorus* (fig. 2D) it has a peculiar diagonal line which seems to represent either an oddly oriented line of fusion or a line of shearing stress between the parts. In both genera postterminal centrum 2 seems to have fused with one or more of the upper hypurals. In *Aphredodorus,* hypurals 2 and 3 are closely associated and hypural 1 has its articular base in part over the preterminal vertebra.

Order Cyprinodontiformes.—As with so many other round-tailed fishes, considerable difficulty has been encountered in interpreting the caudal structure of the Cyprinodontiformes. Also as in other round-tailed groups, the number of branched caudal rays varies greatly. For example, there were 9 branched caudal rays in three specimens of *Chologaster* examined, 13 in a specimen of *Fundulus,* and 17 in a *Belonesox.*

The caudal skeletons of *Amblyopsis* (fig. 3A) and *Chologaster* (fig. 3B) are presumably more "primitive" than those of other members of the order. In these two genera the tip of the vertebral column (presumably represented by *PC2*) fuses with the upper hypural plate. The lower half of the hypural fan seems best interpreted by comparison with the caudal skeleton of *Aphredodorus* (fig. 2D). If the *Aphredodorus* caudal structure really represents a generalized form of that seen in *Amblyopsis* and *Chologaster,* then hypurals 2 and 3 have fused, and hypural 1 has lost all basal attachment. (Seemingly hypural 1 frequently does this in round-tailed fishes, judging by the illustrations in Whitehouse, 1910, and others.)

The caudal skeletons of various nonamblyopsoid cyprinodonts have been illustrated by Hollister (1940). Part of that of *Fundulus* is shown here (fig. 3C). The simplest explanation for *Fundulus* is that the terminal vertebra, postterminal centra, and all the hypurals have fused into a single plate. If this is correct, the intervertebral articulation between the postterminal centra 1 and 2 has been lost in *Fundulus,* leaving it with one fewer vertebra at the base of the caudal fin than *Amblyopsis* and *Chologaster.* However, no sign of the lost intervertebral articulation could be seen in the stained specimen of *Fundulus* examined, or in the juvenile specimens of *Mollienisia* illustrated by Hollister (1940, figs. 7-10).

OrderLampridiformes.—The only caudal skeleton of a member of this order available was one of *Velifer* (fig. 3D). Once again there is the intervertebral type of articulation between postterminal centrum (1?) and the structure behind it (a postterminal centrum fused with a hypural?). This feature sets *Velifer* to one side of the lineage leading to the percoids, as far as caudal skeleton is concerned. The slight resemblance to *Amblyopsis* and *Aphredodorus* seems of highly dubious significance.

Orders Beryciformes, Zeiformes, and *Perciformes.*—As far as basic pattern of the caudal skeleton is concerned, these three orders may be grouped together. There seems no reason why one should not have been derived from the basic stock of another or, alternatively, why all three should not have developed from a single basal stock. The most significant difference, perhaps, is the number of caudal rays; in the Beryciformes this is said to be 17 branched (except for 16 in the Polymixiidae), in the Zeiformes 10 to 13, and in the Perciformes basically 15 branched. In each of the three orders there is a gradation in the caudal skeleton from forms in which this structure is fairly primitive or generalized to forms in which it is considerably fused.

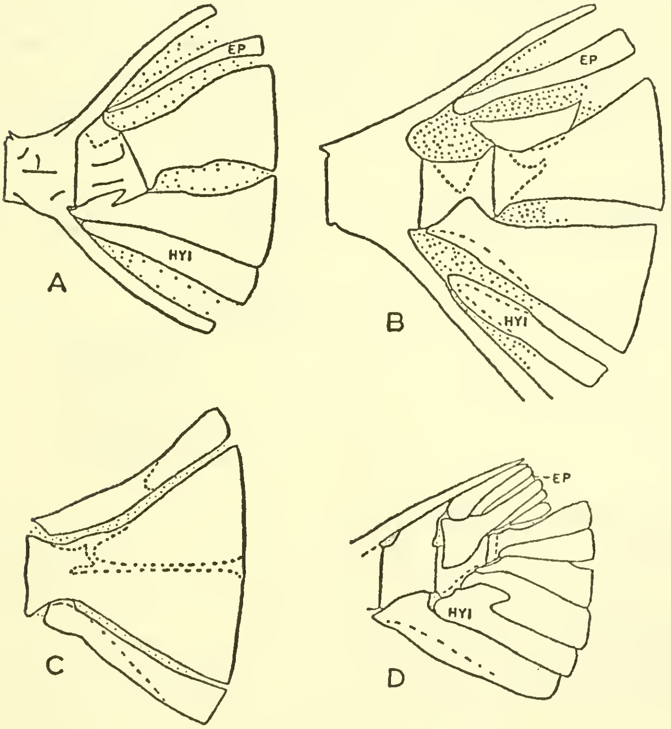

FIG. 3.—A, Caudal skeleton of *Amblyopsis spelaeus* (Cyprinodontiformes). Lettering as in figure 1, A.

B, Caudal skeleton of *Chologaster* sp. (Cyprinodontiformes). Lettering as in figure 1, A.

C, Part of caudal skeleton of *Fundulus olivaceus* (Cyprinodontiformes).

D, Caudal skeleton of *Velifer hypselopterus* (Lampridiformes). Lettering as in figure 1, A.

Among the Beryciformes the two apparently extreme types of caudal skeleton have been well illustrated. In *Polymixia* (Regan, 1911a, fig. 1) the first preterminal vertebra has a normal spine but no neural crest, the anterior uroneural is wedged into the terminal vertebra, and there is one postterminal centrum. In *Hoplopteryx* (Regan, 1911a, fig. 2) the first preterminal vertebra has a crest but no neural spine, the anterior uroneural is fused with the terminal vertebra, and there are no postterminal centra. *Polymixia* is the more primitive of the two in all of the features mentioned. An examination of the caudal skeletons of *Hoplostethus, Myripristis,* and *Holocentrus* indicates that various combinations of the *Polymixia-Hoplopteryx* types occur among berycoids (diagram 2). Thus *Hoplostethus* has the postterminal centrum and free uroneural of *Polymixia* but the neural crest on the preterminal vertebra as in *Hoplopteryx.* In *Holocentrus* the bone fusions are as in *Hoplopteryx* and there is the neural crest on the preterminal vertebra as in *Hoplopteryx,* but the first epural is so oriented as to give the distinct impression that it has arisen from the neural spine of the preterminal vertebra.

	Preterminal vertebra with a normal neural spine but no median crest	Preterminal vertebra with a median crest but no neural spine
Anterior uroneural fused with terminal vertebra No postterminal centrum in adult		*Holocentrus* (Holocentridae) *Myripristis* (Holocentridae) *Hoplopteryx* (Berycidae)
Anterior uroneural wedged into terminal vertebra A separate postterminal centrum	*Polymixia* (Polymixiidae)	*Hoplostethus* (Trachichthyidae)

Diagram 2.

Among the Zeiformes the caudal skeleton of *Antigonia* (fig. 4A) has the same basic structure as that of the percoid *Serranus.* In both, the postterminal centra have fused with the terminal vertebra to form a tapering point (urostyle) on the latter; there is only a single uroneural (which is not fused to the terminal vertebra); there are 3 epurals and 6 hypurals; and the first preterminal vertebra bears a neural crest but no neural spine.

In contrast to *Antigonia,* the caudal skeleton of *Zeus* (cf., Norman, 1934, p. 6, fig. 6D) has undergone so much fusion that its component parts are identifiable only with difficulty.

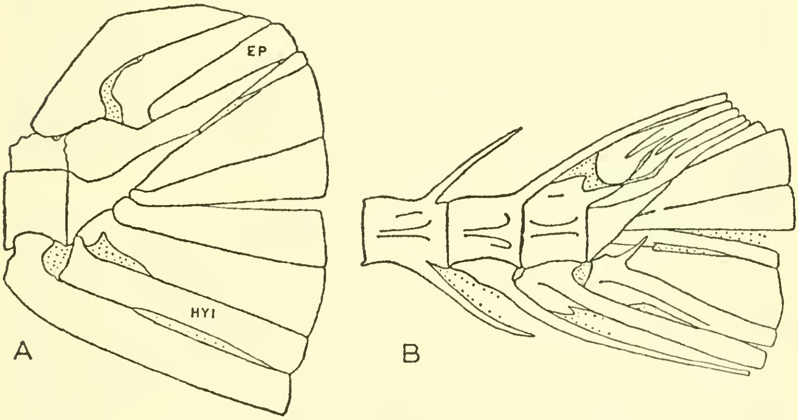

FIG. 4.—A, Caudal skeleton of *Antigonia capros* (Zeiformes). Lettering as in figure 1, A.
B, Caudal skeleton of *Epinephelus bonaci* (Perciformes).

With regard to the Perciformes, the only point that will be made here has to do with two presumably derivative groups, namely, the Mugiloidei (Percesoces) and the Pleuronectiformes (Heterosomata). In both of these (cf., Hollister, 1937a, and Norman, 1934, p. 3, fig. 3, respectively) the caudal skeleton shows considerably more fusion than in the basal percoids (fig. 4B).

Discussion.—Three matters will be taken up here: the sequence in the fusion of parts of the caudal skeleton; the similarities in structure shown by the basal members of various groups; and finally the evolutionary changes that have occurred in the caudal skeleton within groups.

At the different levels of organization between the isospondylous fishes and the percoids there has been a progressive reduction in the number of parts. Some of this has doubtless come about through loss, but perhaps a greater portion has been the result of fusion. The extent to which fusion has occurred differs within and between the various groups of fishes. This secondary simplification of structure has been evolved through a number of steps, and the sequence of these steps seems to have been essentially the same in various groups of fishes. Thus, hypurals 2 and 3 seem to fuse before hypural 1 becomes added to the group, e.g., in cyprinodonts and apparently in eels; postterminal centrum 1 becomes amalgamated with the terminal vertebra, with postterminal centrum 2 coming in in the more advanced forms; etc. When these sequences are changed, other features of the caudal skeleton seem to evolve in other than the usual fashion, or vice versa. In any event the different sequences form the bases upon which the three caudal skeleton types designated here have been established. It may be added that the end point in the evolution of all three would be a simple platelike caudal skeleton which would be essentially the same regardless of what sequence had been followed. Such an end point is represented by *Fundulus* (fig. 3C).

In a very general way there is an association between fusion of parts in the caudal skeleton and reduction in the number of caudal rays. Perhaps no significance should be read into this other than as independent exemplifications of the trend in the evolution of teleostean fishes toward the reduction of the number of parts throughout the head and body. Certainly in the example of the cyprinoids dealt with above there was no relationship between the number of caudal rays and of hypurals.

There seems to be equally little direct relationship between the amount of fusion and fin type or mode of life. There are numerous round-tailed fishes with a fused, platelike caudal skeleton (*Fundulus*) and fork-tailed forms with similar features (Beloniformes); similarly there are slow- and weak-moving forms (pipefishes) and fast-swimming fishes (tunas) with platelike caudal skeletons. The epitome of consolidation is undoubtedly reached in the small, neotenic *Schindleria* (Gosline, 1959, p. 75).

Turning to the three basal types of caudal structure distinguished in the introduction to this section, Type I is by far the commonest. It occurs among all iniomous and in the basal berycoid, zeoid, and perciform fishes. In these the uroneural(s) do not fuse with the vertebral elements and a separate second postterminal centrum is usually visible, though postterminal centrum 1 has fused with the terminal vertebra. This type is also well represented among isospondylous fishes, e.g., salmonoids and stomiatoids. Indeed Type I seems to be a stage in the normal or at least usual route of evolution followed in the modern teleosts.

Types II and III, by contrast, appear to represent divergent evolutionary side lines. It thus seems more probable that the representatives of these types are either phylogenetically related or have evolved their caudal similarities as the results of rather unusual environmental stresses (or both). The (Type II) resemblances between the round herrings and the characin *Brycon* are particularly intriguing in this regard, for the similarities extend to trivialities.

As to Type III, it is difficult to understand why postterminal vertebra 2 should have fused with upper hypurals in such divergent fishes as osteoglossoids, the Percopsiformes, cyprinodonts, *Velifer,* and apparently in eels. Perhaps the best explanation that can be offered is that suggested in a previous paper (Gosline, 1960), namely, that these forms have all had round-tailed ancestral forms, even if they have a forked tail now. Of these groups the caudal skeletons of only *Aphredodorus* and *Amblyopsis* show sufficient similarity in detail to suggest an inquiry into the possibility of phylogenetic relationship.

In the introduction to the paper the within-group evolution of the structures dealt with was noted. Since the caudal skeleton shows this feature the most strikingly of the four characters examined, the subject will be discussed here.

Our present classification of teleostean fishes has been erected chiefly through efforts to distinguish groups, and for purposes of presentation the "orders" are frequently represented as a series of beads attached to one another by longer or shorter strings. As a result, the fact that evolution has occurred within orders has become obscured.

Now it is very possible that the major teleostean orders originally did evolve in response to a particular mode of life (Simpson, 1944), and that if only the characters involved in these adaptations are considered, the orders could be represented as a series of rather separate beads. Nevertheless, such characters would only represent a very small proportion of those found in the fish as a whole. For all other features progressive change would either not occur or might be expected as much within as between orders. As far as the caudal skeleton is concerned, the amount of change that takes place within the ostariophysine fishes and other orders is far greater than the difference between *Albula* and *Epinephelus.* Or, to put the matter differently, the caudal skeletons of the basal berycoids and serranids are nearer the basal clupeiform type than that of *Clupea.*

II. SOME FEATURES OF PELVIC STRUCTURE

The position of the pelvic fin and the number of its rays are almost universally used in the higher classification of teleostean fishes. Internal pelvic structures have been neglected. The most thorough account of pelvic anatomy in fishes is that of Sewertzoff (1934); within groups, Sheldon's (1937) treatment of the pelvic girdle in catfishes appears to be unique. The facets of pelvic structure that will be treated here are the small, curved splint of bone that lies outside of the outermost ray in many lower teleosts, and the radial elements.

The pelvic fins of most lower teleosts are made up of a series of segmented soft rays (lepidotrichia of Goodrich, 1904, Jarvik, 1959, and others), each of which contains a separate upper and lower half. The only exception is the curved splint that runs for most of its length along the outer surface of the upper half of the outermost ray on either side (fig. 5A to C). This splint never shows any transverse segmentation, and its anterior end does not articulate with the pelvic girdle but lies free in the skin. The origin and nature of this structure seem to be unknown. Suffice it to say here that it can be traced back in typical form and condition to *Amia*. In *Lepisosteus* there is a minute, unpaired, diamond-shaped plate on the outside of the base of the lateralmost ray, but whether this is the same element as the curved strut of *Amia* seems open to question.

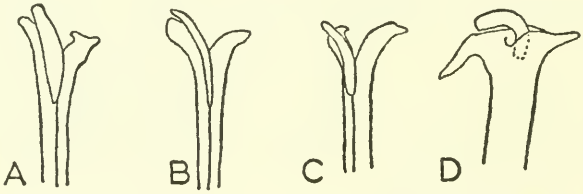

FIG. 5.—Outermost right pelvic ray bases, lateral views.

A, *Tarpon* (Clupeiformes); B, *Solivomer* (Scopeliformes); C, *Aphredodorus* (Percopsiformes); D, *Myripristis* (Beryciformes).

Among the Clupeiformes this curved splint is present in *Tarpon* (fig. 5A), *Pterothrissus, Salmo,* and *Chanos* among the forms examined. In the Dussumieriidae, Clupeidae, and Engraulidae it appears to be missing, at least as a separate element.

There is probably no great systematic significance to be attached to the loss of this splint. Thus, among the haplomous fishes it is present in *Esox* but apparently not in *Umbra.* Among the iniomous fishes it occurs in *Solivomer* (fig. 5B) but not in *Aulopus.* Among ostariophysine fishes it appears in *Brycon,* and among the cyprinodonts, in a specimen of *Fundulus majalis* (but not in another form of *Fundulus* examined). About all that can be said is that, like the orbitosphenoid, it represents, when present, the holdover of a primitive teleostean (holostean?) feature.

Under the circumstances it only remains to point out the high degree of development of this splint in two lower teleostean groups—the Notacanthiformes and Percopsiformes. Among the soft-rayed halosauriform fishes as represented by *Halosauropsis,* this outer splint is present in fairly typical elopoid form. In the spinous *Notacanthus,* however, this same structure has been transformed into one of the several pungent spines at the outside of each pelvic fin. The other spines, as indicated by their forked bases, have formed by the fusion of two halves of a segmented ray. (In this they are similar in construction to the single pelvic spine of the berycoids and percoids.)

In the Percopsiformes (fig. 5C) the outermost ray structure of the pelvic fin is about as in the elopoids. This, like so many other features, indicates the low level of organization of the group.

At this point the question may well be asked: What is a pelvic spine? If *Percopsis* has a pelvic spine, then so have *Tarpon, Salmo,* and others. If the outer splintlike structure should not be considered a spine, then in counting the pelvic spines of *Notacanthus* should one count the number of pungent elements and subtract one? The difficulty cannot satisfactorily be resolved by fiat, but in practice the systematist can easily handle the problem by stating how he is making his pelvic fin counts. As a guide in this matter it may be said that, with the exception of the notacanthids, the author has never found a separate splint developed in those forms that have a true pelvic spine, e.g., holocentrids and percoids.

In living holosteans and in many lower teleosts there are either three or four radials between the pelvic rays and the pelvic girdle on each side (Sewertzoff, 1934). In *Lepisosteus, Amia,* and most isospondylous fishes (fig. 6A) the innermost radial (the metapterygium according to Sewertzoff) is enlarged and runs partly under and partly along the inside of the innermost ray. Lateral to this innermost radial there are either two or three smaller nodules of bone that are more or less hidden between the two halves of the ray bases. These nodules may be, and perhaps always are, enclosed in cartilage.

To summarize concerning these radial elements as a group, the author has found them well developed in isospondylous fishes, in *Aulopus* among iniomous fishes, and in *Holocentrus* among the berycoids. However, a number of lower (and apparently all higher) teleosts lack separate radial ossifications. Indeed, even among the haplomous fishes the pelvic rays seem to articulate, at least in part, with a cartilaginous area that contains no radial ossifications.

The interest here is not so much in the presence or absence of independent radial elements as in the history of two of these, the innermost and outermost, in certain lower teleostean groups. Among the isospondylous fishes the inner radial may be large (as in *Salmo,* fig. 6A, and *Tarpon*), small (as in *Hiodon* and *Yarrella*), or apparently absent (as in *Esox* and *Umbra*). However, in all the isospondylous fishes examined it is either absent or has a movable articulation with the base of the innermost ray.

In apparently the great majority of iniomous fishes, by contrast, this inner radial becomes fused to the lower half of the innermost pelvic ray (Gosline, in press). As a result of this, the two or three rays lateral to the innermost ray appear to articulate with a club-shaped basal extension (as in fig. 6B) of the inner ray. As has been pointed out (Gosline, in press), this fusion of radial and ray is not invariable in the iniomous fishes. The known exceptions occur in *Alepisaurus* where the inner pelvic ray and radial are attached but not fused to one another, and in *Bathypterois* where the two structural elements movably articulate with one another as in most isospondylous fishes.

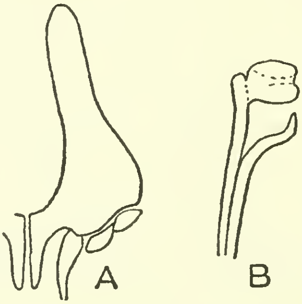

FIG. 6.—A, Pelvic girdle of larval salmon (Clupeiformes). (From Sewertsoff, 1934, fig. 26.)

B, Innermost right pelvic ray of *Myripristis* (Beryciformes). The front of the fish is toward the top, and the bottom of the fish is to the left of the figure.

In both *Halosauropsis* and *Notacanthus* of the Notacanthiformes the innermost ray of the pelvic fin articulates movably with the inner radial as in isospondylous fishes. The same condition holds for *Brycon* among the ostariophysine fishes.

By contrast there are several orders in which the bottom half of the innermost pelvic ray has the club-shaped (radial) extension typical of the iniomous fishes. Among these are at least the Percopsiformes (*Aphredodorus* and *Percopsis* examined), the Beryciformes (*Holocentrus* examined) and the Beloniformes (*Chriodorus* and *Athlennes* examined).

In view of the variability of the radials and the paucity of the material studied it seems inadvisable to push too far the inference that can be drawn from the inner radial regarding genetic relationships. Suffice it then to summarize by suggesting that the Notacanthiformes and Cypriniformes seem to show an isospondylous type of inner radial organization, and the Percopsiformes, Beryciformes, and Beloniformes, an iniomous type.

The history of the outermost radial may be dealt with even more briefly. In a fish like *Salmo* (fig. 6A) or *Synodus,* this radial is a flattish, pebblelike nodule lying between the bases of the halves of the three outermost pelvic rays. In the beloniform *Athlennes* and the syngnathiform *Fistularia* the author has been unable to find any independent radial ossifications. In the beryciform genera *Holocentrus* and *Myripristis* the outer soft ray has been transformed into a rather formidable spine. This spine has a complicated articulation with the pelvic girdle which effectively restricts movement to one plane. (The same thing is true of the holocentrid dorsal spines, which seem to have essentially the same system of basal articulation.) In *Holocentrus* and *Myripristis* there is a small, movable nodule of bone (fig. 5D), flattish except for a curved projection that penetrates a hole in the base of the pelvic spine, that presumably represents the outer radial. In the zeiform genus *Antigonia* and several percoids examined there is no trace of a separate ossification between the base of the pelvic spine and the girdle.

Concerning the pelvic spines formed from soft rays (and not from the outer, curved splint discussed earlier), it has already been noted that there are several of these in notacanthids. Aside from this group, a true pelvic spine seems to occur first in the berycoids and zeoids. At least, the outer rays of the gadid *Lota,* the lampridiform *Velifer,* and others all proved to be of the divided and segmented type (lepidotrichia) found in lower forms. There is, however, no guarantee that a fish with an outer soft pelvic ray has not merely lost the spine as has indeed happened in the majority of the flatfishes (Norman, 1934; Hubbs, 1945).

III. SOME BONES OF THE SNOUT REGION IN MODERN TELEOSTEAN FISHES

The bones discussed in the present section are the supraorbital and certain of the ossifications surrounding the sensory canals of the snout. The evolution of these bones is closely associated with the functions they serve. Originally this function was that of protecting the lateral line canals of the surface of the snout. However, in many lower teleosts three of these bones—the supraorbital, antorbital, and lacrimal—have developed into a system for pumping water in and out of the olfactory capsule. Some aspects of the sensory canal system and its ossicles in certain lower teleosts will be described first. The remainder of the section will be devoted to the pumping system and its ossifications.

Transverse sensory canals of the snout region in certain lower teleosts.—The ethmoidal commissure of the sensory canal system has a rather brief history in modern teleosts. Presumably, like the supratemporal commissure, it was originally enclosed in a series of separate, flat, roofing bones, as in *Amia.*

Among the teleosts the ethmoidal commissure most closely approaches the *Amia* condition in *Elop*s (Nybelin, 1957). Here the median portion of the canal passes through a bone called the rostral by Nybelin (1957, p. 456, fig. 2), but more generally termed the mesethmoid (cf., Starks, 1926, p. 143); in any event all traces of independent, superficial, canal-bearing plates have disappeared. Laterally on each side, the commissure just misses the front of the supraorbital canal and then passes back through two lateral rostral plates to join the infraorbital canal at the front of the lacrimal.

In a young specimen of *Megalops* examined, as in *Tarpon* (Nybelin, 1957, p. 457), there is also a well-developed ethmoidal commissure. But unlike *Elops,* that of *Megalops* fails to connect laterally with the infraorbital canal. Furthermore, there is only one lateral rostral on each side instead of two. Presumably, the posterior lateral rostral with its canal has dropped out, eliminating the junction between the commissure and the infraorbital system.

My efforts to find, by gross dissection, either a bone-enclosed ethmoidal commissure or lateral rostral ossicles in alepocephalids, clupeids, and round herrings have been unsuccessful. Presumably the ethmoidal commissure described for *Clupea* by Wohlfahrt (1937) passes entirely through the flesh of the snout. (The sensory canals of the head in teleosts are by no means always bone enclosed, cf., Gosline, 1949, p. 3.)

The ethmoidal commissures described to this point are easily recognized as such. However, certain other lower teleosts have transverse canals in the snout region so peculiar as to arouse doubt whether or not they are commissure derivatives. One such series has been described in the eels by Allis (1903); this will not be discussed here. Very different canal structures occur in the snouts of the albulids and halosaurids. These will be described below.

At least some of the difficulties with the canal bones of the head in *Albula* and *Pterothrissus* undoubtedly arise in relation to the cavernous trough system of lateral line canals in these fishes. Many deep-water fishes, but also some shallow-water and even some fresh-water forms, have such a system of troughs replacing the usual sensory canals of the head. Such troughs differ from the usual tubes in a number of ways. In the first place the external surface of these troughs is covered by a layer of thin, taut skin. In the second, such a system may have a large number of minute openings to the exterior, but it lacks the usual type of large (primary) sensory canal pores. Whatever the significance of these differences as far as function is concerned, it seems certain that a trough system shows considerable variation as compared to the relatively stable normal canals. Connections may be established between some parts of a cavernous system and membranous closures may be developed between others. Sometimes, e.g., in *Halosauropsis,* there seems to be a separate ossicle developed below each lateral line sense organ (neuromast). With this background, which is based on an examination of such diverse fishes as engraulids, notopterids, macrourids, *Acerina,* and brotulids (see also Garman, 1899; Pfüller, 1914; Omarkhan, 1949), the troughs in the snout region of *Albula, Pterothrissus,* and *Halosauropsis* will be dealt with.

In *Albula* the supraorbital canal of each side passes forward over a nasal and a prenasal ossicle to end blindly at the border of the snout. There is also a rather extensive median cavity in the tip of the mesethmoid. Though this cavity extends laterally into the flesh on either side of the mesethmoid, it does not appear to connect with the supraorbital or infraorbital sensory canals. Whether this cavity represents the ethmoidal commissure of *Elops,* the peculiar median sensory system of eels described by Allis (1903), or whether it is even a part of the sensory canal system is not clear to the present author. In the related *Pterothrissus* (fig. 7), the supraorbital canal extends forward to the snout rim, down which it extends for a short distance before ending blindly. Near its anterior end it is in open connection with its fellow on the other side via a hole through the mesethmoid; on the floor of this transverse opening there is a well-developed neuromast. Other than this opening, there is no median cavity in the mesethmoid.

The infraorbital canal in *Albula* and *Pterothrissus* runs forward to the anterior end of the lacrimal, where it doubles back and up into the antorbital (see below). At its anteriormost point it is joined by another canal which passes through two (*Albula*) or three (*Pterothrissus*) small (lateral rostral?) ossicles and then drops down into the premaxillary, where it runs forward and ends blindly (fig. 7). The canal in the premaxillary of *Albula* and *Pterothrissus* (it also occurs in *Dixonina*) is unique among living teleosts.

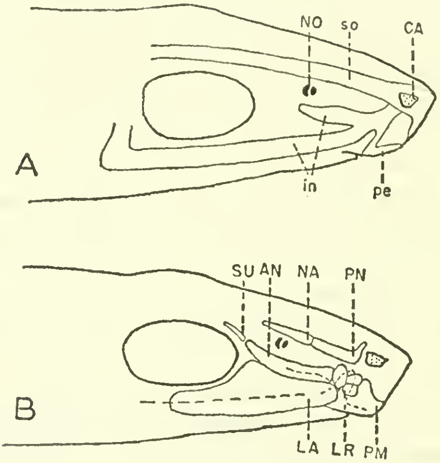

FIG. 7.—Diagrammatic lateral and slightly superior views of the head of *Pterothrissus gissu* (Clupeiformes).

A, Showing the course of the sensory canals of the snout; B, showing the superficial bones of the snout region (the course of the infraorbital system of sensory canals outlined by dashes).

AN, antorbital bone; *CA,* cavity in mesethmoid by means of which the supraorbital sensory canals of either side join; *in,* infraorbital sensory canal; *LA,* lacrimal bone; *LR,* lowermost of the three lateral rostral bones; *NA,* nasal bone; *NO,* nostril; *pe,* premaxillary sensory canal; *PM,* premaxillary bone; *PN,* prenasal bone; *so,* supraorbital sensory canal; *SU,* supraorbital bone.

Halosauropsis (USNM 53615) is the only other fish known to the author besides the elopoids that has small canal-bearing ossicles in front of the lacrimal. Here, as in *Albula* and *Pterothrissus,* there is a trough system of canals and a decidedly subterminal mouth. The supraorbital and infraorbital canals end blindly forward. Just above the premaxillaries on the lower surface of the snout there is a broad cross channel which is only separated from the infraorbital canal on either side by a membrane. Underlying the various canals in the snout region is a series of six small ossicles on each side, several of these bearing a single neuromast.

The supraorbital and antorbital in relation to olfaction.—For present purposes the nasal organs of the lower teleosts may be divided into three types. One, represented in the fishes examined only by the Beloniformes, has no nostrils and no olfactory laminae, at least in *Cololabis* and *Hyporhamphus;* instead, the nasal tract runs directly to the base of a nasal tentacle which protrudes from a nasal fossa. Variations of this nasal organ in the hemiramphids have been described by Weed (1933, p. 44). A second type of nasal structure consists of a series of transverse laminae lying at the bottom of a nasal capsule that is closed above except for two rather small, well-separated nostrils. The anterior of these frequently opens at the tip of a tube. Water is presumably passed across the nasal epithelium of such an olfactory organ by ciliary action as in *Anguilla* (Liermann, 1933). In fishes with either of the types of nasal organs just noted the surrounding bones appear to have little to do with olfaction, and these types will not be dealt with further.

In the majority of living teleosts, by constrast, there are two relatively large, adjacent narial openings leading into the olfactory capsule on the bottom of which lie the olfactory laminae. From the capsule extend one or more nasal sacs or diverticula. Movement of the bones around these sacs alternately contract and expand them, thus pumping water in and out across the nasal epithelium (Eaton, 1956). It is with certain of the bones involved in this pumping system that the present discussion will be concerned.

The *antorbital* (fig. 7B, *AN*) is a bone rather widely represented among the lower teleosts but apparently incorporated into the lacrimal in higher forms. It undoubtedly originated as a sensory canal bone, but in living lower teleosts it serves primarily as part of the nasal pumping system just mentioned.

For purposes of nomenclature, the "type" antorbital is that of *Amia* (Westoll, 1937, p. 519). However, it seems probable that the antorbital of *Amia* is equivalent to the two lateral rostrals plus the antorbital of *Elops* (cf. Westoll, 1937, p. 519, footnote). In modern teleosts the antorbital becomes associated with the supraorbital bone (fig. 7B) above it and reduces or loses its sensory canal. Even so it remains easily identified by its topographic position and relationships: when present it lies above the lacrimal and borders the nasal openings below; forward it usually has a ligamentous connection with the outer surface of the maxillary. Only when the antorbital is greatly reduced is it difficult to identify. Nevertheless it passes under a number of names in the literature. Thus Derschied (1924) calls it the adnasal; Gregory (1933) labels the same bone prefrontal in some illustrations (e.g., fig. 32) and lacrimal in others (e.g., fig. 40); and Wohlfahrt (1937), Berg (1940), Kirkhoff (1958), and others have mistakenly identified it as a supraorbital bone. On the other hand Lekander (1949) has, with more justification, called the bone usually termed the lacrimal, the antorbital. In the cyprinids which Lekander studied, the bone in question is very probably a compound structure made up of a fusion of the lacrimal and antorbital, but the latter bone would seem to have formed at most a very insignificant part of the result.

In living teleosts there is at most only one *supraorbital* bone (fig. 7B, *SU*). It never bears a sensory canal and seems to be the sole remnant of a series of bones that formerly protected the upper border of the orbit. In certain scopeliform fishes (e.g., *Aulopus*) the remaining supraorbital forms part of the rigid roof of the orbit, but its retention in modern teleosts is probably attributable to its secondary association with the antorbital as part of the nasal pumping system.

In the majority of modern isospondylous fishes there are two nasal sacs opening off from the nasal capsule (Derschied, 1924). The lower of these passes down and back in front of and below the orbit. Water is pumped in and out of this sac by movements of the lacrimal dorsolateral to it and the palatine ventromedial to it. (This is the Lacrimalsack of Liermann, 1933; see also Eaton, 1956.) The upper sac, with which the present discussion is concerned, extends up and back to and sometimes above the upper border of the eye. As Kirkhoff (1958) has clearly shown for *Clupea,* the expansion and contraction of this sac is governed by the linkage of the antorbital (supraorbital I of Kirkhoff) and supraorbital. Movement in the superficial bones of the snout associated with both nasal sacs is ultimately controlled by the opening and closing of the mouth. This is brought about by separate ligamentous attachments between the maxillary and the forward ends of the lacrimal and the antorbital.

Neither the presence of an upper (supraorbital) nasal diverticulum nor of an antorbital-supraorbital link are constant features in the isospondylous fishes (Derschied, 1924). It would seem that wherever a well-developed supraorbital nasal sac is present there is also an antorbital-supraorbital pumping mechanism. However, the supraorbital or antorbital bone may be present in fishes with no supraorbital diverticulum. With this introduction, a brief history of the antorbital and supraorbital bones in living teleosts will be given.

In *Elops* both bones are present (Nybelin, 1957, fig. 2) but do not seem to form a movable link, for the supraorbital bone is tightly attached to the frontal; there is no supraorbital nasal sac (Derschied, 1924, fig. 1,*c*). *Megalops* differs only slightly in the possession of a small supraorbital nasal diverticulum (Derschied, 1924, fig. 3). In *Albula* there is an elongate, movable supraorbital bone associated with a canal-bearing antorbital (as in *Pterothrissus,* fig. 7B); the supraorbital diverticulum extends well back under the former bone (Derschied, 1924, fig. 4,*b*).

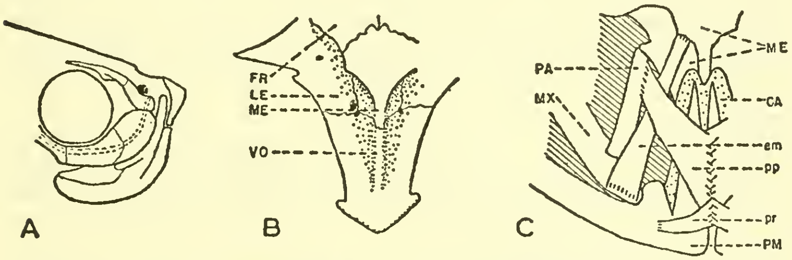

Fig. 8.—A, Snout region of *Pellona* sp. (Clupeiformes).

B, Ethmoid region of cranium of *Mycteroperca* (Perciformes). *FR,* frontal; *LE,* lateral ethmoid; *ME,* mesethmoid; *VO,* vomer.

C, Snout region of *Mycteroperca* (Perciformes). *CA,* cartilaginous area under premaxillary pedicels; *em,* ethmoid-maxillary ligament; *ME,* mesethmoid bone; *MX,* maxillary bone; *PA,* palatine bone; *PM,* premaxillary bone; *pp,* palatine-premaxillary ligament; *pr,* interpremaxillary ligament.

In *Alepocephalus* there is no supraorbital bone and no supraorbital nasal diverticulum of the nasal capsule (Derschied, 1924, fig. 11). There is however an L-shaped antorbital which protects the ventral and posterior borders of the nasal openings, but there is no ligamentous connection between its forward end and the maxillary.

Among the herringlike fishes the suborbital and supraorbital nasal sacs are usually both represented (Derschied, 1924, pp. 98-106, figs. 6-8). The antorbital-supraorbital link is always present (fig. 8A) and perhaps reaches the epitome of its devlopment as a pumping mechanism (Kirkhoff, 1958). Nevertheless, even among this group there seems to be considerable reduction in the size of the diverticula and in the mobility of the dermal bones of the snout in those forms with a heavy covering of adipose tissue in the snout region, e.g., *Dorosoma* and the anchovies. Indeed, in the anchovy examined the supraorbital appears to be rigidly united to the skull.

The great variation in the nasal apparatus and dermal bones of the snout in stomiatoids has been demonstrated by Derschied (1924, pp. 118-128, figs. 12-15). Suffice it to say here that the antorbital-supraorbital link is present in the more primitive genera *Maurolicus, Cyclothone,* and *Gonostoma.*

The salmonoid nasal sacs seem to be similar to those of the herrings in that a supraorbital and suborbital diverticulum are both present (Derschied, 1924, pp. 109-115, fig. 10). However, the antorbital-supraorbital-maxillary link never seems to be so well developed. For example, in *Salmo,* which has a very fleshy snout, an antorbital and supraorbital are both present but so deeply embedded that it is difficult to see how opening the mouth could move them. The antorbital and supraorbital are also present in *Coregonus* (Berg, 1940, p. 235, fig. 122) and *Osmerus,* though in the latter the antorbital is rather feeble.

In *Argentina* there is a well-developed supraorbital covering the supraorbital nasal sac, but apparently no antorbital (Chapman, 1942, p. 106, fig. 4). In *Nansenia,* however, a small antorbital is present (Chapman, 1948, p. 10, fig. 5).

In *Galaxias* there appears to be a supraorbital (?) but no antorbital, and in *Salanx* neither bone is present. Among the haplomous fishes there are apparently no nasal sacs and no antorbital. A movable supraorbital is present in *Esox,* but not in *Umbra.*

In *Chanos,* which resembles *Dorosoma* in the heavy layer of adipose tissue in the snout regions, the nasal sacs are again small. The supraorbital is large but movable and lies on the surface of the skull. The small squarish antorbital covers the outer surface of the nasal capsule. Thus the two bones have planes at right angles to one another, and there seems to be little connection between them.

Gonorhynchus seems to be unique in that there is a large nasal sac extending back in the flesh external to the large lacrimal. Antorbital and supraorbital bones are absent.

According to Derschied (1924, p. 159) *Phractolaemus* is even more peculiar in having a transverse canal running between the nasal capsules of the two sides.

Among the osteolossoid fishes there is a most varied and disconcerting series of dermal bone arrangements on the sides of the snout. All are similar in two respects. First, all the members of the group have a rigid cup around the nasal capsule which gives off no diverticula. Second, the bone arrangements around this capsule in no way resemble those of any fish dealt with up to here.

In *Hiodon* the nasal is a tubular, L-shaped bone hooking over and around the front of the nasal capsule in such a way that the front of the supraorbital lateral line canal runs downward and somewhat backward. The infraorbital canal runs forward and stops in a small bone (the lacrimal?) just behind the nasal capsule. The rear of the capsule is rimmed by the lateral ethmoid; this bone does not reach the surface, but just below the skin gives off a forward flange that in lateral view makes the lateral ethmoid look like a circumorbital (see Ridewood, 1904, pl. 25, fig. 20). There is no separate supraorbital.

Pantodon has the suborbitals continued forward as a ring of tubular ossicles well up on the anterior rim of the orbit. The anteriormost of these overlies but is entirely separate from the lateral ethmoid; that it represents the antorbital of the fishes dealt with above seems somewhat dubious.

In *Osteoglossum, Heterotis,* and *Arapaima* this anteriormost bone becomes progressively expanded and fuses above with the frontals. In *Osteoglossum* at least, it bears a canal that opens out above into a subdermal space above the surface of the frontals. *Notopterus* has a similar channel in its anteriormost circumorbital.

At this point it may be well to summarize for the isospondylous fishes. The osteoglossoids (along with the mormyroid fishes; see Derschied, 1924, pp. 142-157, figs. 21-25) must be separated off at once because they have a rigidly enclosed nasal capsule without diverticula and no supraorbital bone, the place of the latter sometimes being taken by a canal-bearing antorbital (?) that fuses with the frontal above the eye.

Second, *Gonorhynchus* and *Phractolaemus* must be removed from the others, because of the very peculiar (but very different) cavities connected with their nasal capsules.

Among the remaining clupeiform fishes one or two nasal capsule diverticula and an antorbital-supraorbital link are generally present. At least two lines of evolution have developed from this basic pattern. In *Alepocephalus,* which has a long snout with the nostrils far back, there is a large nasal sac extending forward under the lacrimal, but the supraorbital sac and the supraorbital bone are missing. In the salmonoid series a rather different line of development has taken place. The supraorbital sac is generally retained but the anterior end of the antorbital-supraorbital link degenerates; in *Argentina,* for example, the antorbital seems to be completely missing. Among haplomous fishes the antorbital is always missing; a movable supraorbital is present only in *Esox;* and there are apparently no nasal sacs.

With regard to the orders above the isospondylous fishes, I have been able to discover a supraorbital and/or antorbital in only four: the iniomous, ostariophysine, heteromous, and salmopercoid fishes.[2] In no members of these examined was there a well-developed supraorbital nasal sac.

In the iniomous genus *Aulopus* there is a well-developed supraorbital bone. It is, however, rigidly attached to the frontal and seems to function as a protecting bone for the upper portion of the eye. The nasal capsule extends back very slightly below its anterior margin. The antorbital forms a long, somewhat curved strut running forward from the front of the supraorbital bone below the nostrils. In *Chloropthalmus* both supraorbital and antorbital bones are again present. The supraorbital has a somewhat more anterior position than in *Aulopus.* It is less rigidly attached to the frontals, and dips down below the rear border of the nasal capsule. The antorbital is a small ossicle lying above the forward portion of the lacrimal. *Neoscopelus* has a small antorbital but apparently no supraorbital. In the more specialized iniomous fishes examined, e.g., *Parasudis,* neither antorbital nor supraorbital are present, at least as separate elements.

Among the ostariophysine fishes, the antorbital and a somewhat movable supraorbital are present in *Brycon.* The latter bone extends slightly over the nasal cavity. In *Astyanax* there is a small antorbital, but I have been unable to find any supraorbital. In the cyprinids, by contrast, there is usually a supraorbital, but the antorbital generally disappears. Presumably it fuses with the lacrimal.

Among the heteromous fishes there is a very slender antorbital in *"Halosauropsis"* and a somewhat stronger one that bears the anterior end of the infraorbital canal in *Notacanthus.* In neither genus is there any trace of a supraorbital.

Finally in *Percopsis* the infraorbital channel runs forward through the lacrimal, then turns upward through a terminal hoop in that bone and doubles back to end over an ossicle which is undoubtedly an antorbital. The whole arrangement is somewhat reminiscent of *Albula.* In *Aphredodorus* there is no antorbital; the infraorbital canal runs straight forward in the lacrimal and ends there without doubling upward and backward.

In general, it may be said that lower teleostean evolution shows the

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[2] In a stained and cleared specimen of the eel *Ariosoma* there is a minute ossicle above and in front of the lacrimal that may represent the antorbital. Since the above was written an antorbital has also been located in the holocentrid fishes.

antorbital and the one remaining supraorbital bones on their way out. Before disappearing, however, there is a transformation of function of these bones into a pumping mechanism for the supraorbital diverticulum of the nasal capsule. This new function has probably prolonged the evolutionary life of the antorbital and the supraorbital.

The higher teleosts usually have nasal diverticula (cf., Eaton, 1956); however, the supraorbital diverticulum has disappeared. Perhaps it is no coincidence that the supraorbital sac and supraorbital bones drop out just below the level of protrusile premaxillary development (see section IV of this paper), for a protrusile upper jaw would certainly affect the arrangements of any pumping systems in the snout region.

From a phylogenetic standpoint, the antorbital-supraorbital pumping system would seem to be the sort of mechanism that would only have evolved once, for it is made up of rather heterogeneous parts. It seems improbable that the two elements in this link were originally more than casually in contact with one another. If, then, this antorbital-supraorbital link evolved only once, it is evidence that at least the fishes that possess it are of monophyletic origin.

IV. UPPER JAW PROTRUSION IN TELEOSTEAN FISHES

The freeing of the maxillary from the cheek is generally considered a milestone in the evolution of the actinopterygian fishes. The development of a protrusile upper jaw in the teleosts is a further, though probably less fundamental, step in the same general direction.

Probably the principal method of feeding in fishes is to suck the food in with the surrounding water by expansion of the oral and gill cavities. If some method is evolved of shooting the mouth opening forward at the same time the suction is developed, the chances of catching any moving prey should be increased. This, in its barest terms, would seem to be the basic advantage of a protrusile upper jaw.

There are, of course, a number of supplementary considerations. For example, fishes have on the one hand found it possible to adapt such a protrusile jaw for other types of feeding, e.g., the nipping structure of the parrot fishes. On the other, there are some types of feeding in which a protrusile upper jaw may be disadvantageous. Thus, many fishes feeding on large prey have redeveloped fixed premaxillaries, e.g., barracudas, gempylids, tunas, most carangids. Furthermore, even those fishes in which the pipette system of feeding is developed to its greatest extent, i.e., the pipefishes and sea horses, do not have a protrusile upper jaw. On balance, however, there are probably more fish species living today that have a protrusile upper jaw than there are species that do not.

The fact, noted above, that many fishes have lost the protrusile premaxillaries often makes it difficult to state definitely that a fish with a fixed jaw never had a protrusile jaw.

In the percoid type of jaw protrusion the mesethmoid and vomer have a median ridge (fig. 8B) which forms a rail along which the premaxillary heads (pedicels) slide. This prohibits lateral dislocation. The premaxillaries are held pressed to the rail by a series of ligaments. At the front the two premaxillaries are bound to one another, and anterolaterally are held in place by the palatine-premaxillary ligament (fig. 8C); posteriorly they are firmly tied to the maxillary and the lower jaw.

When a fish with protrusile premaxillaries of the percoid type opens its mouth, the upper jaw automatically slides forward and downward along the ethmovomerine ridge. The anterior portions of the premaxillaries are wedged forward by the outward rotation of the anterior maxillary heads; this rotation is associated in turn with movement of the forward end of the palatine (van Dobben, 1935). The posterior ends of the premaxillaries are forced forward and downward by the lowering of the mandible.

Thus protrusion of the premaxillaries is accomplished by a rather complex mechanism. Nevertheless, all the basic elements necessary for the percoid type of premaxillary protrusion would seem to be present at least as far back as the basal scopeliform fishes, e.g., *Aulopus*. Furthermore, even in such clupeiform fishes as *Megalops* and *Clupea* (Kirkhoff, 1958) the whole system of ethmoid-palatine-maxillary-premaxillary articulations and ligamentous connections is present and the premaxillaries are to some extent automatically rotated, if not protruded, when the mouth is opened. In actual practice the only criterion the author has been able to find for whether the premaxillaries can or cannot be protruded is the presence or absence of an infolding of the skin across the front of the snout behind the upper jaw: where a broad or narrow frenum is present between the cranium and the upper lip, it is assumed that the premaxillaries are nonprotrusile.

The teleostean orders (following Berg's 1940 classification) in which a protrusile upper jaw is present are the following: Clupeiformes (*Gonorhynchus* (?) and *Phractolaemus* only), Bathyclupeiformes, Ateleopiformes, Cypriniformes (Cyprinoidei), Gadiformes, Macruriformes, Gasterosteiformes, Lampridiformes, most Cyprinodontiformes, Phallostethiformes, Stephanoberyciformes, Beryciformes, Mugiliformes, and most higher teleostean orders.

Of these, the very peculiar mouth structure of the isospondylous *Phractolaemus* has been taken up briefly by Ridewood (1905, p. 279). It seems to be constructed on a very different plan from that of the percoids. In *Bathyclupea* the protrusile jaw is typically percoid, as indeed is the fish itself. The protrusile, somewhat tubular mouth of ateleopids seems never to have been adequately described; no specimens are available to this author for dismemberment of the mouth parts. The protrusile upper jaw of cyprinoid fishes has been dealt with a number of times (cf. Fiebiger, 1931; Gregory, 1933); its construction is very different from that of the percoid fishes and certainly represents an independent development.

In most of the rest of the fishes with a protrusile premaxillary there is a basic structure essentially similar to that of the percoids. So far as the structural elements mentioned in the description of the percoid jaw are concerned, there would seem to be no basic difference between the protrusile upper jaws of the cods, sticklebacks, holocentrids, and phallostethids and those of the percoids. Whether, however, the peculiar type of jaw protrusion found in the Lampridiformes (Regan, 1907) is of basically percoid type or has been derived independently is a question about which the author has no first-hand information.

The cyprinodonts, some of which have a protrusile and some a fixed upper jaw, form a rather special category. Eaton (1935, pp. 166-167) has stressed the similarities in jaw structure between *Fundulus* and the Percesoces. There are certainly superficial resemblances between *Mugil* and *Fundulus,* but I believe these to be secondary. The peculiarities of the mugilid jaw structure can be traced, via the atherinids and sphyraenids, directly back to the percoid type. The protrusile upper jaw of cyprinodonts operates on a rather different system. In *Fundulus, Belonesox, Rivulus, Goodea, Orestias,* and others the premaxillary ends laterally in a strong downward hook which is membranously attached to the coronoid portion of the lower jaw forward, more or less independently of the maxillary. Lowering of the mandible thus forces the premaxillary forward. The maxillary apparently has very little to do with premaxillary protrusion.

Among cyprinodont genera with a nonprotrusile premaxillary, *Oryzias* has the same downward process at the tip of the premaxillary as *Fundulus* and the others mentioned. Loss of protractile premaxillaries is here undoubtedly a secondary character. In *Chologaster* and

Typhlichthys, however, the premaxillaries are not only nonprotractile, but have no downward hook at the tips, tapering laterally to a point as is usual in fishes. The inference would seem to be that the premaxillaries of these two genera represent the primitive condition, and that a peculiar protractile mechanism has developed within the cyprinodonts.

To summarize the foregoing material, it may be said that the following orders usually placed below the Perciformes have basically protrusile upper jaws: Gadiformes (with Macruriformes), Gasterosteiformes, Lampridiformes, Beryciformes, Zeiformes, Phallostethiformes, and Pleuronectiformes. The following orders have basically fixed premaxillaries but have one or more members developing a protrusile upper jaw: Clupeiformes, Cypriniformes, and Cyprinodontiformes.

A few concluding notes may be added concerning certain groups with nonprotrusile premaxillaries. It would appear, as already mentioned, that all the elements necessary for a protrusile jaw mechanism are present in the basal scopeliform fishes; nevertheless, the final step of actual jaw protrusion has apparently not been taken. What has just been said applies equally well to the Percopsiformes. The possibility, which the author, at least, cannot refute, exists for such groups that the lack of a protrusile jaw is here due to secondary loss.

The upper jaw structure of the Syngnathiformes is very different. Here, in *Fistularia* and *Aulostomus,* at least, the premaxillaries have no pedicels and are bound by a continuous membrane to the anterior heads of both the maxillaries and palatines. Indeed the whole upper jaw structure appears specialized in a direction which is very different from that of the Gasterosteiformes and Perciformes.

DISCUSSION

It remains to integrate the four structural systems that have been followed in the preceding sections with one another and with the existing classification of modern teleostean fishes. This can perhaps best be done by taking up one by one the lower teleostean orders as given by Berg.

Clupeiformes.—In a previous paper the author (Gosline, 1960) has dealt with the classification of this group. There a major line was drawn between a division Clupei, including *Gonorhynchus* and the haplomous fishes, and a division Osteoglossi. The nasal structures noted in the present paper would seem to reinforce such a classification, for the Osteoglossi never have nasal sacs whereas the Clupei usually do. In relation to this structural difference the supraorbital-antorbital and lacrimal pumping mechanisms so typical of the Clupei are never present in Osteoglossi, in which the area usually occupied by these bones is filled by a varied series of bones rather difficult to interpret. Certainly some members of the Clupei have also lost their nasal diverticula, e.g., *Esox* and *Umbra,* but in these the bones of the snout region have never progressed so divergently as in the Osteoglossi.

In the same paper (Gosline, 1960) the elopids and albulids were placed together in the suborder Elopoidei of the division Clupei. The presence of sensory canals in the premaxillaries of albulids, unique among recent teleosts, points up once again the divergence between these two groups.

Bathyclupeiformes.—It has been adequately demonstrated by others that the single contained family belongs in the Perciformes.

Galaxiiformes.—Berg erected this order for the genera *Galaxias* and *Neochanna.* Gosline (1960) has followed the more usual taxonomic procedure of grouping these genera with *Prototroctes, Lovettia, Aplochiton,* and *Retropinna* (and of placing the whole assemblage in the Clupeiformes). The possibility that Berg is correct in removing *Galaxias* and *Neochanna* from the other genera mentioned probably deserves further attention.

Scopeliformes.—The presence of fulcral scales and of well-developed temporal fossae in the rear of the skull of the basal iniomous genus *Aulopus* makes it impossible to derive the Scopeliformes from anything higher in the scale of modern teleosts than the elopoid Clupeiformes. (For a discussion of the relationship between the Scopeliformes and Clupeiformes, see Gosline, in press.)

Ateleopiformes, Giganturiformes, and *Saccopharyngiformes.*—The present author has no new information on these groups.

Mormyriformes.—The close resemblance between the caudal skeleton of these fishes and those of the osteoglossoids (Gosline, 1960) bears out the interrelationship between these groups hypothesized on other grounds.

Cypriniformes.—The rather remarkable similarity between the caudal skeleton of the characin *Brycon* and that of the round herrings has been remarked upon in section I of this paper. In pelvic osteology, however, *Brycon* appears to be more generalized than the modern herrings.

Anguilliformes.—No new information can be added here. Suffice it to say that the eel jaw structure can be derived only from that of the Clupeiformes among living teleosts.

Halosauriformes.—The palatine-maxillary articulation and the sensory canals of the head of halosaurids suggest a relationship with *Albula* and *Pterothrissus.* The pelvic organization is typical of the Clupeiformes.

Notacanthiformes.—Though highly specialized there seems to be no reason to believe that this group is not most closely related to the halosaurids, even though the pelvic structure of notacanthids is unique.

Beloniformes.—This group is so specialized that few inferences concerning relationship can apparently be drawn from the structures treated above. The pelvic osteology does suggest that of the iniomous fishes.

Gadiformes and *Macruriformes.*—The protrusile upper jaw of these fishes seems to be essentially of perciform type.

Gasterosteiformes.—Another group with a typical protrusile perciform upper jaw.

Syngnathiformes.—This group seems to differ from the Gasterosteiformes about as widely as possible in upper jaw structure.

Lampridiformes.—Nothing to be added here.

Cyprinodontiformes.—The protrusile upper jaw, where it occurs in these fishes, is different from that of the percoids and, judging from *Amblyopsis* and *Chologaster* which have fixed upper jaws, a protrusile jaw mechanism has been independently developed within the group. The caudal skeleton of the basal members *Amblyopsis* and *Chologaster* is highly peculiar but bears some resemblance to that of the Percopsiformes.

Phallostethiformes.—A typical perciform upper jaw.

Percopsiformes.—Though the caudal skeleton is specialized in a direction peculiar to this order and apparently the Cyprinodontiformes, the pelvic structure and antorbital bone indicate a "lower" teleostean condition. The ensemble of characters suggests that the Percopsiformes may be an offshoot of a primitive scopeliform or protoscopeliform stock.

Stephanoberyciformes.—Nothing to be added here.

Beryciformes.—In pelvic structure a scopeliform derivation is suggested. The protrusile jaw seems to be typically perciform. So far as the living teleosts are concerned a "true," percoid-type pelvic spine seems to be present for the first time here.

Zeiformes.—The protrusile upper jaw, pelvic structure, and caudal skeleton all appear to be percoid.

Mugiliformes, Polynemiformes, Ophiocephaliformes, and *Symbranchiformes.*—Nothing to be added.

In conclusion it seems relevant to discuss groupings of modern teleostean orders. The older divisions such as that between the Malacopterygii and Acanthopterygii or between Physostomi and Physoclisti need no present consideration. The defect of all such systems lies in the fact that any one character may have been lost or gained independently many times in teleostean evolution. That independent lineages may lose a character, e.g., the connection between the air bladder and the esophagus, is fairly obvious. That a character may be and often is gained in independent lineages is sufficiently indicated by the fact that the consolidation of lepidotrichia into spinelike structures has taken place time and again in teleosts, e.g., in the Cypriniformes, Notacanthiformes, Cyprinodontiformes, and Perciformes. As with the protrusile upper jaw, teleosts seem to have tried out fin spines in a number of ways before developing the generally satisfactory type found in the perciform fishes; or, alternatively (as suggested by the notacanthids), a generally adaptable type of fin spine may have been developed only after the lineage had specialized too far in other ways to allow much adaptive radiation. In any event, a formal division of the teleostean fishes based on a single character, whether one of loss, e.g., Physostomi, or of new development, e.g., Acanthopterygii, is open at least to grave suspicion.

Orders with the following percoid-type structures:

Branchiostegal rays	Protrusile premaxillaries	Pelvic spine
Syngnathiformes	. . .	. . .
Percopsiformes	. . .	. . .
Cyprinodontiformes	. . .	. . .
Gadiformes	Gadiformes	. . .
Macruriformes	Macruriformes	. . .
Lampridiformes	Lampridiformes (?)	. . .
Gasterosteiformes	Gasterosteiformes	Gasterosteiformes
Beryciformes	Beryciformes	Beryciformes
Zeiformes	Zeiformes	Zeiformes
Higher orders	Higher orders	Higher orders

Diagram 3.

Insofar as such a basis of division is valid at all, the characters of the hyoid arch (Hubbs, 1919), the development of a percoid type protrusile upper jaw, and the formation of a single "true" outer pelvic spine would seem to provide the most useful dividing lines (diagram 3). As may be seen from this diagram these three features furnish a division between a "lower" and a "higher" group of orders at roughly but not exactly the same point.

There seems little use in weighing the relative merits of these three dividing lines. Still less is there any point in recognizing the groups on either side of any of these lines in a formal classification. Each of them merely represents a level of organization in a single structure, which, like fin spines, may have been attained independently several times, or secondarily lost. (Nevertheless it is perhaps of some significance that some fishes of questioned affinity, e.g., the sticklebacks, always fall into a "higher" group in whichever of the three ways a dividing line is drawn.) For the present, then, it seems most convenient merely to speak of the percoids and their derivatives as "higher teleosts" and the isospondylous fishes and their derivatives that have not attained the percoid phase as "lower teleosts." To adopt this system, as is done here, has at least the advantage of attempting to recognize phylogenetic rather than level-of-organization groupings.

In further conclusion, a preliminary attempt will be made to carry through the idea of phylogenetic groupings within the "lower" teleosteans. To start at the bottom with the isospondylous fishes, it hardly matters for present purposes whether the group is polyphyletic or not. In either event there seems to be a basic cleavage between a *Hiodon*-osteoglossoid group and the remaining isospondylous forms. The *Hiodon*-osteoglossoid section (division Osteoglossi of Gosline, 1960) seems to have given rise to the mormyrids and their allies. The remainder (division Clupei), judging from the continuity of the supraorbital-antorbital stay (section III), etc., would seem to have given rise to most if not all other teleostean orders.

As a second step it may be noted that there is a series of orders—Clupeiformes, Halosauriformes, Notacanthiformes, and Cypriniformes—in which the basal members at least have the innermost radial of the pelvic fin present as a separate nodule. There is another group—Scopeliformes, Beloniformes, Percopsiformes, and Beryciformes—in which this same radial is fused to the base of the lower half of the inner pelvic ray (section II). Now, this difference is neither of any great structural importance nor is it absolute. Nevertheless, those orders with a free inner radial all have the maxillary typically included in the gape, whereas those orders with the inner radial and ray fused all have the maxillary excluded. Primarily on the basis of this combination of characters it is here suggested that there is a series of lower teleostean orders derived from the division Clupei that never reached a scopeliform stage of evolution and another series derived from the same source that did. (The eels must be included in the former group even though today they have no pelvic fins).

A final grouping of orders may be suggested on the basis of a number of minor features: the presence of a protrusile jaw and of a single pelvic spine developed from a soft ray, general similarity of caudal skeleton, and others. This group includes the berycoids, zeoids, and percoids.

The general relationships hypothesized in the above paragraphs are summarized in diagram 4 (which, incidentally, incorporates the string-of-beads concept objected to earlier in the paper). A number of minor and several major groups have been left out of this diagram (which is after all only a sort of temporary clothes rack to work with and from). The most important of these are the anacanthine, syngnathiform, gasterosteiform, cyprinodontiform, and lampridiform groups. Where any of these came off from what appears to be the main isospondylous-iniomous-berycoid-percoid route of teleostean evolution, the present author is not prepared to say.

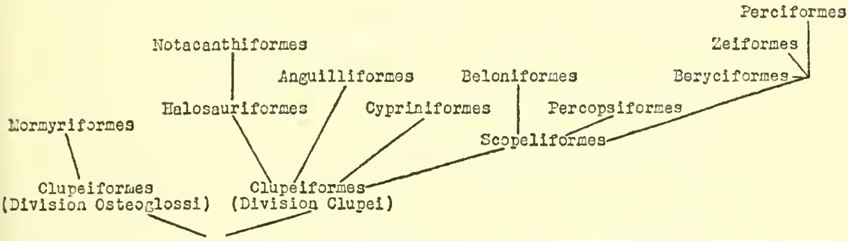

Diagram 4.

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