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## Monophyly of the Euteleostean Clades—Neoteleostei, Eurypterygii, and Ctenosquamata

G. DAVID JOHNSON

Although the integrity of Rosen's Neoteleostei, Eurypterygii, and Ctenosquamata has been maintained in most subsequent classifications, the evidence cited for monophyly of each clade is conspicuously disparate. Previously proposed synapomorphies are reviewed and evaluated based on my own assessment and/or that of other authors. Those that appear least ambiguous with respect to a hypothesis of monophyly for each clade are identified. Three previously unrecognized structural innovations, each congruent with a different clade, afford new evidence of monophyly. At the level of the Neoteleostei (stomiiforms and above), concomitant with the advent of the retractor dorsalis muscle, there is a shift in the insertion of the third internal levator from the dorsal surface of the fourth pharyngobranchial cartilage to the fifth upper pharyngeal toothplate. At the level of the Eurypterygii (aulopiforms and above), the medial pelvic radial fuses with the ventral half of the medial pelvic ray in early ontogeny. At the level of the Ctenosquamata (myctophids, neoscopelids, and above), the fifth upper pharyngeal toothplate is absent and with it the associated third internal levator. Recognition of the unique ctenosquamate synapomorphy follows from the resolution, based partially on ontogenetic evidence, of long-standing confusion about the identity of the fourth and fifth upper pharyngeal toothplates in higher euteleosts.

IN his seminal work emphasizing the dorsal gill arch elements, upper jaws, and caudal skeleton, Rosen (1973) proposed the first ostensibly resolved phylogenetic hypothesis of the cladistic relationships among major groups of higher euteleostean fishes. Among the major conclusions of that work (Fig. 1) were (1) diagnosis of a monophyletic Neoteleostei, in which Rosen included the stomiiforms as the sister group of a monophyletic Eurypterygii (all other neoteleosts); (2) separation of the old myctophiforms (=Iniomi, sensu Gosline et al., 1966) into two monophyletic lineages, a newly restricted Myctophiformes (myctophids and neoscopelids) and the Aulopiformes (all other myctophiforms, giganturids and various fossil genera); and (3) placement of aulopiforms as the sister group of a monophyletic Ctenosquamata, in which the new Myctophiformes is the sister group of the Acanthomorpha. In the introduction to her treatise on the limits and interrelationships of acanthomorph fishes, Stiassny (1986) referred to the "phylogenetic reality" of the Neoteleostei, Eurypterygii, and Ctenosquamata, implying that these groups generally have been accepted by subsequent authors as originally delineated by Rosen (1973). Although it is true that the monophyly of these clades has

not been challenged seriously, except by Rosen himself (1985) (Fig. 2), there is substantial disparity in the evidence that has been cited subsequently in support of their monophyly (i.e., synapomorphy lists for each). For example, of eight synapomorphies listed in total for the Neoteleostei by Rosen (1973), Fink and Weitzman (1982), Lauder and Liem (1983), and Rosen (1985), only one is common to all four lists. This ambivalence is exacerbated by the fact that characters frequently have been rejected or ignored with no justification or discussion.

I encountered this confusing state of affairs in the early stages of an investigation of the affinities of the rare Japanese fish *Pseudotrichonotus altivelis* Yoshino and Araga (in Masuda et al., 1975), described originally as a myctophiform but suggested by Johnson (1982) to be more advanced. To confidently place this fish within one or another clade of higher euteleosts, I found it necessary to attempt to sort out what might be considered "valid" synapomorphies from some of the more ambiguous evidence that has been set forth. My goal was not to undertake an overall parsimony analysis but to examine proposed characters independently to evaluate their homology based on both the morphological evidence and congruence with

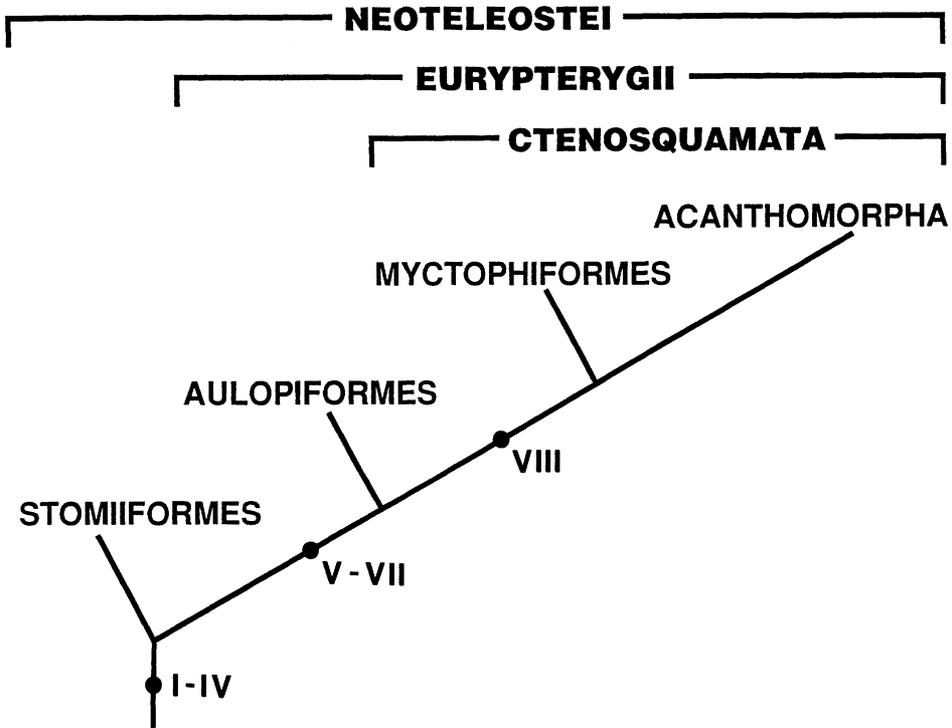


Fig. 1. Cladogram of relationships among three euteleostean clades, as proposed by Rosen (1973). Roman numerals refer to characters so numbered in text.

Rosen's (1973) hypothesis. In particular, because of the apparent ambiguity of many of these characters, I wanted to identify what, if any, were the unique, unreversed synapomorphies of the major clades; these would provide the most satisfying solution to the placement of *Pseudotrichonotus*. In the course of my review, three additional characters came to light, each providing cogent evidence for the monophyly of Rosen's Neoteleostei, Eurypterygii, and Ctenosquamata. The primary purpose of this paper is to describe these unique synapomorphies, two of which are founded in evidence from early ontogeny, and demonstrate their congruence with each clade. Additionally, I discuss my review of previously proposed synapomorphies and identify those that appear to be the least ambiguous based on my own assessment and/or that of other authors. This paper will provide the foundation for a more detailed study of the precise relationships of *Pseudotrichonotus*, which will not be considered further here (see Johnson, Okiyama, and Tominaga, 1989, unpubl. abstract, Third International Conference on Indo-Pacific Fishes).

In this paper, I follow the taxonomic nomenclature of Rosen (1973), unless otherwise stated. The Aulopiformes comprises two subgroups, the Aulopoidei (Aulopidae, Chlorophthalmidae, Bathysauridae, Scopelosauridae, Bathypetroidae, and Ipnopidae) and the Alepisauridae (Alepisauridae, Omosudidae, Scopelarchidae, Evermannellidae, Harpadontidae, Synodontidae, Anopteroidei, Paralepididae, and Pseudotrichonotidae, the latter not considered by Rosen); however, work in progress on *Pseudotrichonotus* indicates that aulopids are the sister group of synodontoids (Synodontidae, Harpadontidae, and Pseudotrichonotidae). The Myctophiformes includes only the Myctophidae and Neoscopelidae. Giganturids and fossil taxa were not considered in the present study.

#### NEOTELEOSTEI

Rosen (1973) diagnosed a monophyletic Neoteleostei (Stomiiformes + Aulopiformes + Myctophiformes + Acanthomorpha) based on three synapomorphies: (1) presence of a retractor dorsalis muscle; (2) presence of ascend-



ambiguous evidence for monophyly of the Neoteleostei:

*I. Exoccipitals and basioccipitals exposed posteriorly and joined by an inverted Y-shaped suture.*—Among the works discussed above, only Lauder and Liem (1983) omitted a tripartite occipital condyle from their list of neoteleost synapomorphies and, because they offered no justification, that omission may have been inadvertent. A detailed examination of this highly complex character was beyond the scope of my study. A comprehensive investigation of its ontogeny is needed and could provide important insight concerning homology. For the present, I have no reason to challenge the assessments of Rosen (1973) and Fink and Weitzman (1982), particularly in light of Rosen's (1985) more critical appraisal of structural homology. In the latter paper, Rosen suggested possible independent origin of a similar configuration below neoteleosts but did not reject the neoteleost configuration as synapomorphic.

*II. Type 4 tooth attachment.*—Fink (1981) and Fink and Weitzman (1982) presented logical arguments for the interpretation of Type 4 depressible teeth as a neoteleostean specialization, even though they occur in a relatively small percentage of neoteleosts. This type of tooth attachment, in which the teeth are hinged with a posterior axis of rotation, results from suppression of mineralization and loss of collagen from the anterior basal surface of the tooth (Fink, 1981). It characterizes juveniles of several primitive stomiiforms as well as adults of some others, is common in primitive eurypterygians, and has been retained in a few acanthopterygians. Type 4 teeth are known to occur among more primitive teleosts only in *Esox*, where parsimony and a different pulp cavity morphology indicate an independent origin.

*III. A retractor dorsalis muscle.*—Of the eight synapomorphies previously proposed for the Neoteleostei, there has been unanimous agreement about only one, the presence of a retractor dorsalis muscle. This muscle, extending from the anterior vertebrae to the dorsal gill arch elements, is a consistent feature of neoteleosts and is surely one of the major structural and functional innovations in teleostean evolution. Although musculature between the vertebral column and dorsal gill arch elements occurs in a few lower euteleosts (e.g., *Pantodon*, *Amia*, *Lep-*

*isosteus*, some muraenid eels, some cyprinids, siluriforms), it generally has been interpreted as nonhomologous with the retractor dorsalis of neoteleosts (for discussion and further references, see Nelson, 1967, 1969). I believe that homology of the neoteleost retractor dorsalis is corroborated by an associated modification of the dorsal gill arch muscles of primitive neoteleosts (stomiiforms and aulopiforms). This modification, a shift in the insertion of the third internal levator, is described below as a fourth neoteleost specialization.

*IV. Insertion of the third internal levator on the fifth upper pharyngeal toothplate.*—Internal levator muscles originate on the cranium and insert on the pharyngobranchials. Primitively, euteleosts have three, the first inserting on the ossified second pharyngobranchial, the second on the ossified third pharyngobranchial, and the third along the dorsal surface of the fourth pharyngobranchial cartilage (Fig. 3A). Insertion of the third internal levator on the fourth pharyngobranchial cartilage characterizes all nonneoteleosts that I have examined, including those mentioned above that have some sort of retractor musculature. With the advent of the neoteleost retractor dorsalis, however, there is a shift in the insertion of all or most of the third internal levator from the fourth pharyngobranchial cartilage to the fifth upper pharyngeal toothplate (Fig. 3B–C). This arrangement appears functionally effectual, because it provides for a forward pull on the fifth toothplate acting antagonistically to the backward pull of the retractor dorsalis on that element. Insertion of the third internal levator on the fifth upper pharyngeal toothplate uniquely characterizes stomiiforms and aulopiforms; the remaining neoteleosts (ctenosquamates) lack both the third internal levator and fifth upper toothplate (see below). Nelson's (1967) erroneous observation that *Aulopus* lacks a third internal levator probably resulted from his failure to recognize the shift in its insertion. I interpret the shift in the insertion of the third internal levator as an unequivocal synapomorphy of the Neoteleostei, one that lends credence to the homology of the neoteleost retractor dorsalis.

Fink (1984) noted the presence of a retractor dorsalis in *Lepidogalaxias*. He cited this as evidence suggesting that *Lepidogalaxias* could be the sister group of neoteleosts, although he pointed out other characters that conflict with this hypothesis. Subsequently, Begle (1991) has

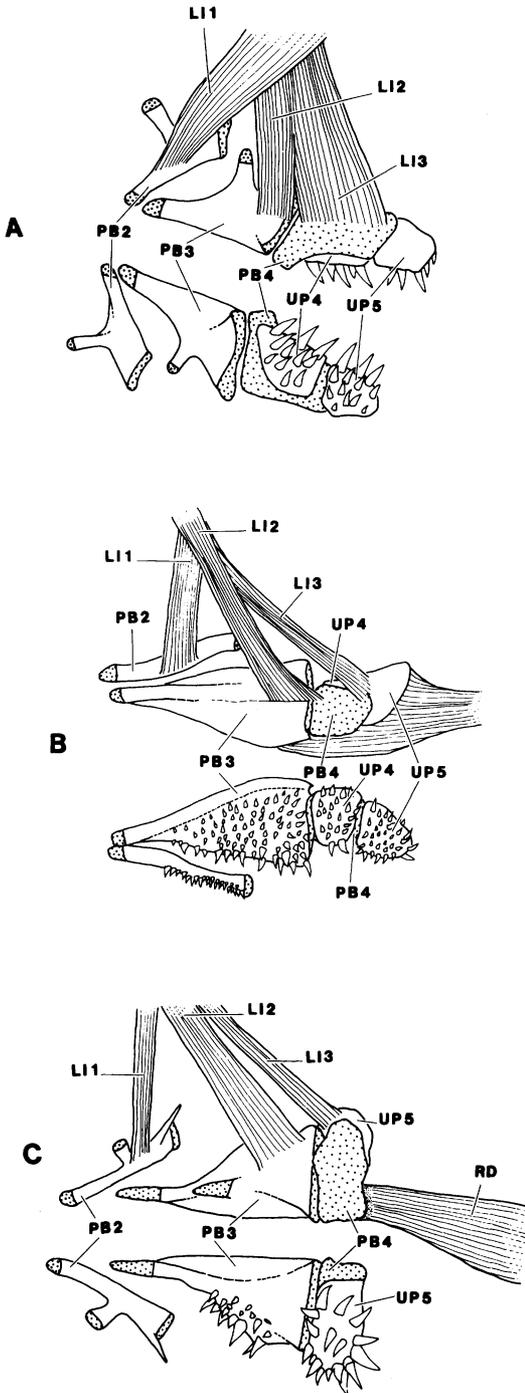


Fig. 3. Pharyngobranchials (PB) 2-4 with toothplates, showing upper pharyngeal toothplates (UP) 4-5, internal levators (LI) 1-3, and retractor dorsalis (RD), right side, medial and ventral views; stippling denotes cartilage. (A) *Argentina striata*, USNM 188212,

proposed that *Lepidogalaxias* is part of a monophyletic Osmeroidei and, thus, could not be the sister group of neoteleosts. It is worth noting, in this regard, that *Lepidogalaxias*, unlike neoteleosts, retains insertion of the third internal levator on the fourth pharyngobranchial cartilage. Lack of the associated neoteleost modification is at least consistent with an independent origin of the "retractor dorsalis" of *Lepidogalaxias*, although it does not specifically refute the *Lepidogalaxias*-neoteleost hypothesis.

#### EURYPTERYGII

Of eight synapomorphies listed by Rosen (1973) for his Eurypterygii (Aulopiformes + Myctophiformes + Acanthomorpha), all but one were seriously challenged by Fink and Weitzman (1982), and most were rejected convincingly. Nonetheless, these authors accepted the monophyly of Rosen's Eurypterygii, diagnosable by the presence of a toothplate fused to the third epibranchial. They also allowed that Rosen's seventh character, reduction of the second preural neural spine to a half spine, might be diagnostic and added a eurypterygian synapomorphy described by Lauder (1982, 1983) but erroneously attributed by Fink and Weitzman (1982) to Lauder (1981), presence of an interoperculothyoid ligament (inappropriately listed by Rosen [1985] as a neoteleostean synapomorphy and erroneously attributed to Lauder and Liem [1983]).

Lauder and Liem (1983), largely following Fink and Weitzman (1982), showed four eurypterygian synapomorphies on their cladogram: (1) reduction of the second preural neural spine to a half spine; (2) replacement of the mandibulothyoid ligament with an interoperculothyoid ligament; (3) fusion of a toothplate to the third epibranchial; and (4) retractor dorsalis with a tendinous insertion on the third pharyngobranchial. No explanation of the fourth character was given, and Rosen's (1973) illustrations and my own observations indicate that it is not diagnostic for eurypterygians. In some aulopiform genera (e.g., *Aulopus*, *Trachinocephalus*), the retractor dorsalis has direct muscular insertion

←

128.5 mm SL; (B) *Aulopus japonicus*, AMNH 28635, 97 mm SL; (C) *Maurolicus mulleri*, USNM 302396, 41.8 mm SL.

on the third pharyngobranchial, and in others (e.g., *Synodus*, *Lesidium*), it has no insertion of any type on that bone. The validity of a reduced neural spine on the second preural as a eurypterygian synapomorphy is also suspect, given its widespread occurrence among preneoteleosts (C. Patterson, pers. comm.). A somewhat shortened NPU2 characterizes some of the most primitive teleosts such as *Pholidophorus*, *Leptolepis*, and *Tharsis* (Patterson and Rosen, 1977, figs. 31, 33, 35). Furthermore, a bladeliike half-spine much like that seen in eurypterygians occurs in the fossil elopoccephalan *Anaethalion* (Patterson and Rosen, 1977, figs. 39, 41–44), in *Elops* (Monod, 1968, figs. 20–24), in the fossil salmoniforms *Gaudryella* and *Humbertia* (Patterson, 1970, figs. 13, 14, 27), and in primitive osmeroids (Patterson, 1970, figs. 42, 43).

Rosen (1985) rejected the monophyly of his (1973) Aulopiformes and Myctophiformes, placing the alepisauroids in an unresolved trichotomy with stomiiforms and the remaining eurypterygians, within which there was also uncertainty about the placement of neoscopelids, "chlorophthalmids" and "aulopoids" in relation to the ctenosquamates (Fig. 2). A consequence of this new proposal, not adequately discussed by Rosen (1985), is that the monophyly of his (1973) Eurypterygii is also rejected. Rosen (1985) suggested that a new Eurypterygii would "come to include the Ctenosquamata and perhaps the Chlorophthalmidae and some aulopoids." However he did not explicitly elaborate his reasons for excluding the alepisauroids and made no mention of the characters cited in Lauder and Liem (1983) as diagnostic of the old Eurypterygii, nor of the unique configuration of the dorsal-gill arch elements that he described (Rosen, 1973) as evidence for monophyly of the Aulopiformes.

Although Rosen (1985) provided an insightful review of occipital anatomy and its bearing on the monophyly of the Neoteleostei, he seems to have brought, in that paper, more confusion than resolution to the problem of eurypterygian limits and intrarelations. I find myself in the awkward position of having to criticize a paper that was written at a time when Rosen was seriously ill, and, as Patterson has pointed out (Rosen and Patterson, 1990), the thoroughness with which he could approach a problem was understandably limited. In so doing, in no way do I intend to demean Rosen's seminal and prodigious contribution to our knowledge of the

anatomy and phylogeny of fishes. Nonetheless, the 1985 paper exists, with its shortcomings, and because I disagree with the conclusions, I have no choice but to explain why.

A major part of the problem with Rosen's (1985) analysis is that many characters are substantially more variable than indicated by their distribution on the cladogram. This is not unique to the 1985 paper (true also of Rosen, 1973), but in the 1985 paper, the confusion is aggravated by a lack of systematic treatment of previously accepted, and subsequently unchallenged, synapomorphies, the use of nebulous taxonomic groupings (e.g., "aulopoids" and "chlorophthalmids"), and by a number of internal inconsistencies in the text. For example, "aulopoids" (said to include at least *Aulopus*, but, for no cited reasons, also possibly bathysaurids, bathypteroids, and ipnopids, but not *Chlorophthalmus*) are hypothesized as the sister group of ctenosquamates based on nine synapomorphies, none of which is discussed and all of which I believe are problematic.

In the following listing of these characters, I briefly note the problems associated with their interpretation as synapomorphic at this level: (1) high-set pectorals and (2) subthoracic pelvics (characters of degree, both variable among aulopiforms and showing advanced states in some alepisauroids; e.g., synodontids, where they are about equivalent in position to those of many myctophiforms); (3) ctenoid scales (true ctenoid scales [sensu Johnson 1984] occur only among percomorphs; the serrate or spiny scales that characterize *Aulopus* also characterize *Chlorophthalmus*, are present among myctophiforms only in the neoscopelid *Solvomer* and the myctophids *Notoscopelus* and a few species of *Myctophum* [see Johnson, 1982] and have a spotty distribution among acanthomorphs; spiny scales are found also among stomiiforms, e.g., *Chauliodus* and ostariophysans); (4) three or fewer supraneurals (three or fewer characterize many stomiiforms, and most aulopiforms, including many alepisauroids); (5) reduced spine on NPU2 (a eurypterygian synapomorphy in Rosen [1973], Fink and Weitzman [1982], and Lauder and Liem [1983] characterizes all aulopiforms, including alepisauroids; treated elsewhere by Rosen [1985] as a synapomorphy of "osmeroids" and neoteleosts, see below); (6) derived premaxillary morphology (not described, but presumably the form of the symphyseal or ascending process; Stiassny [1986] concluded that homologies of the ele-

vation medial to the articular process on the premaxillae of various nonacanthomorphs are not clear); (7) type of retractor dorsalis (not described); (8) toothplate fused to third epibranchial (present in most alepisauroids and treated as a eurypterygian synapomorphy by Rosen [1973], Fink and Weitzman [1982], and Lauder and Liem [1983]); and (9) median rostral cartilage (homologies of rostral structures among aulopiforms and myctophiforms rejected by Hartel and Stiassny [1985]). Having listed those nine synapomorphies of "aulopoids" and ctenosquamates, Rosen (1985), without further discussion, listed only three of them in his final "synapomorphy scheme": median rostral cartilage, subthoracic pelvics, and three supra-neurals. The remaining six were either not mentioned at all or listed as synapomorphies at other levels. This represents only one example of numerous discrepancies that cast doubt on the validity of Rosen's (1985) hypotheses and, at the very least, make them extremely difficult to evaluate.

Stiassny (1986) agreed with Rosen's proposal that neither the Aulopoidei nor the Aulopiformes of Rosen (1973) are monophyletic, but for different reasons. She placed a group of aulopoids, specifically *Aulopus*, *Chlorophthalmus*, and *Parasudis*, as the sister group of the Ctenosquamata based on their possession of an elevated and reoriented cranial condyle of the head of the maxilla and the concomitant exposure of a maxillary saddle for the reception of a "palatine prong" on the head of the palatine. Like Rosen (1985), Stiassny did not mention the distinctive configuration of the dorsal gill arch elements used by Rosen (1973) to defend aulopiform monophyly. That unique configuration involves lateral displacement of the second pharyngobranchial, concomitant elongation of the uncinat process of the second epibranchial, and (not noted by Rosen, 1973) absence of a cartilaginous condyle on the third pharyngobranchial for articulation of the second epibranchial; it is obviously a fairly complex specialization that is unlikely to have arisen independently, as would be the case if aulopiforms are not monophyletic. Stiassny's (1986) hypothesis is also at odds with that of Johnson et al. (1989), which places *Aulopus* as the sister group of the synodontoids. It does not, however, challenge the monophyly of Rosen's (1973) original Eurypterygii, and consequently, Stiassny (1986) did not discuss evidence, pro or con, relating to the integrity of that assemblage, although she

alluded to its "phylogenetic reality" in her introduction.

I conclude from all of this, and from my additional observations, that the monophyly of the Eurypterygii, as originally conceived by Rosen (1973), has not been challenged seriously and that it is supported by three synapomorphies, one of which has not been previously recognized as such.

V. *A toothplate fused to the third epibranchial.*—A fused third epibranchial toothplate (EB3TP) is unique to eurypterygians, though not universally present within the clade. Absence of the EB3TP in some myctophids is most parsimoniously interpreted as reversal. The same is true for its absence in only some members of the alepisauroid families Paralepididae (including *Anotopterus*), Evermanellidae, and Synodontidae and in the highly derived and closely related *Alepisaurus* and *Omosudis*. Loss of the EB3TP is also common among percomorphs (Johnson, 1981, 1984).

VI. *Presence of an interoperculohyoid ligament.*—My cursory observations support those of Lauder (1982, 1983) that a shift in insertion of the mandibulohyoid ligament to the interopercle (i.e., the advent of an interoperculohyoid ligament) diagnoses the Eurypterygii, but I have not done an exhaustive survey, nor did Lauder.

VII. *Fusion of the ventral half of the medial pelvic ray to the medial pelvic radial.*—Gosline (1961) described a specialized feature of the pelvic fin, fusion of the innermost radial with the ventral half of the innermost pelvic ray, and noted that it characterizes the great majority of "inimous" fishes. He also observed this condition in *Aphredoderus*, *Percopsis*, *Holocentrus*, *Chriodorus*, and *Ablennes* and interpreted this as evidence of an inimous derivation for the orders Percopsiformes, Beryciformes, and Beloniformes. Because he observed some variability (two exceptions among inioms, *Alepisaurus* and *Bathypterois*, see discussion below) and had done only a very cursory survey among other groups, and because this feature was not "of any great structural importance," Gosline (1961) believed it "inadvisable to push too far the inference that can be drawn . . . regarding genetic relationships." Gosline et al. (1966) described this character as one of several that distinguishes the Iniomi from isospondylous fishes, but Gosline (1971) did not mention it in his work

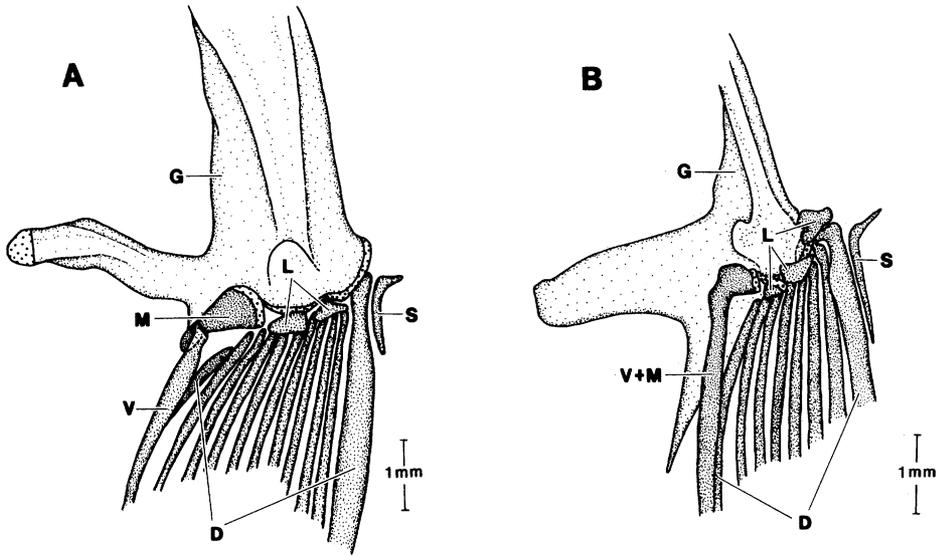


Fig. 4. Pelvic girdle (G), radials (L, lateral; M, medial), and fin rays (D, dorsal half; V, ventral half; V+M, ventral half fused with medial radial; S, splint); left side, ventral views; ventral halves of all except medial-most fin ray removed: (A) *Argentina striata*, USNM 188224, 127 mm SL; (B) *Percopsis omiscomaycus*, USNM 179711, 84.5 mm SL.

on functional morphology and teleostean classification, nor has it been considered in any subsequent treatment of teleostean relationships. My observations indicate that this feature is a synapomorphy of the Eurypterygii, and I describe it in more detail below.

Primitively in teleosts, there are three autogenous radials at the posterior margin of each half of the pelvic girdle with which the pelvic-fin rays articulate (Figs. 4A, 5A). The medial radial is the largest and has a configuration that differs substantially from that of the other two basically ovoid elements. It consists of an ossified, posteriorly tapering cone with a cartilaginous bulb or articular surface anteriorly. This distinctive larger medial radial also is present in more primitive actinopterygians, where there are more than three radials (e.g., *Amia*, Goodrich, 1930, fig. 206; and paleoniscoids, Gardiner, 1984, fig. 138), and it has been suggested (Stensio, 1921; Rosen et al., 1981; Gardiner, 1984) that it may represent a metapterygial element. Most frequently in teleosts, this medial radial is somewhat protracted and is slightly bent near midlength, such that the posterior portion lies approximately parallel to the shaft of the medial pelvic ray, its overall shape more or less resembling that of an inflated comma. An ossified medial pelvic radial with this configuration is lacking in osteoglossomorphs but present

in pholidophorids (C. Patterson, pers. comm.), elopiforms, clupeomorphs (where it is often more irregularly shaped), and lower euteleosts. Among euteleosts, it occurs in at least some ostariophysans (both in anotoophysans and otoophysans), argentinoids (Fig. 4A), osmeroids, salmonoids (Fig. 5A), and stomiiforms but not in esocoids, where there are no separate pelvic radials and the pelvic rays articulate directly with the cartilaginous posterior margin of the pelvic girdle (this is presumably a secondary condition, but I have not attempted to assess it). Although stomiiforms exhibit reductive trends in the morphology of the medial pelvic radial, including its complete absence, the ossified protracted cone or commalike configuration characterizes primitive members of the major stomiiform groups; sternoptychids (e.g., *Thorophos*, Weitzman, 1974, fig. 105), stomiids (e.g., *Neonesthes*, Fink, 1985, fig. 161), and gonostomatids (e.g., *Diplophos*, Fink and Weitzman, 1982, fig. 20).

In noneurypterygian euteleosts, the distinctive medial radial always remains fully autogenous (Figs. 4A, 5A), although in some groups (e.g., salmonids, osmerids, argentinoids), the ventral half of the medial one or two pelvic rays may be firmly attached to it by connective tissue. However, in all aulopiforms (Figs. 5B, 6A), except the Ipnopidae (including bathypteroids), in

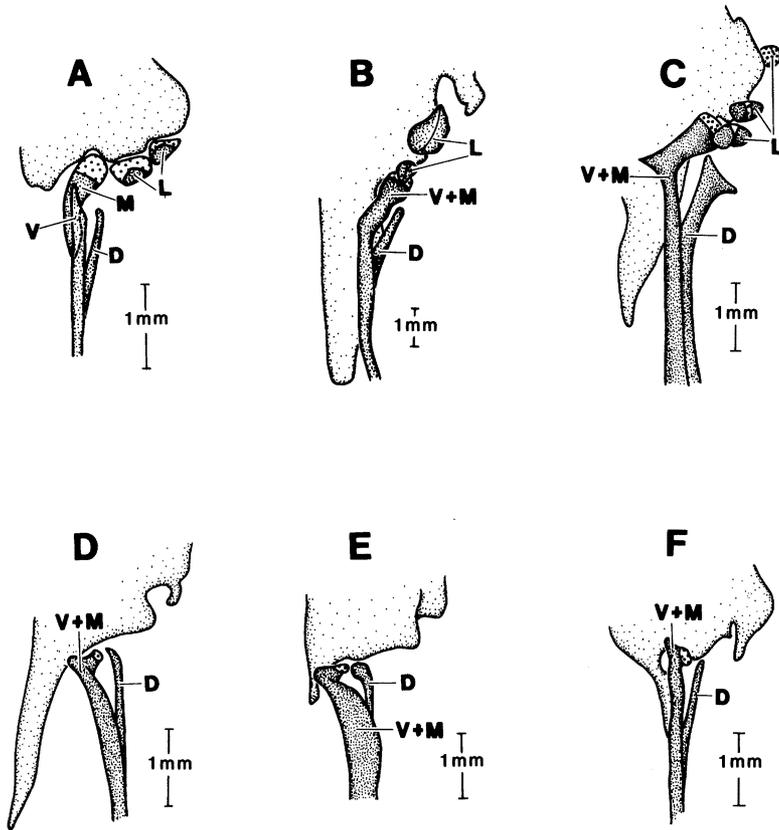


Fig. 5. Medial-most pelvic-fin ray (D, dorsal half; V, ventral half; V+M, ventral half fused with medial radial), radials (L, lateral; M, medial), and girdle margin (G); left side, ventral views: (A) *Salmo salar*, SU 49265, 78.3 mm SL; (B) *Parasudis truculentus*, USNM 159850, 96.1 mm SL; (C) *Neoscopelus macrolepidotus*, AMNH 49533, 100.5 mm SL; (D) *Setarches guentheri*, USNM 157704, 57.6 mm SL; (E) *Pronotogrammus aureorubens*, USNM 185228, 65.7 mm SL; (F) *Menidia beryllina*, USNM 200735, 53.0 mm SL.

all myctophiforms (Fig. 5C), and in most acanthomorphs (Figs. 4B, 5D–F, 6B), the medial radial fuses to the proximal end of the ventral half of the medial pelvic ray early in ontogeny. In its most primitive embodiment, as seen in aulopiforms, myctophiforms, *Polymixia*, and percipiforms (Fig. 4B), the coalesced medial radial remains large, and the ventral half of the medial ray is, consequently, somewhat reminiscent of a golf club. In these groups the two primary lateral radials are also well developed, and in some taxa, there may be an additional lateral radial associated with the lateral most ray.

I have done a broad, but not yet exhaustive, survey of this ventral ray/medial radial fusion among acanthomorphs; it is widespread and undoubtedly primitive for the group. Within acanthopterygians, the primitive golf-club form

characterizes some beryciforms (e.g., holocentrids and berycids), which also have two ossified lateral radials, and in other beryciforms (e.g., trachichthyoids), where the two lateral radials are lacking, the lateral process on the ventral ray is smaller. The latter condition is found among stephanoberycoids (e.g., melamphaeids, *Barbourisia*, *Gibberichthys*), but in *Rondeletia* and *Stephanoberyx* a free medial radial is embraced by the bases of the medial ray. If this free radial is the homolog of that present in noneurypterygians, rather than a neomorph, this is the only instance of reversal of medial radial fusion among acanthomorphs of which I am aware.

In most perciforms (Fig. 5D–E) and atheriniforms (Fig. 5F), wherein the two lateral radials are extremely reduced or more commonly absent, the coalesced medial radial is also

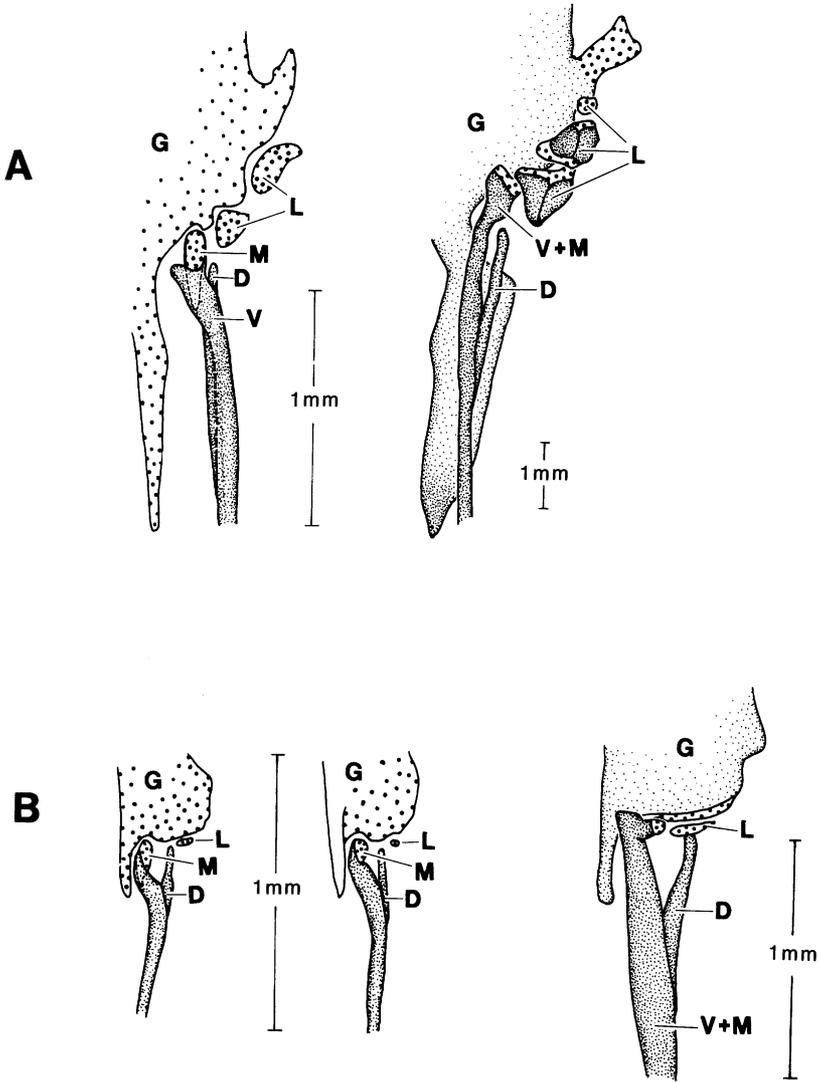


Fig. 6. Medial-most pelvic-fin ray (D, dorsal half; V, ventral half; V+M, ventral half fused with medial radial), radials (lateral, L; medial, M), and girdle margin (G), developing; left side, ventral views: (A) *Synodus* sp., left, USNM 315317, 27.0 mm SL, right, USNM 315318, 79.2 mm SL; (B) *Morone americana*, USNM 315315, left to right, 16.2 mm SL, 17.8 mm SL, 28.1 mm SL.

much reduced and may be detectable only as a small, cartilage-tipped bony prominence or cartilaginous nubbin on the lateral side of the proximal tip of the ventral ray half. Nonetheless, the origin of this structure can be seen in larval specimens to be the result of ontogenetic fusion of the initially elongate cartilaginous medial radial to the ray tip (Fig. 6B). I have found such a modified ventral ray half in the pelvic fin of most percoids and in at least some labroids,

trachinoids, notothenioids, blennioids (including tripterygiids), gobioids (including *Rhyacichthys*), acanthuroids, scombroids, stromateoids, and anabantoids. Where the cartilage-tipped process is lacking in perciforms (e.g., in many blennioids, gobioids, the labroid family Labridae), the medial radial is also lacking, suggesting that this secondary condition, which is not structurally homologous with that in noneurpterygians, arose through reduction of the fused ra-

dial process rather than through pedomorphic truncation (i.e., failure of the radial to fuse in ontogeny). Among scorpaeniforms, the modified medial pelvic ray characterizes anoplomatids, hexagrammids, and at least some scorpaenoids (Fig. 5D), and platycephaloids; however, I have not found it in cottoids except in the problematic *Normanichthys* (which probably is not a scorpaeniform). It is lacking in most pleuronectiforms but well developed in the primitive *Psettodes*.

The distribution of this character in paracanthopterygians is interesting and merits further investigation. In percopsiforms (Fig. 4B), there is a cartilage-tipped, golf-club-like ventral ray half much like that of aulopiforms and myctophiforms and three well-developed lateral radials. All other paracanthopterygians (Anacanthini, sensu Patterson and Rosen, 1989) examined show no evidence of ventral ray/medial radial fusion and either have no pelvic radials (gadiforms and ophidiiforms, all pelvic rays articulate directly with cartilaginous margin of girdle) or have one to several cartilaginous radials (batrachoidiforms and lophiiforms). Absence of ventral ray/medial radial fusion is presumably secondary, because the other option requires a noneurypterygian origin for these groups. Consequently, it has no bearing on the tenuous monophyly of the Paracanthopterygii but could be interpreted as an additional apomorphy of the Anacanthini.

As for exceptions among primitive eurypterygians, specifically aulopiforms, Gosline's (1961) observation that the medial radial is free in *Alepisaurus* was apparently based on a young specimen; ossification and fusion of the medial radial to the ventral half of the medial ray is delayed ontogenetically in *Alepisaurus* and the closely related *Omosudis* as compared to other aulopiforms, but the fusion is complete in large specimens. (In light of this, I examined large specimens of salmonids and other noneurypterygians to confirm that the medial radial remains autogenous throughout development, even though firmly attached to the ventral ray half in some.) Gosline (1961) also noted that the ipnoid *Bathypterois* retains a free medial radial, and I have confirmed this for that genus and *Ipnois*. Ipnoids possess the three other eurypterygian synapomorphies, and thus the lack of medial radial fusion is either a reversal or places them as the sister group of all other eurypterygians. Reversal seems most likely, because the latter hypothesis is at odds with the convincing

dorsal gill arch evidence for monophyly of the Aulopiformes, discussed above. Subsequent work by Sulak (1977) and Johnson (1982) also placed ipnoids as close relatives of other aulopiform subgroups, all of which have a fused medial radial.

Fusion of the medial pelvic radial to the ventral half of the medial pelvic ray apparently has occurred independently once among noneurypterygians in a few, though not all, New Zealand species of *Galaxias*, as reported by Weitzman (1967). My observations confirm those of Weitzman concerning *Galaxias* but are contrary to his statement that this fusion also characterizes *Elops*; I found the medial pelvic radial to be autogenous in larval, juvenile, and adult *Elops*.

#### CTENOSQUAMATA

Of the three major clades under consideration here, the Ctenosquamata (Myctophiformes + Acanthomorpha) has received the least attention. Rosen (1973) listed 10 synapomorphies that purportedly unite myctophiforms and acanthomorphs. Fink and Weitzman (1982) did not consider ctenosquamate monophyly. Lauder and Liem (1983, fig. 14) showed only two synapomorphies at the ctenosquamate node, one comprising two of the 10 listed by Rosen (1973) and an additional one described by Lauder (1982). The latter, a pharyngohyoideus muscle inserting on the urohyal, was said by Lauder and Liem to have been found in some aulopiforms, casting doubt on its validity as a ctenosquamate specialization; I have not attempted to evaluate this observation. Lauder and Liem (1983) did not discuss their reasons for excluding the remaining eight synapomorphies in Rosen's original list, although for many of them, the reasons are obvious.

There are varying degrees of ambiguity associated with all 10 of Rosen's (1973) ctenosquamate synapomorphies; they either are not unique to ctenosquamates, are variable within even primitive ctenosquamates, or both. The last five in his list are the least convincing. For some of these (e.g., "ctenoid" scales, dorsal-fin "spines"), there remain questions of homology on morphological grounds. More important, none of them characterizes all myctophiforms, and most are found in only a few species of myctophids; some are also variously present among primitive acanthomorphs. As Rosen (1973) himself observed with regard to the subocular shelf, "perhaps we are seeing no more

than a proclivity to develop this structure in both groups.”

Rosen's other five putative synapomorphies warrant more extensive discussion:

(1) Reduction of the posterior upper pharyngeal dentition and formation of a hinge joint between the fourth upper pharyngeal toothplate (UP4) and the toothplate of the third pharyngobranchial (PB3). Rosen (1973) was confused about homology and presence or absence of the fourth and fifth upper toothplates, and thus his interpretation of posterior toothplate reduction and articulation is flawed. As described below, the critical feature is not the diminution of the posterior pharyngeal dentition but the unique absence of the fifth upper toothplate (UP5). An overlapping, hingelike articulation between UP4 and the toothplate of PB3 (undoubtedly associated with the loss of UP5) is somewhat difficult to characterize unambiguously and is variable, even among primitive ctenosquamates. Within myctophiforms, for example, *Neoscopelus* has a broad shelf on UP4 that overlaps the toothplate of PB3 ventrally, whereas in *Diaphus* there is no contact of any kind between UP4 and PB3.

(2) Reduction of the fourth pharyngobranchial cartilage (PB4). Here again, there is a trend toward a smaller PB4, but its size is more variable than implied by Rosen (1973). As is clear in Rosen's (1973) illustrations, there is not an unequivocal reduction in size at the ctenosquamate node. In myctophids and neoscopelids, PB4 is substantially shortened compared to most aulopiforms, but most synodontoids have a comparably reduced PB4, and in numerous acanthomorphs (e.g., *Polymixia*, *Percopsis*, *Velifer*, *Caranx*), this cartilage is considerably larger than it is in myctophiforms.

(3) A separate internal division of the retractor dorsalis inserting on the third pharyngobranchial (PB3). There is a general trend toward insertion of the retractor dorsalis more anteriorly, but substantial variation in its insertion exists, and this is evident in Rosen's (1973) illustrations. Most aulopiforms have little or no insertion of the retractor dorsalis on PB3, however in *Aulopus* (Rosen's fig. 4), a major portion inserts on PB3, and a separate division inserting on PB3 occurs in *Scopelarchoides* (Rosen's fig. 13). Within synodontoids there is a large internal division inserting along much of the length of PB3 in *Saurida* and *Harpadon* (not shown in Rosen's fig. 8), whereas the closely related *Trachinocephalus* and *Synodus* (Rosen's fig. 7) have

a single division inserting on UP5. Furthermore, emphasis on insertion of the retractor dorsalis on PB3 is far from universal among ctenosquamates; many acanthomorphs have a single retractor dorsalis bundle inserting on both PB3 and UP4.

(4) A hinge joint between the toothplates of the second epibranchial (EB2) and pharyngobranchial (PB2). Rosen (1973) did not discuss or present any further description of this feature, and I find his characterization oversimplified. Many percoids have a single, large, autogenous, ovoid toothplate at the anterior end of EB2 that articulates with the cartilaginous posterior tip of PB2, frequently contacting the fused toothplate of the latter (see Rosen's [1973] illustrations of *Centropomus*, fig. 93, and *Caranx*, fig. 97). A similar condition is found in some beryciforms, whereas others have a series of small toothplates along the anterior portion of EB2 or lack toothplates there altogether as do many percomorphs, paracanthopterygians, and atherinomorphs. Neoscopelids have a single large toothplate on EB2, similar to, but more asymmetrical than, that of percoids, but it does not form a "hinge-joint" with the fused toothplate of PB2, nor does the smaller second epibranchial toothplate of myctophids, which shows considerable variation in shape and size and frequently does not even reach the anterior tip of EB2. If any generalization can be made, it is, perhaps, that flattened, autogenous toothplates apparently do not occur on EB2 below the Ctenosquamata.

(5) Further reduction of the second preural neural spine to a low crest and extension of the first epural over it. Rosen (1985) later questioned the wisdom of basing "major taxonomic judgements" on the length of NPU2, and the extreme variability in this and the position of the first epural are obvious in his earlier montage of the epural-uroneural complex (Rosen, 1984, figs. 35–37).

Although I view all of Rosen's (1973) ctenosquamate synapomorphies as problematic, I argue below that monophyly of the Ctenosquamata is supported by a reductive restructuring of the dorsal gill arches that uniquely characterizes all members of the clade. For this and other reasons, I disagree with Rosen's later (1985) exclusion of the Neoscopelidae from the Ctenosquamata (Fig. 2). In the preceding section on the Eurypterygii, I explained how Rosen (1985) challenged the monophyly of his (1973) Myctophiformes (Myctophidae + Neoscopeli-

dae), proposing instead that myctophids alone are the sister group of acanthomorphs and placing neoscopelids in an unresolved polytomy immediately preceding the newly restricted Ctenosquamata together with two loosely defined groups, "chlorophthalmids" and "aulopoids." I discussed some specific examples of the myriad problems associated with Rosen's character analysis, most of which relate to questions of structural homology and substantially greater variability in character states than indicated in the character analysis and cladogram. Here, I will briefly touch upon additional problems of a similar nature.

Rosen's (1985) proposal of an unresolved polytomy below ctenosquamates is puzzling in light of his synapomorphy scheme. Although his cladogram (Rosen, 1985, fig. 45) shows 12 synapomorphies at this unresolved node, the synapomorphy scheme indicates that, of these, neoscopelids share eight with ctenosquamates, whereas "aulopoids" share only three and "chlorophthalmids" only one. Thus, even if one accepts Rosen's highly problematic character interpretations and analysis, his putative polytomy is fully resolved on a parsimony basis, and his original Ctenosquamata remains intact. This is not to suggest that Rosen's (1985) new character evidence for ctenosquamate monophyly is any less ambiguous than that of the 1973 paper discussed above, only that the premise that "aulopoids" or "chlorophthalmids" may be more closely related to ctenosquamates than neoscopelids is not logically defended.

Rosen (1985) further argued against a sister group relationship between myctophids and neoscopelids based on eight putative synapomorphies of myctophids and acanthomorphs, all purportedly lacking in neoscopelids. Although this would not necessarily challenge ctenosquamate monophyly (neoscopelids need not be excluded from ctenosquamates if they are the sister group of myctophids + acanthomorphs), it warrants discussion. Of the eight putative myctophid-acanthomorph synapomorphies, presence of a well-developed subocular shelf is the least ambiguous. The others are too variable to be considered unequivocally synapomorphic at this level. Rosen's use of partial closure of the cervical gap, absence of an accessory neural arch, and the associated modifications as synapomorphies that unite myctophids and acanthomorphs is particularly disconcerting given the extreme variability among these features within aulopiforms. Furthermore, al-

though it is true that neoscopelids have a large cervical gap, Rosen's statement (p. 13) that they also have an accessory neural arch is erroneous; my observations indicate that all three neoscopelid genera lack an accessory neural arch. Oddly, Rosen (1985) himself noted that the structure that Rosen and Patterson (1969, fig. 61A) labeled as an accessory neural arch in *Neoscopelus* was actually the first of four supraneurals but did not elaborate further on his conviction that neoscopelids have an accessory neural arch. An interarcual cartilage occurs in only a few myctophid species, and among primitive acanthomorphs only in anomalopids and a few melamphaeids, and in none of these groups does it resemble the rodlike structure that characterizes more advanced acanthomorphs. Number of supraneural ("predorsal") bones is quite variable among aulopiforms, and three or fewer is common. As for the rostral cartilage, I invoke again the persuasive arguments of Hartel and Stiassny (1986) that homology of the rostral cartilage is unclear below acanthomorphs, wherein the configuration has stabilized to a single median chondrified cartilage strongly bound to the premaxillary ascending processes by well-developed maxillo-rostral ligaments.

Stiassny (1986) described four putative synapomorphies of myctophids and neoscopelids, corroborating Rosen's original (1973) Myctophiformes and thus conflicting with Rosen's (1985) myctophid-acanthomorph synapomorphies of which all but the subocular shelf appear equivocal. I agree with Stiassny's assessment of the conelike parapophyses on the first vertebra but have not attempted to evaluate her other three characters, which involve rostral ligaments and subtleties in the configuration of the head of the maxilla that I find difficult to interpret.

The question of monophyly of the Myctophiformes remains somewhat problematic; however, I suspect that Stiassny's corroboration of Rosen's (1973) original hypothesis is valid. As for ctenosquamate monophyly, the evidence presented to date is inconclusive. Nonetheless, I maintain that the Ctenosquamata, as originally delineated by Rosen (1973), is monophyletic, based on a fundamental reductive restructuring of the dorsal gill arches that has gone unrecognized as unique among euteleosts to neoscopelids, myctophids, and acanthomorphs. It may be that certain features of the dorsal gill arches interpreted by Rosen (1973) as ctenosquamate synapomorphies (discussed above) are correlat-

ed with this restructuring. A comprehensive parsimony analysis could demonstrate that some of these features, though variable, are interpretable as ctenosquamate synapomorphies, but only the specialization described below is unique to and unreversed within the Ctenosquamata.

*VIII. Absence of the fifth upper pharyngeal toothplate and the associated third internal levator muscle.*—

The primitive complement of upper pharyngeal toothplates among euteleosts is four (Fig. 3B), one fused to the ossified second pharyngobranchial, one fused to the ossified third pharyngobranchial, one (UP4) associated with the cartilaginous fourth pharyngobranchial, and one (UP5) variously associated with, but not fused with, the fourth epibranchial. There is some question regarding the origin of UP5; Weitzman (1967) suggested that it might have been derived, along with UP4, from the dermal-element series of the fourth, rather than the fifth, arch, and Nelson (1969) discussed the difficulties associated with determining this. The actual origin of this element need not concern us here, so long as it is understood that, among euteleosts, UP5 refers to the homolog of the separate toothplate that lies posterior to UP4, whether or not UP4 is present.

Many euteleosts have only a single toothplate posterior to the third pharyngobranchial (Figs. 3C, 7), one of the posterior ones having been lost, and there has been categorical confusion regarding the identity of the remaining toothplate in various groups. All ctenosquamates have a single posterior toothplate that has been identified, correctly I believe, as UP4 (Fig. 7B–D). The single posterior toothplate that characterizes many nonctenosquamates (Figs. 3C, 7A) also has been identified most frequently as UP4, indicating (incorrectly, as I will argue below) that UP5 is lacking in these groups. For example, Weitzman (1967) observed that the fifth upper pharyngeal toothplate was missing in all esocoids, osmeroids, salmonids, stomiiforms, and synodontids that he examined. The following illustrations of dorsal gill arch elements of various nonctenosquamate fishes have the single posterior toothplate labeled UP4: Rosen (1973), figs. 5 (salmonid), 7–8 (synodontids), 17 (giganterid), 18–22 (stomiiforms), 58 (umbrid); Rosen (1974), fig. 15A (umbrid); Weitzman (1974), figs. 76, 78 (sternoptychids), 79 (osmerid); Lauder (1983), fig. 2B (esocid).

Nelson (1969) recognized and discussed potential confusion about the identity of the two

posterior toothplates but saw no clear resolution. Accordingly, he stated, “The loss of the fourth and fifth toothplates is a character of possible systematic significance, but so far not sufficiently understood,” and it appeared to him that “the fourth and fifth plates seem independently to have been lost many times.” I agree with Nelson (1969) that the fourth upper pharyngeal toothplate has been lost independently many times within both nonctenosquamates and ctenosquamates; however, I believe that the fifth upper pharyngeal toothplate has been lost only once in the evolution of euteleosts, in the common ancestor of ctenosquamates. This conviction follows from resolution of the long-standing homology problem relating to identity of UP4 and UP5. Close scrutiny provides unambiguous evidence that the single toothplate previously identified as UP4 in nonctenosquamate fishes is actually UP5.

Rosen (1973) diagnosed one of his two aulopiform subgroups, the alepisauroids, on the basis of several specializations of the dorsal gill arch elements, including absence of the fifth upper pharyngeal toothplate and concomitant enlargement of UP4 (see his figs. 7–16). As pointed out by Johnson (1982), Rosen’s observations and illustrations indicating a single posterior upper pharyngeal toothplate in most alepisauroids were erroneous. With the exception of synodontoids (*Pseudotrichonotus*, *Synodus*, *Trachinocephalus*, *Saurida*, and *Harpadon*) and *Anotopterus*, all aulopiforms have two posterior toothplates (Johnson [1982] reported that *Alepisaurus* has a single toothplate, but my specimens clearly have two). In alepisauroids, however, unlike aulopoids, the more anterior of the two, UP4, is usually quite small, and in some species (e.g., *Coccorella atrata*, Johnson [1982, fig. 15A]) is edentulous. Rosen (1973) apparently missed the small UP4 in most alepisauroids, assumed that UP5 had been lost, and interpreted the large UP5 as UP4. Because UP4 is substantially reduced among those alepisauroids having two toothplates, it seems reasonable that the remaining toothplate in synodontoids and *Anotopterus* is UP5, not UP4 as previously thought. I extend this hypothesis to include all nonctenosquamates with a single posterior toothplate and maintain that it is corroborated by two independent lines of evidence establishing the identity of each toothplate: ontogeny and associated musculature.

Ontogeny: Examination of developing dorsal gill arch elements (Fig. 8) affords a clear ex-

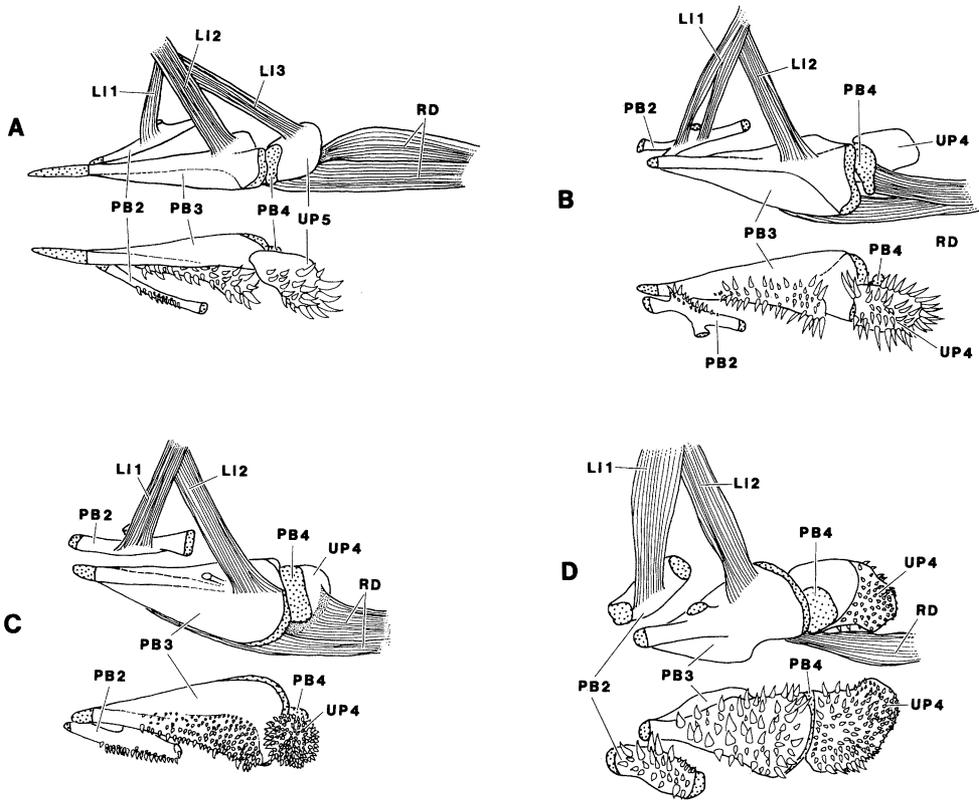


Fig. 7. Pharyngobranchials (PB) 2–4 with fused toothplates, showing upper pharyngeal toothplates (UP) 4–5, internal levators (LI) 1–3, and retractor dorsalis (RD); right side, medial and ventral views; stippling denotes cartilage: (A) *Trachinocephalus myops*, USNM 185861, 124 mm SL; (B) *Diaphus mollis*, AMNH 29449, 38.8 mm SL; (C) *Solivomer arenidens*, USNM 135419, 110 mm SL; (D) *Morone americana*, USNM 109851, 44.5 mm SL.

position of posterior toothplate homology. At their initial appearance in early development the fourth and fifth upper pharyngeal toothplates evince specific positional relationships with respect to the fourth pharyngobranchial cartilage and the fourth epibranchial (EB4). Among taxa possessing both toothplates, UP4 consistently appears on the ventral surface of PB4, whereas UP5 appears at the distal tip of EB4 (Fig. 8A). The specific relationship between UP4 and PB4 is generally obvious in adults; however, UP5 frequently extends anteriorly along the ventral surface of UP4 with growth, such that its primary association with EB4 may be obscured (e.g., Figs. 3C, 7A). Anterior expansion of UP5 occurs most commonly where UP4 is reduced or absent, and this has substantially confounded the UP4–UP5 homology problem. Knowledge of the early ontogenetic positional relationships of the two

posterior toothplates in those taxa having both permits positive identification of the remaining element in taxa with only one. Using these criteria, UP5 is present in all nonctenosquamates examined; in taxa with a single posterior toothplate (Fig. 8B), that element appears initially at the tip of EB4, and the ventral surface of PB4 is vacant until UP5 grows forward to cover it. In contrast, all ctenosquamates lack UP5, UP4 appears initially on the ventral surface of PB4, and there is no toothplate associated with EB4 (Fig. 8C–D).

Internal levators: Euteleosts primitively have three internal levator muscles, the third inserting on the fourth pharyngobranchial cartilage in nonneoteleosts (Fig. 3A) and shifting to the fifth upper pharyngeal toothplate in neoteleosts (Fig. 3B), with the advent of the retractor dorsalis. The first two internal levators insert on the second and third pharyngobranchials, re-

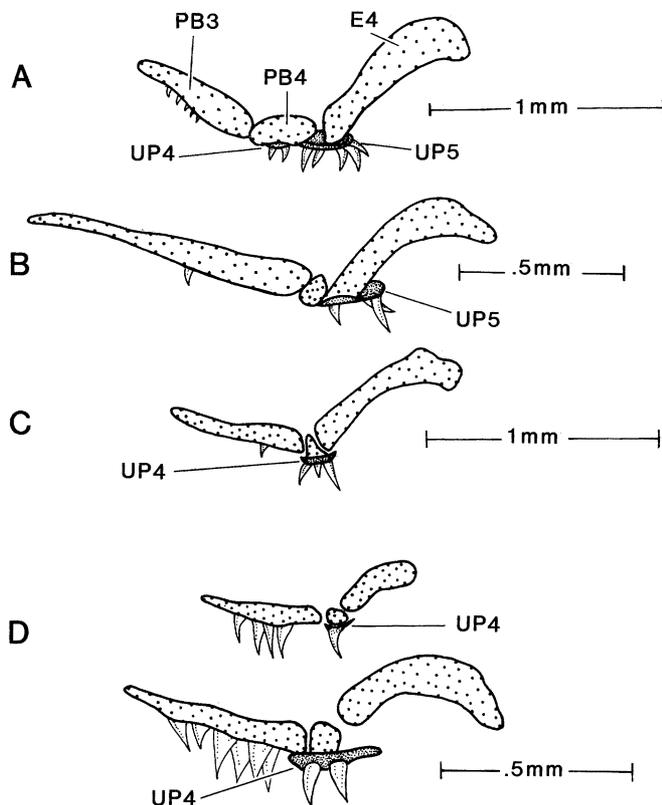


Fig. 8. Selected dorsal gill arch elements at early stage of development, right side, medial views, showing pharyngobranchials (PB) 3–4, upper pharyngeal toothplates (UP) 4–5, epibranchial (E) 4; stippling denotes cartilage: (A) *Scopelarchus* sp., USNM 315316, 28 mm SL; (B) *Synodus* sp., USNM 315317, 22.5 mm SL; (C) *Symbolophorus californiense*, USNM 315314, 16.5 mm SL; (D) *Morone saxatilis*, USNM 315315, upper, 7 mm SL, lower, 8.5 mm SL.

spectively, and UP4 never receives levator muscles. Insertion of the third internal levator on UP5 in primitive neoteleosts provides a marker for the identity of that element in taxa with a single posterior toothplate. Using that criterion, the hypothesis that absence of UP5 is unique to ctenosquamates is corroborated, as it is with the ontogenetic evidence. All nonctenosquamate neoteleosts (stomiiforms and aulopiforms) have three internal levators, the third inserting on the posterior-most toothplate (i.e., UP5; Figs. 3C, 7A). In contrast, all myctophids, neoscolopelids, and acanthomorphs have only two internal levators, the first inserting on the second pharyngobranchial and the second on the third pharyngobranchial (Fig. 7B–D). Identity of the posterior-most toothplate as UP4 is supported by its lack of an associated internal levator.

The dorsal gill arch elements of all ctenosqua-

mate fishes differ from all other euteleosts in having lost UP5 and the associated third internal levator. As with the retractor dorsalis for neoteleosts, this unique, fundamental structural and functional innovation is cogent evidence of the monophyly of the Ctenosquamata.

#### MATERIAL EXAMINED

Comparative observations were made on the pelvic girdle and dorsal gill arch elements in a broad range of euteleosts, and a complete listing of the hundreds of cleared and stained specimens examined would be impractical. Most are part of the permanent skeletal collection of the USNM; a few were borrowed from the AMNH, FMNH, and MCZ collections. In addition to cleared and stained specimens, whole specimens representing over 200 genera in a broad range

of euteleost families were dissected to examine branchial musculature. In most of these dissections, the head of each specimen was sagittally sectioned along the midline, continuing posteriorly through the anterior several vertebrae. One-half of the head (usually the left) was then removed and stained for bone and cartilage to facilitate observation of muscle origins and insertions on the dorsal gill arch elements. Less intrusive dissections were done on some specimens to check only insertions of internal levators.

Listed below are families for which cleared and stained specimens of one or more (for most families) members were examined. Numbers in parentheses indicate the number of genera in which branchial muscles were also examined. The taxonomic groupings are for convenient reference, and no phylogenetic inferences are intended.

*Elopomorpha*.—Albulidae (1), Elopidae, Megalopidae.  
*Clupeomorpha*.—Clupeidae (1), Engraulidae (1).  
*Esocidae*.—Esocidae (1), Umbridae (1).  
*Ostariophysii*.—Ariidae (1), Chanidae, Characidae (1), Cyprinidae (1).  
*Salmonoidei*.—Salmonidae (1).  
*Argentinoidei*.—Argentinidae (1), Bathylagidae (1), Platytrichidae (1).  
*Osmeroidei*.—Galaxiidae (1), Lepidogalaxiidae (1), Osmeridae (1), Plecoglossidae, Retropinnidae.  
*Stomiiformes*.—Gonostomatidae (2), Sternoptychidae (1), Stomiidae (2).  
*Ateleopoidae*.—Ateleopodidae (1).  
*Aulopiformes*.—Alepisauridae (1), Anopteroideae, Aulopidae (1), Bathysauridae (1), Chlorophthalmidae (1), Evermannellidae (1), Harpadontidae (1), Ipnopidae (1), Notosudidae, Omosudidae, Paralepididae (1), Pseudotriconotidae (1), Scopelarchidae (1), Synodontidae (2).  
*Mycetophiformes*.—Mycetophidae (3), Neoscopelidae (1).  
*Polymixioidei*.—Polymixiidae (1).  
*Paracanthopterygii*.—Antennariidae (1), Aphredoderidae (1), Batrachoididae (1), Bregmacerotidae (1), Bythitidae (2), Carapidae (1), Gadidae (4), Macrouridae (1), Merlucciidae (1), Ophidiidae (3), Percopsidae (1).  
*Atherinomorpha*.—Atherinidae (1), Bedotiidae (1), Belonidae (1), Cyprinodontidae, Melanotaenidae (1), Phallostethidae.  
*Lampriformes*.—Lampridae, Lophotidae, Radiicephalidae, Regalecidae (1), Stylephoridae (1), Trachipteridae (1), Veliferidae (1).  
*Beryciformes*.—Anomalopidae (1), Anoplogasteridae (1), Barbouriidae (1), Berycidae (1), Diretmidae (1), Gibberichthyidae (1), Holocentridae (2), Trachichthyidae (2), Melamphaeidae (1), Monocentridae (1), Rondelettiidae (1), Stephanoberyidae (1).  
*Gasterosteiformes*.—Aulorhynchidae (1), Gasterosteidae (1).  
*Zeiformes*.—Caproidae (2), Grammicolepidae (1), Zeidae (1).  
*Scorpaeniformes*.—Agonidae (1), Cottidae (1), Cyclopteridae (1), Hexagrammidae (1), Hoplichthyidae (1), Liparidae (1), Scorpaenidae (2), Triglididae (1), Zaniolepididae (1).  
*Pleuronectiformes*.—Cynoglossidae (2), Pleuronectidae (1), Psettodidae (1).  
*Gobiesociformes*.—Gobiesocidae (2).  
*Mugiloidei*.—Mugilidae (2).  
*Elassomatoidei*.—Elassomatidae (1).  
*Percoidae*.—Acropomatidae (1), Ambassidae (1), Apogonidae (6), Arripidae (1), Bathyclupeidae (1), Caesionidae (1), Callanthiidae (1), Carangidae (4), Centracanthidae (1), Centrarchidae (2), Centropomidae (2), Cepolidae (1), Cirrhitidae (1), Coryphaenidae (1), Dinolestidae (1), Drepaneidae (1), Emmelichthyidae (1), Ephippidae (1), Epigonidae (1), Gerreidae (1), Glaucosomatidae (1), Girellidae (2), Grammatidae (1), Haemulidae (1), Hapalogenysidae (1), Howellidae (1), Kuhlidae (1), Kurtidae (1), Kyphosidae (1), Inermiidae (1), Lactariidae (1), Leiognathidae (1), Lethrinidae (1), Lobotidae (1), Lutjanidae (2), Malacanthidae (1), Moronidae (2), Nemipteridae (1),

Notograpidae (1), Opisthognathidae (2), Oplegnathidae (1), Ostracoberyidae (1), Percichthyidae (6), Percidae (2), Plesiopidae (2), Polynemidae (1), Pomacanthidae (1), Pomatomidae (1), Priacanthidae (1), Pseudochromidae (2), Rachycentridae (1), Scatophagidae (1), Sciaenidae (3), Scombrobracidae (1), Scorpididae (1), Serranidae (6), Sillaginidae (1), Sparidae (1), Terapontidae (1), Toxotidae (1).  
*Stromateoidei*.—Centrolophidae (1).

*Labroidei*.—Cichlidae (1), Embiotocidae (1), Labridae (1), Pomacentridae (1).  
*Scombroidei*.—Gasterochismatidae (1), Gempylidae (1), Istiophoridae (1), Scombridae (2), Sphyraenidae (1).  
*Acanthuroidei*.—Acanthuridae (1), Luvaridae, Siganidae, Zanclidae.  
*Gobioidei*.—Gobiidae (1), Eleotrididae (4), Rhyacichthyidae (1), Schindleriidae (1), Xenisthmidae (1).  
*Blennioidei*.—Blenniidae (9), Chaenopsidae (2), Clinidae (2), Dactyloscopidae (1), Tripterygiidae (1), Labrisomidae (6).  
*Callionymoidei*.—Callionymidae (1).  
*Zoarcoidei*.—Bathymasteridae (1), Zoarcidae (1).  
*Stichaeoidei*.—Pholidae (1).  
*Pholidichthyoidei*.—Pholidichthyidae (1).  
*Ammodytoidei*.—Ammodytidae (1).  
*Trachinoidei*.—Champsodontidae (1), Cheimarrichthyidae, Chiasmodontidae (2), Leptoscopidae, Paraperidae (1), Percophidae (6), Trachinidae (1), Trichodontidae (1), Trichnotidae (1), Uranoscopidae (1).  
*Notothenioidei*.—Bovichthyidae, Harpigeridae (1), Nototheniidae (1).

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