BULLETIN OF MARINE SCIENCE, 52(1): 554–626, 1993

PERCOMORPH PHYLOGENY: A SURVEY OF ACANTHOMORPHS AND A NEW PROPOSAL

G. David Johnson and Colin Patterson

ABSTRACT

The interrelationships of acanthomorph fishes are reviewed. We recognize seven monophyletic terminal taxa among acanthomorphs: Lampridiformes, Polymixiiformes, Paracanthopterygii, Stephanoberyciformes, Beryciformes, Zeiformes, and a new taxon named Smegmamorpha. The Percomorpha, as currently constituted, are polyphyletic, and the Perciformes are probably paraphyletic. The smegmamorphs comprise five subgroups: Synbranchiformes (Synbranchoidei and Mastacembeloidei), Mugilomorpha (Mugiloidei), Elassomatidae (*Elassoma*), Gasterosteiformes, and Atherinomorpha. Monophyly of Lampridiformes is justified elsewhere; we have found no new characters to substantiate the monophyly of Polymixiiformes (which is not in doubt) or Paracanthopterygii. Stephanoberyciformes uniquely share a modification of the extrascapular, and Beryciformes a modification of the anterior part of the supraorbital and infraorbital sensory canals, here named Jakubowski's organ. Our Zeiformes excludes the Caproidae, and characters are proposed to justify the monophyly of the group in that restricted sense. The Smegmamorpha are thought to be monophyletic principally because of the configuration of the first vertebra and its intermuscular bone. Within the Smegmamorpha, the Atherinomorpha and Mugilomorpha are shown to be monophyletic elsewhere. Our Gasterosteiformes includes the syngnathoids and the Pegasiformes (*Pegasus*) and Indostomiformes (*Indostomus*), two groups which are shown to be immediately related to syngnathoids by modifications of the gill filaments and their skeletal supports. Monophyly of the Gasterosteiformes in this sense is justified by several characters. We are unable to resolve the interrelationships among the five subgroups of Smegmamorpha. The remaining percomorphs are the Perciformes (including Caproidae), Scorpaeniformes, Dactylopteriformes, Pleuronectiformes and Tetraodontiformes; we have found nothing to indicate that Percomorpha in that sense are monophyletic, although our survey does not cover Tetraodontiformes. We believe that Scorpaeniformes and Pleuronectiformes are nested within Perciformes, but again have found nothing to indicate that Perciformes in this expanded sense are monophyletic. We recommend extending the Percomorpha to include the Atherinomorpha (and other smegmamorphs), and argue that this larger group is monophyletic. A scheme of relationships of the seven groups Lampridiformes, Polymixiiformes, Paracanthopterygii, Stephanoberyciformes, Zeiformes, Beryciformes and the expanded Percomorpha is presented and supported by apomorphies. New names for higher acanthomorph taxa are proposed as follows: Euacanthomorpha (Acanthomorpha minus Lampridiformes), Holacanthopterygii (Eucanthomorpha minus Polymixiiformes), and Euacanthopterygii (Acanthopterygii minus Stephanoberyciformes). Monophyly of Beryciformes s.l. (including stephanoberyciforms) is rejected because Beryciformes s.s. share several apomorphies with the expanded Percomorpha, all of which are absent in Stephanoberyciformes. The Zeiformes are the most problematic of the acanthomorph groups; with the characters that we have been able to assess, the zeiforms are placed most parsimoniously as the sister-group of Euacanthopterygii (i.e., between stephanoberyciforms and beryciforms on the cladogram), but we do not propose a name for the taxon so formed. There is a disturbing incidence of homoplasy in the characters that we have investigated in acanthomorphs.

Fishes, considered collectively . . . offer to the philosopher an endless source of meditation and surprise.

J.-A. Brillat-Savarin, "The Philosopher in the Kitchen," 1825.

Thus, recent work has resolved the bush at the bottom, but the bush at the top persists.

G. Nelson (1989: 328).

Our original intention, in getting together to produce a concluding paper for this symposium volume on percomorph phylogeny, was to summarize and draw together the contents of the volume. We have, in fact, produced something more pretentious or utopian. The organizer of a symposium on percomorph phylogeny might hope that the result would be a new and well-supported scheme of relationships for the group, or at least for its major clades. That is not what this volume contains; the majority of the included papers deal with phylogenetic relationships within perciform clades. We do not comment on those, not because we disregard them but because they concern disparate twigs of the tree, and so make no connected story. Here we are more concerned with the main branches of the tree, percomorphs and their relatives. We decided, perhaps unwisely, to grasp the nettle, to plunge into the glycerin, and to propose a scheme of relationships for those groups. That was, in part, an aim of the symposium, because in the concluding general discussion the participants collaborated, with more or less enthusiasm, in drawing up such a scheme. Our own concluding cladogram agrees with that post-symposium version in having eight nodes or non-terminal components, but all eight of those components are different in the two, and only six out of a dozen terminals are identical (they are polymixiids, lampridiforms, paracanthopterygians, gasterosteiforms, mugiloids, and atherinomorphs). There are several billion other possibilities, and in presenting ours we recognize one other point that came up in the post-symposium discussion, that any tree can be justified by special pleading, by insisting that certain characters are uniquely derived but others are more labile or plastic. Our adventure with the glycerin convinced us of one thing—very few of the characters found among percomorphs and their relatives are uniquely derived, and progress will not be made without some special pleading.

Reviewing and comparing all of the contributors' manuscripts for this volume has been a stimulus to the development of our own ideas, however misguided they may be. Inevitably, those ideas contradict some of the contributors, most of whom have not had the opportunity to respond. We apologize to them here, and acknowledge the unfair advantage that we enjoyed.

The Percomorph Problem

When Rosen (1973) named Percomorpha, it included beryciforms, perciforms, and the groups placed between and beyond those in Greenwood et al.'s (1966) classification, such as zeiforms, lampridiforms, gasterosteiforms, scorpaeniforms, pleuronectiforms and tetraodontiforms; in others words, Percomorpha = Acanthopterygii minus Atherinomorpha. Rosen gave no characters for his Percomorpha, and to our knowledge, no one has subsequently found any that characterize all the included taxa (e.g., Lauder and Liem, 1983). Possible counter examples to that statement may be found in Stiassny (1990), who cited medial suturing or apposition of the pelvic bones and ventral displacement of the anteromedial process of the pelvic bone, and Roberts (1993), who cites transforming ctenoid scales. But Stiassny's percomorph characters are denied by Stiassny's (1990, 1993) own argument that mugiloids, which have the characters, are related to atherinomorphs, and Roberts's character, strictly applied (as he employs it in this volume), necessitates exclusion from the percomorphs of percoid taxa such as Priacanthidae, Epigonidae, Bramidae, *Ostracoberyx* and *Howella.* Our current understanding of the Percomorpha as circumscribed by Rosen is that they are polyphyletic, and are therefore an unreal and uncharacterizable group. We believe that the situation can be rectified only by modifying the content of Percomorpha,

excluding some of Rosen's percomorphs and including some of his non-percomorphs. Our reasons for these changes include proposals and opinions concerning (1) the lampridiforms, (2) the paracanthopterygians, (3) the beryciforms, (4) the atherinomorphs, (5) the perciforms, and (6) the zeiforms. In the following sections we summarize information on those six groups, discussing characters (given **bold** numbers) of which some are described in detail only in the succeeding character list. Nevertheless, there is unavoidable repetition between the accounts of individual groups and the concluding description of characters. Our conclusions on those six groups lead us to propose names for several new higher taxa within acanthomorphs, a procedure that may seem premature. But our goal is to focus in on the Percomorpha, to characterize the group and to specify what it does and does not contain; we give new names for acanthomorph taxa that we believe to be either more or less inclusive than Percomorpha to achieve that goal and to place Percomorpha in the hierarchy.

Rosen (1964: 220) wrote "In any study that involves taxonomic rearrangements, inevitably there arises the question of what to call various groups during the presentation of new evidence, especially when new group names are proposed and groups of long standing are dismembered and the components are redistributed." We faced the same problem here. In the following we use the name "lampridiforms" in the sense of Olney et al. (1993; i.e., excluding ateleopodids); "paracanthopterygians" and "atherinomorphs" are used in the conventional sense (as circumscribed, for example, respectively by Patterson and Rosen, 1989, and Parenti, 1993); "perciforms" means Perciformes in the conventional sense (Nelson, 1984), and we use "perciforms and their immediate relatives" for a group comprising perciforms, scorpaeniforms, and pleuronectiforms. Our "zeiforms" excludes the Caproidae (*Antigonia, Capros*), which we call "caproids." Our "gasterosteiforms" includes the syngnathiforms, and following Pietsch (1978) and our own examination of the two genera, *Pegasus* and *Indostomus* (=Pegasiformes and Indostomiformes of Nelson, 1984); unlike Pietsch (1978, who is followed by Nelson, 1984) we have found no good reason for associating dactylopterids (Dactylopteriformes of Nelson, 1984) with the gasterosteiforms. For beryciforms in the conventional sense (as in Nelson, 1984, but excluding *Polymixia* among Recent fishes) we use "beryciforms s.l.," and we use "stephanoberyciforms" for the Stephanoberycoidei of Moore (1993: Melamphaidae, Stephanoberycidae, Hispidoberycidae, Gibberichthyidae, Rondeletiidae, Barbourisiidae, Megalomycteridae, Cetomimidae, "and probably the miripinnatoid fishes") and "beryciforms" for the Trachichthyoidei of Moore (1993: Trachichthyidae, Monocentridae, Anomalopidae, Anoplogastridae, Diretmidae) *plus* the Holocentridae and Berycidae. Other group names are introduced and defined seriatim in the following sections.

Lampridiforms

Olney et al. (1993) list characters showing that lampridiforms are a monophyletic group. After reviewing all previously proposed characters that might help to place the group, they conclude that lampridiforms are basal acanthomorphs but make no more precise statement about their relationships. The internal phylogeny proposed by Olney et al. clearly establishes that veliferids (*Velifer* and *Metavelifer*) are the morphologically primitive sister-group of all other lampridiforms. We have been impressed by the condition of the intermuscular bones and ligaments in veliferids, and believe that they resolve the position of lampridiforms as the sister-group of all other acanthomorphs. To explain why, we have to summarize a study of teleostean intermuscular bones and ligaments (Patterson and Johnson,

submitted[1]). We have found that the primitive teleostean condition is to have three series of intermusculars: epineurals, epicentrals and epipleurals. The first two series develop in a rostrocaudal gradient, from the occiput back, whereas epipleurals develop rostrally and caudally from about the level of the first caudal centrum. Epineurals are developed primitively as posterolateral bony outgrowths of the neural arches, but in most teleosts they lose their original continuity with the neural arch, and are attached to it by ligament. Epicentrals and epipleurals are primitively attached to the axial skeleton by ligaments. In many lower teleosts the series of epineural bones continues caudally as a series of discrete ligaments, without included bone, and in most lower teleosts the epicentral series is represented by ligaments alone. The epipleural series of bones may be extended rostrally and caudally by a series of ligaments, or the series may be represented by ligaments alone. *Polymixia* is the only living acanthomorph with ossified epipleurals (**12**), and it also has a series of epineural bones and epicentral liagments (Fig. 1B). *Polymixia* differs from non-acanthomorphs in having the distal part of the first epineural displaced ventrally into the horizontal septum (**8**) and the point of origin of the third to tenth epineurals displaced ventrally from the neural arch to the parapophysis or centrum (**11**). In other acanthomorphs (except lampridiforms) the distal parts of the second and several succeeding epineurals are displaced ventrally into the horizontal septum (**14**), the point of origin of the third and several succeeding epineurals is displaced on to the rib (except in stephanoberyciforms, **20**), and the epicentral series of ligaments, if present, begins only behind the ventrally displaced epineurals (**13**). Beryciforms retain the primitive neural arch or spine origin for the posterior epineurals (where present), and most have an epicentral series of ligaments that begins at about the tenth vertebra. Perciforms and their immediate relatives and atherinomorphs have all the epineurals displaced ventrally on to the rib and the epicentral series, when present, never overlaps the epineural series; the bones conventionally called epipleurals in those fishes are homologous with the epineurals, not the epipleurals, of non-acanthomorph teleosts.

In veliferid lampridiforms all epineurals (Fig. 1C) retain the primitive origin, on the neural arch, and further differ from *Polymixia* (Fig. 1B) and other acanthomorphs in that none of them has the distal part displaced ventrally into the horizontal septum from the primitive dorsolateral position (Fig. 1A). Veliferids also have a series of epicentral ligaments that extends forward to the first centrum in *Velifer,* as in myctophiforms (Fig. 1A), whereas in *Polymixia* there is no epicentral on the first centrum. In having no epineurals with the point of origin displaced ventrally, the distal part of all the epineurals above the horizontal septum, and an epicentral ligament on the first centrum, veliferids are more primitive than any other acanthomorph. There is character conflict here because, unlike *Polymixia,* lampridiforms have no epipleural bones or ligaments; we note that in veliferids the swimbladder extends posteriorly beyond the body cavity in a pair of horn-like processes that occupy the position of the epipleurals in *Polymixia,* and that behind and in series with the pleural ribs of *Velifer* there is a series of segmental ligaments. To our knowledge, that situation is unique, and we suggest the possibility that those ligaments represent the missing, but expected, epipleural series.

Lampris is the one other lampridiform in which we have observed more than one epineural, and the situation is clearly different from that in veliferids. In *Lampris* there are epineurals only on the first five or six vertebrae, and in contrast

[1] Patterson, C. and G. D. Johnson. The intermuscular bones and ligaments of teleostean fishes. Smithson. Contrib. Zool. Submitted.

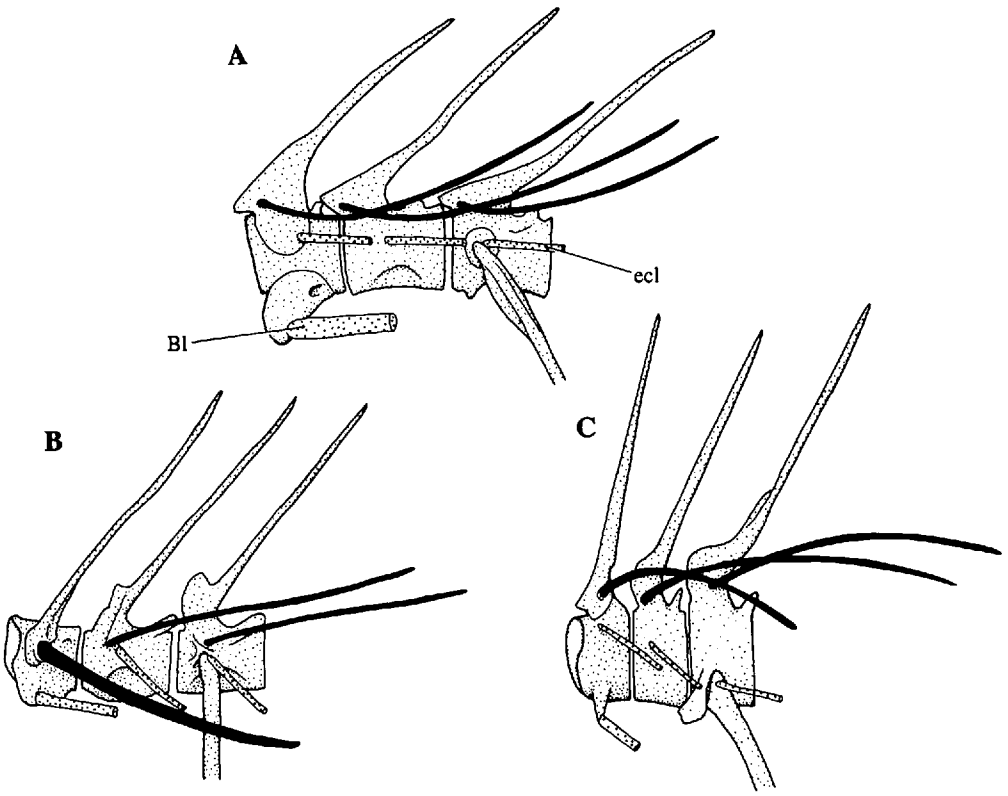


Figure 1. First three vertebrae and associated epineural intermuscular bones, epicentral intermuscular ligaments (ecl) and ribs in: A. *Myctophum obtusirostris,* AMNH 29140SW; B. *Polymixia lowei,* BMNH 1987.12.7.1–5 and USNM 308378; C. *Velifer hypselopterus,* RUSI 13821. Ligaments shown in heavy stipple (Baudelot's ligament, Bl, originates low on the first centrum), epineurals black. Note that B differs from A and C in having the distal part of the first epineural displaced ventrally.

to veliferids (Fig. 1C), the ribs insert high on the centrum, just below the neural arch. The first two epineurals of *Lampris* resemble those of *Velifer* in orientation, but the first is enlarged relative to the second, as in *Polymixia* (Fig. 1B). The third through sixth epineurals originate not on the neural arch, as they do in veliferids, but on the rib, the last one or two by means of a short ligament. The derived displacement of the proximal ends of these epineurals, from neural arch to rib, resembles the condition in higher acanthomorphs, but given that lampridiforms are monophyletic, it has clearly occurred independently in *Lampris,* presumably in association with elevation of the point of origin of the ribs. Epicentral ligaments extend forward to the third vertebra in *Lampris* and are associated with the ventrally displaced epineurals on vertebrae three through six, and thereafter with the ribs. *Trachipterus* has a single epineural, in the primitive position on the first vertebra, no epicentral ligaments, and no ribs.

Olney et al. (1993) cite one further character of lampridiforms corroborating the conclusion that they are the sister-group of other acanthomorphs: absence of the spina occipitalis (**10**), a posteroventral extension of the supraoccipital between the exoccipitals that Stiassny (1986) found to be present in *Polymixia* and other acanthomorphs. We have found one other feature of lampridiforms that corroborates their position as the sister-group of all other acanthomorphs: the posterior process of the pelvic girdle is tipped by cartilage, whereas it is fully ossified (closed distally in bone) in all other acanthomorphs that we have examined (**9**). Our view

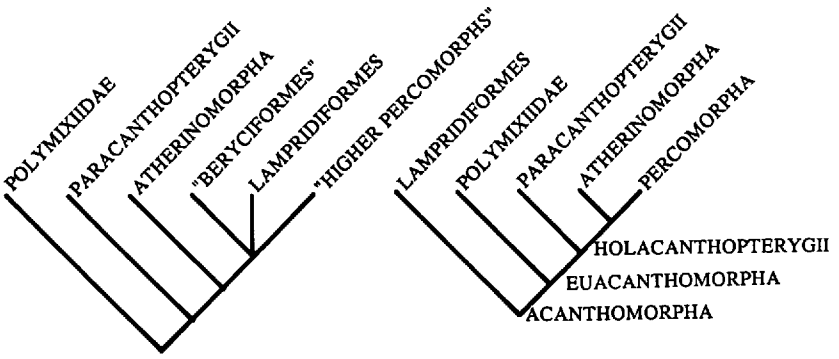


Figure 2. Diagrams contrasting our view of lampridiform relationships (right) with an interpretation of that of Olney et al. (1993; left).

of lampridiform relationships is contrasted with an interpretation of that presented by Olney et al. (1993) in Figure 2, where the new names Euacanthomorpha and Holacanthopterygii are introduced, the first for all acanthomorphs except lampridiforms and the second for euacanthomorphs less polymixiids.

Paracanthopterygians

There is nothing new in this volume on the content or characterization of Paracanthopterygii. Although the monophyly of that group is still poorly documented, we have found no good reason to question it.

Parenti (1993) discusses evidence that supports the proposal that Atherinomorpha are the sister-group of Paracanthopterygii (Fig. 3A), and cites eight characters common to some or all atherinomorphs and paracanthopterygians. Because we find a substantial suite of characters indicating that paracanthopterygians are more remote from atherinomorphs than are beryciforms or stephanoberyciforms, we need to consider those eight characters. Two of them seem either to be primitive or more widely distributed: absence of a ligament between pelvic girdle and postcleithrum, a structure also absent in neoscopelids, myctophids, lampridiforms, zeiforms, gasterosteiforms, most stephanoberyciforms, *Elassoma* and many higher perciforms; and head of the fourth epibranchial larger than that of the third, which is also found in neoscopelids, myctophids, the stephanoberyciform *Barbourisia,* beryciforms such as berycids, trachichthyids, anomalopids, *Anoplogaster* and *Diretmus* (Rosen, 1973: figs. 71, 69, 125, 84, 88–90, 126), some gasterosteiforms (Banister, 1970: fig. 15; Pietsch, 1978: fig. 9A), some mugilids (Harrison and Howes, 1991: fig. 2), synbranchoids (Rosen and Greenwood, 1976: figs. 36–41), mastacembeloids (Travers, 1984a; Rosen and Patterson, 1990: fig. 32) and various perciforms (Rosen and Patterson, 1990: figs. 28–31, 49). One of Parenti's atherinomorph/paracanthopterygian characters, a full neural spine on PU2, is derived, but it is not present in all atherinomorphs (absent in most atherinoids and exocoetoids), and is also found in all zeiforms (Fujita, 1990: figs. 186–191), in *Elassoma,* gasterosteiforms (Fujita, 1990: figs. 193–202), synbranchiforms (Fujita, 1990: fig. 538), and various perciforms and their immediate relatives (e.g., echeneids, anabantoids, non-psettodid pleuronectiforms). Two more characters are also derived but are restricted only to some atherinomorphs and paracanthopterygians as well as occurring outside those groups: (1) a positional homolog of the gadiform "Y" bone, which occurs only in some gadiforms among paracanthopterygians, is recorded only in adrianichthyoids and in one species of *Pseudomugil* among atherinomorphs, but is also constant in the zeiform *Zenopsis*

(Fujita, 1990: fig. 188) and sometimes present in *Zeus*; (2) supernumerary neural and haemal spines on one or more preural centra, normal only in gadiforms amongst paracanthopterygians, are found in some adrianichthyoids alone among atherinomorphs, and are also characteristic of cetomimoids (Moore, 1993) and the perciform *Icosteus,* and are found commonly in zeiforms. The fifth character is reduction of supraneurals; there are none in atherinomorphs, and among paracanthopterygians, there is one in percopsiforms and a few gadiforms, and none in the remainder except for a series of up to six cartilages in some ophidiiforms, which Patterson and Rosen (1989) thought due to secondary increase. Zeiforms show a pattern somewhat like paracanthopterygians, with one supraneural in most genera (Fig. 20E, F) and none in the remainder; there are none in the problematic *Elassoma* (Fig. 14), none in gasterosteiforms, none in synbranchiforms, and, of course, none in many perciforms (e.g., gobioids, blennioids, scombroids). The remaining three characters are long developmental period, which varies within atherinomorphs and paracanthopterygians; short preanal length in larvae, common only to atherinoids and gadids; and two epurals, which also characterizes other groups such as zeiforms, gasterosteiforms (two or fewer), synbranchiforms, and some higher perciforms, such as scombrids and gobioids.

We do not believe that all or any of the above features are sufficient to outweigh the derived features found in atherinomorphs that are absent in paracanthopterygians (as represented by percopsiforms) but present in beryciforms, perciforms and their immediate relatives, and in mugiloids. These include: fewer than three pelvic radials (**16**), anteromedial process of pelvic bone (**17**), a complex pelvic spine (**21**), and Baudelot's ligament originating on the occiput (**18**). A further suite of derived characters, lacking in beryciforms, is shared by atherinomorphs, perciforms and their immediate relatives, and mugiloids. These include: pelvics with no more than five soft rays (**29**), complete absence of free pelvic radials (**31**), absence of second ural centrum (**27**), absence of sixth hypural (**28**), 17 or fewer principal caudal rays with the 17 rays (when present, as in atherinids) arranged in a I,8,7,I pattern (**33**), and presence of a rod-like interarcual cartilage (**26**). We are convinced therefore that atherinomorphs are more closely related to perciforms than to beryciforms or paracanthopterygians (Fig. 3B).

Beryciforms s.l.

Stiassny and Moore (1992) and Moore (1993) proposed that beryciforms s.l. are paraphyletic, with holocentrids more closely related to "higher Percomorpha" (Zeiformes + Scorpaeniformes + Perciformes in Stiassny and Moore's sample of taxa) than are trachichthyoids and stephanoberyciforms (which together comprise the Trachichthyiformes of Stiassny and Moore, 1992, and Moore, 1993). They placed the berycids as one component of an unresolved trichotomy with Trachichthyiformes and their unnamed group comprising holocentrids and "higher Percomorpha" (Fig. 4A). Stiassny and Moore's evidence for this is two apomorphous features of the pelvic girdle shared by holocentrids and "higher Percomorpha:" sutured medial processes, and an interpelvic ligament linking the bases of the left and right pelvic fin bases.

Our own observations have resulted in a totally different picture of "beryciform" interrelationships, summarized in Figure 4B. We have been impressed by two neglected and independent sets of observations. Jakubowski (1974) showed that "berycoids" (trachichthyids, monocentrids, berycids, holocentrids) share a distinctive feature of the supraorbital sensory canal. The nasal bone turns laterally

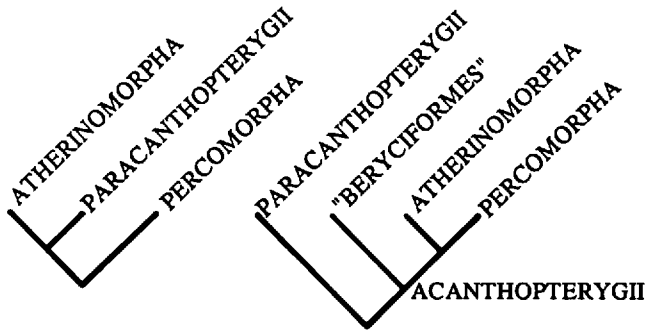


Figure 3. Diagrams contrasting Parenti's (1992) proposal of paracanthopterygian/atherinomorph relationships (left) with our view (right).

anteriorly and contacts the lacrimal, and the nasal contains two neuromasts, the second of which (adjacent to the lacrimal) is innervated by the buccal nerve rather than by the supraorbital nerve, which invariably innervates neuromasts of the supraorbital canal. Independently, Freihofer (1978) reported the same condition in "berycoids," saying that he had found one (Fig. 5) or two (Fig. 7) buccal-innervated neuromasts in the distal part of the nasal in every family, but that this condition does not occur in stephanoberyciforms (Stephanoberycidae, Melamphaidae, Gibberichthyidae). Freihofer (1978: 44) wrote that he would give a detailed account of the beryciform condition in a future paper, but although he gave a presentation on it at the 1979 ASIH meeting (abstract printed in program for that meeting), the paper was not published before his death. However, through the help of S. H. Weitzman and Gail Freihofer we have access to his extensive notes, a grant proposal summarizing the work, and some drawings (four are included here as Figs. 5–8). Whereas Jakubowski (1974) believed that the "captured" buccal-innervated neuromast in the nasal of berycoids is the result of fusion with a rostral ossicle, Freihofer believed that superficial, free lateralis organs on the snout have been "engulfed" by the nasal bone and incorporated in the terminal part of the supraorbital canal. Freihofer's theory seems to have been influenced

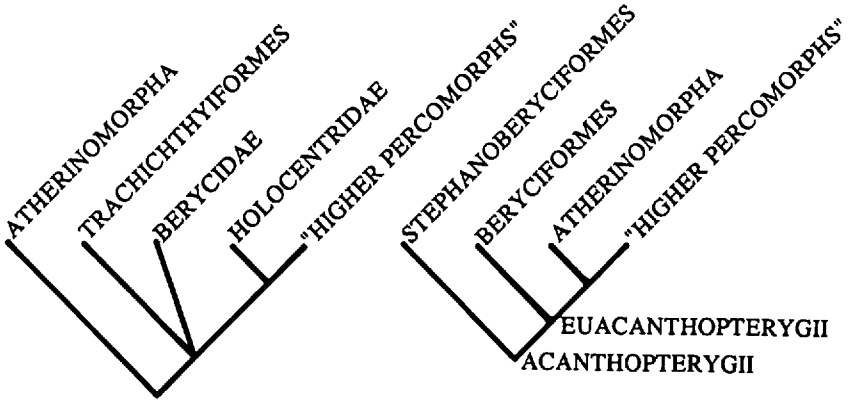


Figure 4. Diagrams contrasting the views of Moore (1993) and Stiassny and Moore (1992) of beryciform relationships (left) with our view (right).

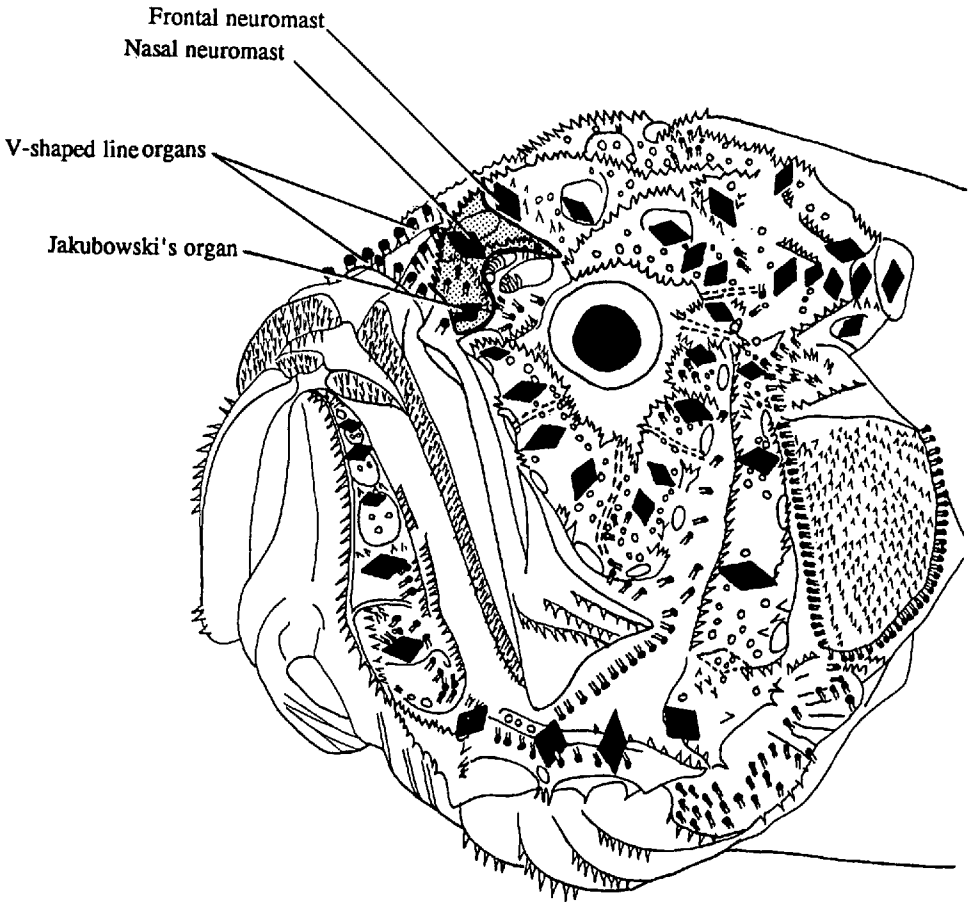


Figure 5. Head of the trachichthyid *Hoplostethus pacificus* in anterolateral view, drawn by W. C. Freihofer, with outline of nasal bone added (mechanical stipple). Neuromasts are shown as black diamonds. Black-tipped fingerlike processes are free lateral line organs on papillae. Open circles are holes in the skin overlying the sensory canals. The innervation of the neuromasts in *Hoplostethus* is shown by Jakubowski (1974: fig. 3).

by his belief that *Polymixia* shows a precursor of the berycoid condition in having "three free lateralis organs in a membranous canal that . . . is connected across the tip of the snout with a similar canal on the other side of the head. Another lateralis organ lies at the midpoint of the crossing canal" (Freihofer, 1978: 44). We have checked the condition in *Polymixia* and find that the canal described by Freihofer looks like the rostral commissure found in primitive neopterygians (e.g., *Lepisosteus, Amia, Elops,* Jollie, 1969), but differs in that it connects with the terminal part of the supraorbital canal, not with the infraorbital canal, as does a true rostral commissure. *Polymixia* seems therefore to have developed a "pseudorostral" commissural sensory canal, a condition that must be seen as autapomorphous, because no other clupeocephalan (euteleosts and clupeomorphs) retains the primitive type of rostral commissure.

We therefore believe that *Polymixia* has no bearing on interpretation of the berycoid condition, and regardless of whether the latter arose by the process

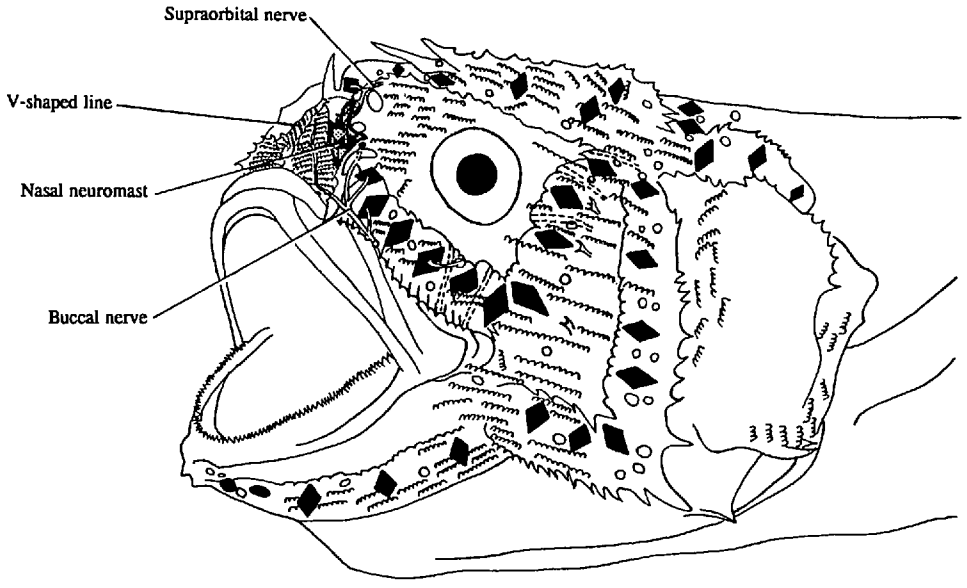


Figure 6. Head of the melamphaid *Poromitra capito* in anterolateral view, drawn by W. C. Freihofer, with outline of nasal bone added (mechanical stipple). As in Figure 5, neuromasts are shown as black diamonds and open circles are holes in the skin overlying the sensory canals. The zig-zag lines on the cheek and lower jaw indicate rows of free lateral line organs on papillae.

envisioned by Jakubowski or by Freihofer, the buccal-innervated terminal supraorbital neuromast(s), with the associated modification of the nasal bone and contact between the tips of the supraorbital and infraorbital canals, is a synapomorphy unique to the berycoid families investigated by Jakubowski and Freihofer [Anomalopidae, Anoplogastridae, Berycidae, Diretmidae, Holocentridae (Fig. 7), Monocentridae, Trachichthyidae (Fig. 5)]. Because the stephanoberyciforms [Barbourisiidae, Cetomimidae (Fig. 8), Gibberichthyidae, Hispidoberycidae, Megalomycteridae, Melamphaidae (Fig. 6), Rondeletiidae, Stephanoberycidae] lack this character (all families except Hispidoberycidae and Megalomycteridae examined by Freihofer) and show what Freihofer took to be the more primitive state of free lateralis organs in the skin outside the terminal pore of the supraorbital canal, the implication is that the beryciforms are a monophyletic group to which stephanoberyciforms do not belong.

We have found seven other characters bearing on this separation of beryciforms and stephanoberyciforms. First, in all stephanoberyciforms Baudelot's ligament originates on the first centrum, as it does in most non-ctenosquamates and in neoscopelids, myctophids, lampridiforms, *Polymixia* and percopsiforms. In beryciforms, as in almost all other acanthopterygians, the ligament originates on the basioccipital (**18**). Second, the supraneurals of all adult beryciforms except *Anoplogaster* (which has one small, remote supraneural) show a derived state, shared with perciforms and their immediate relatives, in having their distal tips closed in bone, with no free cartilage (**23**). Stephanoberyciforms share the primitive type of cartilage-tipped supraneurals with neoscopelids, myctophids, lampridiforms, *Polymixia*, some zeiforms, and lower euteleosts. Third, all beryciforms except *Anoplogaster* (which has no dorsal spines) and diretmids (which have only one) show the "chain-link" type of articulation of the dorsal spines described by

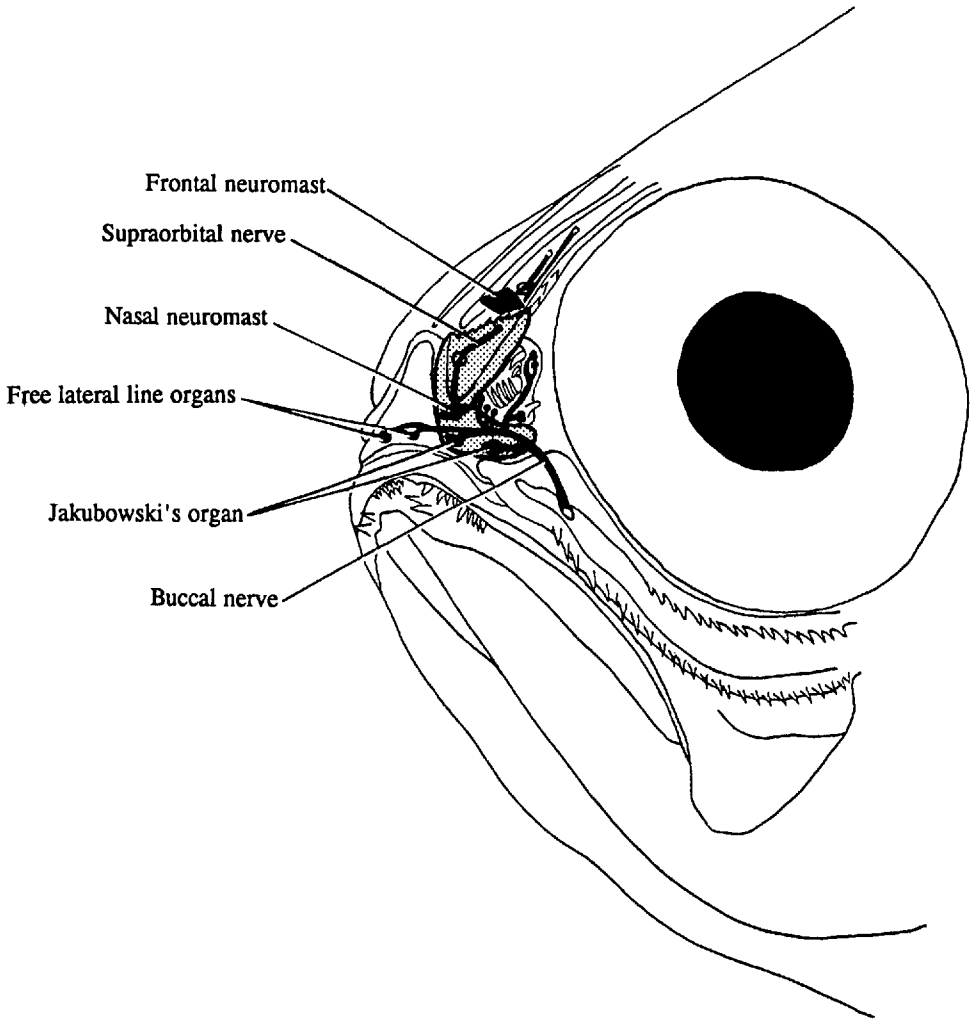


Figure 7. Head of the holocentrid *Myripristis pralinius* in anterolateral view, drawn by W. C. Freihofer, emphasizing the sense organs of the snout and their innervation, with outline of nasal bone added (mechanical stipple).

Bridge (1896) (**22**), whereas all stephanoberyciforms lack it. Of course, most stephanoberyciforms have no dorsal spines, but they are present primitively in the group (three in melamphaids, one or two in *Stephanoberyx,* four to five in *Hispidoberyx,* and six in *Gibberichthys,* in which the anterior ones fuse with proximal radials during ontogeny) and the distal radials bearing the spines are unmodified (Fig. 23). Fourth, the pelvic spine of stephanoberyciforms (present in melamphaids, *Gibberichthys,* and *Hispidoberyx*) is a simple, symmetrical structure with a widely open base, lacking the more elaborate, asymmetrical articular surface that characterizes the pelvic spine of beryciforms (Gosline, 1961: fig. 5; Rosen and Patterson, 1969: fig. 43) and perciforms (Mok and Chang, 1986: fig. 1) (**21**, Fig. 22). Fifth, the ventral procurrent rays of stephanoberyciforms show the condition described by Johnson (1975) as typical of non-acanthopterygian teleosts, in which the proximal ends of the ventral procurrent rays are a mirror image of

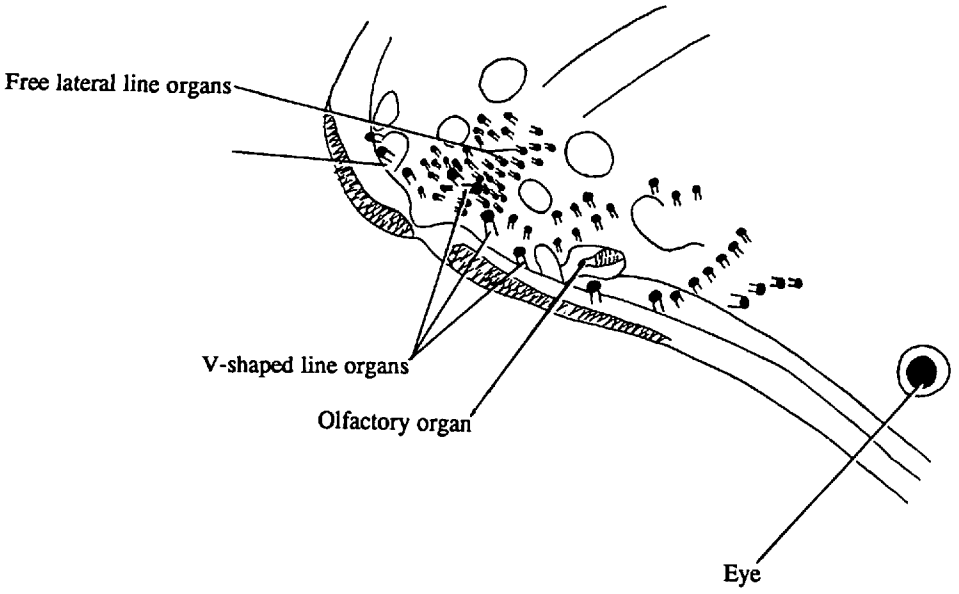


Figure 8. Snout of *Cetomimus craneae* in anterodorsolateral view, drawn by W. C. Freihofer.

those of the dorsal procurrent rays. In beryciforms, we have confirmed that all families show the condition described for anomalopids, anoplogastrids, berycids, holocentrids and trachichthyids by Johnson (1975), with the base of the second ventral procurrent ray truncated, as it is in many perciforms (**24**). Sixth, all stephanoberyciforms except melamphaids have a fourth pharyngobranchial cartilage (PB4), a structure absent in all adult beryciforms, and absent in the ontogeny of at least berycids, holocentrids and trachichthyids [the cartilage identified as PB4 in Rosen's (1973: figs. 84, 85) illustrations of *Beryx splendens* is not a separate element but an extension of the cartilaginous posteromedial corner of PB3]. In some stephanoberyciforms, e.g., *Hispidoberyx* and *Barbourisia* (Rosen, 1973: fig. 116), PB4 is quite large, as it is in myctophiforms, veliferid lampridiforms, *Polymixia* and percopsiforms (Rosen, 1973: figs. 70, 82, 83, 86, 104). Seventh, as summarized under lampridiforms (above) there is a transformation series in the epineural intermuscular bones of acanthomorphs. Primitively, in non-acanthomorphs, the epineurals originate on the neural arch or spine. The most derived state, as in atherinomorphs and perciforms, is to have all but the first two epineurals displaced ventrally so that they originate on the rib (anteriorly) or parapophysis (posteriorly) (**20**). Beryciforms have the anterior epineurals on the ribs, but stephanoberyciforms have them on the parapophysis (except in *Barbourisia,* where they are on the ribs), as in *Polymixia.*

The seven characters described in the preceding paragraph ally beryciforms with higher acanthopterygians, and, together with the absence of "Jakubowski's organ" (as we shall call the buccal-innervated terminal supraorbital neuromasts) in stephanoberyciforms they imply that stephanoberyciforms are the sister-group of beryciforms + atherinomorphs + "higher Percomorpha" (Fig. 4B). Of course, it is possible that the stephanoberyciform condition represents a reversal of the beryciform condition in all eight features. The assumption of reversal would be necessary only if there were numerous or trenchant characters indicating that stephanoberyciforms form a monophyletic group with beryciforms as a whole or

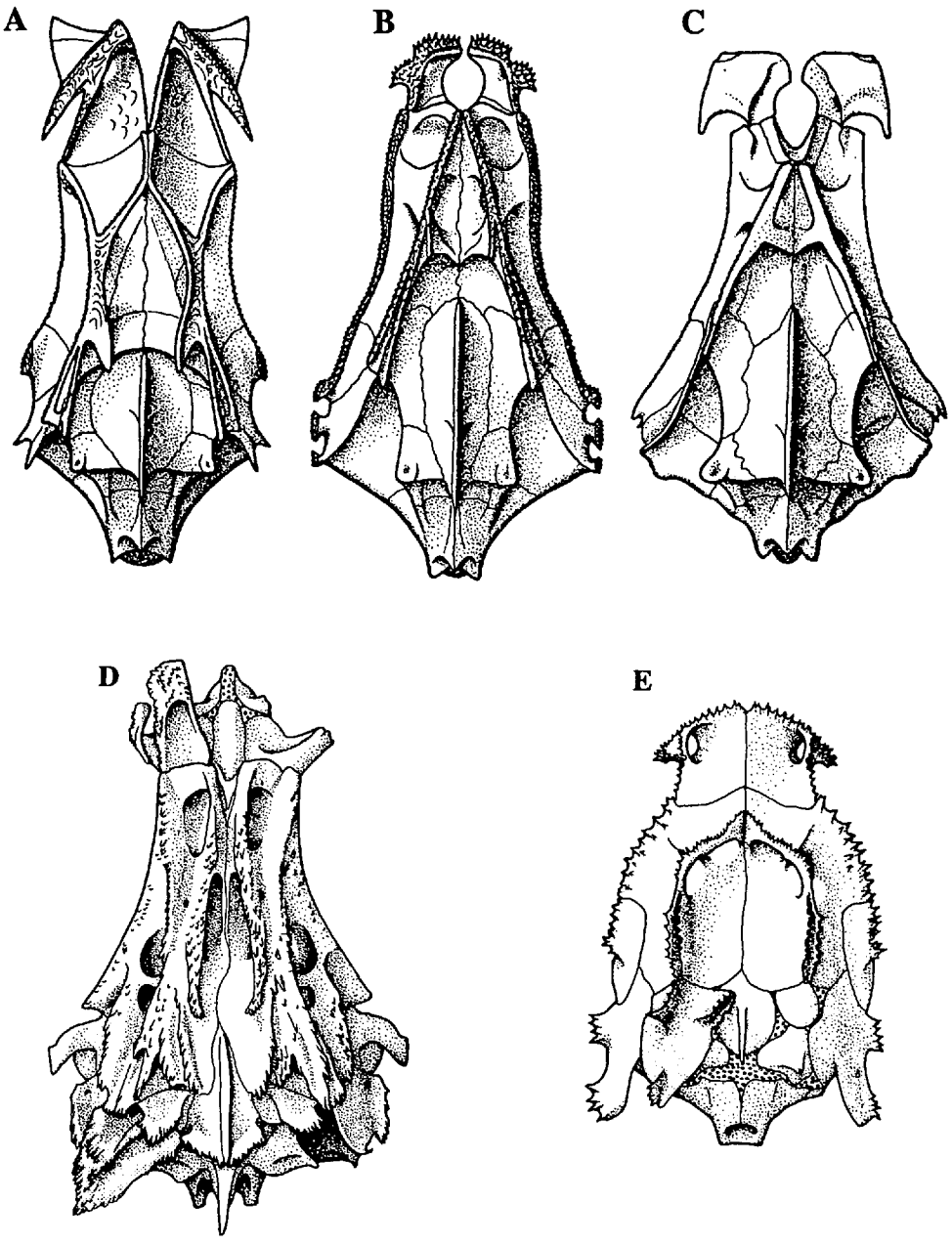


Figure 9. Beryciform (A–D, F, G) and stephanoberyciform (E) skull roofs. A. the trachichthyid *Hoplostethus mediterraneus*; B, C. the berycids *Centroberyx affinis* and *Beryx decadactylus*; D. the holocentrid *Ostichthys trachypoma*, USNM 320099; E. *Stephanoberyx monae*, USNM 20824; F, G. the Cretaceous trachichthyoids *Hoplopteryx lewesiensis* and *Hoplopteryx simus*; H. the Cretaceous holocentroid *Caproberyx superbus*. A–C, F–H after Patterson (1964). Both nasals are in position in A–C and E–G; the left nasal and antorbital are in position in D; and both nasals are missing in H. The left extrascapular is in position in D and E and is indicated by mechanical stipple. Figure 9F–H, opposite page.

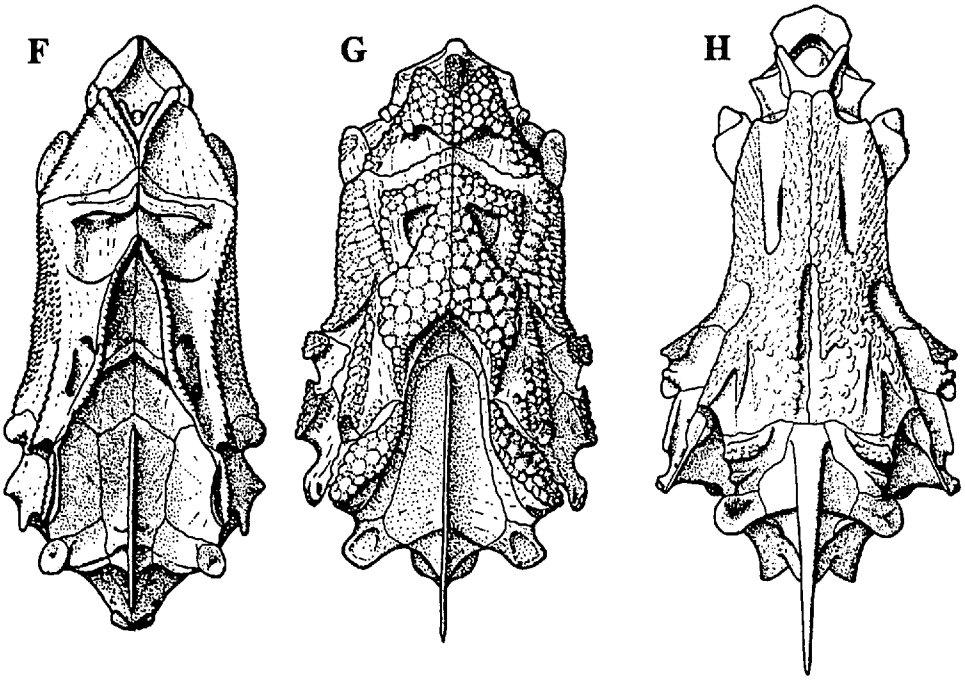


Figure 9 cont. See Figure 9 caption.

with a subgroup of them. Characters having that potential are discussed in the following paragraphs.

In Moore's cladogram (1993: fig. 5) of trachichthyiforms there are three characters placing stephanoberyciforms within that group as the sister-taxon of trachichthyoids. These are: 1, sclerotic ossifications absent; 2, first neural spine fused to centrum; and 3, anterior supramaxilla lost. Comments on these characters are given below. In citing them, Moore's intention was to demonstrate not only that stephanoberyciforms are nested within trachichthyiforms, but that berycids and holocentrids are unrelated to them, since those two groups differ from trachichthyiforms in all three. 1) Sclerotic ossifications absent. These are also absent in neoscopelids, myctophids, zeiforms, *Aphredoderus,* most gasterosteiforms, and many other fishes. In stephanoberyciforms we interpret the absence of ossified sclera as a consequence of the obvious reduction in ossification, and not as a synapomorphy with trachichthyoids. 2) First neural spine fused to centrum. The fusion also occurs in lampridiforms (veliferids, *Lampris*), percopsiforms, zeiforms, atherinomorphs, gasterosteiforms, mugiloids, and many perciforms. 3) Anterior supramaxilla lost. Moore (1993) notes that this character also occurs in "numerous acanthomorph lineages." Further, all anomalopid genera except *Anomalops* have two supramaxillae. Johnson and Rosenblatt (1988) interpreted the condition in *Anomalops* as reversion, but were tentative about rejecting the alternative, that the anterior supramaxilla in anomalopids is primitive. The character is problematic.

We are aware of three other features that might place stephanoberyciforms with or within beryciforms: the relations between the extrascapular and parietal bones, and between the supraorbital and occipital sensory canals; the pattern of crests on the frontal; and the pattern of free lateralis organs on the snout.

In beryciforms, the dorsal limb of the extrascapular articulates with the parietal,

and the occipital commissural sensory canal passes from the extrascapular into a groove or channel on the parietal. This pattern also occurred in Cretaceous beryciforms (Patterson, 1964: figs. 46, 54, 66). In stephanoberyciforms, the extrascapular is much larger than in beryciforms. In melamphaids, this large extrascapular articulates with and covers the posterior part of the parietal, whereas in other stephanoberyciforms the parietal is completely hidden beneath the extrascapular (e.g., *Stephanoberyx,* Fig. 9E, and Moore, 1993: fig. 4); no doubt because of this, Kotlyar (1990), in his osteology of stephanoberycids and gibberichthyids, failed to find the parietal. In all beryciforms and in melamphaids among stephanoberyciforms the primitive posterior or parietal branch of the supraorbital canal is retained (as it is in myctophids and *Polymixia*), and in all beryciforms and stephanoberyciforms the epiphysial commissure between the supraorbital canals is expanded into a spacious median "mucus cavity" or chamber between the frontals above the orbit (Fig. 9). Together with the presence of the occipital commissural canal on (beryciforms) or above (stephanoberyciforms) the parietal, this brings the supraorbital canal and occipital commissural canals into proximity, an unusual condition among teleosts, and in some beryciforms and stephanoberyciforms the two canals become confluent, an even more unusual condition. This confluence may come about in two ways. First, the median mucus cavity (modified epiphysial commissure) may extend posteriorly and communicate with the occipital commissure, a condition that may be unique in teleosts. Freihofer, in his unpublished notes, recorded a communication between the median chamber and the occipital sensory canal in the stephanoberyciforms *Rondeletia, Barbourisia, Gibberichthys* and *Stephanoberyx,* but not in melamphaids, *Cetomimus* or *Ditropichthys* (the connection also occurs in *Hispidoberyx,* Kotlyar, 1991b: fig. 4). Among beryciforms, Freihofer recorded that connection in the trachichthyids *Trachichthys* and *Paratrachichthys* (but not in *Hoplostethus* or *Gephyroberyx*) and in all the holocentrids he examined, including both holocentrines and myripristines. He did not find a connection in anomalopids, *Anoplogaster,* berycids, *Diretmus* or *Monocentris.* Second, there may be a connection between the parietal branch of the supraorbital canal and the occipital commissure, which are already in proximity because of the extension of the commissure on to the parietal. Freihofer's notes record such a connection in the holocentrids *Flammeo, Myripristis* and *Ostichthys,* and do not mention the absence of the connection in any holocentrid; it may be apomorphous for holocentrids. In *Polymixia,* the extrascapular articulates with the parietal in a way similar to that in beryciforms (Fig. 10), and the occipital canal passes on to the parietal; the same condition occurred in Cretaceous polymixiids (Patterson, 1964: figs. 24, 35). Freihofer (unpubl. notes) recorded that in *Polymixia* the occipital canal "curves anteromedially and ends very close to the end of the fronto-parietal canal but there is no confluence of the two canals; there is a connective tissue wall between the two." That pattern is similar to the one he recorded in several non-holocentrid beryciform families. In *Polymixia* the epiphysial commissure is hardly modified; Freihofer (unpubl. notes) called it "not just a cross-commissure but a noticeable enlargement, but it lies beneath a thin bony roof."

Summarizing all this, the articulation between the extrascapular and parietal and the presence of a terminal branch of the occipital commissural sensory canal on the parietal is common to beryciforms, *Polymixia,* and at least some zeiforms (Fig. 10). The hypertrophied extrascapular of stephanoberyciforms can be interpreted in two ways, either as autapomorphous for the group, or as a further modification of the beryciform condition. Because the beryciform condition is not substantially different from the polymixiid or zeiform, one can choose between

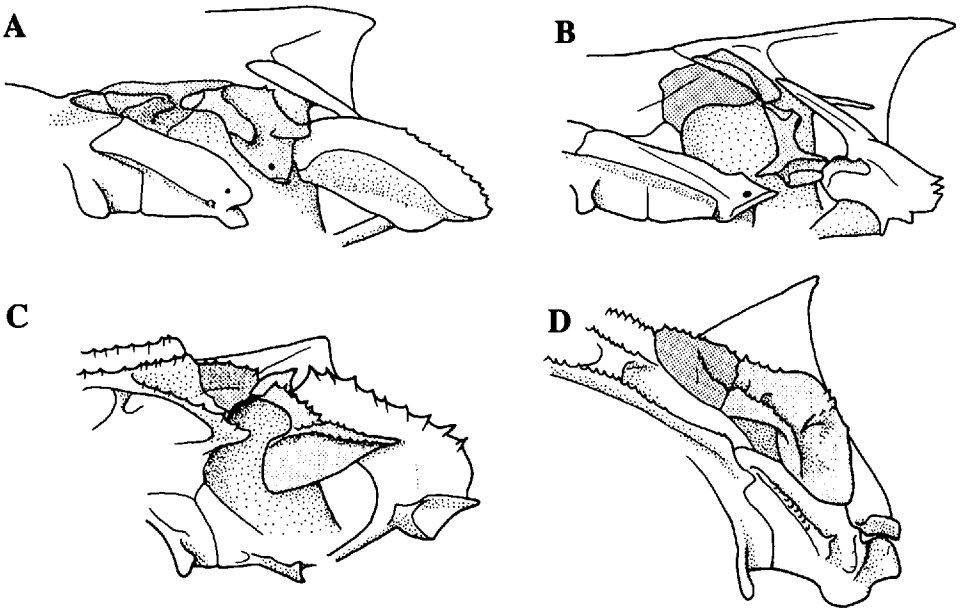


Figure 10. Relation of extrascapular(s) (light mechanical stipple) to parietal (darker mechanical stipple) in: A. *Polymixia lowei*, USNM 308378; B. *Dicentrarchus labrax*, USNM 218915; C. *Hoplostethus mediterraneus*, VIMS 4900; D. *Zenion hololepis*, CAS 38409.

the two alternatives only on grounds of congruence with other characters. The enlarged median mucus cavity is common to stephanoberyciforms and beryciforms, and is responsible for the pattern of crests on the frontal (below). A connection between the median mucus cavity and the occipital commissure occurs in some stephanoberyciforms, a subgroup of trachichthyids, and in holocentrids, a distribution implying that it is not synapomorphous for any group.

The pattern of crests on the frontal in beryciforms and stephanoberyciforms is mentioned by Moore (1993). He discriminates two conditions, a "modified X pattern," interpreted as synapomorphous for trachichthyoids (anomalopids, anoplogastrids, diretmids, monocentrids, trachichthyids), and a "Y-shaped" pattern, interpreted as synapomorphous for *Gibberichthys, Hispidoberyx,* and stephanoberycids. In that interpretation, the two patterns are non-homologous and do not bear on the monophyly or paraphyly of beryciforms s.l. But Moore also mentions the possibility of the pattern of crests having wider generality, writing "It is possible that the patterns of cranial ridges among all trachichthyiforms are related. It is easy to imagine the transformations that could produce the various patterns found in the entire group." One of us has also been impressed by the similarity between the pattern of crests in trachichthyids and stephanoberyciforms, writing that trachichthyids "seem to be the stem group" of the latter (Patterson, 1967: 104). But those transformations necessarily bring in the berycids, in which the frontal crests are readily comparable with those of trachichthyids (Fig. 9), and also holocentrids, where some of the Cretaceous genera (e.g., *Trachichthyoides*) and deeper-living Recent genera such as *Ostichthys* (Fig. 9D) have relatively large mucus cavities (enlarged sensory canals) separated by crests and ridges comparable with those in other beryciforms. In our view, the differences between the various patterns of crests on the frontals are determined primarily by the relative sizes of the median mucus cavity (the expanded epiphysial commissure between the supraorbital sen-

sory canals) and the supratemporal fossa, the median depression on the skull roof that houses trunk musculature, is bisected by the supraoccipital crest, bounded laterally by crests on the frontals and parietals, and separated from the median mucus cavity anteriorly by a V-shaped crest on the frontals. Four patterns can be recognized. In the first, perhaps the most generalized, the median mucus cavity and the supratemporal fossa are about equal in size, and there is an X-shaped pattern of ridges on each frontal, as in the trachichthyid *Hoplostethus* (Fig. 9A). In the second, the supratemporal fossa is enlarged, extending well forward on to the frontals, and the median mucus cavity is small, as in berycids (Fig. 9B, C). In the third, the supratemporal fossa is unrecognizable, the median mucus cavity extends back to the supraoccipital, there is a Y-shaped pattern of ridges on each frontal, and the enlarged extrascapulars cover the parietals and approach the median mucus cavity, as in stephanoberycids (Fig. 9E). And in the fourth, the supratemporal fossa is small because the frontals extend almost to the hind margin of the skull roof, and the median mucus cavity is narrow but elongate, extending posteriorly between the frontals, as in holocentrids (Fig. 9D). The Cretaceous "trachichthyid" *Hoplopteryx* (Fig. 9F, G) shows a pattern intermediate between the trachichthyid *Hoplostethus* and the berycid *Centroberyx,* and the Cretaceous "holocentrid" *Caproberyx* (Fig. 9H) shows a pattern intermediate between *Hoplopteryx simus* (Fig. 9F) and Recent holocentrids. As Moore says (1993), it is easy enough to imagine transformations between these patterns, and the Cretaceous fossils may imply that the trachichthyid, berycid and holocentrid patterns are part of a transformation series. The stephanoberyciform pattern, developed only in *Gibberichthys, Hispidoberyx,* and stephanoberycids, with the associated hypertrophied extrascapular (in all stephanoberyciforms) is the odd-man-out.

The other potential beryciform s.l. character that impressed Freihofer was "a V-shaped line of enlarged, free, finger-shaped neuromasts on the snout. The complete V-shaped line, or different character states of it, is present in all families (most genera examined) of berycoids, trachichthyoids, stephanoberycoids, cetomimoids, and probably also in polymixioids" (1979 ASIH meeting abstract). In a more complete summary, in a grant proposal, Freihofer wrote that the "V-shaped line is seen in full development in the Monocentridae, Trachichthyidae [Fig. 5], Anoplogastridae, Stephanoberycidae, and Gibberichthyidae. It is seen in a modified state in the Melamphaidae [Fig. 6]. Here the single, enlarged organs of the V-shaped line of the Trachichthyidae is changed such that each single organ has been divided into about eight much smaller organs arranged in a horizontal line. The V-shaped line is modified in somewhat the same way in the Barbourisiidae, Rondeletiidae, and Cetomimidae [Fig. 8]. In these families the number of enlarged organs is reduced but a V-shaped line of organs is still discernible in a field of small, irregularly placed organs on the snout." Freihofer added that a "V-shaped line" is not present in any other teleost that he knew, although in neoscopelids "there is a short line of enlarged organs from near the anterior corner of the nasal over to the edge of the side of the snout." In *Polymixia* he interpreted the "pseudorostral commissure" (above) as a possible homolog of the V-shaped line. Figures 5, 6 and 8 show Freihofer's view of the V-shaped line in *Hoplostethus,* the melamphaid *Poromitra,* and *Cetomimus.* In holocentrids, Freihofer's notes record the V-shaped line only in *Plectrypops,* but are not explicit about conditions in any other genus except *Myripristis,* where he found only two free organs on the snout (Fig. 7). In berycids and anomalopids he also recorded only two or three paired organs on the snout, and his notes say nothing of conditions in diretmids. Study and interpretation of these free neuromasts requires experience and special techniques, and we have not tried to follow up Freihofer's work. But as recorded

by him, his observations imply that a well-developed V-shaped rostral line is shared only by *Anoplogaster,* monocentrids and trachichthyids among beryciforms, and by stephanoberycids and *Gibberichthys* among stephanoberyciforms, but may exist in modified form in other stephanoberyciforms.

We have set out these potential characters of beryciforms s.l. in detail because of the obvious conflicts that they imply. There is no doubt that there is a striking resemblance between the skull roof of *Gibberichthys* or *Stephanoberyx* and that of a trachichthyid, anomalopid or monocentrid. Yet *Gibberichthys* and *Stephanoberyx* share with other stephanoberyciforms, and with more primitive outgroups, a suite of primitive characters concerning: 1, the dorsal fin (lack of chain-link spine articulation, **22**); 2, the supraneurals (cartilaginous tips, **23**); 3, the pelvic spine (simple base, **21**); 4, the ventral caudal procurrent rays (unmodified, **24**); 5, Baudelot's ligament (to first centrum, **18**); and 6, the intermusculars (to parapophyses rather than ribs, **20**), whereas beryciforms share derived states of all those characters with perciforms and their immediate relatives. And stephanoberyciforms primitively have a large fourth pharyngobranchial cartilage, absent in all beryciforms, and lack Jakubowski's organ, present in all beryciforms. We propose that stephanoberyciforms (as Stephanoberyciformes) and beryciforms (as Beryciformes) are each monophyletic, and are successive sister-groups of higher acanthopterygians (Fig. 4). We shall call the groups defined by those two nodes Acanthopterygii and Euacanthopterygii.

One consequence of that proposal is that the two derived features of pelvic anatomy used by Stiassny and Moore (1992) to relate holocentrids to higher percomorphs must be seen in another light, either as common to beryciforms and higher euacanthopterygians but reversed in non-holocentrid beryciforms, or as derived independently in holocentrids. Those two features are medial suturing of the pelvic bones (versus overlap, as in most beryciforms), and presence of an interpelvic ligament between the left and right fin bases (versus paired intrapelvic ligaments, from fin base to ipsilateral medial process of girdle). We comment on the two separately.

Regarding the median apposition of the girdle halves in holocentrids, because a similar configuration also occurs within beryciforms in monocentrids, independent derivation there, in holocentrids, and in higher percomorphs is more parsimonious than the multiple reversals within beryciforms that would be required by a single origin for the feature. Furthermore, contrary to Stiassny and Moore, we believe the mode of suturing differs in holocentrids and percomorphs. We have seen the "deep interdigitating suture" described by those authors only in higher euacanthopterygians, whereas in holocentrids there is close apposition of two smooth vertical surfaces, a condition like that in veliferids, where it must have arisen independently. We recognize, nonetheless, that the holocentrid condition could be seen as a precursor to the higher euacanthopterygian condition.

In our view, the interpelvic versus intrapelvic ligament differentiation may not be so clear cut as implied by Stiassny and Moore (1992). In Stiassny and Moore's sample, an interpelvic ligament always co-occurs with a medially sutured girdle except in the zeiform *Zeus,* in which they recorded an interpelvic ligament and "loosely apposed and non-overlapping" pelvic bones. In the zeiform *Parazen,* which has broadly overlapping pelvic bones, we find intrapelvic ligaments (as in *Polymixia* or *Percopsis,* for example), whereas *Zenopsis* has no ligaments at all, and *Zenion* has small intrapelvic ligaments attaching to the ipsilateral pelvic bone behind the area of apposition between them. In *Zeus* we see a heavy investment of connective tissue connecting the bases of the two fins and also the girdle halves. In beryciforms, where Stiassny and Moore recorded intrapelvic ligaments in the

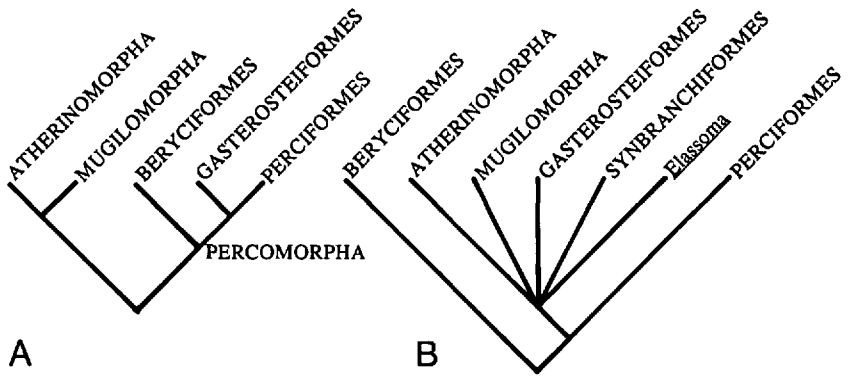


Figure 11. Diagrams contrasting Stiassny's (1990, 1993) view of the relationships of atherinomorphs (A) with our view (B). According to B, the Percomorpha of A are polyphyletic unless the group is expanded to include atherinomorphs and mugilomorphs.

trachichthyid *Hoplostethus,* we find the same condition in the anomalopid *Kryptophanaron,* but in *Anomalops* and *Trachichthys* we find an interpelvic ligament, as in holocentrids. A more detailed and extensive survey would be desirable.

Atherinomorphs

Stiassny (1993) amplifies the case (first proposed in Stiassny, 1990) for a sister-group relationship between mugiloids (which she named Mugilomorpha in 1990) and atherinomorphs (Fig. 11A). As Stiassny (1993) notes, placing mugiloids with atherinomorphs entails the independent acquisition of three features of the pelvic girdle and fin in mugiloids and in perciforms and their relatives, or reversal of those features in atherinomorphs. The three features are: suturing of the medial processes of the girdle (they overlap in atherinomorphs), interpelvic ligament linking the fin bases (atherinomorphs have intrapelvic ligaments), and ventral displacement of the anterior processes of the girdle (they are in the plane of the girdle in atherinomorphs). Again, we consider the first two correlated. Roberts (1993) adds another character, present in mugiloids but absent in atherinomorphs, that must therefore also evolve twice or reverse in atherinomorphs: transforming ctenoid scales. Johnson (1993) was not convinced by the evidence for the mugiloid–atherinomorph connection, but felt that it might involve one other problematic taxon, the North American freshwater *Elassoma,* conventionally placed in the Centrarchidae, which shares some derived features with mugiloids.

In our survey of teleostean intermuscular bones (Patterson and Johnson, submitted), one feature was unique to four taxa among all those that we examined. The taxa are *Elassoma,* Mugiloidei, Atherinomorpha, and Gasterosteiformes. The feature concerns the first two epineurals, which primitively originate on the neural arches of the first two centra. In these four taxa, there are transverse processes or fused parapophyses on the first two centra, and the epineural originates at the tip of the parapophysis. The distal end of that epineural is free in the musculature in *Elassoma* (Fig. 12B) and in exocoetoid atherinomorphs, is associated with the medial face of the dorsal postcleithrum in mugiloids (*Agonostomus,* Fig. 12D) and atherinoid atherinomorphs (*Bedotia,* Fig. 12E), and is associated with the medial face of the cleithrum in gasterosteoids (*Culaea,* Fig. 12C; *Aulorhynchus* has no epineurals and the transverse process of the first centrum is associated

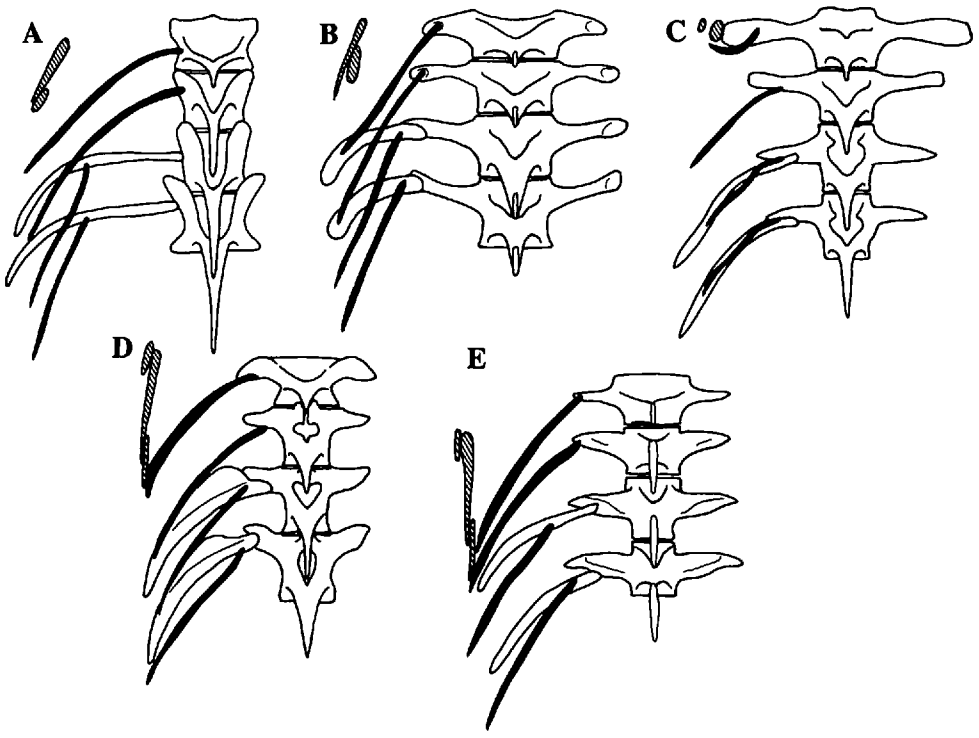


Figure 12. Dorsal view of the first four vertebrae and associated epineurals and ribs of the left side in: A. the percopsiform *Aphredoderus sayanus,* USNM 188576; B. *Elassoma zonatum,* USNM 313100; C. the gasterosteiform *Culaea inconstans,* USNM 196818; D. the mugiloid *Agonostomus monticola,* USNM 7342; E. the atherinomorph *Bedotia* sp., USNM 301513. The epineurals are black. The left cleithrum and supracleithrum, and in D and E, the dorsal postcleithrum, are cross-hatched and shown as if cut through in horizontal section at the level of the tip of the first epineural.

with the cleithrum distally). *Hypoptychus,* which was transferred to the gasterosteiforms (from Ammodytoidei) by Ida (1976), has no intermuscular bones, but has a transverse process on the first centrum, with an epineural ligament running from its tip to the cleithrum. These observations suggest that the gasterosteiforms, whose relationships are as obscure as are those of *Elassoma,* might also be part of the atherinomorph–mugilomorph problem. Before tackling that, it is necessary to review the composition of the Gasterosteiformes.

Composition and Interrelationships of the Gasterosteiforms.—Divergent viewpoints on the composition of the gasterosteiforms are provided by Pietsch (1978) and Nelson (1984), as summarized in their classifications:

Pietsch (1978)
Order Gasterosteiformes
  Suborder Gasterosteoidei
    Superfamily Aulorhynchoidea
      Families Aulorhynchidae, Hypoptychidae
    Superfamily Gasterosteoidea
      Family Gasterosteidae
  Suborder Syngnathoidei
    Infraorder Syngnatha

Superfamily Pegasoidea
Families Pegasidae, Rhamphosidae
Superfamily Syngnathoidea
Families Solenostomidae, Syngnathidae
Infraorder Macrorhamphosa
Superfamily Macrorhamphosoidea
Families Macrorhamphosidae, Centriscidae
Superfamily Aulostomoidea
Families Aulostomidae, Fistulariidae

Nelson (1984)
Order Gasterosteiformes
Families Hypoptychidae, Aulorhynchidae, Gasterosteidae
Order Indostomiformes
Family Indostomidae
Order Pegasiformes
Family Pegasidae
Order Syngnathiformes
Suborder Aulostomoidei
Superfamily Aulostomoidea
Families Aulostomidae, Fistulariidae
Superfamily Centriscoidea
Families Macrorhamphosidae, Centriscidae
Suborder Syngnathoidei
Families Solenostomidae, Syngnathidae
Order Dactylopteriformes
Family Dactylopteridae

Regarding the last order, Nelson wrote "Pietsch (1978) gives reasons to believe that this group may bear some affinity with the pegasids and syngnathiforms." We add some remarks on dactylopterids at the end of this section. Pietsch (1978) also commented on *Indostomus* and the possibility that it is related to his syngnathiforms, whereas Nelson (1984) placed *Indostomus* "between the groups to which it seems to come closest." Neither Pietsch nor Nelson studied *Indostomus,* and Banister (1970), who gave the only complete account of the osteology of the genus, did not compare it with *Pegasus.* We have examined Banister's alizarin-stained material of *Indostomus* and other specimens.

In their original description of *Indostomus* Prashad and Mukerji (1929) described "four complete lobate gills." Bolin (1936) denied that, writing "The Syngnathidae, however, of all the fish which I have been able to examine, are the only ones in which the gills are so sharply modified in form and structure that they deserve the special designation lobate." Banister (1970) did not comment on the gills of *Indostomus.* Figure 13 shows that the gills of *Indostomus* share two striking specializations with those of *Pegasus,* syngnathids and *Solenostomus.* First, the gill filaments are of the type called "lophobranch" (by Cuvier, designating a group containing syngnathids and *Solenostomus*), resembling an ostrich plume rather than the flight feather pattern normal in teleosts (*Fistularia,* Fig. 13A). In the "lophobranch" pattern the lamellae are reduced in number (about 25 per filament in *Pegasus* and *Indostomus,* 30 in *Solenostomus* and *Hippocampus,* and 40 in *Syngnathoides,* the illustrated syngnathid, compared with about 140 in *Aulorhynchus* or *Fistularia*), and are relatively widely spaced; there are about 30 lamellae per mm in *Aulichthys, Aulorhynchus* and *Fistularia* and about 20 per mm in *Pegasus, Solenostomus, Hippocampus* and *Syngnathoides* (*Indostomus* is excep-

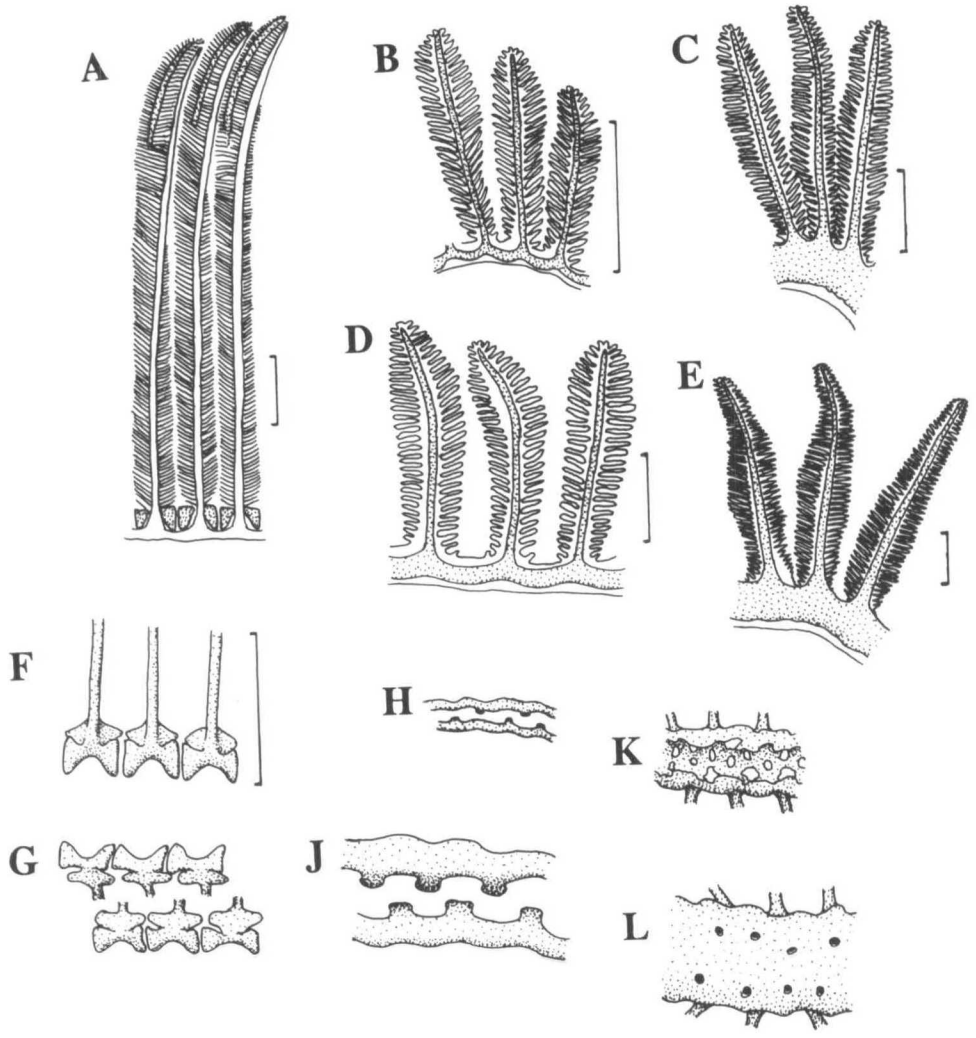


Figure 13. Gill filament structure in Syngnatha and other gasterosteiforms. A–E. Sketches of three adjacent filaments of one hemibranch, viewed from the gill slit, in cleared and stained specimens of A. *Fistularia petimba,* USNM 210463; B. *Indostomus paradoxus,* BMNH 1986.2.14.9–19; C. *Pegasus natans,* BMNH unreg.; D. *Solenostomus paradoxus,* USNM 76598; and E. *Syngnathoides* sp., USNM 243319. F. sketch of the skeleton of the base of three adjacent filaments of one hemibranch, viewed from the gill slit, in *Aulorhynchus flavidus,* BMNH 1979.7.20.7–15. G–L. sketches of the skeleton of the bases of three adjacent filaments from two hemibranchs, viewed from the gill arch, in G. *Aulorhynchus flavidus,* H. *Indostomus paradoxus,* J. *Pegasus natans,* K. *Solenostomus paradoxus,* and L. *Syngnathoides* sp. G–L are respectively from the same specimens and to the same scale as F and B–E. Cartilage and bone are stippled; the unstippled "rachis" of the filament in A is the afferent artery. Scale bars beside A–F = 0.5 mm.

tional here, having about 30 lamellae per mm like the unmodified gasterosteiforms). Second, the skeletal supports of the individual gill filaments, the gill rods or gill rays, are fused basally in the "lophobranchs" so that the skeleton of each hemibranch has the form of a comb (Fig. 13B–E, H–L), which may be entirely cartilaginous (*Indostomus, Pegasus, Solenostomus*) or partially ossified (some syngnathids). In *Solenostomus* the two "combs" are also partially fused as a

Table 1. Distribution of certain characters in gasterosteiform subgroups (see also Pietsch, 1978: table 1)

Character	Aulorhynchids	*Hypoptychus*	Gasterosteids	*Pegasus*	*Indostomus*	*Solenostomus*	Syngnathids	Macrorhamphosids	Centriscids	*Aulostomus*	*Fistularia*
1.	–	–	–	+	+	+	+	–	–	–	–
2.	1–5	1–5	1–4/5	2–3	1–5	0	1–3; 1–2; 0	1–4; 1–3,5	1–4; 1–3,5	1,2,4,5	1,2,4,5
3.	3	3	3	1–2	3	2	1–2	3	3	3	3
4.	4	4	4	4	4	0	3	4	4	3	3
5.	N	N	N	E	E	–	–	N	N	–	–
6.	–	–	–	–	–	–	–	–	–	+	+
7.	−++±−	−++−c	−++−−	−−+−−	−−++−	−++−−	−++−−	c+++−	c+++c	−+++−	−+++−
8.	P	–	P	P	P	–	N	C	C	P	P
9.	4	4	3–4	5	6	1	1–3	4–5	3–5	4	5
10.	+	+	+	+	–	–	–	–	–	–	–
11.	±	+	+	–	–	–	–	–	–	–	–
12.	–	–	–	–	–	+	+	+	+	+	+
13.	3	2	3	3	2	1	2–3	1	1	1	1
14.	C	D	D	C	D	D	D	D	D	D	D
15.	–	–	–	+	–	–	+	+	+	–	+
16.	1	1	0	2	0	0	0	0	0	0	0
17.	+	–	–	+	+	+	+	+	+	+	+
18.	+	+	+	–	+	–	+	+	+	+	+
19.	0–3	(3)	c. 16	0	0	0	0	0	0	0	0
20.	0–21	27–28	9–16	2	0	0	0	0	0	0	0
21.	0	0	0	6	0	4	3	5	6	4	4
22.	E	+	E	+	+	+	+	+	+	E	+
23.	4	4	4	3	3	4	4	4	4	4	4
24.	0	0	0	0	0	0	0	1	1	1	1
25.	–	(–)	+	–	+	–	(–)	–	–	–	–
26.	1	2	1	0	0	1	0	1	1	2	0
27.	PH–H5	PH–H5	PH–H5	PH–H5	PH–H5	PH–H5	PH–H5	PH–H5	PH,H1–5	PH,H1–2,3–5	PH–H5
28.	I	–	I	–	I	P	–	F	F	I	–
29.	+	–	+	–	–	–	–	–	–	–	–
30.	L	0	L	P	P	P	P	P	P	C	P

The original information in this table comes from our examination of cleared-and-stained specimens of the aulorhynchids *Aulorhynchus* and *Aulichthys*, the gasterosteids *Culaea*, *Gasterosteus* and *Spinachia*, of the monogeneric families Hypoptychidae, Pegasidae, Indostomidae, Solenostomidae, Aulostomidae and Fistulariidae, and of the syngnathids *Syngnathus* and *Hippocampus*, the macrorhamphosid *Macrorhamphosus*, and the centriscid *Aeoliscus*. Characters: 1) Gill filaments lophobranch, with skeleton fused basally (Fig. 13) (+) or unmodified (−). 2) Basibranchials present, numbered from 1 to 5, including cartilaginous elements; basibranchial 5 is a small median cartilage at the base of the fifth ceratobranchials (e.g., Nelson, 1969: fig. 17A, *Aulostomus*). The alternative entries under gasterosteids for basibranchial 5 refer to the presence of the cartilage in *Spinachia* and its absence in the other gasterosteids examined. Alternative entries under macrorhamphosids and centriscids refer to a difference between our own observations, on double-stained specimens of both taxa, of a small fourth basibranchial and no fifth, and those of Jungersen (1908), of no fourth and a small fifth in both; we have found Jungersen's work remarkable for accuracy, and can only note this consistent difference. 3) Number of hypobranchials. 4) Number of epibranchials. 5) Condition of fourth epibranchial: N indicates normal, associated with third; E, enlarged, and dissociated

cartilaginous network between the bases of the two hemibranchs (Fig. 13K) and in *Syngnathoides* the fusion is more extensive, forming a cartilaginous tube enclosing the afferent artery (Fig. 13L). In other syngnathids there may be paired "combs" like those in *Pegasus* (*Hippocampus,* Riess, 1881: fig. 27; pers. obs.), or less extensive fusion between the "combs" (*Syngnathus,* Rauther, 1925: pl. 19, fig. 210). In *Solenostomus* and syngnathids the bases of the two hemibranchs are rather widely separated and the gill rods run along the curved outer margin of each filament, so that they lie on the inhalant side, adjacent to the efferent artery (Fig. 13K, L). In *Indostomus* and *Pegasus* the bases of the hemibranchs are still closely approximated and gill rods arise in the primitive position, near the inner margin (exhalant side) of each filament, adjacent to the afferent artery (Fig. 13H, J). In *Indostomus* the distal parts of the gill rods remain in that position, but in *Pegasus* the distal parts of the rods curve outwards to the inhalant side, the same position as in *Solenostomus* and syngnathids. The primitive form of the teleostean gill-filament skeleton is as in *Fistularia* and *Aulorhynchus* (Fig. 13A, F, G), where the cartilaginous or bony gill rods are separate (unfused) proximally, and have intricate bases that articulate with their neighbors and have a wing grooved for the descending efferent artery (*Esox, Salmo,* Riess, 1881: figs. 17, 31, 32; Bijtel, 1949: pls. 10–12).

These unique specializations of the gills imply that *Pegasus* and *Indostomus* are most closely related to Pietsch's Syngnathoidea (syngnathids + *Solenostomus*), or in other words that *Indostomus* belongs within Pietsch's (1978) Syngnatha. Pietsch listed several additional characters which support that relationship, including the remarkable similarity between the body armor of *Indostomus* and syngnathids. Another character bearing on this relationship is an unusual feature of the lower jaw mechanism listed by Pietsch (1978) as common to dactylopterids and his Syngnatha. We have checked this character and agree that in both groups the interopercle is reduced to a thin rod, decoupled from the remaining opercular bones, and is attached exclusively to the hyoid via the interoperculohyoid ligament. As a consequence, depression of the lower jaw is apparently accomplished solely through contraction of the sternohyoideus, without the usual participation of the levator operculi. (For reasons discussed below, we are convinced that this condition must have arisen independently in dactylopterids.) In *Pegasus* (Pietsch, 1978: fig. 6A), both the opercle and subopercle are extremely reduced, and the preopercle is greatly enlarged, essentially forming the entire operculum. In syngnathids (Jungersen, 1910: pl. 5), the opercle remains large, and the preopercle has

←

from third; −, absent. 6) Presence (+) of interarcual cartilage. 7) Pharyngobranchial elements present (+), cartilaginous (c), or absent (−), in the following order: PB1–PB2–PB3–UP4–PB4. Alternative entries under UP4 for aulorhynchids refer to its presence in *Aulorhynchus* and absence in *Aulichthys.* 8) Form of ceratohyal suture: a dorsal prong (P), none (−), complex interdigitation (C, see Jungersen, 1908), or no distal ceratohyal (N, see Jungersen, 1910). 9) Number of branchiostegals. 10) Parietals present (+) or absent (−). 11) Intercalar present (+) or absent (−). 12) Pterotic meeting basioccipital and separating exoccipital from prootic (+) or exoccipital contacting prootic (−). 13) Number of infraorbitals, including lacrimal but excluding dermosphenotic. 14) Infraorbital series continuous (C) or discontinuous (D). 15) Posttemporal incorporated in skull roof (+) or distinct (−). 16) Number of extrascapulars. 17) First four vertebrae joined by interdigitating sutures at the base of the neural arch (+) or unmodified (−). 18) Parapophyses (transverse processes) on first two vertebrae present (+) or absent (−). 19) Number of pairs of epineural bones or (in parentheses) ligaments. 20) Number of pairs of ribs. 21) Number of elongated anterior vertebrae. 22) Posterior extension of coracoid: present (+), absent (−), or with superficial ornamentation (E = "ectocoracoid"). 23) Number of pectoral radials. 24) Number of postcleithra. 25) Pelvis with a superficial, ornamented portion present (+) or absent (−). (Pelvic girdle absent indicated by (−).) 26) Number of epurals. 27) Condition of hypurals: PH–H5 indicates a single fan-shaped plate incorporating the parahypural and five hypurals; PH,H1–5 indicates the same configuration but with a separate parahypural; and PH, H1–2,3–5 indicates separate upper and lower hypural plates and a separate parahypural. 28) Condition of dorsal spines: I indicates isolated dorsal spines, unconnected by membrane; − indicates no dorsal spines; P indicates the modified "pseudospines" of *Solenostomus*; and F indicates spines fused with their pterygiophores (Jungersen, 1908: pl. 2). 29) Presence (+) of rayless dorsal and anal pterygiophores caudally, extending beyond the fins. 30) Condition of scales: L indicates lateral line scutes only; P indicates plates or scutelike scales forming a more or less complete carapace; 0 indicates scales absent; and C indicates the small ctenoid scales of *Aulostomus* (Roberts, 1993). Because the latter occur in conjunction with segmental lateral line scales, each equal in length to four scale rows, we interpret them as secondary, not as the primary squamation in which body and lateral line scales are similar.

a reduced upper limb and extends as a plate between the opercle and quadrate. Banister (1970: fig. 13) described and illustrated the interopercle in *Indostomus* as an ovoid plate extending between the large opercle and the quadrate and the hind end of the very elongate lower jaw. The positional relationships of that bone (it contacts the quadrate) indicate that it is, in fact, the preopercle and we believe that the rectangular bone posterior to the orbit, identified by Banister as the preopercle, is part of the discontinuous infraorbital series. *Indostomus,* then, lacks an interopercle, and shares with other Syngnatha lower jaw depression exclusively via the hyoid, from which there is a strong (interoperculohyoid?) ligament to the dentary.

It is also worth noting that in both *Indostomus* and *Pegasus* the subopercle is reduced to a small splint of bone lying posteromedial to the opercle. Further features unique to *Indostomus* and *Pegasus* among gasterosteiforms are the relatively enlarged fourth epibranchial and the presence of only three pectoral radials (Banister, 1970: figs. 8, 15; Pietsch, 1978: figs. 9, 11).

Characters bearing on gasterosteiform interrelationships are set out in Table 1. We can discern no fully consistent pattern in the data in Table 1, but note first that with the inclusion of *Hypoptychus* in the Gasterosteoidei there is little evidence for monophyly of that group. Nelson (1978, 1984) was not convinced by Ida's (1976) argument for placing *Hypoptychus* with the gasterosteoids, but the only counterargument that he (Nelson, 1978) offered was "numerous differences" between *Hypoptychus* and *Aulichthys,* the western Pacific gasterosteoid with which *Hypoptychus* (also western Pacific) shares one remarkable feature pointed out by Ida (1976): in both *Hypoptychus dybowskii* and *Aulichthys japonicus* (the two genera are monotypic) the premaxilla is toothed in the male, but toothless in the female. Nelson (1978) added another character shared by the two, a postmaxillary process on the premaxilla, a structure absent in all other gasterosteiforms. We have noted two further features shared by *Hypoptychus* and *Aulichthys*: first, the metapterygoid is reduced to a straight, narrow splint; and second, *Hypoptychus* has a "basimandibular" (de Beer, 1937: 418), a small median cartilage behind the upper part of the mandibular symphysis, whereas *Aulichthys* has a small bone in that position (BMNH 1979.7.20.25). In other gasterosteiforms we have seen occasional minute nodules or lenses of bone behind the ventral part of the mandibular symphysis, but these appear to be sesamoids in the tendon of the geniohyoideus, non-homologous with the cartilage (*Hypoptychus*) or bone (*Aulichthys*) behind the upper part of the symphysis. These features suggest that *Hypoptychus* is not just a dubious gasterosteoid, but the sister-taxon of *Aulichthys.* There are, as Nelson (1978) said, many differences between those two genera, but most of them can be seen as reductive in *Hypoptychus* (e.g., absence of scales, of lateral line scutes, of median fin spines, of ceratohyal suture, of spina occipitalis, and of pelvic skeleton and fin; epineural ligaments rather than bones). The only non-reductive characters distinguishing *Hypoptychus* from *Aulichthys* that we have observed are nos. 7 and 26 in Table 1; the presence of two epurals in *Hypoptychus* vs. one in *Aulichthys,* and the presence of PB4 in *Hypoptychus* vs. its absence in *Aulichthys.* There are also many differences between the two aulorhynchid genera *Aulichthys* and *Aulorhynchus* (e.g., absence in the latter of intercalar, medial limb of posttemporal, ribs, intermusculars, and supracleithrum; the lower jaw in *Aulichthys* is much longer than the upper, and the first haemal spine in *Aulichthys* is placed behind the first two or three anal pterygiophores rather than adjoining the first anal pterygiophore; UP4 is present in *Aulorhynchus* but absent in *Aulichthys*), and in all of those cited *Hypoptychus* agrees with *Aulichthys* rather than *Aulorhynchus.* If, as we therefore suspect, *Hypoptychus* is most closely related to

Aulichthys, the Aulorhynchidae are paraphyletic, and the Gasterosteoidei may also be paraphyletic, because the only derived character in Table 1 that is unique to Gasterosteidae and Aulorhynchidae, no. 29 (rayless dorsal and anal pterygiophores extending caudally beyond the fin), must have been lost in *Hypoptychus* and may therefore also have been lost in Syngnathoidei, all of which have the median fins much modified. Three of the derived features in which *Aulorhynchus* differs from *Aulichthys,* loss of intercalar, of spina occipitalis and of ribs/epineurals, are shared with Syngnathoidei [the only recorded ribs in Syngnatha are the bones on the seventh and eighth vertebrae of *Pegasus* that Pietsch (1978) described as ribs, but they may, as Jungersen (1915) thought, be intermusculars]. The implication is that *Aulorhynchus* is more closely related to Syngnathoidei than to other gasterosteoids; this is also implied by the fact that we are unable to specify any derived character common to all Syngnathoidei (Table 1). The elongate anterior centra cited as a character of Syngnathoidei by Pietsch (1978) are not found in *Indostomus,* but will serve to define the group if the condition in *Indostomus* is accepted as secondary because the lophobranch gill-filament skeleton of *Indostomus* (Fig. 13) establishes it as a member of the subgroup Syngnatha.

The possibility that dactylopterids are related to gasterosteiforms (Pietsch, 1978) was mentioned at the beginning of this section. Pietsch cited a number of derived characters shared by dactylopterids and one or other gasterosteiform subgroup, but none common to dactylopterids and all gasterosteiforms. The proposition of relationship can best be evaluated by reference to a list of the derived characters of gasterosteiforms. Neither Pietsch (1978) nor Nelson (1984) provided any. We propose the following characters: 1) There is a cartilaginous fifth basibranchial articulating with the tips of the fifth ceratobranchials. This structure was illustrated in *Aulostomus* by Nelson (1969: fig. 17A) and described by him as a secondarily separate rudiment. The structure is widespread though not universal in gasterosteiforms (Table 1, no. 2), being present in *Spinachia* among gasterosteids, in aulorhynchids and *Hypoptychus,* in *Indostomus* among Syngnatha, in aulostomoids, and questionable in macrorhamphosoids. 2) Baudelot's ligament is absent. 3) The coracoid has a posteroventral extension (Table 1, no. 22), which is sometimes superficial and ornamented (ectocoracoid of Nelson, 1971; infraclavicle of Ida, 1976). In *Pegasus* and *Indostomus* we take the long, slender process extending back beneath the lowermost pectoral radial to be the homolog of the "ectocoracoid." 4) The pelvic bone has no anterior process (Stiassny and Moore, 1992). 5) The caudal skeleton includes a full neural spine on PU2; HPU2 and HPU3 fused to their centra; and the parhypural and five hypurals fused with each other and with the terminal centrum. There are two exceptions to that last character (Table 1, no. 27): centriscids, where the parhypural is free and does not articulate with the centrum; and *Aulostomus,* where the parhypural is distinct and there are separate upper and lower hypural plates. But all the hypurals are fused to the terminal centrum in the Eocene aulostomids *Eoaulostomus* and *Synhypuralis.* 6) The dorsal spines, when present, are separate (isolated), not joined by membrane, and articulate at or posterior to the midpoint of the protracted dorsal surface of each pterygiophore. 7) Scales, when present, are represented by plates or scutes, except in *Aulostomus,* which has peripheral ctenoid scales that we take to be secondarily developed (Table 1, no. 30). In addition, the first four vertebrae are joined by interdigitating sutures at the base of the neural arches. This feature is lacking only in *Hypoptychus* and gasterosteids, each of which shares unique specializations with other gasterosteiforms, as listed above.

There are also a number of characters that gasterosteiforms share with atherinomorphs and other fishes discussed in the following section (Table 2), including

the presence of transverse processes (lacking only in *Solenostomus*), primitively bearing epineurals, on the first two vertebrae; pelvic girdle dissociated from cleithrum; two or fewer infraorbitals behind the lacrimal; no supraneurals; supracleithrum reduced or absent; dorsal suturing of the ceratohyal; absence of distal radials on spine-bearing dorsal pterygiophores; a reduced first pectoral ray; and two or fewer epurals.

Comparing dactylopterids against this list of characters, they agree with gasterosteiforms in lacking Baudelot's ligament; in having scute-like scales (Roberts, 1993); in having a reduced supracleithrum, although the form and position of the supracleithrum in dactylopterids (Allis, 1909) are unique; in lacking supraneurals and distal radials on the spine-bearing dorsal radials; and in having a reduced first pectoral ray and two epurals. Dactylopterids differ from gasterosteiforms in lacking a fifth basibranchial and a posteroventral extension of the coracoid; in having an anterior process on the pelvic girdle; in having no neural spine on PU2, HPU2 and HPU3 autogenous, and a different pattern of hypural fusion, with PH and H1 fused but autogenous, H2 free, and H3–5 fused but autogenous; in having the dorsal spines joined by membrane; in lacking transverse processes (and epineurals) on the anterior vertebrae; in having the pelvic girdle connected to the cleithrum; in having three infraorbitals between the lacrimal and dermosphenotic; and in having the normal perciform pattern of ceratohyal suture. The first three vertebrae of dactylopterids are sutured together, but the suturing involves the centrum as well as the neural arches, and the first vertebra is also sutured to the occiput; we agree with Pietsch (1978) that this pattern is unlikely to be homologous with the gasterosteiform pattern. Evaluating this series of similarities and differences convinces us that dactylopterids are not closely related to gasterosteiforms, or to the other fishes discussed in the following section; but the characters shared by dactylopterids and gasterosteiforms (or some gasterosteiform subgroup) are another instance of the horrors of homoplasy.

Our examination of dactylopterids has not yielded any convincing evidence of their relationships, or any further indication that they are related to scorpaenoids.

Relationships between Atherinomorphs, Mugiloids, Gasterosteiforms, and Other Groups.—We are encouraged in the idea that gasterosteiforms might be related to atherinomorphs and mugiloids by two pieces of information in W. C. Freihofer's unpublished papers, whose existence was mentioned above under Beryciformes. This information comes from portions of the manuscript published as Freihofer (1978) that were omitted at the editor's request, and which Freihofer evidently intended to publish separately. The first, mentioned briefly in Freihofer (1978: 44), concerns the innervation pattern of the adductor mandibulae. In the published text, Freihofer said that a particular and distinctive pattern is found only in the seven families of atherinomorphs that he examined and in gasterosteids. In the unpublished text the primitive pattern of adductor innervation was described as a single branch of the ramus mandibularis trigeminus, and the atherinomorph pattern as from three to six separate, well-spaced branches detaching sequentially from the nerve as it runs forwards below the eye and above the muscle. Two branches of the nerve were described in mugiloids (*Myxus, Xenomugil*), and Freihofer wrote "mugilids resemble atherinomorphs in having more than one branch . . . The mugilid pattern is uncommon among perciform fishes, if not unique. The only other fishes examined so far other than atherinomorphs having a series of sequential . . . branches . . . are the sticklebacks [gasterosteids] and tubesnouts [aulorhynchids], syngnathoids not yet being examined." Freihofer went on to describe five branches in *Gasterosteus* and four or five in *Aulorhynchus*.

The other piece of information concerns the dorsal longitudinal lateral line collector nerve, mentioned in Freihofer (1978: 46) as being present in all the other perciforms that he examined, but absent in zoarcids, gobiids, mugilids, and in all atherinomorphs. Freihofer amplified this in the unpublished text by saying that the zoarcids and gobiids "either show drastic specialization away from a percoid pattern of their trunk lateral line nerves or their pattern is a retained, modified preacanthopterygian pattern." Furthermore, he noted that *Gasterosteus* also shows no sign of the collector nerve, and concluded that gasterosteiforms and atherinomorphs might be sister-groups, because of the numerous branches of the mandibular nerve to the adductor mandibulae, a unique specialization with which the absence of the lateral line collector nerve, though not unique, is consistent.

[Freihofer's unpublished papers also provide one more synapomorphy for atherinomorphs, described in the unpublished text as "unique premaxillary extension of the supraorbital trunk" and mentioned in the published text (Freihofer, 1978: 44) by a reference to Herrick's (1899: fig. 3) illustration of *Menidia*. Freihofer observed this extension in members of the Atherinidae, Melanotaeniidae, Cyprinodontidae, Anablepidae, Oryziatidae, Exocoetidae and Hemirhamphidae. The published text says that the same extension also occurs in holocentrids, but there is no mention of that in the unpublished notes. In those notes, however, what seems to be the same condition is described in *Mastacembelus*. Finally, Freihofer's manuscript suggests a synapomorphy for gasterosteiforms (gasterosteoids and syngnathoids): the fin-ray nerves course external to the hemitrichs rather than between (internal to) them. That feature is not unique to gasterosteiforms, being recorded in pleuronectiforms, ophidioids, cottids, and other benthic forms. But Freihofer remarked that the gasterosteoids and syngnathoids are the first non-benthic fishes known to have external fin-ray nerves.]

We have checked Parenti's (1993) 14 atherinomorph characters in *Elassoma*, mugilids and gasterosteiforms and find that several of them are present in all or some of these four groups. We discuss them below, as numbered by Parenti: 6. One or two laminar, disclike mesethmoid ossifications. Johnson (1984) noted the similarity between the discoidal mesethmoids of *Elassoma* and atherinomorphs. This is discussed further by Parenti (1993), who remains unconvinced that the two conditions are homologous. The mesethmoid is unmodified in mugiloids and its configuration is variable in gasterosteiforms. But we note one feature of the ethmoid region that appears to be common to all four groups: the vomer lacks ascending processes and the direct articulation between the vomer and lateral ethmoid identified by Stiassny (1986) as an acanthomorph synapomorphy is lacking. 7. Infraorbital series represented by a lacrimal and a dermosphenotic, and two, one, or no anterior infraorbital bones. The infraorbital series is reduced in all four groups. Gasterosteiforms have no more than a lacrimal and two adjacent infraorbitals, and, as in atherinomorphs, the infraorbital canal is discontinuous in all except aulorhynchids and *Pegasus* (Table 1). Nelson (1971: 435) reported that aulorhynchids have four infraorbitals in addition to the dermosphenotic, but our observations indicate that there are only three, although the lacrimal may give a false impression of being sutured at midlength. *Elassoma* has only the lacrimal, and mugilids have a pronounced gap between the lacrimal and a continuous chain of infraorbitals posteriorly. We note that reduction and/or interruption of the infraorbital series is not unique to these groups, but is known in a number of other percomorphs, including gobioids, gobiesocids and callionymids (Springer, 1983; Winterbottom, 1993). 8. Lateral processes of pelvic bone and distal end of pleural rib in close association and, in some taxa, connected by a ligament. With one exception, primitive gasterosteiforms, we agree with Parenti

(1993: fig. 2B) that this feature is unique among acanthomorph fishes to atherinomorphs. In gasterosteids a broad laminar process arises from the posterolateral corner of the pelvic girdle and is associated dorsally with the distal tips of one or more pleural ribs (Nelson, 1971: figs. 1, 3, 4). In aulorhynchids the process is present, but is reduced or directed posteriorly (Nelson, 1971: fig. 2), so that it does not contact the ribs. In *Elassoma,* the tip of the third rib is connected to the slightly expanded posterolateral corner of the girdle by a myocomma, but there is no differentiated ligament. Stiassny (1993) proposes that a posterolateral pelvic process in mugilids that is ligamentously connected to the postcleithrum is homologous with the rib-associated process of atherinomorphs. Although that interpretation may be correct, we note that the tip of the postcleithrum is ligamentously connected to a similar process in polynemids and sphyraenids, two unrelated groups (Johnson, 1986, 1993) in which the process and the connection are probably convergent. Atherinomorphs, *Elassoma,* mugilids and gasterosteiforms have the pelvic girdle dissociated from the cleithrum (as do polynemids and sphyraenids), but only atherinomorphs have overlapping, rather than sutured pelvic bones. We interpret both conditions as secondary. 9. Supracleithrum reduced or absent. The supracleithrum is notably reduced in all gasterosteiforms (Starks, 1902: figs. 1–6; Jungersen, 1908, 1910, 1915; Banister, 1970: fig. 7; Nelson, 1971: figs. 2–5; Ida, 1976: fig. 5) except solenostomids (Jungersen, 1910: pl. 7). It is also reduced in mugiloids (Stiassny, 1993) but not in *Elassoma* (Fig. 14). An additional feature of the supracleithrum of atherinomorphs, shared by all the above taxa, is that it lacks a sensory canal. Stiassny (1993) cites a reduced supracleithrum without a sensory canal as a feature found only in atherinomorphs and mugilomorphs. Absence of a supracleithral sensory canal also characterizes all gobioids, and has apparently arisen several times within perciforms, but reduction of the supracleithrum is much less common. 12. Supraneural bones absent. This reductive feature is not uncommon among percomorphs. Supraneurals are also absent in *Elassoma* (Fig. 14). They appear to be present in some gasterosteids (e.g., *Pungitius* and *Culaea,* Nelson, 1971: figs. 1, 3), but the structure of these bones and comparison with the anterior pterygiophores of gasterosteiforms with a dorsal fin beginning immediately behind the head (e.g., *Aulichthys, Apeltes,* Nelson 1971: fig. 2) implies that they are predorsals (secondarily rayless radials) rather than supraneurals. We guessed that the same interpretation might apply to the three supraneurals of mugiloids, but examination of mugilid larvae confirmed that those three elements develop in rostrocaudal sequence, unlike the spinous dorsal pterygiophores of most acanthomorphs, and thus must be supraneurals. Gasterosteiforms, at least primitively, have the dorsal fin origin anterior to the third neural spine, a euacanthopterygian character present in most percomorphs. Atherinomorphs, mugilids and *Elassoma* share a posteriorly displaced dorsal-fin origin with the neural spines anterior to the fin expanded. 14. Olfactory sensory epithelia arranged in sensory islets. This condition is not unique to atherinomorphs, but it is very uncommon among acanthomorph fishes. Yamamoto (1982: table 3.1) reported that it also occurs in the gasterosteiforms *Pungitius* and *Fistularia* (but not in the syngnathoid *Hippocampus*), as well as in *Hexagrammos, Upeneus, Ammodytes* and *Fugu.* He did not find it in *Mugil,* and *Elassoma* was not examined.

As for Parenti's (1993) eight possible atherinomorph + paracanthopterygian characters (cited above, under paracanthopterygians), six of them are not among her 14 atherinomorph characters. Three of those six characters occur in gasterosteiforms (no ligamentous connection between postcleithrum and pelvic girdle; full neural spine on PU2; two or fewer epurals—Table 1), whereas two others,

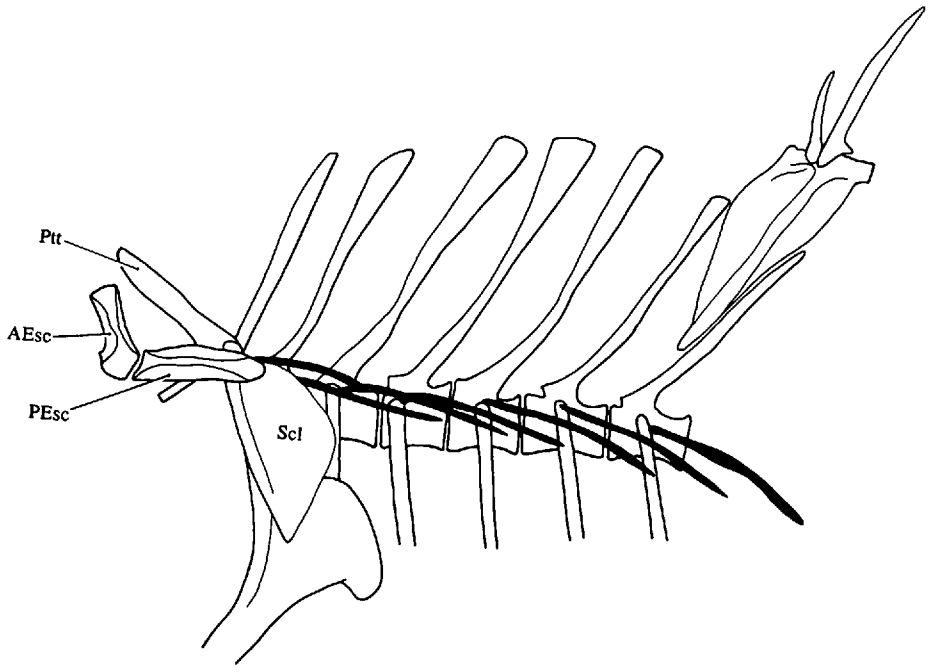


Figure 14. *Elassoma zonatum*; lateral view of anterior vertebrae and surrounding structures, to show the unreduced supracleithrum (Scl), elongate posterior extrascapular ossicle (PEsc) overlying the posttemporal (Ptt), absence of supraneurals, posteriorly displaced dorsal fin, and expanded neural spines. Epineurals black. USNM 313100.

each with limited distribution in both atherinomorphs and paracanthopterygians, do not occur there ("Y" bone and doubled caudal neural and haemal arches).

Stiassny (1993: fig. 1) lists seven characters common to atherinomorphs and mugiloids. One of these (no. 4, reduced supracleithrum) is discussed above. Among the remainder, nos. 3 (neural spines anterior to dorsal fin expanded, e.g., *Hypoptychus*), 6 (posteriorly directed dorsal cleithral process, Nelson, 1971), and 7 (extensive abductor profundis) occur in at least some gasterosteiforms and elsewhere in some perciforms. And two of those characters occur in *Elassoma,* nos. 3 and 7 in Stiassny's list: expanded anterior neural spines (Fig. 14) and orientation of abductor profundis.

Another character discussed by Johnson (1993) and Stiassny (1993) is the configuration of the extrascapulars. Stiassny found that extrascapulars are generally absent in atherinomorphs, except in a few atherinoids [the notocheirid (=isonid) *Iso* and some atherinids amongst those surveyed], but that mugiloids are unusual in having three extrascapulars, the supernumerary one (the most posterior) an elongate tubular ossicle overlying the posttemporal, which does not bear a sensory canal. She reported a similar but shorter ossicle in the atherinoid *Melanorhinus.* As described by Johnson (1993) *Elassoma* (Fig. 14) also lacks a sensory canal in the posttemporal and has an elongate posterior extrascapular ossicle, resembling that of mugiloids but extending back to the supracleithrum. Among gasterosteiforms, *Pegasus* has two extrascapulars, aulorhynchids and *Hypoptychus* have one, and the remainder have none.

One further character may bear on a relationship between atherinomorphs and gasterosteiforms: the relation between the distal and proximal ceratohyals. Figure 15E–J illustrates the ceratohyals of *Elassoma,* two mugiloids, a gasterosteiform,

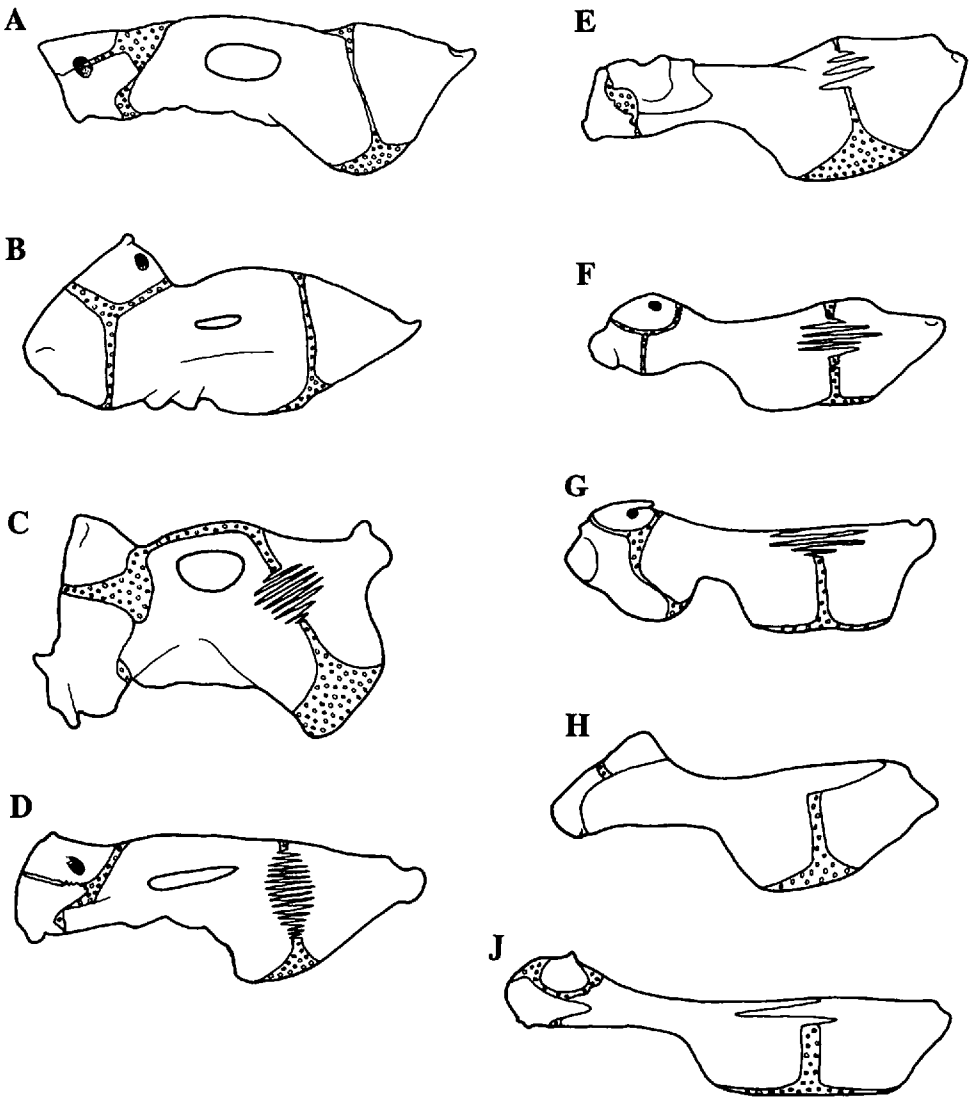


Figure 15. Medial view of the right hyoid bar in: A. the beryciform *Hoplostethus mediterraneus*, VIMS 4900; B. the zeiform *Cyttopsis roseus*, AMNH 29460; C. the caproid *Antigonia combatia*, USNM 266901; D. the percoid *Pomatomus saltatrix*, USNM 236806; E. *Elassoma zonatum*, USNM 313100; F, G. the mugiloids *Agonostomus monticola*, USNM 7342, and *Mugil* sp., USNM 297255; H. the gasterosteiform *Culaea inconstans*, USNM 196818; J. the atherinomorph *Bedotia* sp., USNM 301513.

and an atherinomorph. In the last two, the two ceratohyal ossifications are sutured along the dorsal margin by long spatulate prongs. In *Mugil* (Fig. 15G) there is suturing along the dorsal margin, whereas *Agonostomus* (Fig. 15F) shows a more typical perciform pattern with the suturing confined to the middle part of the junction between the bones (Fig. 15C, D), as does *Elassoma*. Illustrations in McAllister (1968), Jungersen (1908, 1910), Rosen (1964: fig. 14), Banister (1970: fig. 14), Pietsch (1978: fig. 8) and Parenti (1981: fig. 28) indicate that the dorsal spatulate suturing is general in atherinomorphs and gasterosteiforms (except *Hypoptychus*, Ida, 1976: fig. 4; and *Solenostomus*, Jungersen, 1910: pl. 6, fig. 3). To

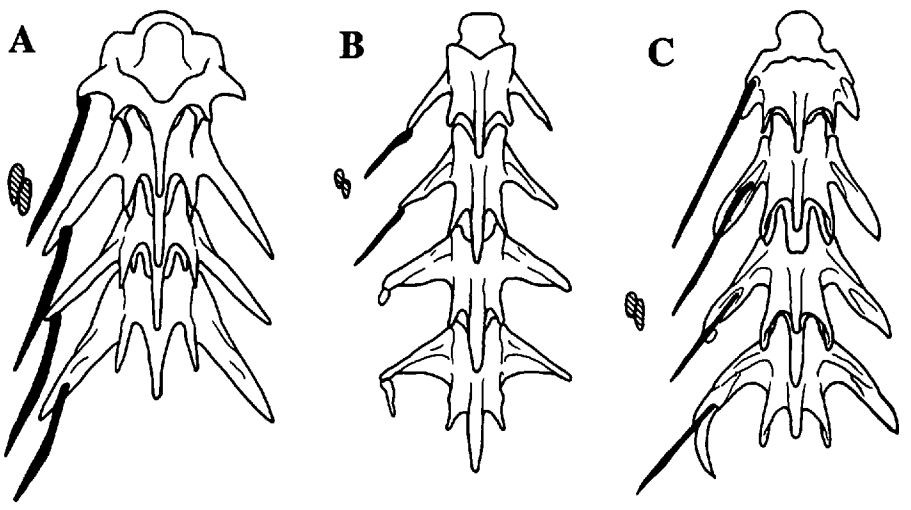


Figure 16. Dorsal view of the first four vertebrae and associated epineurals and ribs of the left side in: A. the synbranchoid *Monopterus albus*, BMNH 1976.4.2.71; B. the mastacembeloid *Chaudhuria caudata*, MCZ 47058; C. the mastacembeloid *Rhynchobdella sinensis*, BMNH 1927.10.1.19. The epineurals are black. The left cleithrum and supracleithrum are cross-hatched and shown as if cut through in horizontal section at the level of the tip of the first epineural.

our knowledge, a similar pattern occurs elsewhere only in anguilliforms, where it differs in that the dorsal suturing is accomplished by a posteriorly directed spur from the distal ceratohyal, a condition that has obviously developed independently.

Summing up, if the characters cited by Stiassny (1990, 1993) as common to atherinomorphs and mugiloids are indicative of a relationship between those two groups (as we believe they are), then the mugilomorph + atherinomorph assemblage also involves two other taxa, *Elassoma* (=Elassomatidae Jordan and Gilbert, 1882) and Gasterosteiformes.

Synbranchiformes. Our association of *Elassoma* and gasterosteiforms with the atherinomorphs and mugilomorphs was initially prompted by the realization that they shared a modified pattern of the first two vertebrae and intermuscular bones that was unique among the groups surveyed in our review of intermusculars (Patterson and Johnson, submitted[1]). We extended that survey and have found a similar pattern in four other teleostean taxa: in the carangoid *Echeneis*; in the gobiid *Gnatholepis* (pointed out to us by A. C. Gill); and in the synbranchoids and mastacembeloids, which were together included in the Synbranchiformes by Gosline (1983) and Travers (1984a, 1984b). *Echeneis* and *Gnatholepis* are each nested within well-characterized monophyletic groups (carangoids, gobioids), and the modifications of their first two vertebrae and intermusculars can therefore only be interpreted as convergent with those in *Elassoma*, gasterosteiforms, atherinomorphs and mugilomorphs; in *Echeneis* we suggest that the pattern developed in connection with dorsoventral compression of the cranium and support of the dorsal-fin sucking disc. The other two taxa, synbranchoids and mastacembeloids, are thought to be percomorphs (Rosen and Greenwood, 1976; Travers, 1984b) or "percomorphous" (Gosline, 1983), but their relationships are otherwise obscure. Although the characters used by Gosline (1983) and Travers (1984b) to relate synbranchoids and mastacembeloids in the Synbranchiformes are not fully

convincing, we have found no reason to question the monophyly of that group, and suggest that further evidence for it is the similarity in configuration of the anterior vertebrae (Fig. 16) in the two groups, and the resemblance between the "pluglike" (Rosen and Greenwood, 1976: 45) anterior surface of the first centrum in synbranchoids and the "ball and socket" (Travers, 1984b: 108) occipital joint in mastacembeloids.

An alternative scheme, proposed by Lauder and Liem (1983) and Roe (1991), is that the sister-group of synbranchoids is the Channidae (*Channa*). Unfortunately, Lauder and Liem (1983), although they cited Travers's proposal of mastacembeloid–synbranchoid relationships (as a personal communication), did not evaluate the mastacembeloids, and Travers (1984b), in his comparison of mastacembeloids with synbranchoids and other groups, did not discuss Lauder and Liem's proposal, although he included *Channa* in his comparisons. Travers's account of mastacembeloids throws into question some of the characters cited by Lauder and Liem (e.g., features of the adductor mandibulae complex; supposed enlarged, toothed endopterygoid in synbranchoids). In addition, Yamamoto's (1982) summary of the structure of the olfactory organ in *Channa* and a synbranchoid denies the similarity between the two suggested by Lauder and Liem, and Rosen and Patterson (1990) pointed out the dissimilarities between the dorsal gill arches of *Channa* and synbranchoids, and derived similarities shared by *Channa,* nandids and anabantoids. The anterior vertebrae and epineurals of *Channa* are unmodified; among the other derived characters listed in Table 2, those shared by *Channa* and one or more groups in that table are dissociation of the pelvic girdle from the cleithrum, absence of supraneurals, a caudal skeleton with a full-length NPU2 and two or fewer epurals (as in nandids and anabantoids), and head of the fourth epibranchial larger than the third (as in anabantoids, Rosen and Patterson, 1990: figs. 28–31). We do not feel that *Channa* is more closely related to the synbranchoids than are the mastacembeloids, or that *Channa* is related to the other fishes under discussion here.

Above, we have reviewed a number of characters bearing on the proposed relationship between *Elassoma,* gasterosteiforms, mugilomorphs and atherinomorphs. We now review those characters in synbranchiforms. Rosen and Greenwood (1976) provided a phylogeny of synbranchoids in which *Macrotrema* is the sister-group of the remainder (Synbranchinae) and *Ophisternon* is the sister of the remaining synbranchines. We have seen no cleared-and-stained material of the rare and poorly known *Macrotrema,* and take *Ophisternon* as a representative synbranchoid. Travers (1984b) provided a phylogeny of mastacembeloids in which the Chaudhuriidae (*Chaudhuria* and *Rhynchobdella*) are the sister-group of the remainder. We find certain problems with Travers's characterization of the Chaudhuriidae (1984b: 132), because some of the characters seem to be primitive (e.g., nos. 26, presence of spina occipitalis, 33, absence of ventral process on basibranchial 2), others may be primitive (e.g., nos. 25, 28), and others may not exist (nos. 32, 34), but we have taken *Chaudhuria* and *Rhynchobdella* as primitive mastacembeloids. 1. Epineurals originating at the tip of parapophyses or transverse processes on the first two vertebrae. In synbranchoids, there is a transverse process on the first (and succeeding) vertebra with a bone articulating at its tip (Fig. 16A; Rosen and Greenwood, 1976: fig. 63). Rosen and Greenwood (1976) and Travers (1984b: 126) interpreted the bone on the first vertebra as a pleural rib. It is in series with similar bones on the succeeding vertebrae that are posterodorsally directed and lie not in the wall of the pleural cavity (the normal position of a pleural rib) but in or close to the horizontal septum (observations on *Ophisternon,*

Synbranchus and *Monopterus,* and cf. Rosen and Rumney, 1972: figs. 21, 22). There are no other riblike bones, and Regan (1912) interpreted the single series of bones as epipleurals. Although orientation is not an infallible guide in discriminating intermusculars and ribs, we know of no other teleosts with ribs on the first centrum, and interpret the single series of bones on the transverse processes of synbranchoids as epineurals. They therefore show the same condition as *Elassoma,* gasterosteiforms, atherinomorphs and mugilomorphs. In mastacembeloids, Travers (1984a) described and illustrated epicentral bones (on the first one to four vertebrae), an epipleural bone (on the third, fourth or fifth vertebra), and pleural ribs (first appearing on the third to sixth vertebra, except in a few species that lack them on the first 14 or more vertebrae). He did not say how he distinguished epipleural bones from epicentrals or pleural ribs, but judging by his cleared-and-stained specimens, including the illustrated individual of *Mastacembelus mastacembelus* (Travers, 1984a: fig. 12), his single epipleural is the first pleural rib and his epicentrals are the epineurals. In *Chaudhuria,* where the only epineurals are on the first one or two vertebrae, they originate on substantial transverse processes (Fig. 16B; Travers, 1984a: fig. 21), in the same pattern as in synbranchoids, *Elassoma,* gasterosteiforms, atherinomorphs and mugilomorphs. In *Rhynchobdella* (Fig. 16C), which Travers placed as the sister-taxon of *Chaudhuria,* there are four epineurals (not three, cf. Travers, 1984b: 126) all originating on transverse processes, but the process on the first centrum is shorter than those on the second and third. In mastacembelids the pattern illustrated for *Mastacembelus mastacembelus* (Travers, 1984a: fig. 12) is exemplary; the epineurals are on transverse processes on the second and third vertebrae, but those processes are shorter than in *Rhynchobdella,* and the epineural is on a still shorter process on the first vertebra. 2. Association between tip of first epineural and shoulder girdle. The first epineural is directed towards the cleithrum in mastacembeloids, but does not contact it (Fig. 16B, C). The shoulder girdle is displaced posteriorly in several synbranchoids, but in the less modified forms (e.g., *Monopterus*) where the shoulder girdle is still connected to the cranium, the first epineural ends behind the cleithrum (Fig. 16A). 3, 4. Innervation of adductor mandibulae and absence of dorsal longitudinal lateral line collector nerve. We have no information on conditions in synbranchoids. Freihofer (unpubl. notes, 1973) recorded a single branch of the ramus mandibularis trigeminus to the adductor mandibulae and a dorsal longitudinal collector nerve in *Mastacembelus,* so that it does not show the specializations found in atherinomorphs, mugilomorphs and gasterosteiforms. But, as recorded above, Freihofer's notes imply that *Mastacembelus* shares a premaxillary extension of the supraorbital trunk with atherinomorphs. 5. Infraorbital series represented by a lacrimal, a dermosphenotic, and two or fewer infraorbital bones. In synbranchoids, there is only one infraorbital, the lacrimal (Rosen and Greenwood, 1976: 49). In mastacembeloids, there is a large lacrimal and a series of from one to five small, tubular ossicles surrounding the canal (Travers, 1984a: 56, fig. 3); when complete, as with the chain of five ossicles in *Mastacembelus mastacembelus* (Travers, 1984a: fig. 3), the infraorbital canal is uninterrupted. But it is interrupted in *Rhynchobdella* and *Chaudhuria,* which we take to be primitive mastacembeloids and the distribution of the uninterrupted condition in Mastacembelidae requires further study. 6. Lateral processes of pelvic bone and distal end of pleural rib in close association, and in some taxa, connected by a ligament. Synbranchiforms have no pelvic girdle or fin. 7. Supracleithrum reduced or absent. The supracleithrum is small or very small in synbranchoids (Travers, 1984b: fig. 6) and lacks a sensory canal. All mastacembeloids lack a

posttemporal and have two or three tubular ossicles between the cranium and the posteriorly displaced pectoral girdle. The mastacembeloid supracleithrum is slender but not much reduced and bears a fused tubular ossification similar to the free tubules anterior to it (Travers, 1984a: figs. 11, 21, 67–73). 8. Supraneural bones absent. There are no supraneurals in synbranchiforms. 9. Olfactory sensory epithelia arranged in sensory islets. Only one synbranchiform has been examined (Yamamoto, 1982: table 3.1). Yamamoto reported that the sensory epithelia of *Monopterus albus* (=*Fluta alba*) are not in discrete islets but mixed irregularly with the indifferent epithelium. 10, 11. Full neural spine on PU2, two epurals. The only synbranchoid with a recognizable caudal skeleton is *Macrotrema* (Rosen and Greenwood, 1976: fig. 2); PU2 has a full neural spine and there are no epurals according to Rosen and Greenwood's interpretation. Mastacembeloids (Travers, 1984a: figs. 14, 23, 75–78; Fujita, 1990: fig. 538) all have a full neural spine on PU2, and there may be no epurals, or one or two. Travers identified three epurals in *Macrognathus pancalus* and *Mastacembelus unicolor* (1984a: 114, fig. 75a), but in his cleared-and-stained specimen of *M. unicolor* we see only one, and we do not believe that the diminutive "third epural" in his *M. pancalus* merits that interpretation. 12. Dorsal-fin origin displaced posteriorly. There is no dorsal fin in synbranchoids. In mastacembeloids the first dorsal pterygiophore is behind the fourth neural spine (*Mastacembelus mastacembelus*) or further posteriorly. 13. Anterior neural spines expanded distally. The anterior four or more neural spines are expanded in mastacembeloids (Travers, 1984a: 101, figs. 12, 21), and they are somewhat expanded in synbranchoids (Rosen and Rumney, 1972: fig. 21). 14. Distal and proximal ceratohyals sutured dorsally by spatulate prongs. In synbranchoids the distal and proximal ceratohyals are described as "suturally united dorsally, in some cases completely ankylosed" (Rosen and Greenwood, 1976: 23, figs. 25, 42–50; cf. Fig. 17A). In mastacembeloids the sutured region is close to the dorsal margin of the hyoid bar, much as in *Mugil* (cf. Figs. 17B, 15G; Travers, 1984a: figs. 7, 51), except in *Chaudhuria,* where there is one dorsal strut (Travers, 1984a: fig. 19), as in gasterosteids and atherinomorphs (Fig. 15H, J). 15. A long third (posterior) extrascapular. Synbranchoids have one extrascapular or none (Travers, 1984b: fig. 6). Mastacembeloids have no posttemporal and have the medial extrascapular incorporated in the skull roof. Between the skull and the supracleithrum there are usually two tubular ossicles (Travers, 1984a: table 4, figs. 11, 67–72), but some mastacembeloids have none and three occur occasionally. Travers (1984a) interpreted these ossicles as remnants of the posttemporal.

A further character, discussed by Stiassny (1992), is the insertion of the levator operculi muscle. Stiassny found that part of the muscle inserts on the lateral face of the opercle in atherinoid atherinomorphs and primitive mugiloids, and considered this modification to be unique to those taxa among acanthomorphs. However, Travers (1984a, 1984b) reported a lateral insertion of the levator operculi in all mastacembeloids and synbranchoids, and in some blennioids. Stiassny did not use the levator operculi as a character relating mugiloids and atherinomorphs, because the derived lateral insertion is lacking in non-atherinoid atherinomorphs and in the more derived mugiloids. Occurrence of the lateral insertion in all synbranchiforms is no more than suggestive.

Two characters previously proposed as atherinomorph synapomorphies are also found in synbranchiforms. First, most synbranchoids and mastacembeloids have the head of the fourth epibranchial larger than that of the third (character 10 of Parenti, 1993; Rosen and Greenwood, 1976: figs. 27–41; Travers, 1984a: figs. 10, 20, 64–66). Second, mastacembeloids lack an interarcual cartilage, but the (os-

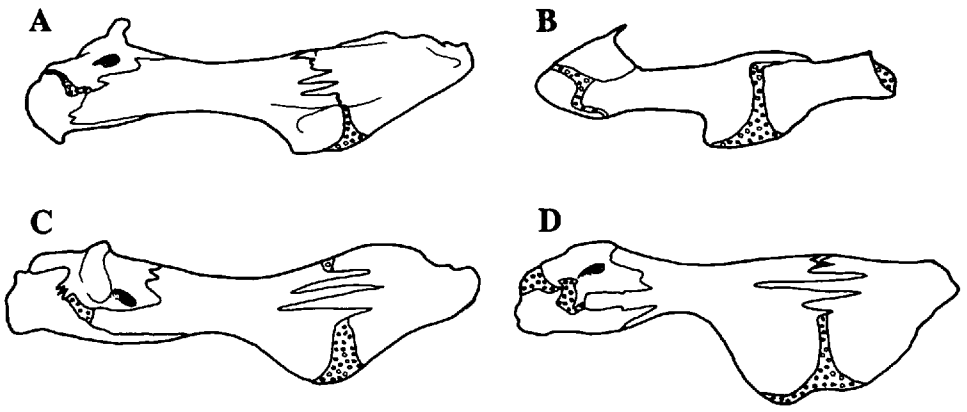


Figure 17. Hyoid bars of synbranchoids (A, C) and mastacembeloids (B, D). A. *Macrotrema caligans*, in lateral view, after Rosen and Greenwood (1976: fig. 25); B. *Chaudhuria caudata*, in lateral view, after Travers (1984a: fig. 19a); C. *Monopterus albus*, in medial view, BMNH 1976.4.2.71; D. *Rhynchobdella sinensis*, in medial view, BMNH 1927.10.1.19.

sified) interarcual cartilage of synbranchoids articulates near the proximal base of the first epibranchial (character 12 of Rosen and Parenti, 1981).

Synbranchiforms share one character with gasterosteiforms, absence of Baudelot's ligament, and mastacembeloids share a further feature with them, dorsal spines that are isolated, not joined by membrane (there is no dorsal fin in synbranchoids).

Conclusions

The foregoing review of characters shared by synbranchiforms, atherinomorphs, mugilomorphs, *Elassoma* and gasterosteiforms leads us to believe that synbranchiforms are related to the other four taxa. We therefore advocate a grouping of the five taxa: Atherinomorpha, Mugiloidei, Gasterosteiformes, Elassomatidae, Synbranchiformes. We need a name by which to refer to that group in the ensuing discussion. To expand the Atherinomorpha to include the other taxa is unlikely to generate more than misunderstanding or dismay, and Stiassny (1990) has already used Mugilomorpha for mugiloids alone. Rather than erect yet another "-morpha" name based on a genus, we will call the group Smegmamorpha, using the initials of the six components, Synbranchoidei, Mastacembeloidei, Elassomatidae, Gasterosteiformes, Mugilomorpha and Atherinomorpha. The name derives from the Greek and Latin *smegma*, a cleansing agent or means of cleaning, and refers to our expectation that grouping these taxa will have the effect of cleaning up or tidying the systematics of higher teleosts, since the taxa concerned were previously assigned (Nelson, 1984) to about ten different orders or suborders, most of them of unknown relationships.

The distribution of shared derived characters among smegmamorph taxa, indicated in Table 2, shows no consistent pattern, and is not yet amenable to further evaluation because of missing information. Johnson (1993) felt that a mugiloid–elassomatid relationship was possible, but there is little in Table 2 apart from extrascapular configuration (no. 24) to support that. Stiassny's (1990, 1993) mugilomorph–atherinomorph relationship also receives surprisingly little support from Table 2, for there are only two characters exclusive to those two groups

Table 2. Distribution of selected shared derived characters in Atherinomorpha, Mugilomorhpa, Elassomatidae, Gasterosteiformes, Synbranchoidei, and Mastacembeloidei

Character	Atherino-morpha	Mugilo-morpha	Elassom-atidae	Gasteros-teiformes	Synbran-choidei	Mastacem-beloidei
1.	+	+	+	+	+	+
2.	+	+	+	+	NA	NA
3.	+	+	+	+	NA	NA
4.	+	−	+	+	+	−
5.	+	+	+	±	+	±
6.	+	−	+	+?	+	+
7.	+	+	+	−	NA	±
8.	+	+	+	+	+	+
9.	+	+	−	+	+	−
10.	±	−	+	+	+	+
11.	+	±	−	+	+	+
12.	+	+	−	+	NA	+
13.	RA	R	A	RA	A	RA
14.	+	+	+	+	+	+
15.	+	+	+	+	+	+
16.	+	+	+	+(−)	+	±
17.	1–3	3	3	1–2	0	0–2
18.	3–6	2	?	4–5	?	1
19.	+	+	?	+	?	−
20.	+	−	+	+	NA	NA
21.	+	−	+	+	NA	NA
22.	+	+	−	−	−	−
23.	+	+	−	−	−	−
24.	−	+	+	−	−	−
25.	+	−	?	+	−	?
26.	−	−	+	+(−)	−	+
27.	±	±	−	−	+	+
28.	−	−	−	+	+	+
29.	−	−	−	+	NA	+
30.	+	−	−	±	+	+
31.	±	−	+	+	−	−
32.	++	+−	++	++	++	+−
33.	cy	ct	cy	sc(ct)	cy	cy

Characters: 1) First epineural originates at the tip of a transverse process on the first vertebra. 2) Pelvic girdle dissociated from cleithrum. 3) Pelvic girdle without differentiated external dorsal and ventral wings (presence of these wings is character 8 of Stiassny and Moore, 1992). 4) Infraorbital series with three or fewer bones between lacrimal and dermosphenotic. 5) Infraorbital series discontinuous. 6) Supraneurals absent. 7) Dorsal fin origin displaced posteriorly. 8) Anterior neural spines expanded distally. 9) Supracleithrum reduced or absent. 10) Full neural spine on PU2. 11) Distal and proximal ceratohyals sutured dorsally by spatulate prongs. 12) Spinous dorsal fin pterygiophores lack distal radials. 13) First pectoral ray reduced (R) to medial hemitrich with articular base, or lacks articular base (A). 14) First neural arch fused to centrum. 15) Vomer without lateral wings that articulate with lateral ethmoid. 16) PB4 absent. 17) Number of epurals. 18) Number of branches of mandibular branch of trigeminal nerve innervating adductor mandibulae. 19) Lateral line collector nerve absent (+) or present (−). 20) Pelvic bones not sutured medially (+). 21) Lateral process of pelvic bone associated with tip of a pleural rib (+), not with postcleithrum. 22) Subdivision of pharyngocleithralis muscle into anterior and posterior sections. 23) Levatores interni 1–2 separate first levator externus from remainder. 24) A long third (posterior) extrascapular, and no sensory canal in posttemporal. 25) Olfactory sensory epithelium arranged in islets. 26) Interarcual cartilage present (−) or absent (+). 27) Levator operculi inserts on outer face of opercle (+). 28) Baudelot's ligament absent (+) or present (−). 29) Dorsal spines isolated, not joined by membrane (+). 30) Head of fourth epibranchial larger than third (+). 31) Presence (−) or absence (+) of basisphenoid. 32) HPU3 and HPU2 both fused to centrum (++), both autogenous (−−). 33) Condition of scales: cycloid (cy), ctenoid (ct), or scutelike plates (sc). The ctenoid entry under gasterosteiforms refers to *Aulostomus*.

(nos. 22 and 23); gasterosteiform–atherinomorph relationships are as strongly supported (nos. 18 and 25).

If the case for aligning mugiloids, gasterosteiforms, synbranchiforms and *Elassoma* with atherinomorphs is accepted (to us, it is at least as strong as that linking percopsiforms with other paracanthopterygians; Patterson and Rosen, 1989), the link between four percomorph subgroups and a non-percomorph group will affect our ideas about the content and the possible characterization of Percomorpha, and the fact that two of those four percomorph groups (mugiloids, *Elassoma*) were previously placed in Perciformes raises the "perciform problem"—what does that group contain and how is it characterized?

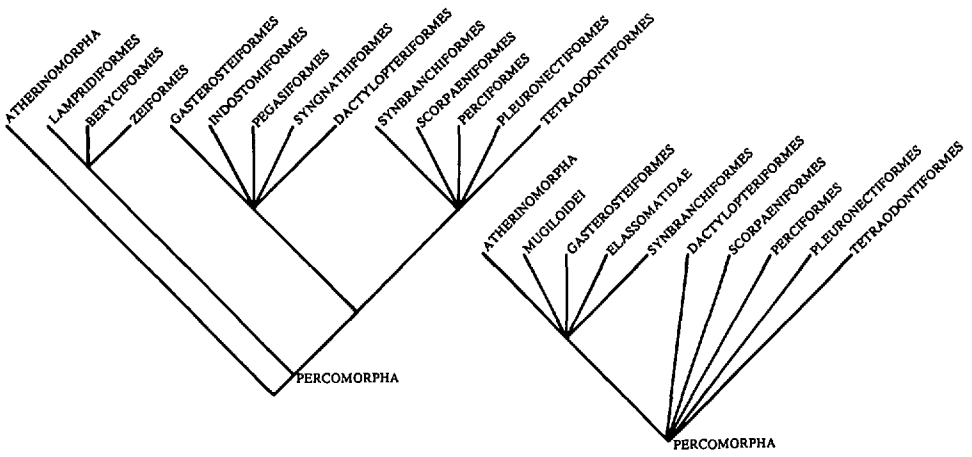


Figure 18. Diagrams of percomorph relationships. Left, an interpretation of Nelson (1984) at the ordinal level. The grouping of lampridiforms, beryciforms and zeiforms is based on Nelson's statement that the three "seem to have a relatively close relationship," and the grouping of the five orders from Gasterosteiformes to Dactylopteriformes is based on Nelson's interpretation of Pietsch (1978). Right, our own interpretation. In comparison with the left-hand diagram, Syngnathiformes, Pegasiformes, Indostomiformes and Syngnathiformes are included in Gasterosteiformes; Mugiloidei, Elassomatidae and Mastacembeloidei are extracted from Perciformes, with the latter included in Synbranchiformes; Atherinomorpha, Mugiloidei, etc. are considered to form a monophyletic group within Percomorpha; and Lampridiformes, Beryciformes and Zeiformes are placed outside the Percomorpha.

Perciforms and Percomorphs

A long tradition in teleostean classification, perpetuated by Greenwood et al. (1966) and Nelson (1984), for example, is to precede the Perciformes by several "pre-perciform" orders (e.g., Zeiformes, Gasterosteiformes, Dactylopteriformes, Scorpaeniformes) and to follow them by two derived or "post-perciform" orders (Pleuronectiformes, Tetraodontiformes) (Fig. 18A). In cladistic terms, the "post-perciform" orders are better seen as nested within Perciformes, and we have no doubt that this is the correct place at least for pleuronectiforms (Chapleau, 1993). The "pre-perciform" order Zeiformes is more problematic (see below), but we know of no characters to indicate that Scorpaeniformes are less closely related to perciform fishes than are (say) pleuronectiforms or gobies. Maintaining a string of separate orders for "pre-perciforms" and "post-perciforms" has no merit until characters are provided to justify them, and is more likely to render Perciformes para- or polyphyletic than monophyletic. We considered dropping Scorpaeniformes back into the perciform pot, if only to stimulate the search for characters justifying their individuality. That proposal would entail ranking the scorpaeniforms on the same level as the other perciform suborders, and is unlikely to be accepted. But we know of no sound characters justifying a pre-perciform position for Scorpaeniformes, and this emphasizes the tenuity of the distinction between our Smegmamorpha (above) and the Perciformes (Fig. 18B).

That last statement brings in the topic of this volume, the Percomorpha. As emphasized at the beginning of this account, no one has yet proposed any unambiguous characters for the Percomorpha. The scheme we have presented so far has placed some "percomorphs" (the lampridiforms) more distant from perciforms than is *Polymixia,* other "percomorphs" (stephanoberyciforms, beryciforms) more distant from perciforms than are atherinomorphs, and other "percomorphs" (gasterosteiforms, mugiloids, *Elassoma,* synbranchiforms) closer to

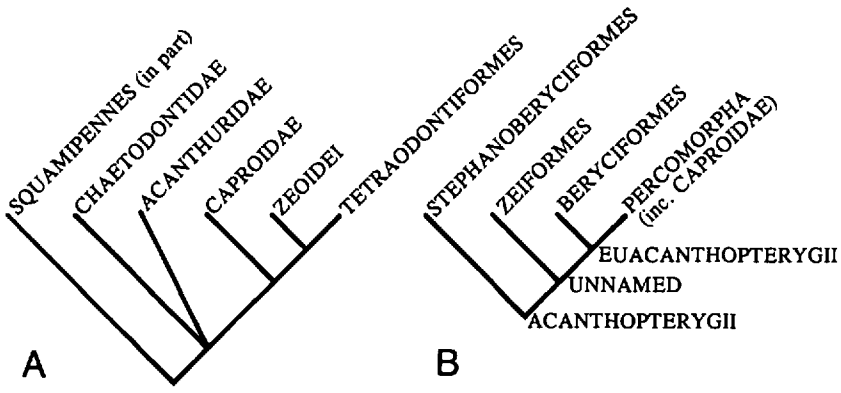


Figure 19. Diagrams summarizing: A. Rosen's (1984) view of zeiform relationships; B. our own interpretation.

atherinomorphs than to perciforms. Within that framework, the Percomorpha as defined by Rosen (1973) or Nelson (1984), Acanthopterygii minus Atherinomorpha, has shrunk to what we have been informally referring to as "perciforms and their immediate relatives," i.e., Perciformes, Scorpaeniformes, and Pleuronectiformes, with or without more problematic taxa like the tetraodontiforms and dactylopterids. As we have just argued, we believe that this informal grouping should be subsumed under Perciformes, although we are still unable to characterize it. This raises the embarrassing or mortifying possibility that we should wind up a volume on percomorph phylogeny by concluding that the group does not exist. The alternative is to save the Percomorpha by expanding it to include fishes that were originally excluded from it, the atherinomorphs. We believe that there is a monophyletic group comprising "perciforms and their immediate relatives" and our smegmamorphs. That group can be characterized by a series of apomorphies (**26–33**), and we propose to name it Percomorpha. We appreciate that in so doing we have lost the original distinction between percomorphs and atherinomorphs that Rosen (1973) intended by the term Percomorpha, but guess that he would not have flinched.

Zeiforms

In this volume, there is no more than passing mention of zeiforms (Johnson, 1993; Roberts, 1993), and the most recent substantial contribution is still Rosen (1984) (Fig. 19). Rosen's ideas, that zeiforms in the traditional sense (caproids + zeoids) are paraphyletic, that zeoids are the sister-group of tetraodontiforms, and that the "immediate outgroup" for zeiforms + tetraodontiforms is acanthurids and chaetodontids (so that zeiforms are nested well within percomorphs), have been commented on briefly by Mok and Chang (1986), Zehren (1987), Tyler et al. (1989), Bannikov (1991), Stiassny and Moore (1992), and Johnson (1993). One consequence of Rosen's proposal, whether or not he was correct about the connection with tetraodontiforms, is that it throws doubt on the monophyly of zeiforms, because all the characters that he cited as common to caproids and zeoids also occur in tetraodontiforms. Heemstra (1980), Mok and Chang (1986), and Bannikov (1991) questioned the reality of the relationship between caproids and zeiforms, an idea that goes back at least to Rosen (1973: 479). Bannikov (1991), who believed that caproids are related to acanthuroids, reviewed the evidence for separating them from zeiforms (principally that provided by Rosen,

1973), but did not suggest where zeiforms belong. His account contains some inaccuracies, such as crediting zeiforms with three epurals (they all have two) and with lacking ribs (see below). Rosen (1973) cited the perciform-like vertebral number (21–23), pelvic count (I,5) and caudal skeleton of caproids, as opposed to vertebral counts of 31–46, higher pelvic ray number and modified caudal skeleton of zeiforms, concluding that caproids "fit our present definition of a perciform" whereas zeiforms fail to fit only in pelvic and vertebral counts. In fact, the zeiform *Zenion* has only 26–27 vertebrae (Kotthaus, 1970, records 25 or 26 plus the terminal centrum in his *Z. longipinnis,* which is a synonym of *Z. hololepis* according to Heemstra, 1986; our four *Z. hololepis* all have 27 vertebrae, 10 + 17), and a number of perciforms (e.g., scombrids, bramids, cepolids, some trachinoids and stromateoids) have vertebral counts as high as those of other zeiforms. In any case, in his 1984 paper Rosen neglected his earlier remarks and assumed that caproids are related to zeiforms. Mok and Chang (1986) suggested that caproids might be related to tetraodontiforms, because both share a closed chain-link pelvic spine articulation, but that zeiforms, which lack that structure, "probably are not related to these fishes." Zehren (1987), in his osteology of *Antigonia,* was primarily concerned with monophyly of and relationships within that genus; he used *Capros,* zeiforms and tetraodontiforms as outgroups, and as evidence of caproid monophyly and zeiform monophyly merely referred to Rosen (1984: 31). But Zehren did find that one of the most striking characters cited by Rosen (1984) as common to caproids, zeiforms and tetraodontiforms does not have that distribution; the character is to have the halves of the first neural arch spread apart and firmly attached to the occipital bones, with the first dorsal radial inserted into the occiput between these bones. Zehren found that the first neural arch is attached to the occiput in caproids and zeiforms, but that the first radial inserts behind the first neural spine in the zeiforms *Parazen* and *Grammicolepis,* and is not inserted between the exoccipitals in *Capros*; we expand on these observations below.

Stiassny and Moore (1992), in their parsimony analysis of characters drawn from the pelvic girdle, found it necessary to constrain the monophyly of zeiforms (represented by *Capros* and *Zeus* in their sample). Without that constraint, *Capros* fell out with perciforms whereas *Zeus* was separated from it by some or all beryciforms (Stiassny and Moore, 1992: fig. 16).

Our observations on zeiforms are based on examination of cleared-and-stained specimens of the following genera: *Allocyttus, Capromimus, Cyttopsis, Neocyttus, Oreosoma, Parazen, Pseudocyttus, Stethopristes, Xenolepidichthys, Zenion, Zenopsis,* and *Zeus.* These include representatives from all five families recognized by Heemstra (1980) and (*Capromimus*) one of his two incertae sedis genera. We accept zeiforms as monophyletic and identify the following (none of which is present in caproids) as synapomorphies of the group (see also Rosen, 1984: 31): Baudelot's ligament originates high on the exoccipital, immediately under the vagus foramen; the dorsal fin endoskeleton has the distal portions of the proximal-middle radials laterally expanded, and there are no distal radials in the spinous portion except as tiny cartilaginous or partially ossified structures under the last few spines (Fig. 23); the palatine has a specialized, mobile articulation with the ectopterygoid, which is truncated dorsally, and the metapterygoid is extremely reduced; the anterior vertebral centra have an unusually flexible articulation, and ribs, when present, never occur anterior to the fourth vertebra; there is a distinctive configuration of the dorsal gill arch elements, including upright columnar processes on PB2 and PB3, and absence of PB4 and UP4 (Rosen, 1973: figs. 101, 102; 1984: figs. 22, 23); below the frontals, there is a continuous median cartilage extending

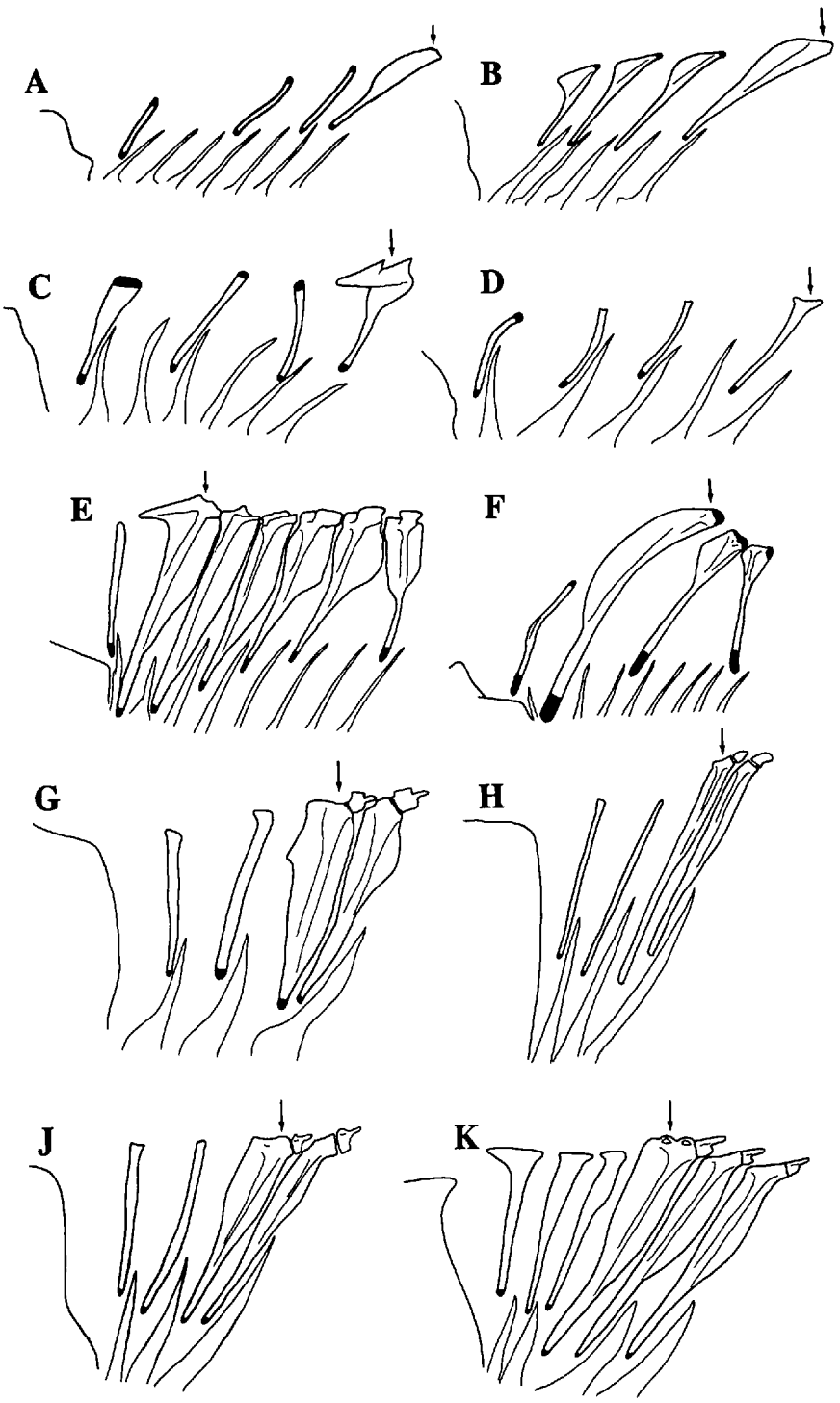


Figure 20. Supraneurals (black denotes cartilage) and anterior dorsal pterygiophores (vertical arrow marks head of first pterygiophore) in relation to neural spines in: A. *Myctophum obtusirostris,* AMNH 29140SW; B. *Polymixia lowei,* USNM 308378; C, D. the stephanoberyciforms *Gibberichthys pumilis,* USNM 207512, and *Poromitra crassiceps,* USNM 296944; E, F. the zeiforms *Zenion hololepis,* USNM

between the ethmoid cartilage and the pterosphenoids; and in the caudal skeleton there is a full neural spine on PU2, two epurals, and the parhypural is truncated proximally (in *Parazen* and *Xenolepidichthys* among the genera that we have examined there is a small, vertically directed hypurapophysis, which obscures the lack of articulation between the parhypural and the centrum, cf. Fujita, 1990: fig. 186).

Given that zeiforms are monophyletic, as are caproids (Zehren, 1991), there are many possible resolutions of their relationships. The tetraodontiform problem is beyond our scope, and we will not comment further on the evidence presented by Rosen (1984) for relationship between zeiforms and tetraodontiforms. There are similarities between zeiforms and lampridiforms, in the jaws, for example, and in the pelvic girdles of some (veliferids and *Zeus*), but we think a relation between the two is unlikely given the derived configuration in zeiforms of the spina occipitalis (**10**), Baudelot's ligament (originating on the occiput, **18**), the epineural intermusculars (in the horizontal septum, and originating on the ribs in *Zenopsis* and on the parapophyses in *Xenolepidichthys,* where there are no ribs; no epicentral ligaments; **11**, **13**), the caudal skeleton (five hypurals, 15 or fewer principal rays; **28**, **33**), the gill arches (head of EB3 enlarged, no UP4 or PB4), the differentiated spinous dorsal fin, and the pelvic radials (reduced, one radial in addition to the fused medial radial in *Parazen,* one free radial in *Zenopsis, Oreosoma,* and *Neocyttus,* **16**).

The single impressive character common to caproids and zeiforms that we have observed is the way the first vertebra is modified, with the neural arch tilted forward and tightly attached or fused (by suture) to the occiput; however, on close examination there are at least three different conditions involved. In caproids, the first neural spine is rostrocaudally compressed and plastered against the epioccipitals, and the neural arches are expanded posteriorly as laminar plates between which the first dorsal pterygiophore inserts. Most zeiforms have a condition resembling that of caproids in that the first dorsal pterygiophore inserts between the neural arches of the first vertebra, which are also plastered to the epioccipitals. In these zeiforms, however, either the neural spine is not flattened or the neural arches do not meet anterodorsally to form a neural spine, although there may instead be a small strap of bone joining the two arches posterior to the first pterygiophore. In other zeiforms (e.g., *Zenion, Parazen, Xenolepidichthys*) the neural arches meet to form an upright neural spine that is not attached to the occiput, and the first dorsal pterygiophore inserts posterior to it or along its posterior margin (Fig. 20E, F). Because this condition is clearly more primitive than the caproid condition, and because there is good evidence that zeiforms and caproids are monophyletic, the similar derived state common to caproids and to some zeiforms cannot be a synapomorphy of the two groups.

Although we find no reason to question the percomorph affinity of caproids, several characters of zeiforms imply that they occupy a more primitive position among acanthopterygians. Some of the most convincing evidence for this is in the pelvic girdle (Stiassny and Moore, 1992) and fin, where the girdle is not sutured medially (there is a broad overlap in *Parazen* and *Zenion*), the pelvic spine, when present, has a symmetrical base (Fig. 22D; **21**), there are more than five soft rays

---

←

307305, and *Oreosoma atlanticus,* AMS I.21370034; G–I. the beryciforms *Anomalops katoptron,* SIO 72-289, *Diretmus argenteus,* VIMS uncat., and *Hoplostethus mediterraneus,* VIMS 4900; J. the percoid *Dinoperca petersii,* USNM 269543.

(29), and, as described above, some taxa have a free pelvic radial. Our survey of zeiforms implies that the more primitive members of the group are *Parazen* (only member of the Parazenidae) and *Zenion* (type genus of the Zeniontidae). *Parazen* has a less modified parhypural, with a hypurapophysis, and both genera have the dorsal fin inserting behind the first neural spine, which is not plastered to the occiput, and only one vacant interneural space below the spinous dorsal fin (Fig. 20E). *Xenolepidichthys* is the only other zeiform we have examined with the first two conditions, but it shares with the remaining genera what we believe to be a derived feature of the spinous dorsal fin and vertebral column: there are several interneural spaces in which no pterygiophores insert and the neural spines converge distally (Fig. 20F). *Parazen* and *Zenion* each have seven pelvic-fin rays, the lateralmost a spine in *Zenion*. *Parazen* is the only zeiform we have examined that has a medial pelvic radial fused to the base of the ventral hemitrich of the medial pelvic ray (*Parazen* also has a free radial lateral to the fused one, and as mentioned above, three other genera, *Neocyttus, Oreosoma* and *Zenopsis,* have a single small free radial associated with the medial ray). We believe this fused radial, a eurypterygian character (Johnson, 1993), establishes that the medial ray of *Parazen* is the primitive medial ray, and indicates that the seven pelvic rays of *Parazen* are not the result of secondary addition of rays. The only zeiform we have examined with the typical percomorph pelvic count of one spine and five rays, *Pseudocyttus,* does not have the medial radial fused to the medial ray, suggesting that I,5 is not the primitive zeiform complement. If this interpretation is correct, zeiforms are not percomorphs (29).

Additional features of zeiforms that suggest they are not percomorphs include a supraneural tipped distally in cartilage in some taxa (23), the lack of chain-link articulation in the dorsal fin (22, Fig. 23), a separate U2 early in ontogeny (Fig. 21, and observations of larval *Zeus*), and a deep perforate ceratohyal that is not sutured (Fig. 15B) and is reported to bear as many as eight branchiostegals. These are discussed more fully below.

A single supraneural occurs in all zeiforms that we examined, except *Parazen, Zenopsis* and *Zeus*. In *Xenolepidichthys* and *Oreosoma* (Fig. 20F) the supraneural is not ossified distally, a primitive condition that, to our knowledge, is never realized among percomorphs.

Zeiforms have five to ten dorsal-fin spines, the first a supernumerary element on the first pterygiophore, the remainder resting on the pterygiophore succeeding the one with which they are serially associated. The proximal-middle radials have broad, shelf-like expansions dorsally, but the expanded distal radials that form the chain-link arrangement in beryciforms and percomorphs are either absent or represented by tiny, usually cartilaginous, elements that are embedded in connective tissue and lie within the partially open bases of the spines (Fig. 23D). Absence of distal radials in the spinous dorsal fin characterizes several percomorph groups, including most smegmamorphs, but the abrupt transition between spinous and soft-ray pterygiophore configuration that characterizes beryciforms and percomorphs is lacking in zeiforms, wherein the proximal-middle and distal radials associated with the last spine and first soft ray are very similar. Although we consider it unlikely, we cannot discount the possibility that the zeiform condition was derived from a chain-link arrangement. It is also possible that the shelf-like expansions on the proximal-middle radials represent a first step in the transition to chain-link articulation.

Adult zeiforms, like percomorphs (27), lack a free second ural centrum, however this element appears to develop separately in the larval zeiforms we have examined (*Zenion,* 8.9 mm SL, Fig. 21, and *Zeus,* 10 mm SL). A separate second ural

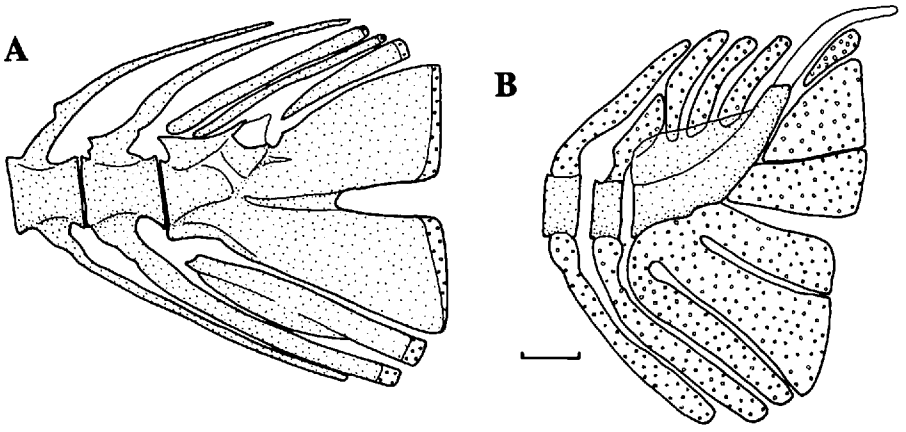


Figure 21. Caudal skeleton in larvae of: A. *Zenion hololepis*, SL 8.9 mm, DANA Colln, St. 3744 II; B. *Antigonia* sp., 5.2 mm SL, USNM 324760. In B, the caproid, the terminal centrum is ossified as a continuous cylinder, with no trace of a separate U2, whereas in A, the zeiform, there is a conspicuous bony partition within the cylinder, separating U2 from PU1 + U1. Scale bar = 0.1 mm.

centrum has also been reported in some diminutive atherinomorphs (Parenti, 1993) and in some larval percoids (Arratia, 1982; Mabee, in press). As Figure 21 shows, larval caproids have no sign of a second ural centrum, and it is also absent in the two tetraodontiforms where ontogeny is known (Matsuura and Katsuragawa, 1985; Fujita, 1992).

The ceratohyal of zeiforms has a configuration most like that of beryciforms (Fig. 15A, B). The deep-bodied anterior ceratohyal contains a fenestra (the "beryciform foramen" of McAllister, 1968) along the groove for the hyoid artery and is not sutured to the posterior ceratohyal. Although a "beryciform foramen" occurs in the ceratohyal of many perciforms, it is always associated there with a strong suture between the anterior and posterior ceratohyals (Fig. 15C, D). In those percomorphs that lack a fenestra, suturing may be present or absent (Mok and Shen, 1983: fig. 12). We have observed a ceratohyal like that of zeiforms only among non-percomorph acanthomorphs.

There is a persistent legend (Regan, 1910; McAllister, 1968; Heemstra, 1980) that some zeiform taxa have eight branchiostegals, like most beryciforms and stephanoberyciforms, rather than the seven found in most zeiforms and perciforms (caproids have six). McAllister (1968) credited *Zenion* with eight, but all Kotthaus's (1970) specimens and our own have seven. He also credited the zeid *Cyttus* with seven to eight, but discounted Starks's (1898) record of eight in *Zeus*. Heemstra (1980) attributed seven branchiostegals to Zeidae (including *Cyttus*), but seven to eight to Zeniontidae. The legend seems to originate with Günther's (1860) record of eight branchiostegals in his two species of *Cyttus, C. australis* (type species) and *C. roseus* (now *Cyttopsis roseus*), and to have been reinforced by Goode and Bean's (1896) record of eight branchiostegals in *C. hololepis* (now *Zenion hololepis*). Heemstra (1980) referred to Günther's count for *C. roseus* as an error; our own examination of the types of the three species (*C. australis* and *C. roseus* in BMNH, *Z. hololepis* in USNM) shows seven branchiostegals in *C. roseus, Z. hololepis,* and one of the two syntypes of *C. australis,* whereas the other has eight. Further specimens of *C. australis* have seven. We have observed eight branchiostegals in one AMNH specimen of *Allocyttus verrucosus*; four other specimens have seven. Thus the situation in zeiforms seems to be as in generalized

perciforms, with seven branchiostegals the rule, and eight occurring only in exceptional individuals.

In the scheme of relationships outlined in the preceding sections (Figs. 2–4, 11, 18), zeiforms appear to be related to euacanthopterygians (i.e., they fit above paracanthopterygians and stephanoberyciforms in the cladogram) because they have all the characters of euacanthomorphs (**8–11**) and holacanthopterygians (**12–14**), they have two out of three acanthopterygian characters, a pelvic spine (**15**) and no more than one free pelvic radial (**16**), and they have three out of eight euacanthopterygian characters: Baudelot's ligament is on the occiput (**18**, though on the exoccipital rather than basioccipital); the dorsal fin is advanced (**19**); and the anterior epineurals are on the ribs (**20**) in the few zeiforms that have both ribs and epineurals (e.g., *Zenopsis*). Zeiforms lack one acanthopterygian character, an anteromedial process on the pelvic bone (**17**); that process is also absent in various stephanoberyciforms, beryciforms and percomorphs (e.g., gasterosteiforms), but is generally retained in percomorphs which have the pelvic girdle in contact with the cleithra, as it is in zeiforms. Zeiforms lack several euacanthopterygian characters, including truncation of the second ventral procurrent caudal ray (**24**), a complex pelvic spine (**21**), chain-link articulation of the dorsal fin-spines (**22**), and a postcleithral-pelvic ligament (**25**); all of these are inferred to reverse in one or another percomorph subgroup, but the pelvic spine reverts to the primitive condition only when greatly reduced (e.g., the percichthyid *Gadopsis*, Rosen and Patterson, 1969: fig. 43G), and when chain-link articulation of the dorsal spines is secondarily absent, the configuration does not resemble that seen in zeiforms, where the minute distal radials lie within the spine base and there is no abrupt transition between the spine-bearing and more posterior radials. Further, the zeiforms *Xenolepidichthys* and *Oreosoma* have a supraneural that is not closed in bone distally, the primitive state of a character (**23**) that is not known to reverse in percomorphs, though it has reversed in the beryciform *Anoplogaster*. Finally, zeiforms have a number of percomorph characters: they lack a second ural centrum (**27**), have five or fewer hypurals (**28**), all the epineurals in the horizontal septum (**32**, although we know of no zeiform with epineurals posterior to the eleventh or twelfth centrum), and fewer than 17 principal caudal rays (**33**, although no zeiform has the I,8,7,I caudal count so characteristic of basal percomorphs). Zeiforms lack the following four percomorph characters: interarcual cartilage (**26**), six or fewer pelvic rays (**29**), transforming ctenoid scales (**30**), and absence of free pelvic radials (**31**). Two of those four characters (**26**, **30**) have evidently been lost independently several times within percomorphs, whereas reversal in the other two is exceptional (more than six pelvic rays in the gasterosteiform *Solenostomus* and in some cyprinodontids and pleuronectiforms; a free pelvic radial in the gasterosteiform *Indostomus* and in gobiesocids and callionymids).

Given the information summarized in the preceding paragraph, there are three possible positions for zeiforms in our scheme (for the moment, we neglect one further possibility, zeiforms as the sister-group of beryciforms). They could be percomorphs, but if so they show reversal in ten characters (17, 19, 20, 21, 23, 25, 26, 29, 30, 31). They might fit between beryciforms and percomorphs, with which they share one character absent in beryciforms (33, reduced caudal ray count), and three characters that also develop independently within beryciforms (27, 28, 32); if so they show reversal in six characters (17, 19, 20, 21, 23, 25). And they might fit between stephanoberyciforms and euacanthopterygians (beryciforms + percomorphs), with which they share three characters (18, 22, 24); if so, they show reversal in one character (17) and independent acquisition of four (27, 28, 32, 33), the first three of which are also independently acquired in par-

acanthopterygians, stephanoberyciforms and beryciforms. The first of these alternatives, requiring ten reversals, can be excluded on grounds of parsimony. The second alternative, requiring six reversals, is less parsimonious than the third, which requires one reversal and four independent acquisitions, three of them concerning reductions in the caudal skeleton and fin. Advocating that last alternative (zeiforms are the sister-group of euacanthopterygians) would necessitate naming another higher taxon, something we are unwilling to do on the admittedly tenuous evidence available. That would not be necessary for the one remaining alternative, zeiforms as the sister-group of beryciforms. There is one character, the mode of articulation between the extrascapular and parietal (Fig. 10), that might support that alternative, but in terms of parsimony such a placement would require exactly the same reversals (characters 17, 19, 20, 21, 23, 25) as placing zeiforms as the sister-group of percomorphs, and would also entail independent acquisition in zeiforms of the four characters that they share with percomorphs (characters 27, 28, 32, 33). On the information currently available we must reject that last alternative, and so provisionally place zeiforms as the sister of euacanthopterygians (Fig. 19). We do not expect the taxon so formed to endure, and will not propose a name for it.

Character (Apomorphy) List

Acanthomorpha

1. *Dorsal and anal fin-spines.* True fin-spines, i.e., azygous, unsegmented, bilaterally fused anterior fin-rays, are present in the dorsal and anal fins of veliferid lampridiforms, polymixiids, percopsiforms and some other paracanthopterygians, the less derived stephanoberyciforms, zeiforms, and most other acanthopterygians. These spines occur both in supernumerary association with the first pterygiophore and in serial association with the first and one to many succeeding pterygiophores. Elsewhere in teleosts, one to three dorsal spines occur in some cypriniforms and in siluriforms, but those spines often have segmented tips and have a paired (rather than median) internal cavity, and there are numerous dorsal and anal spines (with a median cavity) in *Lipogenys* and notacanthids. The spines in these two groups (otophysans, notacanthoids) are clearly of independent origin, and so are not homologous with those of acanthomorphs. Rosen's (1973: 452) report of two dorsal and an anal spine in myctophids, based on his examination of a dry skeleton of *Lampanyctus crocodilus* (BMNH 1885.7.1.4) and a cleared-and-stained *Myctophum spinosum* (AMNH 18152), was incorrect in our view. We have examined both specimens and several other myctophids, and find that the elements in question are paired throughout their length.

2. *Rostral cartilage.* A "rostral cartilage" has been identified as a synapomorphy of various euteleostean clades, e.g., neoteleosts (Fink and Weitzman, 1982), and "aulopoids" plus ctenosquamates (Rosen, 1985). Hartel and Stiassny (1986) pointed out the highly variable configuration and composition of this structure (or structures) in aulopiforms and stomiiforms, which raises still unsolved questions of homology at these levels. They wrote "By the level of the Acanthomorpha, the situation has stabilized such that there appears little doubt of the homology of the single median chondrified rostral cartilage strongly bound to the premaxillary ascending processes by a well-developed rostro-premaxillary ligament." We concur that this consistent rostral cartilage configuration, in which the maxillo-rostroid ligament arises from the lateral face of the medial maxillary process (Stiassny, 1986), is unique to acanthomorph fishes.

3. *Median caudal cartilages absent.* One or two ovoid or triangular cartilages lie between the distal tips of the second and third hypurals of most argentinoids, osmeroids, salmonoids, stomiiforms, aulopiforms and myctophiforms (Fujita, 1990: figs. 56–135 and table 3). These structures, termed median caudal cartilages (CMC) by Fujita (1990), are lacking in all the more primitive teleosts (Fujita, 1990: figs. 1–55; there is a small cartilage in the position of the ventral CMC in the cyprinid *Tanakia,* fig. 34), and we interpret them as a synapomorphy of Euteleostei minus Esocoidei and Ostariophysi (Neoteleostei plus Salmonoidei and the Osmerae of Begle, 1991). CMC are lacking in the caudal skeleton of all acanthomorph fishes with the exception of the beryciforms *Beryx* (Fujita, 1990: fig. 180; absent in *Centroberyx,* pers. obs.), *Anomalops* (Fujita, 1990: fig. 178; absent in other anomalopid genera, pers. obs.) and *Diretmus* (pers. obs.), and the trichiurine gempylid *Benthodesmus* (Fujita, 1990: fig. 522). Parsimony demands that the CMC in these acanthomorphs are secondary or independent occurrences, like the single CMC in *Tanakia,* and we interpret the general absence of CMC in acanthomorphs as a reductive synapomorphy of the group.

4. *Anterior and medial infracarinales separate.* Stiassny (1993) suggests that separation of the anterior and medial infracarinalis muscles might corroborate acanthomorph monophyly. Our observations support her surmise. In myctophiforms, aulopiforms, and more primitive euteleosts that we have examined the anterior infracarinalis is continuous with the medial infracarinalis, through a tendon that passes over the ventral surface (Winterbottom, 1974: 287, mistakenly stated dorsal surface) of the pelvic girdle (Stiassny, 1993: fig. 5A). In lampridiforms, *Polymixia,* paracanthopterygians, stephanoberyciforms and acanthopterygians, these two muscles are not connected and the anterior infracarinalis either inserts directly on the pelvic bone (usually on the anterior process, if present) or has no association with it (Stiassny, 1993: fig. 5B–E).

5. *Dorsal limb of posttemporal firmly bound to epioccipital.* Our observations support those of Stiassny (1986); a relatively tight and immobile connective-tissue attachment of the posttemporal to the epioccipital is an acanthomorph synapomorphy. The loose connection through an elongate ligament that characterizes more primitive neoteleosts is lacking in all the acanthomorphs that we have examined.

6. *Medial pelvic process ossified distally.* Primitively in neoteleosts, the contralateral halves of the pelvic girdle are associated by abutment or continuity of cartilage-capped medial processes, varying in form from broad-based (e.g., aulopiforms, Johnson, 1974: fig. 15; Stiassny and Moore, 1992: fig. 2A) to columnar (e.g., myctophiforms, Jollie, 1954: fig. 21; Nafpaktitis and Paxton, 1978: figs. 2, 3; Stiassny and Moore, 1992: fig. 2C). Stiassny and Moore (1992) identified overlap of the medial pelvic processes as a synapomorphy of the Acanthomorpha. Our observations indicate that the medial processes also overlap in neoscopelids (cf. Stiassny and Moore, 1992: fig. 2B). As Stiassny and Moore (1992) showed, there is much variation in the way the medial processes are associated in basal acanthomorphs, ranging from loose apposition through broad overlap to direct abutment with suturing or strong connective-tissue binding. One feature of the acanthomorph medial pelvic process that is universally lacking in more primitive neoteleosts is the complete ossification (no remaining cartilage) of their distal tips, a condition characterizing *Polymixia,* percopsiforms, stephanoberyciforms, zeiforms, beryciforms, and those atherinomorphs in which medial processes are discernible. In lampridiforms, monocentrids, holocentrids and most percomorphs there are no distinct medial processes, but the area of contact between the two pelvic bones is fully ossified. We interpret the cartilage-tipped medial pelvic

process of gadiforms, the stephanoberyciforms *Scopelogadus, Gibberichthys* and *Barbourisia,* and a few derived perciforms (e.g., *Notothenia*) as secondary.

7. *First centrum with anterior surface bearing distinct facets that articulate with the exoccipital condyles.* This is a character proposed by Rosen (1985: 47): "the anterior vertebra has developed ossified autocentral prezygapophyses that articulate directly with the exoccipital condyles." We agree with Rosen that the specialized configuration of the anterior surface of the first centrum is unique to acanthomorphs.

Other Possible Acanthomorph Characters.—Stiassny (1986) proposed that acanthomorphs differ from non-acanthomorphs in the configuration of the ethmoid cartilage and in the relation between the lateral ethmoid and vomer. She described the character as "reduction of the ethmoid cartilage and a close approximation (often sutural union) of the lateral ethmoids with the vomer" (p. 449). Reduction of the ethmoid cartilage includes "displacement of the anterolateral plate [present in *Aulopus*] by an enlarged ethmoid–vomerine complex" (p. 442). Stiassny illustrated variations in the acanthomorph configuration (1986: figs. 21, 22), and noted that acanthomorphs such as *Zeus, Gasterosteus, Aphredoderus* and *Percopsis* lack the association between the lateral ethmoid and vomer (although the lateral ethmoid does have an anterolateral process), and also that such an association is present in cypriniform and characiform otophysans. We feel that Stiassny is probably correct in seeing a characteristic pattern in the acanthomorph ethmoid region, and in her surmise that the pattern is associated with a kinetic jaw system. But we have not coded the character as a numbered apomorphy because of difficulty in precisely describing it and recording its distribution, and because it may well be correlated with the rostral cartilage (2 above), and so not be independent. As we noted above, this feature is lacking in all smegmamorphs.

EUACANTHOMORPHA
(Acanthomorpha minus Lampridiformes)

8. *First epineural displaced ventrally into horizontal septum.* The first epineural is primitively an outgrowth of the neural arch, and among euteleosts this continuity with the arch is maintained in *Esox,* argentinoids, stomiiforms, and in some salmonoids and aulopiforms. In all primitive teleosts the first epineural is in series with the succeeding epineurals, and is directed dorsolaterally (e.g., Fig. 1A; Hartel and Stiassny, 1986: fig. 6, of aulopiforms; Rosen, 1985: figs. 13, 15–17, of *Salmo, Prosopium, Aulopus,* and two myctophids). In all acanthomorphs except lampridiforms, the first epineural, although it generally maintains its origin on the neural arch, is deflected ventrally into the horizontal septum (Fig. 1B; Patterson and Johnson, submitted[1]). We have observed a slight ventral deflection of the first epineural, like that in *Velifer* (Fig. 1C), in some argentinoids and aulopiforms, and in the neoscopelid *Neoscopelus* (but not in the neoscopelia genera *Solivomen* and *Scopelengys*). No non-acanthomorph has the first epineural in the horizontal septum.

9. *Posterior pelvic process ossified distally.* In myctophiforms (Jollie, 1954: fig. 21c), aulopiforms (Johnson, 1982: fig. 19), stomiiforms (Fink, 1985: figs. 67, 68), and other primitive euteleosts the posterior process of the pelvic bone is either fully cartilaginous or tipped with cartilage distally. [In Stiassny and Moore's (1992: fig. 2) illustrations of *Synodus, Neoscopelus,* and *Lampanyctus* the cartilage tip on the posterior process is correctly depicted only in *Lampanyctus,* but it does occur in the other two genera.] Among the acanthomorphs that we have examined,

only lampridiforms have cartilage at the tip of the posterior process (Olney et al., 1993: fig. 4; not correctly depicted for *Lampris* in Stiassny and Moore, 1992: fig. 11). In all other acanthomorphs, the tip of the posterior process is closed by bone (Stiassny and Moore, 1992: figs. 1, 3, 5, 9, 10, 12, 13). The stephanoberyciform *Gibberichthys* is exceptional in having the pelvic bone poorly ossified and the entire posteromedial margin cartilaginous, although there is no discrete posterior process. Woods and Sonoda (1973: 265) reported cartilaginous posterior processes in the beryciform *Trachichthys australis* (size not specified), but they are fully ossified in our 103 mm SL specimen (AMS I.16861004).

10. *Spina occipitalis.* Stiassny (1986) identified the spina occipitalis of Allis (1909) as a synapomorphy of her Acanthomorpha. The spina occipitalis is a ventral projection from the supraoccipital that extends between the exoccipitals to the dorsal margin of the foramen magnum. Stiassny found that the spina occipitalis is absent in non-acanthomorphs except for some osteoglossomorphs (*Hiodon* and *Heterotis*) and cypriniforms. In *Hiodon* and *Heterotis* (Taverne, 1977: figs. 6, 97) the pattern appears to be different, for the spina does not contact the exoccipitals. Among acanthomorphs, Stiassny found the spina occipitalis to be absent only in some ammodytoids, mastacembeloids and tetraodontiforms, and she argued that because the spina is present in some mastacembeloids and tetraodontiforms, the absence in others is secondary. The spina has also been lost within acanthuroids (Tyler et al., 1989: character 29). Stiassny found no exception to the absence of a spina in ammodytoids, but our cleared-and-stained specimens of *Ammodytes tobianus* (BMNH 1971.5.4.5–7 and unreg.) have a well-developed spina occipitalis; there is none in *Hypoptychus,* however, which was once thought to be an ammodytoid (Ida, 1976). The spina is present primitively in gasterosteiforms, but is absent in *Aulorhynchus,* aulostomoids, and the Syngnatha of Pietsch (1978).

We believe that there is some subjectivity in recognizing this character, and considerable variation in the extent to which the spina reaches and/or contributes to the foramen magnum. Nonetheless, a median posteroventral process on the supraoccipital does characterize *Polymixia,* percopsiforms, stephanoberyciforms, and most other acanthopterygians. Such a process is lacking in all lampridiforms (Olney et al., 1993).

11. *Point of origin of anterior epineurals displaced ventrally on to centra or parapophyses.* Primitively, the anterior epineurals originate on the neural arch (references cited under character 8, above), as they do in veliferid lampridiforms (see above, p. 000, on the situation in *Lampris*; other lampridiforms have lost all the epineurals or all but the first). In *Polymixia,* the first two epineurals originate on the neural arch, but those on vertebrae 3–10 originate on the parapophysis or centrum. More posterior epineurals originate on the neural arch or spine. In stephanoberyciforms the third and succeeding epineurals originate on the centrum or parapophysis [we have not found epineurals beyond the tenth vertebra (*Rondeletia*) in any stephanoberyciform], and in other acanthomorphs the anterior epineurals originate on the rib (these are the intermuscular bones commonly described as epipleurals, Patterson and Johnson, submitted[1]).

HOLACANTHOPTERYGII
(Acanthomorpha minus Lampridiformes and Polymixiiformes)

12. *Epipleurals absent.* The epipleurals are a series of intermuscular bones originating on the posterior ribs in the abdominal region and the anterior haemal spines in the caudal region. They are widespread in lower teleosts, and among euteleosts they occur in esocoids, ostariophysans, argentinoids, stomiiforms, au-

lopiforms and myctophiforms. In salmonoids and osmeroids they are represented only by a series of ligaments. *Polymixia* has epipleurals on the last three or four ribs and the first six or seven haemal spines. They are absent in all other Recent acanthomorphs. We have found no epipleural bones or ligaments in lampridiforms, and must assume that this represents an independent loss. We note that veliferids, the most primitive lampridiforms, have paired posterior extensions of the swimbladder in the position of the epipleurals.

13. *Epicentral ligaments absent anteriorly.* The epicentral series of intermusculars is represented by a series of bones or ligaments in the horizontal septum, originating from the neural arch or centrum of the first two vertebrae, and from the centrum, parapophysis or head of the rib on more posterior vertebrae. The epicentral series develops in a rostrocaudal gradient, and epicentral bones or ligaments are usually absent on posterior caudal vertebrae. In non-acanthomorph euteleosts, epicentral bones are present in gonorynchiforms, gymnotoids and some aulopiforms, and epicentral ligaments are present in otophysans, esocoids, salmonoids, osmeroids, stomiiforms and myctophiforms. Veliferid lampridiforms have epicentral ligaments from the first (*Velifer*) or third (*Metavelifer*) vertebra back to about the tenth (*Metavelifer*) or 25th (*Velifer*), *Lampris* has them from the third vertebra (posterior extent unknown, no cleared material seen), and *Polymixia* has them from the second back to about the 25th. Elsewhere in acanthomorphs, we have found a discrete series of epicentral ligaments only in beryciforms (trachichthyids, monocentrids, anomalopids, diretmids, holocentrids, berycids), where they begin at about the ninth vertebra and overlap the epineural series, and in a few zeiforms (e.g., *Xenolepidichthys*) and percomorphs (e.g., Centropomids, *Morone,* mugilids) where they begin at about the same level as in beryciforms, but never overlap the epineurals. This character is presumably associated with the next one.

14. *Distal parts of anterior epineurals displaced ventrally into horizontal septum.* Whereas *Polymixia* has the first epineural displaced into the horizontal septum from its primitive dorsolateral position, other acanthomorphs (except lampridiforms) have several epineurals so displaced. In beryciforms (except *Monocentris*) about the first five epineurals lie in the horizontal septum, and in other acanthomorphs (including *Monocentris*) all the epineurals are in the horizontal septum.

Other Possible Holacanthopterygian Characters.—Rosen (1985:53) suggested another possible holacanthopterygian character, "Complete closure of the notochordal-connective tissue space between the basioccipital and the centrum of the first vertebra." In *Polymixia* Rosen (1985:fig. 18) illustrated what he called a notochordal plug" remaining on the anterior face of the disarticulated first vertebra, and a "cervical gap" occupied by the notochordal sheath between the ventral part of that vertebra and the basioccipital. Rosen saw this condition as part of a transformation series, beginning with the wide cervical gap that he reported in aulopiforms (*Chlorophthalmus, Aulopus*) and neoscopelids, and with *Polymixia* intermediate between the narrower gap in myctophids, and the absence of a gap in other acanthomorphs. We have been unable to convince ourselves that there is any gap between the lower part of the first centrum and the basioccipital condyle in *Polymixia.* But we have been struck by a similarity between the occipital joint (as seen in dry skeletons) of lampridiforms (*Velifer, Lampris*) and *Polymixia*: in those fishes, the surface of the basioccipital portion of the condyle resembles the surface of the exoccipital portion, both having a plane, granular surface, and the notochordal pit lies at the top of the basioccipital portion of the condyle, at the junction of the limbs of the inverted Y-shaped suture in the condyle. The opposing

surface of the first vertebra has the same texture as the basioccipital condyle, and differs from the articular surfaces of normal vertebrae. In other acanthomorphs, whereas the exoccipital condyles have the same plane, granular surface as in lampridiforms and *Polymixia,* the basioccipital portion resembles the surface of a vertebra, with the notochord pit in its center, and with a smooth surface marked by concentric growth lines. The opposing surface of the first vertebra has the same structure as the basioccipital condyle and as other vertebrae. However, we have also found the lampridiform/*Polymixia* type of occipital joint in berycids (*Centroberyx, Beryx*), which share other acanthopterygian (15–17) and euacanthopterygian (18–25) characters.

ACANTHOPTERYGII
(Stephanoberyciformes + Zeiformes
+ Beryciformes + Percomorpha)

15. *Pelvic spine present.* In non-acanthomorphs, lampridiforms, percopsiforms and some stephanoberyciforms, the first (most lateral) pelvic ray is segmented distally and consists of paired hemitrichs. In some stephanoberyciforms (some melamphaids, *Gibberichthys, Hispidoberyx*), some zeiforms (e.g., *Zenion, Xenolepidichthys, Neocyttus,* and *Allocyttus*), all beryciforms except *Anoplogaster* and some anomalopids, and most percomorphs, the first pelvic ray is an unpaired, unsegmented spine. We interpret the presence of a pelvic spine as a synapomorphy of acanthopterygians, requiring secondary loss of the spine within stephanoberyciforms, zeiforms, beryciforms, and in a few percomorph subgroups (including some atherinomorphs). Because the pelvic spine of stephanoberyciforms and zeiforms differs in structure from that of other acanthopterygians (beryciforms and percomorphs, character 22 below), there is an alternative interpretation, that a complex spine developed in the latter group and a simple spine developed independently in stephanoberyciforms and zeiforms. However, a pelvic spine occurs in all three of Kotlyar's (1991a, 1991b) groups of stephanoberyciforms (*Gibberichthys* among stephanoberycoids, melamphaids, *Hispidoberyx*), and is most parsimoniously interpreted as primitively present in Moore's (1993) phylogeny of stephanoberyciforms. In zeiforms, a pelvic spine occurs in four of the five recognized families, including one of the genera we consider most primitive. Therefore, we prefer the interpretation of primitive presence of the spine in acanthopterygians.

16. *Free pelvic radials reduced in size and/or number.* Primitively in euteleosts there are three or four autogenous radials at the posterior margin of the pelvic bone, between the bases of the pelvic fin-rays (Johnson, 1992: figs. 4A, 5A). Stiassny and Moore (1992) stated that these radials "divide off from the pelvic cartilage" in early ontogeny, but we have seen no evidence for this and believe that in acanthomorphs the pelvic radials are separate from their earliest appearance. In eurypterygian euteleosts the medial radial fuses with the ventral hemitrich of the medial pelvic fin-ray (Johnson, 1992: figs. 4B, 5B, C). In veliferid lampridiforms (Olney et al., 1993), *Polymixia* and percopsiforms, there are three large, free cartilaginous or ossified radials forming an essentially continuous row from the fused medial radial to the first (outermost) fin-ray, so that all the rays embrace some part of a radial. In most stephanoberyciforms and beryciforms, there is just one small, ossified radial, within or just medial to the base of the pelvic spine (or first ray), and most of the fin-rays do not embrace a radial. Berycids have a large ossified radial outside the upper half of the base of the pelvic spine and a small one within the base of the spine, but nothing between there and the fused medial radial. Holocentrids are most like *Polymixia* and percopsiforms in having two

radials associated with the base of the spine (as in berycids), and one more free radial medial to them (between the bases of the first and second soft rays in *Ostichthys,* between the bases of the middle rays in *Optivus*), but there is no continuous row of radials. Zeiforms have zero to two free cartilaginous radials associated with the medial rays. We consider the reduction in size and/or number of the pelvic radials to be a synapomorphy of acanthopterygians.

17. *Anteromedial process of pelvic bone.* Stiassny and Moore (1992) identified the presence of an ossified styliform process, projecting anteriorly from the ventromedial surface of each pelvic bone (Stiassny and Moore's figs. 3, 5, 10, 12, 13), as a synapomorphy of their Acanthopterygii (=our Stephanoberyciformes + Eucanthopterygii). We confirm their observation that similar structures are lacking in non-acanthomorphs and in lampridiforms, *Polymixia,* paracanthopterygians, zeiforms, and some atherinomorphs. We interpret the absence of an anterior pelvic process in zeiforms as a reversal (loss), a justification that must be used for those percomorphs that lack the process (e.g., some atherinomorphs, all gasterosteiforms), but because the process is also absent in non-melamphaid stephanoberyciforms (we differ from Kotlyar, 1991b, in finding no anterior process in *Hispidoberyx*) it is equally parsimonious to treat it as a euacanthopterygian character, independently acquired in melamphaid stephanoberyciforms.

UNNAMED GROUP
(Zeiformes + Euacanthopterygii)

18. *Baudelot's ligament originates on occiput.* In beryciforms and almost all percomorphs, Baudelot's ligament originates on the ventrolateral surface of the basioccipital, passes round a dorsal process on the cleithrum, and inserts on the medial face of the supracleithrum. With the exception of ophidioid (Howes, 1992) and batrachoidid (Markle, 1989) paracanthopterygians, all other acanthomorphs, including stephanoberyciforms, retain the primitive euteleostean (and teleostean) site of origin of Baudelot's ligament, on the first vertebra. It has been argued (by Greenwood et al., 1966: 389) that the difference between these two conditions is due to fusion of the first centrum with the braincase in those fishes having Baudelot's ligament on the basioccipital, but many features of the occiput, first vertebra and adjacent structures show that this is not so. Veliferid lampridiforms are exceptional in having Baudelot's ligament bifid proximally, with one branch originating from a ventrolateral process on the first centrum (Fig. 1C) and the other from the occiput, but on the ventrolateral corner of the exoccipital rather than the basioccipital. This encroachment of a portion of Baudelot's ligament onto the occiput may be related to the anterior placement of the dorsal fin, which has occurred in lampridiforms independently of that in euacanthopterygians (character 20 below). Zeiforms, in which Baudelot's ligament always originates on the exoccipital, are the only other group in which we have found any part of the ligament on that bone. Among stephanoberyciforms, *Rondeletia* and the cetomimids have two ligaments, one from the first vertebra and one from the basioccipital. We homologize the ligament from the first vertebra with Baudelot's, because it passes round the cleithrum to the supracleithrum. The occipital ligament inserts on the cleithrum. Within percomorphs a few groups (e.g., agonid scorpaeniforms, Kanayama, 1991; champsodontids; some zoarcoids) have Baudelot's ligament from the first vertebra, a condition that we interpret as secondary. Among the percomorphs that we have examined, Baudelot's ligament is absent in dactylopterids, synbranchiforms, gasterosteiforms, gobiesocids and callionymids. Because the occipital origin of the ligament differs in zeiforms (exoccipital) and

euacanthopterygians (basioccipital), it would be possible to regard those origins as two separate characters respectively defining zeiforms and euacanthopterygians.

19. *Dorsal fin advanced.* In what we believe to be primitive zeiforms, in all beryciforms, and in basal percomorphs the first dorsal pterygiophore is inserted anterior to at least the fourth neural spine (berycids), and is usually anterior to the third (all others; Fig. 20E–K). In either case, all interneural spaces anterior to the first pterygiophore are occupied by supraneurals. Where three supraneurals are present (berycids and most basal percomorphs), the third lies in the third or (more rarely) the second interneural space, never more posteriorly. *Anoplogaster* has the dorsal fin advanced like other beryciforms, but apparently has lost the first two supraneurals so that the first two interneural spaces are vacant. In myctophiforms, *Polymixia, Percopsis* and fossil percopsiforms (Patterson and Rosen, 1989: fig. 9A–C), and all stephanoberyciforms the first dorsal pterygiophore is inserted posterior to the fourth neural spine, and there are one to several vacant interneural spaces anterior to it (Fig. 20A–D). *Aphredoderus* has the first dorsal pterygiophore between the third and fourth neural spines, and there are two vacant interneural spaces in front of it. Various non-percopsiform paracanthopterygians also have the first dorsal pterygiophore anterior to the fourth neural spine or further forward (e.g., some ophidiiforms, lophiiforms, many gadiforms). Among Recent acanthomorphs, a dorsal fin originating as far forward as that of beryciforms and percomorphs occurs elsewhere only in lampridiforms (0+0+1/1/1/ in *Velifer,* 0+1/1/1/ in *Metavelifer* and *Lampris,* Olney, 1984: table 100), where it must have been derived independently. This character serves as a euacanthopterygian character among Recent acanthomorphs (independently acquired in lampridiforms, and in various paracanthopterygians), but it is weakened or rendered problematic by the fact that the derived euacanthopterygian pattern (0/0/0/1 or 0/0/0/2) occurs in all Cretaceous polymixiids (and in at least one juvenile individual of *Polymixia,* MCZ 58857). Further, in the Cretaceous ctenothrissiforms, which may be related to acanthomorphs, the pattern is 0/0/0+2/ or 0/0/0/2; a lampridiform-like pattern (0+0+1/ or 0+0+0/1+1) occurs in the Cretaceous aipichthyids and *Pharmacichthys* and *Pycnosteroides* (Patterson, 1993). Within percomorphs, secondary posterior displacement of the dorsal origin must have occurred a number of times (e.g., most smegmamorphs, gobioids), but unlike the primitive condition, this secondary one is usually evinced by absence of supraneurals. Mugilids are exceptional among percomorphs in having a posteriorly displaced dorsal preceded by three widely spaced supraneurals (Parenti, 1993: fig. 7).

20. *Anterior epineurals displaced ventrally on to ribs.* In veliferid lampridiforms all the epineurals originate on the neural arches, whereas in *Polymixia* and stephanoberyciforms those on vertebrae 3–10 originate on the centrum or parapophysis (character 11 above). In all beryciforms, zeiforms and most percomorphs the anterior epineurals are displaced further ventrally and originate on the rib (except when ribs are secondarily absent, e.g., various zeiforms, and in gobiesocids, where the rib originates on the epineural, pers. obs. and Gosline, 1970: 376). The epineurals originate on the rib only on a few vertebrae (3–5 or 3–6) in some beryciforms (e.g., *Centroberyx, Anomalops, Adioryx vexillaris*), rising successively on to the parapophysis, centrum, and neural arch posteriorly. *Anoplogaster* has no epineurals, and in *Diretmus* and trachichthyids there are epineurals only on the first one or two centra. The epineurals are on the ribs of all rib-bearing centra in percomorphs (including smegmamorphs). There is character conflict here because they are also on the ribs in paracanthopterygians (there are epineurals on vertebrae

1–5 in *Percopsis* and 1–8 in *Aphredoderus*, and those behind the second vertebra originate on the rib).

EUACANTHOPTERYGII
(Beryciformes + Percomorpha)

21. *Complex pelvic spine.* As discussed above (character 15), we interpret the pelvic spine as synapomorphous for acanthopterygians. The pelvic spine of stephanoberyciforms has a broadly open symmetrical base (Fig. 22A–C) that grasps the unmodified cartilaginous margin of the pelvic girdle. That of zeiforms (Fig. 22D) also has a symmetrical base and frequently has the two hemitrichs unfused proximally along a substantial portion of its length. Beryciforms (Fig. 22E, F) and percomorphs (Fig. 22G–Q), including smegmamorphs, share a specialized configuration of the spine base. It is asymmetrical, and has medial processes that grasp a bony shelf or ring at the posterolateral corner of the pelvic girdle (Gosline, 1961: fig. 5; Rosen and Patterson, 1969: fig. 43; Mok and Chang, 1986: fig. 1). In some percomorphs the medial processes are fused through a bony ring on the girdle, forming a complete "chain-link" attachment. We agree with Stiassny and Moore (1992) that the distribution of the latter condition renders it phylogenetically ambiguous, but we interpret the complex spine base as apomorphous for euacanthopterygians.

22. *Chain-link articulation of dorsal fin-spines.* A distinctive articulation between the dorsal fin-spines and pterygiophores is found exclusively in beryciforms and percomorphs (Fig. 23E–G). The proximal-middle radial of each pterygiophore bends near its distal end and the associated distal radial articulates with the anterolateral corner of the succeeding proximal-middle radial, where the serial spine is borne. The main body of each distal radial lies anterior to the serial spine and is not embraced by it. Instead, each distal radial bears a posterior process that is linked by ligament through a foramen at the base of the spine to the dorsal surface of the succeeding proximal-middle radial. A further distinctive feature is the development of wing-like lateral expansions of both the distal radial and the distal end of the proximal-middle radial, so that there is strong articulation between the two elements, frequently involving suturing. Various modifications of this chain-link articulation occur within percomorphs, ranging from loss or reduction of the distal radials (e.g., all smegmamorphs except *Elassoma*; gobioids; *Dactylopterus*; triglids) to dissociation of the distal radial from its serial member and, in some, fusion of the isolated distal radial to the succeeding proximal-middle element to form a complete bony link through the base of the spine (e.g., blennioids, labrids, some plesiopids; see Mooi, 1993). A consistent feature of the dorsal fin of beryciforms and percomorphs, including those that lack or have reduced distal radials, is that there is an abrupt transition between spinous and soft-ray pterygiophore configuration. Further, when distal radials are reduced in these fishes, they remain anterior to, rather than within, the spine base.

In lampridiforms, *Polymixia* (Fig. 23A), percopsiforms and stephanoberyciforms (Fig. 23B, C) the proximal-middle and distal radials have no wing-like lateral expansions and usually do not articulate strongly with each other, although there may be strong articulation between succeeding proximal-middle radials. If the distal radial bears a ligament, it connects with the succeeding distal radial, not with the succeeding proximal-middle element. There is no abrupt transition in configuration between pterygiophores bearing spines and those bearing soft rays. The condition in zeiforms (Fig. 23D) differs from that described above only

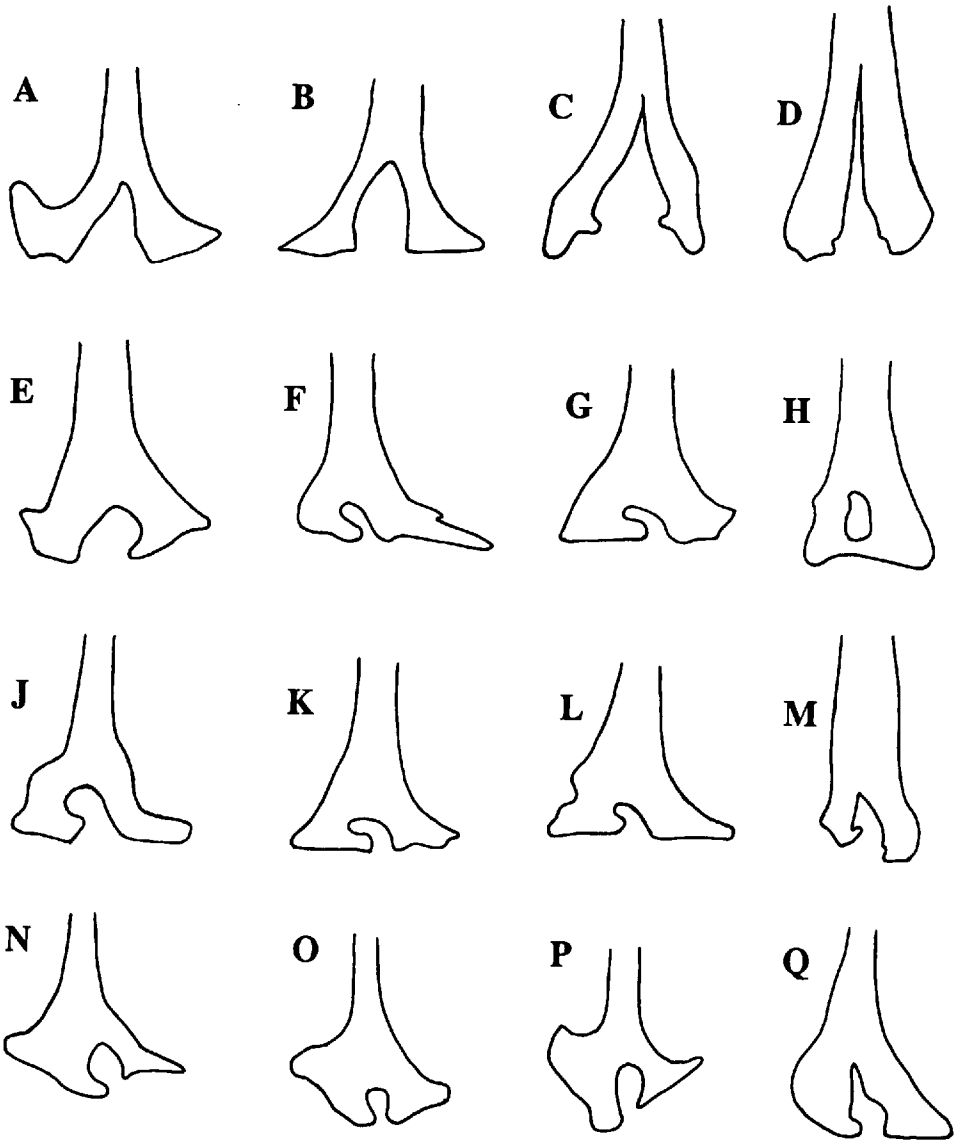


Figure 22. Base of left pelvic spine, in lateral (frontal) view, of: A–C, stephanoberyciforms, D, a zeiform, E, F, beryciforms, G, a percoid, H, a caproid, J, *Elassoma,* K, a mugiloid, L, an atherinomorph, M, a gasterosteiform, N, a gobioid, O, a notothenioid, P, a trachinoid, and Q, a pleuronectiform. A. the melamphaid *Poromitra crassiceps,* USNM 296944; B. *Melamphaes* sp., USNM 320098; C. *Gibberichthys pumilis,* USNM 207512; D. the oreosomatid *Allocyttus verrucosus,* AMS I.20068031; E. *Diretmus argenteus,* VIMS uncat.; F. the trachichthyid *Optivus* sp., AMS I.17033061; G. *Dinoperca petersii,* USNM 269543; H. *Capros aper,* USNM 268912; J. *Elassoma zonatum,* USNM 313100; K. the mugilid *Agonostomus monticola,* USNM 73742; L. *Bedotia* sp., USNM 301513; M. *Aulorhynchus flavidus,* UW 22052; N. *Gobionellus schufeldti,* USNM uncat.; O. *Notothenia sima,* USNM 214435; P. the uranoscopid *Gnathagnus egregius,* USNM 268438; Q. *Psettodes belcheri,* USNM 261532.

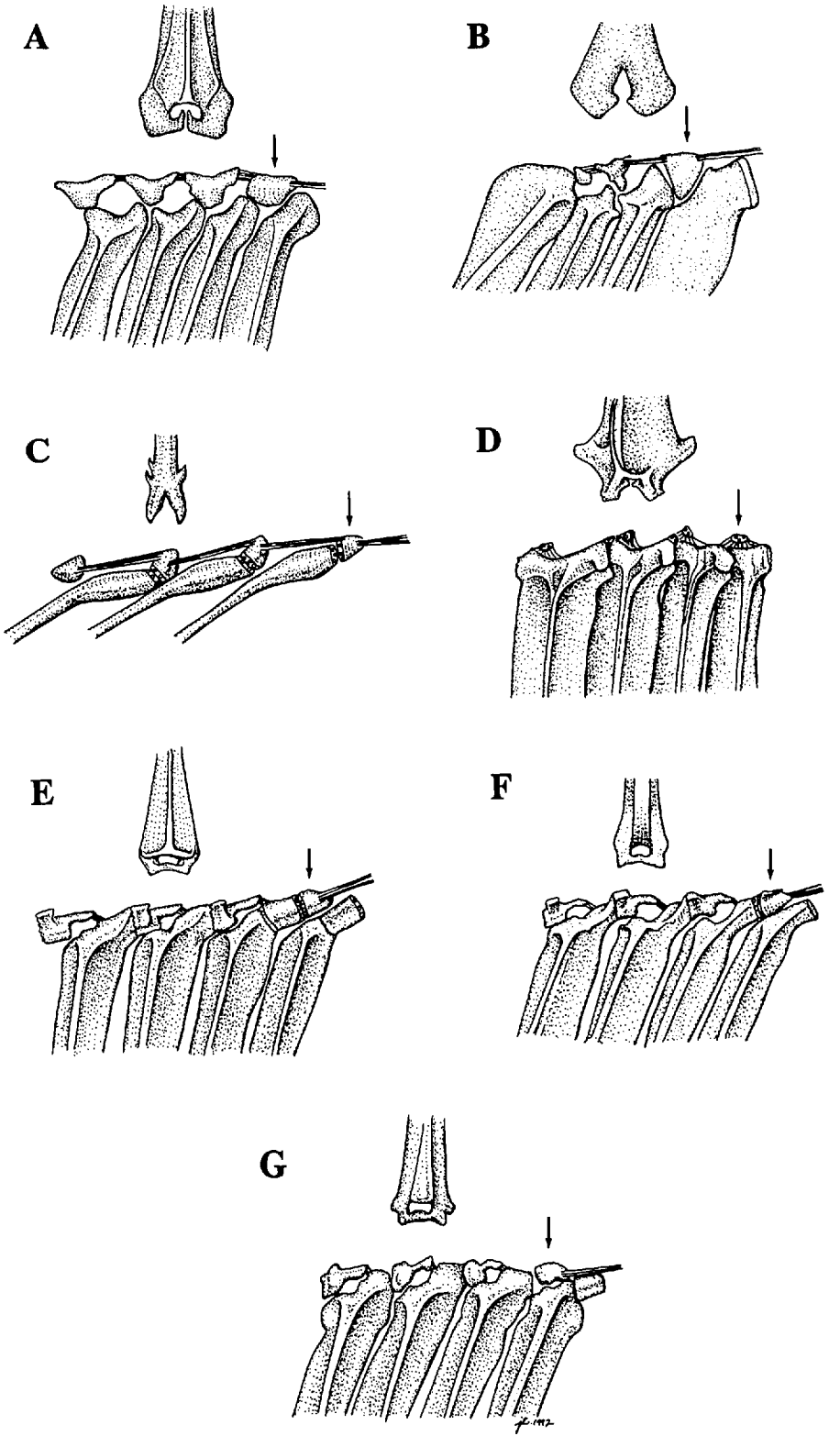
in having wing-like expansion of the proximal-middle radials; distal radials are either lacking or are tiny (usually cartilaginous) and lie within the partially open bases of the spines. The spine-bearing distal radials of lampridiforms and stephanoberyciforms (Fig. 23B, C) lie within the base of their serial spines and lack

posterior processes; those of *Polymixia* (Fig. 23A) and percopsiforms rest directly over the (sutured) junction between successive proximal-middle elements and are anvil-shaped, with anterior and posterior processes projecting towards or into the bases of the preceding and succeeding spines.

23. *Supraneurals ossified distally.* In all beryciforms (except the single supraneural of *Anoplogaster*) and all percomorphs, the distal tips of all supraneurals are fully ossified (closed in bone). As in almost all other teleosts, the proximal tips are cartilaginous. In non-acanthomorphs, lampridiforms, *Polymixia* and stephanoberyciforms each supraneural (only the first in melamphaid stephanoberyciforms) is tipped with cartilage distally. The single supraneural of percopsiforms is unusual in being closed in bone at both ends. Supraneurals are present elsewhere in paracanthopterygians only in ophidioids (Patterson and Rosen, 1989: fig. 9D, E, J, K; Markle and Olney, 1990: figs. 2, 3, 6), where they are entirely cartilaginous, and gadiforms (Patterson and Rosen, 1989: fig. 9F, G; Markle, 1989: 77), where they are cartilage-tipped at both ends. Among zeiforms, we have found the single supraneural (present in all examined genera except *Parazen, Zenopsis* and *Zeus*) to be cartilage-tipped distally in the grammicolepid *Xenolepidichthys* and the oreosomatid *Oreosoma*; it is closed in bone in the others. The beryciform *Anoplogaster* appears to have lost the first two supraneurals, and we interpret the cartilage tip of the small, obliquely oriented remaining supraneural as a reversal, the only one of which we are aware in euacanthopterygians. The situation in zeiforms is ambiguous because it is equally parsimonious to regard the cartilage-tipped supraneural in *Xenolepidichthys* and *Oreosoma* as primitive or as a reversal; we regard it as primitive.

24. *Second ventral procurrent caudal fin-ray shortened proximally.* In all beryciforms the second ventral procurrent caudal ray is truncated proximally, so that its base is set back from the bases of the adjacent rays (Fujita, 1990: figs. 174–184). In non-acanthomorphs, lampridiforms, *Polymixia,* paracanthopterygians, stephanoberyciforms (Fujita, 1990: fig. 173; Kotlyar, 1990: figs. 3, 4, 6; 1991b: fig. 2), and zeiforms there is no such modification and the ventral procurrent rays are essentially a mirror image of the dorsal series. [Johnson (1975: table 1) erroneously reported the beryciform condition in melamphaids; it does not occur there.] The same truncation of the second ventral procurrent ray is found elsewhere among acanthomorphs only in perciforms, where it almost invariably co-occurs with a ventrally directed spur at the base of the first ventral procurrent ray (Johnson, 1975: fig. 2). This "procurrent spur" characterizes stromateoids, basal scombroids, basal acanthuroids, and about 50 families and *incertae sedis* genera of percoids (Johnson, 1975, 1984). Johnson (1975) noted that the percoid *Symphysanodon* is similar to beryciforms in having a truncated second ray without a spur on the first. Although it seems a trivial feature, we are impressed by the unique presence of the truncated second ventral procurrent ray in beryciforms and basal perciforms, and interpret it as evidence of their relationship. This hypothesis requires that both the truncated second ray and the procurrent spur have been lost numerous times within percomorphs; they are, for example, absent in all smegmamorphs.

25. *"Myoseptal" ligament from postcleithrum to posterolateral corner of pelvic girdle.* Stiassny and Moore (1992) proposed that ligamentous attachment of the pelvic girdle to the distal postcleithrum is a synapomorphy of Acanthomorpha. Although we agree that placement of the pelvic girdle anterior to the distal postcleithrum is, for the most part, congruent with the acanthomorph clade, ligamentous attachment between the two elements is not a consistent feature of basal acanthomorphs. Stiassny and Moore (1992) did not discuss the condition in lampri-


A
B
C
D
E
F
G

diforms, but indicated that a ligamentous attachment is present in that group in their data matrix (their table 1). There is no ligament between the postcleithrum and pelvic girdle in lampridiforms. In *Polymixia* we were unable to identify the discrete ligament described and illustrated by Stiassny and Moore (1992: fig. 7A), but agree that the tip of the postcleithrum is bound by diffuse connective tissue to a broad area of the dorsal surface of the pelvic bone. Among percopsiforms, Stiassny and Moore noted that *Percopsis* and *Amblyopsis* lack a postcleithral-pelvic ligament, but that it is well developed in *Aphredoderus*. Stiassny (1993: fig. 4D) illustrated and described this ligament as "inserting onto a ventral bony flange near the articulation of the first pelvic ray." Our examination of several specimens of *Aphredoderus* indicates that the ligament passes from the tip of the postcleithrum to the lateral radial and the base of the first pelvic ray, and so has no attachment to the pelvic girdle. This is a substantially different arrangement from that in *Polymixia*. All the zeiforms that we have examined lack a ligament between the postcleithrum and pelvic girdle, and among stephanoberyciforms, only some melamphaids have a weak ligament from the shaft of the postcleithrum to the dorsal surface of the pelvic bone, about midway along its length (Stiassny and Moore, 1992: fig. 7D, *Scopeloberyx*). In fact, we have observed a discrete ligament from the tip of the postcleithrum to the pelvic girdle only in three unrelated percomorph taxa, mugilids, sphyraenids, and polynemids, where it must have arisen independently in association with posterior displacement of the pelvic girdle and concomitant dissociation from the cleithrum.

We conclude that the sparse occurrence and variable configuration of the postcleithral-pelvic ligament in non-acanthopterygian acanthomorphs casts doubt on the validity of the feature as an acanthomorph synapomorphy. However, we believe that beryciforms and percomorphs share a specific postcleithral-pelvic ligamentous association not found in other acanthomorphs. In this condition, a variously developed ligament running within a myoseptum of the body wall originates from a point proximal to the tip of the postcleithrum, extends approximately at right angles to that bone, and inserts on the posterolateral corner of the pelvic bone (Stiassny and Moore, 1992: figs. 7C, 8A–C; Stiassny, 1993: fig. 4B). As noted above, a similar ligament occurs elsewhere in acanthomorphs only in some melamphaids, where its insertion is further forward on the dorsal surface of the pelvic bone. The acanthopterygian/beryciform type of ligament characterizes all beryciforms and the majority of percomorphs, including most percoids. It has been lost or modified in all smegmamorphs, wherein the pelvic girdle is posteriorly displaced.

Other Possible Euacanthopterygian Characters.—A feature unique to the Euacanthopterygii is the propensity for larvae of marine species to develop elaborate ornamentation on the dermal bones of the head. This ontogenetically ephemeral ornament may be extensive, consisting of variously configured spines and serrate ridges of the opercular bones, pectoral girdle, skull roof, jaws, infraorbitals and nasals. Larvae of all beryciform families (postflexion anomalopid larvae are un-

←

Figure 23. Configuration of spinous dorsal pterygiophores, with frontal view of one spine base, in: A. *Polymixia lowei*, USNM 308378; B, C. the stephanoberyciforms *Poromitra crassiceps*, USNM 296941, and *Hispidoberyx ambagiosus*, AMS I.2808001; D. the zeiform *Zeus faber*, USNM 307842; E, F. the beryciforms *Centroberyx affinis*, USNM 176984, and *Hoplostethus mediterraneus*, VIMS 4900; G. the percoid *Dinoperca petersii*, USNM 269543. Arrows denote the distal radial serially associated with the first soft ray.

known) have prominent spines and/or serrate ridges on several to many head bones, ranging from relatively small but abundant spines in berycids (Mundy, 1990: fig. 5) to larger spines and serrate ridges in trachichthyids, extremely long rostral, supraoccipital and preopercular spines in holocentrids, and horn-like parietal and elongate preopercular spines in diretmids and anoplogastrids (Keene and Tighe, 1984: figs. 204, 208; Okiyama, 1988: 356–360). Larval head spines are widespread, though not universally present, among marine percomorphs (all primary freshwater groups lack them). Within the Perciformes, the majority of marine families exhibit some larval spination, and extensive ornamentation is found within the Percoidei (Johnson, 1984), Scombroidei (Collette et al., 1984), Acanthuroidei (Johnson and Washington, 1987) and Trachinoidei (Watson et al., 1984); less extensive head spination characterizes at least some larvae of labroids, polynemoids, blennioids, gobioids and stromateoids. Dactylopteriform larvae have enormous posttemporal and preopercular spines. In scorpaeniforms, larvae of most scorpaenoids exhibit a complex elaboration of spines on many head bones, and many cottoid larvae have similar patterns, though the spines are weaker (Washington et al., 1984). Larvae of most tetraodontiforms lack head spination, but those of molids have large pyramidal spines on various bones (Leis, 1984a: fig. 243) and those of balistids and monacanthids have a small cluster of spines on the preopercle (Leis, 1984b; Aboussouan and Leis, 1984: figs. 248, 249). No pleuronectiform larva is extensively ornamented, but there are small to moderate spines on the preopercle, cleithrum and skull roof in several families (Ahlstrom et al., 1984: table 173). Among smegmamorphs, larval head spination is found in syngnathoid gasterosteiforms (sensu Pietsch, 1978), where it is most extensively developed as serrate cranial ridges and preopercular spines in macrorhamphosids (Fritzsche, 1984: figs. 216–219). Larval spination would not be expected in the freshwater *Elassoma* and synbranchiforms, but it is also lacking in mugiloids and atherinomorphs, which include marine representatives.

The extensive larval head spination that characterizes most beryciforms and many percomorphs is unknown elsewhere in fishes, and we suggest that it supports euacanthopterygian monophyly. With two exceptions, the larvae of all other acanthomorphs not only lack elaborate bony ornamentation but are essentially devoid of head spination. One exception is postlarvae of one species of melamphaid, *Poromitra capito,* which have substantial spines on the preopercle and weaker spines or serrations on several other head bones (Ebeling and Weed, 1973: fig. 20). Although their configuration changes somewhat in ontogeny, these spines are not restricted to the postlarva; serrate ridges and spines on the adult head are diagnostic among melamphaids for *Poromitra,* and "sharp head spines" in adults are unique within the genus to *P. capito* (Ebeling and Weed, 1973). Known larvae of other species of *Poromitra,* other melamphaid genera, and all other stephanoberyciforms lack transient head spines, and we infer that the spines in *P. capito* are not homologous with those of euacanthopterygians.

A second exception is zeiforms, but knowledge of zeiform larvae is limited (Tighe and Keene, 1984). We have examined larvae of *Zeus, Zenion* and *Grammicolepis* and find that they all possess a row of small supraorbital spines; *Grammicolepis* has an additional row of small spines on the frontal, some on the preopercle, and a laterally projecting serrate ridge on the pterotic; and *Zenion* has laterally projecting spines on the pterotic and bones of the opercular and pectoral series, and a large spine at the angle of the preopercle. This information is congruent with our placement of zeiforms between stephanoberyciforms and beryciforms.

Among non-acanthomorph teleosts, we know of only two groups in which there

is larval head spination. Small spines occur on the preopercle and one or more additional head bones in the larvae of some sternoptychids (Okiyama, 1988: 111), and the larvae of three aulopiform genera, *Sudis, Omosudis* and *Alepisaurus,* have preopercular spines and serrate cranial ridges (Okiyama, 1988: 234, 252).

PERCOMORPHA (new usage, includes Atherinomorpha)

26. *Rod-like interarcual cartilage.* A rod-like interarcual cartilage linking the widely-separated uncinate processes of the first epibranchial and second pharyngobranchial is present in most percoids and is widespread in percomorphs, including atherinomorphs (Travers, 1981). Although a small ovoid cartilage between the closely approximated uncinate processes of the two gill-arch elements has arisen independently in anomalopids and some myctophids, melamphaids (Johnson and Rosenblatt, 1988), and gadiforms (Markle, 1989: figs. 2C, 3A–C; Patterson and Rosen, 1989: fig. 12A–C, E), a rod-like interarcual cartilage like that of percomorphs occurs elsewhere only in some ophidiiforms (ossified in some carapids). We interpret the absence of the interarcual cartilage in a number of percomorph groups (e.g., *Elassoma,* all gasterosteiforms except aulostomids, echeneids, blennioids, gobiesocoids, acanthuroids) as secondary. In most of these groups the articulation between the first epibranchial and second pharyngobranchial differs from the primitive acanthomorph condition (contact between the two uncinate processes) in that the uncinate process of the epibranchial is either absent or has its tip widely separated from that of the second pharyngobranchial (examples in Travers, 1981, and Rosen and Patterson, 1990: figs. 28–48). The same is true of zeiforms (Rosen, 1973: figs. 101, 102), which also lack an interarcual cartilage; whether that absence is primary (zeiforms are not percomorphs, our inference) or secondary can be assessed only by congruence of other characters.

27. *Second ural centrum absent.* There is a well-developed second ural centrum (U2), fused to the upper hypurals, in lampridiforms and most paracanthopterygians, and U2 is free in *Polymixia.* A free U2 occurs in all stephanoberyciforms except melamphaids, where it is fused with PU1 + U1 and with the stegural and one or more upper hypurals (Kotlyar, 1990, 1991a, 1991b). In beryciforms, U2 is free in trachichthyids, monocentrids, *Anoplogaster,* anomalopids and *Diretmus* (Patterson, 1968; Zehren, 1979; Fujita, 1990). In berycids U2 is fused with PU1 + U1, and there is no indication that it is separate in early ontogeny. In Recent holocentrids U2 usually fuses with PU1 + U1 during ontogeny, but it remains free in *Pristilepis* (Randall et al., 1982) and occasionally in *Myripristis* (Fujita, 1990: fig. 182), and U2 is free in Cretaceous holocentroids (Stewart, 1984). A free second ural centrum is lacking in all adult percomorphs, including smegmamorphs (Fujita, 1990: table 2). It is also unknown in adult zeiforms, but it is recognizable in an 8.9 mm SL larva of the putatively primitive genus *Zenion* (Fig. 21) and in a 10 mm SL specimen of *Zeus.* The significance of a distinct U2 in early ontogeny is unclear, as it has also been reported in three diminutive atherinomorphs (Parenti, 1993: fig. 10) and several perciforms (Arratia, 1982; Mabee, in press).

28. *Five or fewer hypurals.* There are six hypurals in most aulopiforms, all myctophiforms, veliferid lampridiforms, *Polymixia,* percopsiform paracanthopterygians, all stephanoberyciforms except melamphaids, and all beryciforms except berycids, Tertiary and Recent holocentroids, and diretmids (Fujita, 1990; Olney et al., 1993; Kotlyar, 1990, 1991a, 1991b; Patterson, 1968; Stewart, 1984). A sixth hypural is unknown in zeiforms and percomorphs (Fujita, 1990: table 2).

29. *Pelvic fins with fewer than six soft rays.* Most percomorphs, including smegmamorphs, have pelvic fins with one spine and five or fewer soft rays. Although

there are numerous exceptions within paracanthopterygians (ophidiiforms, pediculates, various gadiforms), stephanoberyciforms (all but melamphaids and *Hispidoberyx*) and lampridiforms (many of the elongate forms), and some within beryciforms (anomalopids, monocentrids), and zeiforms (*Pseudocyttus*), the general condition inferred for *Polymixia* and all these non-percomorph acanthomorphs is to have a total of six or seven rays in addition to the first ray, which is primitively a spine in acanthopterygians (character 15 above). The decrease to five soft rays in percomorphs evidently involves loss of rays other than the medial one, because at least in the basal members that ray retains the cartilaginous tip evincing its ontogenetic fusion with the medial pelvic radial, a fusion diagnostic of eurypterygians (Johnson, 1992). We are aware of secondary increase to more than six pelvic soft rays among percomorphs only in the gasterosteiform *Solenostomus,* and in some cyprinodontids (e.g., *Aphanius*) and pleuronectiforms, none of which has a cartilage-tipped medial ray. The pelvic fin of *Solenostomus* is highly modified to serve as a brood chamber in females and to our knowledge is unique among fishes in having the hemitrichs of all seven rays fused so that the rays are unpaired (as they are in all the fins, a condition we call "pseudospines" in Table 1).

30. *Transforming ctenoid scales.* Roberts (1993) describes and documents the character of transforming ctenoid scales as a synapomorphy of the Percomorpha. This type of scale, in which ctenii arise as separate ossifications in two or three alternating rows marginally and transform into truncated spines submarginally, occurs nowhere else among fishes and offers cogent evidence for monophyly of all groups possessing it. Roberts excluded several groups from his Percomorpha (notably, Atherinomorpha, Gasterosteiformes, Synbranchiformes, Zeiformes, Tetraodontiformes) because they lack transforming ctenoid scales, though he also acknowledged that transforming ctenii must have been lost independently several times within percomorphs. Because we have no criterion to distinguish primitive and secondary absence of transforming ctenii, we are unwilling to exclude groups that lack them from Percomorpha unless there is other evidence that they are cladistically more primitive (e.g., zeiforms). Most percomorphs that lack transforming or peripheral ctenoid scales (see Roberts, 1993, for definitions) have cycloid scales, and those that have spinoid scales exhibit a wide diversity of spinoid configuration.

31. *Free pelvic radials lost.* As discussed above (character 16), free pelvic radials (excluding the medial radial fused with the ventral hemitrich of the innermost ray) are variously developed in basal acanthomorphs, but one or more is present in veliferid lampridiforms, *Polymixia,* percopsiforms, most stephanoberyciforms (lacking in *Stephanoberyx, Gibberichthys, Rondeletia,* and, of course, in all whalefishes, which lack pelvic fins), some zeiforms (*Parazen, Zenopsis*), and all beryciforms except *Anoplogaster.* With few exceptions, all percomorphs lack free pelvic radials (except occasionally as larvae), and we treat this as synapomorphous for Percomorpha. Among smegmamorphs, the single exception we have observed is in the gasterosteiform *Indostomus,* where there is a small separate ossicle between the bases of rays two and/or three. Among other percomorphs, Winterbottom (1992) reports a free cartilaginous pelvic radial in gobiesocids, callionymids, dactyloscopids and leptoscopids. We have been unable to identify a free radial in dactyloscopids or leptoscopids and believe that Winterbottom is mistaken about its presence in those groups. However, in gobiesocids and callionymids a free cartilaginous radial lies within the base of the pelvic spine, a condition we have not seen elsewhere, corroborating Gosline's (1970) proposal of a close relationship between the two families, for which Winterbottom (1993) provides additional

support. Gosline stated that in both these groups "the ribs start on the second vertebra." That character should be stated "first epineural absent, ribs absent (callionymids) or inserting on epineurals anteriorly (gobiesocids)." Springer's (1988) report of one or two autogenous cartilaginous radials in the pelvic fins of gobioids (character 17 in Winterbottom, 1993) was erroneous. The "relatively large" lateral element is the unossified posterolateral corner of the pelvic plate, and the medial element is fused to the ventral hemitrich of the medial ray.

Stiassny and Moore (1992) identified absence of free pelvic radials as a synapomorphy of their "higher percomorphs," but they placed atherinomorphs outside that group, requiring an independent loss in them. They also suggested that loss of free pelvic radials "is probably the result of a fusion of the radial elements with the fin-ray articular surface on the pelvic plate," but presented no evidence to support that hypothesis. To the contrary, in those percoids where a small cartilaginous radial is present in early ontogeny (e.g., *Morone,* Johnson, 1992: fig. 6B), there is no point in development at which the posterior margin of the pelvic cartilage exhibits a configuration consistent with its having incorporated the oblong radial. Instead, the radial simply stops growing and is apparently resorbed in the surrounding connective tissue.

32. *Point of origin of all but the first two epineurals displaced ventrally, and the distal parts of all epineurals displaced ventrally into the horizontal septum.* The first two epineurals retain their origin on the neural arch in all acanthomorphs (except smegmamorphs, character 34 below), but the distal part of the first is displaced ventrally into the horizontal septum in all except lampridiforms (character 8 above), and in holacanthopterygians the second is also so displaced (character 14 above). In percomorphs all the epineurals are displaced ventrally, and the general pattern (e.g., the acanthuroids and related forms illustrated in Tyler et al., 1989: figs. 23–33) is for the epineural to originate on the rib of rib-bearing vertebrae, on the parapophysis or haemal arch of any posterior abdominal verbebrae that do not bear ribs, and on the base of the haemal spine or the centrum of caudal vertebrae. The distal parts of all the epineurals lie in the horizontal septum, and their tips lie beneath the lateral line. This pattern differs from that found in beryciforms (e.g., berycids, holocentrids, anomalopids; in trachichthyids and diretmids there are only one or two epineural bones, and *Anoplogaster* has none) where the posterior epineurals lie above the horizontal septum and retain their primitive origin on the neural arch. There is character conflict here, first with paracanthopterygians, where the epineurals show the percomorph pattern (e.g., *Aphredoderus,* gadiforms), second with stephanoberyciforms, where most taxa have only a few epineurals but *Rondeletia* has 10–12, again in the percomorph pattern, third with zeiforms, where epineurals are commonly present on about the first ten vertebrae (e.g., *Capromimus, Cyttopsis, Parazen, Xenolepidichthys*) and are in the horizontal septum, and fourth with beryciforms, where *Monocentris* has no anterior epineurals but has them from vertebra 7–8 back to 12–13, again in the percomorph pattern. Doubtless correlated with ventral displacement of the epineurals is the truncation or loss of the series of epicentral ligaments which are absent in paracanthopterygians and stephanoberyciforms, but are retained in some beryciforms, zeiforms, and percomorphs (character 13 above). It would be more parsimonious to treat descent of the epineurals as a holacanthopterygian character, reversed (posterior epineurals elevated in beryciforms), but we think it improbable that beryciforms should exactly mimic the primitive pattern if their epineurals are secondarily developed.

33. *Seventeen principal caudal-fin rays, in I,8,7,I pattern.* No percomorph has more than 17 principal caudal rays, and the typical pattern is I,8,7,I (outermost

principal rays unbranched, branched rays eight in the upper lobe and seven in the lower). The primitive euteleostean pattern of I,9,8,I is retained in stephanoberyciforms, beryciforms, and veliferid and lampridid lampridiforms, whereas *Polymixia* and percopsiform paracanthopterygians have I,8,8,I. The I,8,7,I pattern appears to be unique to percomorphs among teleosts (Fujita, 1990: table 2). Further reduction in principal caudal ray number is common among percomorphs, as it is in other groups of teleosts (Fujita, 1990: table 2). The instances of secondary increase recorded by Fujita (1990) in percomorphs are either individual variants with one extra ray (e.g., in the gobies *Gobiodon, Mugilogobius* and *Taenioides*) or extra branched rays (e.g., the plesiopid *Plesiops* with 9/8 branched rays and the goby *Luciogobius* with 9/9). In the belontiid *Colisa* Fujita records two species with 8/8 branched rays, but our specimen has only 6/7. Zeiforms have no more than 15 principal rays (in grammicolepids: I,6,7,I), and we interpret this reduction as independent of that in percomorphs.

Other Possible Percomorph Characters.—Suturing of the distal and proximal ceratohyals, first noted by McAllister (1968), was recorded by him as present in some cypriniforms and in percopsiforms, ophidiiforms, gadiforms, lophiiforms, batrachoidiforms, atheriniforms, zeiforms, syngnathiforms, gasterosteiforms, and a range of percomorph orders. In zeiforms, McAllister reported suturing between the ceratohyal ossifications only in *Zeus,* where it was said to be represented by "interdigitating prongs (an incipient suture)." We have seen no suturing in zeiforms, and given its absence in lampridiforms, *Polymixia,* stephanoberyciforms and beryciforms, it may be a percomorph character independently acquired within paracanthopterygians. Loss of the orbitosphenoid is frequently cited as a perciform or percomorph character. The bone is present in lampridiforms, *Polymixia* and beryciforms, and is absent in all paracanthopterygians, stephanoberyciforms, zeiforms and percomorphs.

SMEGMAMORPHA
(Synbranchiformes + *Elassoma* + Gasterosteiformes
+ Mugiloidei + Atherinomorpha)

34. *First epineural on parapophysis.* As noted above (characters 7, 11, 24, 32), the first epineural primitively originates from the neural arch, to which it is either fused (primitive) or attached by ligament. All smegmamorphs have a distinctive condition in which the first epineural originates on a parapophysis or lateral process of the centrum (e.g., the atherinoids *Bedotia, Menidia* and *Atherinichthys,* the exocoetid *Exocoetus,* the hemirhamphid *Hemirhamphus,* the scomberesocid *Scomberesox,* the aulorhynchid *Aulichthys,* the gasterosteids *Culaea* and *Spinachia,* the mugilids *Agonostomus, Aldrichetta* and *Chaenomugil,* the mastacembeloids *Rhynchobdella* and *Chaudhuria,* the synbranchoid *Monopterus,* and *Elassoma*). Among all the teleosts that we have surveyed, we have found a similar condition in only two other teleosts, the carangoid *Echeneis* and the gobiid *Gnatholepis,* both nested within well-characterized monophyletic percomorph groups and where we presume its origin is independent.

Other possible smegmamorph characters are set out in Table 2, and discussed in the accompanying text.

CONCLUSIONS

Our main conclusions are summarized in the cladogram in Figure 24. Entered on the main axis of that diagram are the numbered characters from the preceding list, with numbers repeated beside the names of terminal taxa in which the char-

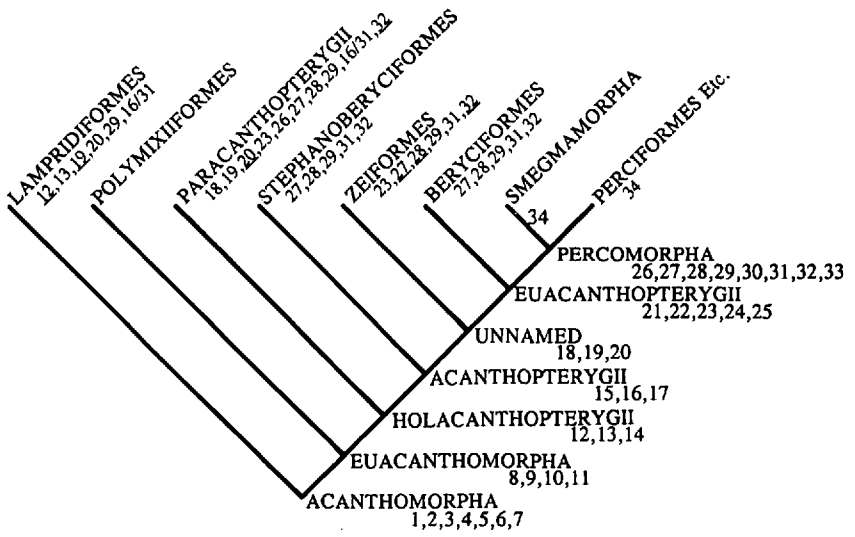


Figure 24. Cladogram summarizing our views on acanthomorph interrelationships. The names on the axis of the cladogram are those that we propose for major groups, and the numbers beneath those names refer to the characters listed in the text. Numbers beneath the names of terminal taxa indicate characters from that list that must be assumed to have originated independently in all (underlined numbers) or some members of those groups. Reversals that must also be assumed to have occurred within terminal taxa are not entered in the cladogram but summarized in the text.

acter in question must be assumed to have developed independently in those members where it occurs. Details of those independent gains or losses are as follows: Character 12, loss of epipleurals, has occurred independently in all lampridiforms, and character 13, loss of epicentral ligaments anteriorly, has occurred in some lampridiforms. Characters 16, reduction (Acanthopterygii), and 31, eventual loss (Percomorpha) of free pelvic radials, has occurred independently within lampridiforms, paracanthopterygians, stephanoberyciforms, zeiforms, and the beryciform *Anoplogaster*. Character 18, Baudelot's ligament on the occiput, has occurred independently in ophidioid and batrachoidid paracanthopterygians. Character 19, dorsal fin advanced, has occurred independently in all lampridiforms and in some paracanthopterygians. Character 20, anterior epineurals displaced ventrally on to ribs, has occurred independently in *Lampris* and in all paracanthopterygians. Character 23, supraneurals ossified distally, has occurred independently in percopsiform paracanthopterygians and within zeiforms. Character 26, rod-like interarcual cartilage, has developed independently in ophidiiform paracanthopterygians. Character 27, loss of second ural centrum, has occurred independently in lophiiform paracanthopterygians, melamphaid stephanoberyciforms, all zeiforms, and berycid and most holocentrid beryciforms. Character 28, five or fewer hypurals, has occurred independently in amblyopsids and non-percopsiform paracanthopterygians, melamphaid stephanoberyciforms, all zeiforms, and holocentrid, berycid and diretmid beryciforms. Character 29, pelvic fins with fewer than seven rays, has occurred independently in most elongate lampridiforms, many paracanthopterygians (amblyopsids, ophidiiforms, pediculates, various gadiforms), most stephanoberyciforms (all but melamphaids and *Hispidoberyx*), some beryciforms (anomalopids, monocentrids), and a few zeiforms (*Pseudocyttus*). Character 32, all epineurals displaced ventrally so that all but the first two originate on the rib, parapophysis or haemal arch, and all are in

the horizontal septum distally, has occurred independently in all paracanthopterygians, in the stephanoberyciform *Rondeletia,* in all zeiforms, and in the beryciform *Monocentris.* Character 34, first epineural originating on a transverse process of the first centrum, has occurred independently in the carangoid *Echeneis* and the gobioid *Gnatholepis.*

Beyond the homoplasy indicated in Figure 24 is the inferred independent acquisition of acanthomorph characters in non-acanthomorph taxa. Those acquisitions include the development of fin spines (character 1) in *Lipogenys* and notacanthids; the loss of median caudal cartilages (character 3) in galaxiids, stomiids, and a subgroup of aulopiforms (aulopids, synodontids, harpadontids) (Fujita, 1990: table 3); development of a spina occipitalis (character 10) in cypriniforms (Stiassny, 1986); and the loss of epipleural bones (character 12) in salmonoids, osmeroids and some aulopiforms (Patterson and Johnson, submitted[1]).

In addition to those multiple origins or losses, our scheme of relationships also requires one or more independent losses or reversals of the derived state of the majority of our characters. We have tried to detail those reversals in the character descriptions, but the following list will serve as a summary. Character 1, dorsal and anal fin spines, reverses (spines are absent in both fins) within every terminal group in Figure 24 except for zeiforms. Character 2, rostral cartilage, reverses (there is no rostral cartilage) in certain acanthomorph subgroups with specialized jaw mechanisms, e.g., synbranchiforms (Gosline, 1983). Character 3, loss of median caudal cartilages, reverses within beryciforms and in a gempylid. Character 6, fully ossified medial pelvic process, reverses within gadiforms, the stephanoberyciform *Gibberichthys,* and notothenioids. Character 9, fully ossified posterior pelvic process, reverses in *Gibberichthys.* Character 10, spina occipitalis, reverses (no spina) within mastacembeloids, gasterosteiforms, acanthuroids and tetraodontiforms. Character 15, presence of pelvic spine, reverses within stephanoberyciforms, zeiforms, beryciforms and a few percomorph subgroups. Character 17, presence of anteromedial process of pelvic bone, reverses in stephanoberyciforms, zeiforms, beryciforms, and within percomorphs in gasterosteiforms and a few other groups. Character 18, Baudelot's ligament originating on occiput, reverses in champsodontids and within scorpaeniforms and zoarcoids. Character 19, dorsal fin advanced, reverses in most smegmamorphs, gobioids, etc. In most cases the reversal is not to the primitive condition because supraneurals are absent, but in mugiloids they are retained. Character 21, complex pelvic spine, reverses in the percoid *Gadopsis* (Rosen and Patterson, 1969: fig. 43G) which has a greatly reduced pelvic spine. Character 23, supraneurals closed in bone distally, reverses in *Anoplogaster.* Character 24, foreshortening of base of second ventral procurrent caudal ray, reverses numerous times within percomorphs, for example, in all smegmamorphs. Character 25, postcleithral-pelvic ligament, reverses (is absent) in all smegmamorphs, where the pelvic girdle is posteriorly displaced, and in some other percomorphs. Character 26, a rod-like interarcual cartilage, is absent in a number of percomorph groups (e.g., *Elassoma,* all gasterosteiforms except aulostomids, echeneids, blennioids, gobiesocids, acanthuroids, some percoids), but the reversal (inferred loss of IAC) is not to the primitive state of an articulation between PB2 and the uncinate process of EB1. Character 29, pelvics with six or fewer rays, reverses in *Solenostomus* and some pleuronectiforms. Character 30, presence of transforming ctenoid scales, reverses many times in percomorphs (Roberts, 1993). Character 31, loss of all free pelvic radials, reverses in *Indostomus,* gobiesocids and callionymids.

Finally, there are a number of other characters, not considered in our list, which

Table 3. Matrix for 39 characters in 16 genera of ctenosquamates. The characters are drawn from those discussed in the preceding text, except for nos. 37–39, which are apomorphies respectively of Beryciformes, Stephanoberyciformes and Zeiformes

	Character							
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–39
Neoscopelus	00000	00000	00000	00000	00000	00000	00010	0000
Myctophum	00000	00000	00000	00000	00000	10000	00010	0000
Velifer	11111	11000	01000	00010	00000	00000	00001	0000
Polymixia	11111	11111	10000	00000	00000	00000	01000	0000
Percopsis	11111	11111	11110	00001	01000	00000	11110	0000
Gibberichthys	11111	01101	11111	10000	00000	00101	10010	0010
Stephanoberyx	11111	11211	21120	10002	00000	00101	20010	0010
Melamphaes	11111	11111	11111	11000	00000	11000	10010	0010
Parazen	11111	11111	11110	10223	02002	11000	12010	0001
Xenolepidichthys	11111	11111	11111	10213	00002	11001	12011	0001
Holocentrus	11111	11111	11112	11111	11110	11000	00002	0100
Centroberyx	11111	11111	11112	11111	11110	11000	00000	0100
Hoplostethus	11111	11111	21112	11112	11110	00000	20000	0100
Elassoma	11111	11111	11112	11131	12022	11101	12112	1000
Aulichthys	11111	11111	11112	10321	22022	11101	12212	1000
Dinoperca	11111	11111	11112	11111	11111	11111	12112	0000

Characters (* = run unordered): 1) Dorsal and anal fin spines absent (0), present (1); 2) Rostral cartilage absent (0), present (1); 3) Median caudal cartilages present (0), absent (1); 4) Infracarinalis muscles joined (0), separate (1); 5) Posttemporal loosely attached to epioccipital (0), tightly attached (1); 6) Medial pelvic process ends in cartilage (0), in bone (1); 7) First centrum unmodified anteriorly (0), with exoccipital facets (1); 8) First epineural dorsolateral (0), in horizontal septum (1), absent (2); 9) Posterior pelvic process ends in cartilage (0), in bone (1); 10) Spina occipitalis absent (0), present (1); 11) Anterior (3–6) epineurals originate on neural arch (0), on centrum, parapophysis or rib (1), absent (2); 12) Epipleurals present (0), absent (1); 13) Epicentral ligaments present on vertebrae 1–8 (or some of them) (0), absent on those vertebrae (1); 14) Distal parts of epineurals 2–5 dorsolateral (0), in horizontal septum (1), absent (2); 15) Pelvic spine absent (0), present, with symmetrical base (1), with complex base (2); 16) Pelvic radials a continuous row (0), discontinuous (1); 17) Anteromedial process of pelvic bone absent (0), present (1); *18) Baudelot's ligament originates on first vertebra (0), on basioccipital (1), on exoccipital (2), absent (3); *19) Dorsal fin originates behind fourth neural spine, supraneurals present (0), in front of fourth neural spine, supraneurals present (1), in front of fourth neural spine, supraneurals absent (2), behind fourth neural spine, supraneurals absent (3); *20) Epineurals on vertebrae 3–6 on neural arch, centrum or parapophysis (0), on rib (1), absent (2), present but ribs absent (3); 21) Dorsal fin spines absent or without chain-link articulation (0), with chain-link articulation (1), spine-bearing radials with no distal radials (2); *22) Supraneurals end distally in cartilage (0), in bone (1), absent (2); 23) Second ventral procurrent caudal ray unmodified (0), shortened proximally (1); 24) No ligament from shaft of postcleithrum to posterolateral corner of pelvic girdle (0), ligament present (1), no ligament, girdle secondarily displaced posteriorly (2); *25) Uncinate process present on E1, no interarcual cartilage (0), interarcual cartilage present (1), no uncinate process, no IAC (2); 26) Second ural centrum distinct (0), fused with PU1 + U1 (1); 27) Six hypurals (0), five or fewer (1); 28) Pelvics with seven or more rays (0), with six or fewer (1); 29) Transforming ctenoid scales absent (0), present (1); 30) One or more free pelvic radials (0), none (1); 31) All or some epineurals above horizontal septum (0), all in horizontal septum (1), two or fewer epineurals (2); *32) Principal caudal rays 19 (0), 18 (1), 17 or fewer (2); *33) Distal and proximal ceratohyals separated by cartilage (0), sutured (1), sutured with dorsal prong (2); 34) Orbitosphenoid present (0), absent (1); *35) Pelvic bones loosely attached or overlapping medially (0), broad median contact (1), sutured (2); 36) First epineural on neural arch or absent (0), on transverse process (1); 37) Jakubowski's organ absent (0), present (1); 38) Extrascapular unmodified (0), enlarged and covering parietal (1); 39) Parahypural articulates with PU1 (0), truncated proximally (1).

require multiple gain or loss in our scheme of acanthomorph relationships. These include: 1. The pelvic splint and adipose fin, two primitive features retained among percopsiform paracanthopterygians. Our scheme demands that both were lost independently in lampridiforms, in polymixiiforms, and in acanthopterygians (as well as in non-percopsiform paracanthopterygians), or that both were reacquired in percopsiforms. 2. The antorbital is a primitive feature retained in *Polymixia, Percopsis* and some fossil percopsiforms among paracanthopterygians, and holocentroids and some Cretaceous trachichthyoids among beryciforms. Our scheme requires that it was lost independently in lampridiforms, stephanoberyciforms and percomorphs (as well as within paracanthopterygians and beryciforms). 3. The orbitosphenoid is a primitive feature retained in lampridiforms, polymixiiforms and beryciforms. Our scheme demands that the orbitosphenoid was lost independently in paracanthopterygians, stephanoberyciforms, zeiforms and percomorphs (and also in myctophiforms), or that it was lost in holacanthopterygians and redeveloped in beryciforms. 4. Medial suturing of the pelvic bones is a derived character identified by Stiassny and Moore (1992) as a synapomorphy of holocentrids plus "higher percomorphs," with medial overlap of the girdles as the primitive state. Our scheme demands either that medial suturing developed in-

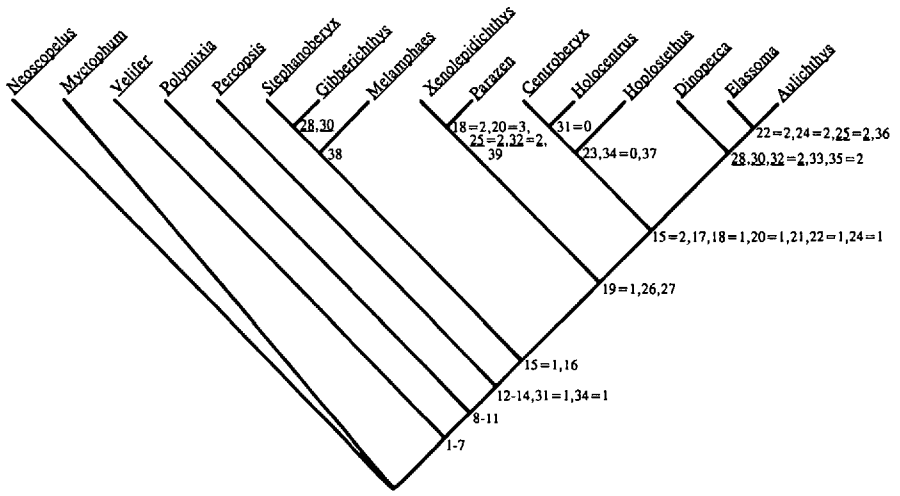


Figure 25. Shortest tree (length 92 steps, CI 0.64, RI 0.76) found by the implicit enumeration option in Hennig86 (Farris, 1988) for the data in Table 3, with *Neoscopelus* and *Myctophum* as the outgroup. Tree length was increased by two steps through weighting character 38 at 3 in order to maintain the monophyly of stephanoberyciforms. Without that weighting (in a consensus of two trees of length 89, CI 0.64, RI 0.76), *Melamphaes* falls out in a trichotomy with zeiforms and euacanthopterygians because it differs from the other two stephanoberyciforms in having derived states of characters 17, 26 and 27. With character 38 weighted at 2, the program found three trees (length 91, CI 0.63, RI 0.76) with a consensus tree showing a tetrachotomy of *Gibberichthys* + *Stephanoberyx, Melamphaes,* zeiforms and euacanthopterygians. Unambiguous changes at internal nodes are shown on the diagram by character numbers referring to Table 3 (numbers without suffix indicate change from state 0 to state 1; reversals are indicated by the suffix =0; parallel changes in characters 25, 28, 30, and 32 underlined).

This cladogram agrees with that in Figure 24 in topology, but differs in the resolution of several characters: anteromedial process of pelvic bone (no. 17 here) is not resolved as an acanthopterygian character but as a character of euacanthopterygians independently developed in *Melamphaes*; origin of Baudelot's ligament (no. 18 here) falls out not as a character of zeiforms + euacanthopterygians but as two separate characters, ligament on exoccipital (zeiforms) and on basioccipital (euacanthopterygians); descent of the anterior epineurals (vertebrae 3–6) on to the ribs (no. 20 here) is not resolved as a character of zeiforms + euacanthopterygians but as euacanthopterygian character because the two zeiforms in the sample both lack ossified ribs on those centra; modified second ventral procurrent caudal ray (no. 23 here) emerges not as a euacanthopterygian character but as a beryciform character, equally parsimoniously interpreted as independently developed in *Dinoperca* or lost in the two smegmamorphs in the sample; the interarcual cartilage (no. 25 = 1 here) and transforming ctenoid scales (no. 29 here) are not resolved as percomorph characters but as autapomorphies of *Dinoperca*; loss of distinct U2 and of sixth hypural (nos. 26, 27 here) are both resolved as characters of zeiforms + euacanthopterygians reversed within beryciforms (*Hoplostethus*), not as percomorph characters; and descent of the epineurals into the horizontal septum (no. 31 here) is resolved not as a percomorph character but (like the absence of the orbitosphenoid, no. 34) as a holacanthopterygian character reversed within beryciforms. Among these differences from Figure 24, those in characters 20, 23, 25 and 29 are due merely to the limited sample in Table 3. The resolution of characters 26, 27, 31 and 34 here as reversed in some (26, 27, 31) or all (34) beryciforms is more parsimonious than our interpretation of those characters (Fig. 24 and in the text), but we prefer to regard characters like loss of the sixth hypural and orbitosphenoid, and descent of the epineurals (coupled with loss of anterior epicentral ligaments) as effectively irreversible, given the strong evidence that each must have occurred more than once within teleosts, and the lack of evidence that any has reversed elsewhere within teleosts. The alternative interpretations of characters 17 (anteromedial process of pelvic bone) and 18 (Baudelot's ligament) here and in Figure 24 are equally parsimonious, as noted in our discussion of those characters in the text.

dependently in holocentrid (and monocentrid) beryciforms, and in percomorphs, or that it developed once and was reversed within beryciforms. Either alternative also entails independent reversal in atherinomorphs. 5. There are two supramaxillae in *Polymixia* and most beryciforms, one in stephanoberyciforms, a few paracanthopterygians and many basal percomorphs, and none in lampridiforms or zeiforms. Our scheme demands that both supramaxillae were lost independently in lampridiforms and zeiforms, and that the anterior supramaxilla was also lost independently in paracanthopterygians, stephanoberyciforms, percomorphs, and within beryciforms.

Given that we acknowledge homoplasy on this massive scale, it will doubtless be asked why we did not do things properly: present a data matrix and the results of parsimony analysis. Currently available parsimony programs can find the shortest tree for only a limited number of taxa, particularly where there is much incongruence. The number of taxa that we have surveyed and wish to include in our sample far exceeds that limit. But Table 3 is a data matrix for an abbreviated sample; because our conclusions on the relationships of stephanoberyciforms, zeiforms and beryciforms are likely to be the most controversial part of our analysis, we have included three stephanoberyciforms and beryciforms and two zeiforms in that sample. Figure 25 shows the most parsimonious tree found by Hennig86 (Farris, 1988; see comments in caption). By trimming our sample to the few representatives of each major taxon shown in Figure 25 we have been obliged to conceal much of the homoplasy that we acknowledge (that which is not universal in terminal taxa). We admit that our scheme is far from perfect, and look forward to its replacement by something either more consistent with known facts or supported by new ones.

Acknowledgments

For unpublished information, we are grateful to T. Gill, G. Howes, R. Mooi, J. Moore, L. Parenti, M. Stiassny, S. Weitzman, and in particular to G. Freihofer. For access to specimens, we thank K. Hartel (MCZ), J. Moore (YPM), J. Olney (VIMS), J. W. Orr (UW), J. Paxton (AMS), R. Rosenblatt (SIO) and J. Tyler (USNM). We are most grateful to L. Parenti and M. Stiassny for comments on the manuscript, and regret that we could not do more to accommodate them.

Literature Cited

Aboussouan, A. and J. M. Leis. 1984. Balistoidei: development. Pages 450–459 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Ahlstrom, E. H., K. Amaoka, D. A. Hensley, H. G. Moser and B. Y. Sumida. 1984. Pleuronectiformes: development. Pages 640–670 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Allis, E. P. 1909. The cranial anatomy of the mail-cheeked fishes. Zoologica, Stuttgart 22(57): 1–219.

Arratia, G. 1982. A review of freshwater percoids from South America (Pisces, Osteichthyes, Perciformes, Percichthyidae, and Perciliidae). Abhandl. Senck. Naturforsch. Gesell. 540: 1–52.

Banister, K. E. 1970. The anatomy and taxonomy of *Indostomus paradoxus* Prashad and Mukerji. Bull. Brit. Mus. Nat. Hist. (Zool.) 19: 181–209.

Bannikov, A. F. 1991. On the systematic position of the family Caproidae with reference to the Eocene genus *Acanthonemus*. J. Ichthyol. 31: 179–188.

de Beer, G. R. 1937. The development of the vertebrate skull. Oxford University Press, Oxford. xxiv + 552 pp., 143 pls.

Begle, D. P. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. Syst. Zool. 40: 33–53.

Bijtel, J. H. 1949. The structure and mechanism of movements of the gill filaments in Teleostei. Arch. Neerl. Zool. 8: 267–288.

Bolin, R. L. 1936. The systematic position of *Indostomus paradoxus* Prashad and Mukerji, a freshwater fish from Burma. J. Wash. Acad. Sci. 26: 420–423.

Bridge, T. W. 1896. The mesial fins of ganoids and teleosts. J. Linn. Soc. Zool. 25: 530–602.

Chapleau, F. 1993. Pleuronectiform relationships: a cladistic reassessment. Bull. Mar. Sci. 52: 516–540.

Collette, B. B., T. Potthoff, W. J. Richards, S. Ueyanagi, J. L. Russo and Y. Nishikawa. 1984. Scombroidei: development and relationships. Pages 591–620 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Ebeling, A. W. and W. H. Weed. 1973. Order Xenoberyces (Stephanoberyciformes). Mem. Sears Found. Mar. Res. 1, 6: 397–478.

Farris, J. S. 1988. Hennig86 version 1.5. Published by the author. 19 pp.

Fink, W. L. 1985. Phylogenetic interrelationships of the stomiid fishes (Teleostei: Stomiiformes). Misc. Publ. Mus. Zool. Univ. Mich. 171: 1–127.

——— and S. H. Weitzman. 1982. Relationships of the stomiiform fishes (Teleostei), with a redescription of *Diplophos*. Bull. Mus. Comp. Zool. 150: 31–93.

Freihofer, W. C. 1978. Cranial nerves of a percoid fish, *Polycentrus schomburgkii* (family Nandidae), a contribution to the morphology and classification of the order Perciformes. Occas. Pap. Calif. Acad. Sci. 128: 1–78.

Fritzsche, R. A. 1984. Gasterosteiformes: development and relationships. Pages 398–405 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Fujita, K. 1990. The caudal skeleton of teleostean fishes. Tokai University Press, Tokyo. xiii + 897 pp.

———. 1992. Development of the caudal skeleton in the tetraodontid fish, *Takifugu niphobles*. Jap. J. Ichthyol. 38: 438–440.

Goode, G. B. and T. H. Bean. 1896. Oceanic ichthyology. Spec. Bull. U.S. Nat. Mus. 2: xxxv + 1–553.

Gosline, W. A. 1961. Some osteological features of modern lower teleostean fishes. Smithson. Misc. Coll. 142: 1–42.

———. 1970. A reinterpretation of the teleostean fish order Gobiesociformes. Proc. Cal. Acad. Sci. 38: 363–382.

———. 1983. The relationships of the mastacembelid and synbranchid fishes. Jap. J. Ichthyol. 29: 323–328.

Greenwood, H. P., D. E. Rosen, S. H. Weitzman and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131: 339–456.

Günther, A. C. L. G. 1860. Catalogue of the acanthopterygian fishes in the collection of the British Museum, Vol. 2. British Museum, London. xxi + 548 pp.

Harrison, I. and G. Howes. 1991. The pharyngobranchial organ of mugilid fishes; its structure, variability, ontogeny, possible function and taxonomic utility. Bull. Brit. Mus. Nat. Hist. (Zool.) 57: 111–132.

Hartel, K. E. and M. L. J. Stiassny. 1986. The identification of larval *Parasudis* (Teleostei, Chlorophthalmidae); with notes on the anatomy and relationships of aulopiform fishes. Breviora 487: 1–23.

Heemstra, P. C. 1980. A revision of the zeid fishes (Zeiformes: Zeidae) of South Africa. Ichthyol. Bull. J. L. B. Smith Inst. 41: 1–18.

———. 1986. No. 141: Family Zeniontidae. Page 441 *in* M. M. Smith and P. C. Heemstra, eds. Smith's sea fishes. Springer-Verlag, Berlin.

Herrick, C. J. 1899. The cranial and first spinal nerves of *Menidia*; a contribution upon the nerve components of the bony fishes. J. Comp. Neurol. 9: 157–455.

Howes, G. J. 1992. Notes on the anatomy and classification of ophidiiform fishes, with particular reference to the abyssal genus *Acanthonus* Günther, 1878. Bull. Brit. Mus. Nat. Hist. (Zool.) 58: 95–131.

Ida, H. 1976. Removal of the family Hypoptychidae from the suborder Ammodytoidei, order Perciformes, to the suborder Gasterosteoidei, order Syngnathiformes. Jap. J. Ichthyol. 23: 33–42.

Jakubowski, M. 1974. Structure of the lateral-line canal system and related bones in the berycoid fish *Hoplostethus mediterraneus* Cuv. et Val. (Trachichthyidae, Pisces). Acta Anat. 87: 261–274.

Johnson, G. D. 1975. The procurrent spur, an undescribed perciform character and its phylogenetic implications. Occas. Pap. Calif. Acad. Sci. 121: 1–23.

———. 1984. Percoidei: development and relationships. Pages 464–498 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

———. 1986. Scombroid phylogeny: an alternative hypothesis. Bull. Mar. Sci. 39: 1–41.

———. 1992. Monophyly of the euteleostean clades—Neoteleostei, Eurypterygii, and Ctenosquamata. Copeia 1992: 8–25.
———. 1993. Percomorph phylogeny: progress and problems. Bull. Mar. Sci. 52: 3–28.
——— and R. H. Rosenblatt. 1988. Mechanisms of light organ occlusion in flashlight fishes, family Anomalopidae (Teleostei: Beryciformes), and the evolution of the group. Zool. J. Linn. Soc. 94: 65–96.
——— and B. B. Washington. 1987. Larvae of the moorish idol, *Zanclus cornutus*, including a comparison with other larval acanthuroids. Bull. Mar. Sci. 40: 494–511.
Johnson, R. K. 1974. A revision of the alepisauroid family Scopelarchidae (Pisces, Myctophiformes). Fieldiana (Zool.) 66: ix + 1–249.
———. 1982. Fishes of the families Evermanellidae and Scopelarchidae: systematics, morphology, interrelationships, and zoogeography. Fieldiana (Zool.) N.S. 12: xiii + 1–252.
Jollie, M. 1954. The general anatomy of *Lampanyctus leucopsarus*. Unpubl. Ph.D. Dissertation, University Microfilms, Ann Arbor, Michigan. 239 pp.
———. 1969. Sensory canals of the snout of actinopterygian fishes. Trans. Ill. Acad. Sci. 62: 61–69.
Jungersen, H. F. E. 1908. Ichthyotomical contributions. I. The structure of the genera *Amphisile* and *Centriscus*. K. Dansk. Vidensk. Selsk. Skrifter (7) 2: 6–107.
———. 1910. Ichthyotomical contributions. II. The structure of the Aulostomidae, Syngnathidae and Solenostomidae. K. Dansk. Vidensk. Selsk. Skrifter (7) 8: 267–364.
———. 1915. Some facts regarding the anatomy of the genus *Pegasus*. Rep. Br. Ass. Advmt. Sci. 1914: 420–422.
Kanayama, T. 1991. Taxonomy and phylogeny of the family Agonidae (Pisces: Scorpaeniformes). Mem. Fac. Fish. Hokkaido Univ. 38: 1–199.
Keene, M. J. and K. A. Tighe. 1984. Beryciformes: development and relationships. Pages 383–392 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.
Kotlyar, A. N. 1990. Osteology of the suborder Stephanoberycoidei. Communication 1. The Stephanoberycidae and Gibberichthyidae. J. Ichthyol. 30: 804–816.
———. 1991a. The osteology of the suborder Stephanoberycoidei. 2. Melamphaidae. J. Ichthyol. 31: 24–39.
———. 1991b. Osteology of *Hispidoberyx ambagiosus* (Hispidoberycidae) and its position within the Beryciformes. J. Ichthyol. 31: 355–362.
Kotthaus, A. 1970. Fische des Indischen Ozeans. A. Systematischer Teil, VI: Anacanthini (2), Berycomorphi, Zeomorphi. "Meteor"-Forsch.-Ergebnisse D5: 53–70.
Lauder, G. V. and K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes. Bull. Mus. Comp. Zool. 150: 95–197.
Leis, J. M. 1984a. Tetraodontoidei: development. Pages 447–450 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.
———. 1984b. Tetraodontiformes: relationships. Pages 459–463 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.
Mabee, P. M. In Press. Phylogenetic interpretation of ontogenetic change: sorting out the actual and artifactual in an empirical case study of centrarchid fishes. Zool. J. Linn. Soc.
Markle, D. F. 1989. Aspects of character homology and phylogeny of the Gadiformes. Pages 60–88 *in* D. M. Cohen, ed. Papers on the systematics of gadiform fishes. Nat. Hist. Mus. Los Angeles County Sci. Ser. 32.
——— and J. E. Olney. 1990. Systematics of the pearlfishes (Pisces: Carapidae). Bull. Mar. Sci. 47: 269–410.
Matsuura, Y. and M. Katsuragawa. 1985. Osteological development of fins and their supports of larval grey triggerfish, *Balistes capriscus*. Jap. J. Ichthyol. 31: 411–421.
McAllister, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. Bull. Nat. Mus. Canada, 221, xiv + 239 pp.
Mok, H. and H. Chang. 1986. Articulation of the pelvic spine in acanthopterygian fishes, with notes on its phylogenetic implications. Jap. J. Ichthyol. 33: 145–149.
——— and S. Shen. 1983. Osteology and phylogeny of Squamipinnes. Spec. Publ. Taiwan Mus. 1: 1–87.
Mooi, R. D. 1993. Phylogeny of the Plesiopidae (Pisces: Perciformes) with evidence for the inclusion of the Acanthoclinidae. Bull. Mar. Sci. 52: 284–326.
Moore, J. A. 1993. The phylogeny of the Trachichthyiformes (Teleostei: Percomorpha). Bull. Mar. Sci. 52: 114–136.

Mundy, B. C. 1990. Development of larvae and juveniles of the alfonsins, *Beryx splendens* and *B. decadactylus* (Berycidae, Beryciformes). Bull. Mar. Sci. 46: 257–273.

Nafpaktitis, B. and J. R. Paxton. 1978. *Idiolychnus*, a new genus of Myctophidae based on *Diaphus urolampus*. Copeia 1978: 492–497.

Nelson, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Am. Mus. Nat. Hist. 141: 475–552.

———. 1989. Phylogeny of major fish groups. Pages 325–336 *in* B. Fernholm, K. Bremer and H. Jörnvall, eds. The hierarchy of life. Excerpta Medica, Amsterdam.

Nelson, J. S. 1971. Comparison of the pectoral and pelvic skeletons and of some other bones and their phylogenetic implications in the Aulorhynchidae and Gasterosteidae (Pisces). J. Fish. Res. Bd. Canada 28: 427–442.

———. 1978. Review of "The biology of the sticklebacks" by R. J. Wooton. Copeia 1978: 552–554.

———. 1984. Fishes of the world, 2nd ed. John Wiley and Sons, New York. xv + 523 pp.

Okiyama, M., ed. 1988. An atlas of the early stage fishes in Japan. Tokai University Press, Tokyo. (In Japanese)

Olney, J. E. 1984. Lampriformes: development and relationships. Pages 368–379 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

———, G. D. Johnson and C. C. Baldwin. 1993. Phylogeny of lampridiform fishes. Bull. Mar. Sci. 52: 137–169.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). Bull. Am. Mus. Nat. Hist. 168: 335–557.

———. 1993. Relationships of atherinomorph fishes (Teleostei). Bull. Mar. Sci. 52: 170–196.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. Phil. Trans. R. Soc. London 247: 213–482.

———. 1967. New Cretaceous berycoid fishes from the Lebanon. Bull. Brit. Mus. Nat. Hist. (Geol.) 14: 67–109.

———. 1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bull. Brit. Mus. Nat Hist. (Geol.) 17: 47–102.

———. 1993. An overview of the early fossil record of acanthomorphs. Bull. Mar. Sci. 52: 29–59.

——— and D. E. Rosen. 1989. The Paracanthopterygii revisited: order and disorder. Pages 5–36 *in* D. M. Cohen, ed. Papers on the systematics of gadiform fishes. Nat. Hist. Mus. Los Angeles County Sci. Ser. 32.

Pietsch, T. W. 1978. Evolutionary relationships of the sea moths (Teleostei: Pegasidae) with a classification of gasterosteiform families. Copeia 1978: 517–529.

Prashad, B. and D. D. Mukerji. 1929. The fish of Indawgyi Lake and the streams of the Myitkyina district (Upper Burma). Rec. Indian Mus. 31: 161–213.

Randall, J. E., T. Shimizu and T. Yamakawa. 1982. A revision of the holocentrid fish genus *Ostichthys*, with descriptions of four new species and a related new genus. Jap. J. Ichthyol. 29: 1–26.

Rauther, M. 1925. Die Syngnathiden des Golfes von Neapel. Fauna Flora Golfo Napoli 36: i–xi + 1–365.

Regan, C. T. 1910. The anatomy and classification of the teleostean fishes of the order Zeomorphi. Ann. Mag. Nat. Hist. (8) 6: 481–484.

———. 1912. The anatomy and classification of the symbranchoid eels. Ann. Mag. Nat. Hist. (8) 12: 387–390.

Riess, J. A. 1881. Der Bau der Kiemenblatten bei Knochenfischen. Arch. Naturgesch. 47: 518–550.

Roberts, C. 1993. The comparative morphology of spined scales and their phylogenetic significance in the Teleostei. Bull. Mar. Sci. 52: 60–113.

Roe, L. J. 1991. Phylogenetic and ecological significance of Channidae (Osteichthyes, Teleostei) from the early Eocene Kuldana Formation of Kohat, Pakistan. Contr. Mus. Paleont. Univ. Mich. 28: 93–100.

Rosen, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Bull. Am. Mus. Nat. Hist. 127: 217–268.

———. 1973. Interrelationships of higher teleostean fishes. Pages 397–513 *in* P. H. Greenwood, R. S. Miles and C. Patterson, eds. Interrelationships of fishes. Academic Press, London.

———. 1984. Zeiforms as primitive plectognath fishes. Am. Mus. Novit. 2782: 1–45.

———. 1985. An essay on euteleostean classification. Am. Mus. Novit. 2827: 1–57.

——— and P. H. Greenwood. 1976. A fourth Neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes. Bull. Am. Mus. Nat. Hist. 157: 1–70.

——— and L. R. Parenti. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. Am. Mus. Novit. 2719: 1–25.

——— and C. Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. Bull. Am. Mus. Nat. Hist. 141: 357–474.

——— and ———. 1990. On Muller's and Cuvier's concepts of pharyngognath and labyrinth fishes and the classification of percomorph fishes, with an atlas of percomorph dorsal gill arches. Am. Mus. Novit. 2983: 1–57.

——— and A. Rumney. 1972. Evidence of a second species of *Synbranchus* (Pisces, Teleostei) in South America. Am. Mus. Novit. 2497: 11–45.

Springer, V. G. 1983. *Tyson belos,* new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobiod osteology and classification. Smithson. Contrib. Zool. 390: 1–40.

———. 1988. *Rotuma lewisi,* new genus and species of fish from the southwest Pacific (Gobioidei, Xenisthmidae). Proc. Biol. Soc. Wash. 101: 53–539.

Starks, E. C. 1898. The osteology and relationships of the family Zeidae. Proc. U.S. Nat. Mus. 21: 469–476.

———. 1902. The shoulder girdle and characteristic osteology of the hemibranchiate fishes. Proc. U.S. Nat. Mus. 25: 619–634.

Stewart, J. D. 1984. Taxonomy, paleoecology, and stratigraphy of the halecostome-inoceramid associations of the North American Upper Cretaceous epicontinental seaways. Ph.D. Thesis, University of Kansas, Lawrence. 201 pp.

Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. J. Zool. London (B) 1986: 411–460.

———. 1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). Am. Mus. Novit. 2979: 1–33.

———. 1993. What are grey mullets? Bull. Mar. Sci. 52: 197–219.

——— and J. A. Moore. 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph intrarelationships. Zool. J. Linn. Soc. 104: 209–242.

Taverne, L. 1977. Ostéologie, phylogénèse et systématique des téléostéens fossiles et actuels du superordre des Ostéoglossomorphes. Première partie. Ostéologie des genres *Hiodon, Eohiodon, Lycoptera, Osteoglossum, Scleropages, Heterotis* et *Arapaima.* Mém. Cl. Sci. Acad. R. Belgique, 8^vo^, 2, 42: 1–234.

Tighe, K. A. and M. J. Keene. 1984. Zeiformes: development and relationships. Pages 393–398 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Travers, R. A. 1981. The interarcual cartilage; a review of its development, distribution and value as an indicator of phylogenetic relationships in euteleostean fishes. J. Nat. Hist. 15: 853–871.

———. 1984a. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part I: Anatomical descriptions. Bull. Br. Mus. Nat. Hist. (Zool.) 46: 1–133.

———. 1984b. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: Phylogenetic analysis. Bull. Br. Mus. Nat. Hist. (Zool.) 47: 83–150.

Tyler, J. C., G. D. Johnson, I. Nakamura and B. B. Collette. 1989. Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). Smithson. Contrib. Zool. 485: 1–78.

Washington, B. B., H. G. Moser, W. A. Laroche and W. J. Richards. 1984. Scorpaeniformes: development. Pages 405–428 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Watson, W., A. C. Matarese and E. G. Stephens. 1984. Trachinoidea: development and relationships. Pages 554–561 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. no. 1.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the Teleostei. Proc. Acad. Nat. Sci. Philadelphia 125: 225–317.

———. 1993. The search for the gobioid sister group (Actinopterygii; Percomorpha). Bull. Mar. Sci. 52: 395–414.

Woods, L. P. and P. M. Sonoda. 1973. Order Berycomorphi (Beryciformes). Mem. Sears Found. Mar. Res. 1, 6: 263–396.

Yamamoto, M. 1982. Comparative morphology of the peripheral olfactory organ in teleosts. Pages 39–59 *in* T. J. Hara, ed. Chemoreception in fishes. Developments in Aquaculture and Fisheries Science 8. Elsevier Sci. Publ. Co., Amsterdam.

Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei). Evol. Monog. 1: 1–389.

———. 1987. Osteology and evolutionary relationships of the boarfish genus *Antigonia* (Teleostei: Caproidae). Copeia 1987: 564–592.
———. 1991. Phylogenetic relationships of the boarfishes (Teleostei: family Caproidae). Am. Zool. 31: 61A.

DATE ACCEPTED: August 3, 1992.

ADDRESSES: *(G.D.J.) Division of Fishes, Department of Vertebrate Zoology, National Museum of Natural History, Washington, D.C. 20560; (C.P.) Department of Palaeontology, British Museum (Natural History), London SW7 5BD, U.K.*