PERCOMORPH PHYLOGENY: PROGRESS AND PROBLEMS

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Publication of the revised classification of Greenwood et al. (1966) heralded a new era of research on the phylogeny of teleostean fishes, with cladistic methodology playing an ever increasing and eventually all-important role. As the largest and most diverse teleostean assemblage (some 10,000 species in well over 200 families), the Percomorpha have been the subject of considerable work in the ensuing period. Our changing perception of the intrarelationships of percomorph fishes has led to many classificatory changes at the ordinal, subordinal, and family levels. Such changes offer one measure of the "progress" that has been made in our understanding of percomorph relationships over the past 25 years. My purpose here is to review briefly that progress and to offer some thoughts about major unresolved problems and future directions. The result is, at best, a highly personal view of the current status of percomorph classification, and the coverage of specific groups varies depending on my knowledge of them. This paper was largely completed prior to submission of the manuscripts for this symposium. So that it can also serve as a guidepost to the symposium volume, I refer to conclusions and new hypotheses presented in the included papers, but do not discuss them further.

The series Percomorpha was first recognized in a cladistic framework by Rosen (1973, fig. 129), who treated it as the most derived clade in his euteleostean phylogeny but provided no evidence for its monophyly. As delineated by Rosen the Percomorpha are equivalent to the Acanthopterygii of Greenwood et al. (1966), i.e., all acanthomorph fishes with the exception of paracanthopterygians and atherinomorphs. Rosen's Percomorpha has persisted in subsequent classifications, but it is only recently that putative synapomorphies have been identified, and there remains considerable disagreement about the limits and monophyly of the group. The only cladogram depicting interrelationships among percomorph orders, that of Lauder and Liem (1983), was acknowledged by those authors to be inadequate and based on many "poor" characters. It has not been viewed seriously by subsequent authors. Stiassny (1990) proposed that monophyly of Rosen's Percomorpha is supported by a distinctive pelvic girdle morphology in which there is a central union of the two pelvic bones and ventrally displaced anteromedial processes. Stiassny and Moore (1992), in a more extensive review of the pelvic girdle, found that only the latter of those characters (together with attachment of the pelvic girdle to the cleithrum or coracoid) diagnoses percomorphs; they used central union of the pelvic bones and presence of an interpelvic ligament to diagnose a more restricted group comprising holocentrids and "higher percomorphs," from which the remaining beryciforms were excluded. Roberts (1993) recognizes a more restricted Percomorpha (which excludes all beryciforms and gasterosteiforms, among other groups) based on the synapomorphy of transforming ctenoid scales. Johnson and Patterson (1993) present yet another concept of the Percomorpha, from which beryciforms and zeiforms are excluded but atherinomorphs and gasterosteiforms are included.

The ordinal and subordinal classification of Greenwood et al. (1966) (hereafter referred to as G. et al.) for the Percomorpha (=Acanthopterygii) is given in Table 1 and their familial classification for the Percoidei in Table 2. Bold type denotes those groups in which subsequent research has led to new hypotheses about limits and/or affinities—information that has or potentially could result in classificatory changes.

Table 1.   Ordinal classification of Percomorpha and subordinal classification of Perciformes after Greenwood et al. (1966). Boldface names denote those groups affected by subsequent hypotheses of limits and/or interrelationships

Superorder Acanthopterygii = Percomorpha	
Order Beryciformes	**Order Perciformes**
	Suborder Percoidei
Order Zeiformes	**Suborder Mugiloidei**
	Suborder Sphyraenoidei
Order Lampridiformes	**Suborder Polynemoidei**
	Suborder Labroidei
Order Gasterosteiformes	**Suborder Trachinoidei**
	Suborder Notothenioidei
Order Channiformes	**Suborder Blennioidei**
	Suborder Icosteoidei
Order Synbranchiformes	**Suborder Schindleroidei**
	Suborder Ammodytoidei
Order Scorpaeniformes	**Suborder Callionymoidei**
	Suborder Gobioidei
Order Dactylopteriformes	**Suborder Kurtoidei**
	Suborder Acanthuroidei
Order Pegasiformes	**Suborder Scombroidei**
	Suborder Stromateoidei
Order Pleuronectiformes	Suborder Anabantoidei
	Suborder Luciocephalidae
Order Tetraodontiformes	**Suborder Mastacembeloidei**

Beryciformes.—Our perception of the limits and intrarelationships of the Beryciformes has continued to change, and additional hypotheses are presented in this volume. Perhaps the most notable modification since G. et al. involves the removal of the Polymixioidei. Rosen and Patterson (1969) placed polymixioids (including fossil forms) as the sister group of all other paracanthopterygians, but their inclusion there was relatively short-lived (Fraser, 1972b; Rosen, 1973). Zehren (1979) presented evidence that *Polymixia* is primitive with respect to beryciforms in several osteological characters and suggested that it be removed from the order; however, he did not suggest paracanthopterygian affinities, nor have others since then. Rosen (1985) and Stiassny (1986) placed *Polymixia* as the sister group of all other acanthomorphs, each identifying two different acanthomorph apomorphies lacking in *Polymixia*. At least one of Rosen's characters, presence of an interarcual cartilage, is not valid at this level; among beryciforms, only anomalopids and a few melamphaeids have an interarcual cartilage, and in neither is it the elongate rod-like structure that characterizes (when present) percomorphs, atherinomorphs and ophidioid paracanthopterygians, but rather a small nodule of cartilage similar to that seen in some myctophids (Jollie, 1954). Rosen's (1973) other character, complete closure of the cervical gap, may be an acanthomorph synapomorphy, but the variability of partial closure among aulopiforms and myctophiforms renders it ambiguous. Stiassny's (1986) higher acanthomorph synapomorphies, absence of the median palato-maxillary ligament and division of the palatovomerine ligament, have not been challenged.

Another major alteration in composition of the Beryciformes is the inclusion of the cetomimoids, which were considered protacanthopterygians by G. et al. Rosen and Patterson (1969) placed the cetomimoids in the Beryciformes. Rosen (1973) aligned cetomimoids and mirapinnatoids with stephanoberycoids, based on evidence from dorsal gill-arch elements and the caudal skeleton, an hypothesis further supported by Moore (1993).

Table 2. Familial classification of suborder Percoidei, after Greenwood et al. (1966). Boldface names denote those groups affected by subsequent hypotheses of limits and/or interrelationships

Suborder Percoidei		
Centropomidae	Lactariidae	**Pempherididae**
Percichthyidae	**Pomatomidae**	Bathyclupeidae
Serranidae	**Rachycentridae**	**Toxotidae**
Grammistidae	**Echeneidae**	Coracinidae
Grammidae	**Carangidae**	**Kyphosidae**
Pseudogrammidae	**Coryphaenidae**	**Ephippidae**
Pseudochromidae	**Formionidae**	**Rhinoprenidae**
Pseudoplesiopidae	Menidae	**Scatophagidae**
Anisochromidae	Leiognathidae	**Chaetodontidae**
Acanthoclinidae	Bramidae	Enoplosidae
Glaucosomidae	Caristiidae	Pentacerotidae
Terapontidae	**Arripididae**	Nandidae
Banjosidae	**Emmelichthyidae**	**Oplegnathidae**
Kuhliidae	**Lutjanidae**	**Embiotocidae**
Gregoryinidae	Nemipteridae	**Cichlidae**
Centrarchidae	Lobotidae	**Pomacentridae**
Priacanthidae	Gerreidae	**Gadopsidae**
Apogonidae	**Haemulidae**	Cirrhitidae
Acropomatidae	**Lethrinidae**	Aplodactylidae
Percidae	**Pentapodidae**	Cheilodactylidae
Sillaginidae	**Sparidae**	Latrididae
Branchiostegidae	**Sciaenidae**	**Owstoniidae**
Labracoglossidae	Mullidae	**Cepolidae**
	Monodactylidae	

Although there is general agreement about the placement of *Polymixia* and the whalefishes and relatives, other aspects of beryciform relationships remain controversial. Two new, but opposing, hypotheses, challenging the monophyly of the Beryciformes and some of Zehren's (1979) proposed relationships are presented in this volume (Moore, 1993; Johnson and Patterson, 1993).

Lampridiformes.—G. et al. included lampridiforms in their Acanthopterygii (=Percomorpha), as have most subsequent classifications (Rosen, 1973; Nelson, 1974, 1984). Stiassny and Moore (1992: fig. 15) proposed two possible placements based only on characters of the pelvic girdle, one within percomorphs, the other at the base of the Acanthomorpha. Olney et al. (1993) conclude that lampridiforms are not percomorphs, and Johnson and Patterson (1993) present additional evidence to support their position as the sister group of all other acanthomorphs.

Although Rosen and Patterson (1969) suggested that ateleopodids might be closely related to lampridiforms, Rosen (1973) rejected that hypothesis based on configuration of the dorsal gill arch elements, which he believed to be more primitive in ateleopodids. Olney et al. (1993) demonstrate that ateleopodids are not acanthomorphs and present evidence for monophyly of the Lampridiformes as delineated in G. et al.

Zeiformes and Tetraodontiformes.—The Zeiformes of G. et al. comprised six families, Parazenidae, Macrurocyttidae, Zeidae, Grammicolepididae, Oreosomatidae, and Caproidae and were placed near the Beryciformes. Rosen (1973) thought that caproids might be more closely related to perciforms than the other zeiforms, and subsequent authors also challenged the caproid-zeiform relationship. However, in a radical departure from the convention accepted by G. et al., Rosen (1984) proposed a close relationship between zeiforms and tetraodonti-

forms, specifically that caproids are the sister group of zeoids plus tetraodonti-forms. Tyler et al. (1989) tentatively accepted Rosen's proposal as a working hypothesis, including his rejection of a close relationship between balistoids and acanthurids, but noted the need for a careful reexamination. Johnson and Patterson (1993) argue that zeiforms (from which they exclude caproids) are not percomorphs, but they do not address Rosen's proposed relationship to tetraodontiforms. Rosen's proposal aside, the composition of the Tetraodontiforms has not been challenged, but there have been several major studies of intrarelationships (Winterbottom, 1974; Tyler, 1980).

Gasterosteiformes and Pegasiformes. — G. et al. treated the Pegasidae (*Pegasus*) as a separate order Pegasiformes, which they placed near the Scorpaeniformes, following Jungerson (1915). Their Gasterosteiformes comprised three suborders, gasterosteoids (in which they included the Indostomidae), aulostomoids, and syngnathoids. Banister (1970) removed the indostomids and placed them as a separate order within the Paracanthopterygii. Ida (1976) removed the Hypoptychidae from the perciform Ammodytoidei and placed it within the Gasterosteiformes. Pietsch (1978) argued that the distinctively specialized jaw mechanism of pegasids is shared by the fossil gasterosteiform ramphosids, indicating a gasterosteiform ancestry for the former. Structural homology of these jaw mechanisms is difficult to evaluate, because the evidence that would test it, i.e., the associated myology and syndesmology, is unavailable in the fossil. In his new classification of the Gasterosteiformes, Pietsch (1978) placed the Pegasoidei (pegasids plus ramphosids) as the sister group of the Syngnathoidei (syngnathids plus solenostomids), these together forming the sister group of gasterosteoids, in which he included the Hypoptychidae. He did not identify synapomorphies uniting those three groups, but defended the monophyly of his Gasterosteiformes based on his observation that "the pegasids are clearly intermediate between the gasterosteoids and the typical syngnathoids." Although Pietsch (1978) did not include *Indostomus* in his new classification of the gasterosteiforms, he concluded that Banister (1970) provided no justification for excluding it, and listed several specializations shared by pegasids and indostomids (some of which are also present in some other gasterosteiforms). Nelson (1984) accepted Ida's (1976) placement of hypoptychids, but was apparently not convinced by Pietsch's arguments, retaining as separate orders the gasterosteiforms, indostomiforms, pegasiforms and syngnathiforms. Johnson and Patterson (1993) argue that Pietsch's Gasterosteiformes are monophyletic with inclusion of the Indostomidae in his syngnathoids and propose a new hypothesis of their relationship to other percomorphs.

Scorpaeniformes. — The composition of the Scorpaeniformes as accepted by G. et al. has not been altered subsequently (except see dactylopteriforms, below), although monophyly of the group has often been questioned. Several authors, including G. et al., have suggested that the primary character uniting the scorpaeniforms, a posterior extension of the third suborbital that usually attaches to the preopercle, may have arisen independently in one or more of the subgroups. A detailed investigation, incorporating developmental information, is needed to test the homology of the suborbital stay. One uncommon feature of most scorpaeniforms that warrants further study with regard to monophyly of the order is the presence of distinct parietal spines in the larvae, otherwise known among acanthomorphs only in some beryciforms (Johnson, 1984). This ornamentation is apparently associated with the supratemporal sensory canal, which, in most scorpaeniforms has a bone-enclosed passage through the parietal. In most scorpaenoids and at least some cottoids the larval parietal spine is retained in adults, and the supratemporal sensory canal passes through an opening in it.

Dactylopteriformes. —G. et al. placed dactylopterids as a separate order near the scorpaeniforms. Pietsch (1978) enumerated several specializations that dactylopterids share with various gasterosteiform subgroups, but concluded that their phylogenetic position remains problematic, a conclusion shared by Johnson and Patterson (1993). Washington et al. (1984) included dactylopterids in their Scorpaenoidei, noting that the intrinsic musculature of their swimbladder is similar to that of triglids, but also citing several trenchant differences in the osteology of the two groups. They did not provide specific evidence for their "working hypothesis ... that the Apistinae, triglids, peristediids and dactylopterids share a common ancestry." It may be worth noting that, unlike most scorpaeniforms (including apistine scorpaenids, triglids and peristediids), the parietals of dactylopterids lack spines and a bone-enclosed supratemporal canal at all stages of development.

Synbranchiformes, Gobiesociformes and Channiformes. —G. et al. included the Alabetoidei (comprising the single genus *Alabes*) in their Synbranchiformes. Rosen and Greenwood (1976) removed *Alabes* from the Synbranchiformes, suggesting that it might be related to blennioids. Springer and Fraser (1976) demonstrated that *Alabes* is a highly specialized member of the Gobiesocidae with which it shares a uniquely specialized condylar articulation between the cleithrum and supracleithrum. Inclusion of the Gobiesocidae (=Gobiesociformes) in the Paracanthopterygii by G. et al. was challenged by Gosline (1970), who suggested possible affinities with the percomorph callionymoids. Patterson and Rosen (1989) agreed that there is no evidence relating gobiesocids to other paracanthopterygians, and Winterbottom (1993) and Johnson and Patterson (1993) support Gosline's hypothesis of a gobiesocid-callionymid relationship.

G. et al. recognized synbranchiforms as a separate acanthopterygian order, whereas mastacembeloids were considered a suborder of the Perciformes. Lauder and Liem (1983) proposed that the Channidae, treated as a separate order by G. et al., are the sister group of the synbranchiforms, an hypothesis also supported by Roe (1991). Travers (1984a, 1984b), however, proposed that synbranchoids and mastacembeloids are sister groups and placed them both in the Synbranchiformes, without mention of the Lauder and Liem proposal. Johnson and Patterson (1993) concur with Travers and include his Synbranchiformes in a previously unrecognized percomorph assemblage.

Pleuronectiformes. —The composition of the Pleuronectiformes as given in G. et al. remains unmodified. Chapleau (1993) reviews the recent classificatory history of the group, discusses evidence for monophyly, and presents a cladistic hypothesis of pleuronectiform intrarelationships. The relationship of pleuronectiforms to other percomorphs remains obscure.

Perciformes. —This largest and most diverse of the percomorph orders is probably polyphyletic. There has not been a serious attempt to diagnose a monophyletic Perciformes, nor to challenge monophyly of the order as currently recognized (sensu G. et al.). Rosen and Greenwood's (1976) proposal that the interarcual cartilage is a perciform synapomorphy was rejected by Travers (1981) based on his broad survey of that character. Perciforms are treated below at the subordinal level.

Mugiloidei. —G. et al. assigned the Mugilidae, Sphyraenidae, and Polynemidae to separate suborders, although they have frequently been placed together in a single suborder. Rosen (1964) discounted a close relationship between these three families and atherinomorphs, but did not resolve the question of their relationship

to one another. Gosline (1968, 1971) continued to recognize a close relationship among mugilids, sphyraenids, polynemids, and atherinoids, as proposed in an earlier (1962) paper, noting (1971) that the principal common character is lack of attachment of the pelvic girdle to the cleithra. Johnson (1986) briefly discussed and discounted the primary characters (including the pelvic girdle) usually cited as evidence of close relationship among mugilids, sphyraenids and polynemids, and placed the Sphyraenidae in the suborder Scombroidei (see below). Stiassny (1990) hypothesized that mugilids are the sister group of the Atherinomorpha (sensu Rosen, 1964) based on four putative synapomorphies, but cautioned that that relationship is challenged by the fact that mugilids also share a derived pelvic girdle morphology exclusively with percomorphs. As she noted, three of the four mugilid-atherinomorph synapomorphies involve pharyngeal myology and thus may be functionally correlated. For two of those three (pharyngocleithralis and pharyngohyoideus), I am unable to identify Stiassny's derived configuration in the primitive mullet *Agonostomus,* and in *Mugil* the pharyngohyoideus appears derived but not the pharyngocleithralis. The third myological character, involving arrangement of the dorsal branchial musculature, is, as Stiassny noted, similar but not identical in mugilids and atherinomorphs. There is, then, some evidence to suggest independent derivation of three of Stiassny's four mugilid-atherino-morph apomorphies. Stiassny (1993) and Johnson and Patterson (1993) discuss additional evidence for a mugilid-atherinomorph relationship, and the latter authors include both in a new assemblage within the Percomorpha. Parenti (1993) rejects a mugilid-atherinomorph relationship in favor of the hypothesis that atherinomorphs are more closely related to paracanthopterygians.

Polynemoidei.—As discussed above there is no convincing evidence that polynemids are related to mugilids or sphyraenids. Their specific relationship to other perciforms has not been examined, but assignment to a separate suborder seems unwarranted. Like many families in the Percoidei, at least some genera have a well-developed procurrent spur (Johnson, 1975), and possible affinities with the Sciaenidae are suggested by the striking resemblance of their larvae to those of that family (de Sylva, 1984). Furthermore, Freihofer (1978) reported that sciaenids and polynemids share a deep, complicated membranous prenasal canal extension. Of 21 putative synapomorphies for the Sciaenidae identified by Sasaki (1989) (many of which are not unique among percoids to sciaenids), polynemids share five. Three of these, extension of epaxial musculature onto the frontals, absence of trisegmental pterygiophores and absence of a supramaxilla, occur commonly in other percoids. Of the other two, insertion of a single branchiostegal ray on the posterior ceratohyal occurs in a few other perciforms (e.g., pseudochromids and most gobioids), and medial interdigitation of the metapterygoid and quadrate may be unique. Further investigation is desirable, but I believe the evidence at hand supports the hypothesis that the Sciaenidae and Polynemidae are sister groups and recommend that both families be included in a superfamily Polynemoidea.

Sphyraenoidei.—Johnson (1986) placed the Sphyraenidae in the suborder Scombroidei, as the sister group of all other scombroids based on several shared osteological specializations. The most compelling evidence of scombroid affinity is found in the unique configuration of the primary jaw dentition and gill arches.

Labroidei.—The Labroidei of G. et al. comprised the families Labridae, Scaridae and Odacidae. Liem and Greenwood (1981) proposed that those three families plus the Embiotocidae and Cichlidae (treated as percoids in G. et al.) constitute

a monophyletic group because they share unique morphological and functional specializations associated with pharyngognathy. Kaufman and Liem (1982) diagnosed this expanded Labroidei by three morphological specializations of the pharyngeal jaws and added to it the family Pomacentridae. Stiassny and Jensen (1987) reviewed and added to the evidence supporting monophyly of Kaufman and Liem's Labroidei, listing a total of eight putative synapomorphies, all of which are associated with the branchial complex, seven being features of the pharyngeal jaw apparatus. It may be worth noting, however, Nelson's (1967) conclusion that "Aside from the fused fifth ceratobranchials there is little in gill-arch structure to indicate that these fishes are particularly closely related to one another."

Although the integrity of the new Labroidei has been widely accepted, evidence for monophyly of the group has been found only in the pharyngeal apparatus; other aspects of the skeletal anatomy provide no suggestion of close relationship among them. This lack of clearly independent corroborating evidence is more unsettling when one considers that none of Stiassny and Jensen's (1987) eight synapomorphies of the branchial apparatus is unique to labroid fishes. All can be found elsewhere among unrelated acanthomorphs, though there is no other group known to have them all (nor, in fact, do all labroids). Branchial muscles in particular have not been extensively surveyed. Stiassny and Jensen stated that embiotocids are unique among acanthomorphs in having the transversus dorsalis anterior (TDA) represented only by the musculus transversus epibranchialis 2 (MTE2). However, Sasaki (1989) pointed out that this condition also characterizes haemulids, cheilodactylids, gerreids, and sciaenids. I have seen it in a few other percoid families and perciform suborders (e.g., gobioids and blennioids), and it appears to characterize all gadiforms. I agree with Sasaki's conclusion that various superficially similar TDA modifications have occurred independently in many lineages and suggest that it applies to other branchial muscles as well. For example, an undivided sphincter oesophagi muscle, said to be lacking in all nonlabroid percomorphs examined by Stiassny and Jensen, occurs in several perciforms (e.g., *Scorpis, Kuhlia, Toxotes, Kyphosus* and *Pholidichthys*). Another important synapomorphy of labroids, though lacking in some pomacentrids, is the muscle sling directly suspending the lower pharyngeal jaws from the neurocranium, effected by a shift in insertion of the fourth internal levator to the fifth ceratobranchial. Stiassny and Jensen reported that a remarkably similar condition characterizes beloniforms, and it has apparently arisen independently many times. In only a cursory survey, I have observed a fourth internal levator sling in the atherinomorphs *Bedotia* and *Melanotaenia* and among percomorphs in *Callionymus*, the enigmatic *Pholidichthys*, the blennioids *Paraclinus* and *Malacoctenus*, and the percoid *Leiognathus*.

Certain putative labroid synapomorphies enumerated by Stiassny and Jensen (1987) are somewhat difficult to evaluate when compared to conditions found in other groups, e.g., characteristic form of the neurocranial apophysis (viewed by Greenwood, 1978, as quite dissimilar in labrids and cichlids), and structural union of the lower pharyngeal jaws, found in a number of percomorph groups but interpreted as unique in labroids because it occurs there even in the absence of pharyngeal hypertrophy and durophagy. Another, ventrorostral displacement of an elongate, cylindrical first basibranchial to lie partially below the basibranchial, is a character of degree, and I see no clear-cut difference between the condition in labroids (itself variable) and that in a number of percoids. Rosen (in Rosen and Patterson, 1990) believed that he could identify the basibranchial condition described by Stiassny and Jensen, but concluded that it "properly defines some

group of pharyngognathous 'percoids,' including pomacentrids, cichlids, embiotocids, gerreids, labrids, and possibly also kyphosids . . . ."

The Labroidei of Kaufman and Liem (1982) may be monophyletic, but I remain skeptical in the absence of corroborative evidence independent of the pharyngeal apparatus. Because of the extensive evolutionary diversification of these fishes, they have been and will continue to be studied heavily by systematists, functional morphologists, ecologists, behaviorists, geneticists, etc., and the information from these investigations will be interpreted increasingly in a historical context in which labroid monophyly is an underlying tenet. As a consequence it is critical that the hypothesis of a monophyletic Labroidei does not become dogma but that it continues to be tested by careful scrutiny of the available evidence. Labroid monophyly will be an important hypothesis to test with molecular data.

Blennioidei. — The Blennioidei of G. et al. comprised fifteen families: Blenniidae, Anarichadidae, Xenocephalidae, Congrogadidae, Notograptidae, Peronedysidae, Ophiclinidae, Tripterygiidae, Clinidae, Chaenopsidae, Stichaeidae, Ptilichthyidae, Pholididae, Scytalinidae, and Zaproridae. Springer and Freihofer (1976) and George and Springer (1980) followed Springer (1975, oral presentation at 1975 Meetings of American Society of Ichthyologists and Herpetologists) in restricting the Blennioidei to six families: Clinidae (including Ophiclinidae and Peronedysidae), Tripterygiidae, Dactyloscopidae (treated as trachinoids by G. et al.), Labrisomidae, Chaenopsidae, and Blenniidae. Springer (1993) presents evidence to support his diagnosis of the Blennioidei. I believe that blennioid monophyly is further corroborated by the shared absence of a neural spine on the first one to several vertebrae, although a few other perciforms (e.g., *Cheimarrichthys, Parapercis, Champsodon*) also appear to lack a neural spine on the first vertebra. Godkin and Winterbottom (1985) placed congrogadids as a subfamily of the percoid Pseudochromidae, and Gill and Mooi (1993) suggest that *Notograptus* is related to acanthoclinine plesiopids. Relationships of the remaining families excluded from the Blennioidei by Springer have not been completely resolved; however most authors (Springer, 1968, Nelson, 1984) have agreed with Gosline (1968) that the Anarichadidae, Stichaeidae, Pholidae, Ptylichthyidae, Scytalinidae, and Zaproridae are most closely related to the Zoarcidae (placed in the Paracanthopterygii by G. et al.).

G. et al. erroneously included the Pholidichthyidae as a junior synonym of the gobioid family Microdesmidae. Based on a detailed study of the osteology and neuroanatomy of *Pholidichthys,* Springer and Freihofer (1976) found some evidence in the dorsal longitudinal lateral-line nerve to suggest a possible relationship to Springer's Blennioidei, but no corroborative evidence in the osteology.

Gobioidei and Schindleroidei. — No changes in the composition of the Gobioidei have been proposed since the classification of G. et al. There have been, however, numerous studies dealing with higher level relationships within the suborder, and evidence supporting gobioid monophyly has grown substantially (Miller, 1973; Birdsong, 1975; Springer, 1978, 1983; Hoese, 1984; Birdsong et al., 1988). Winterbottom (1993) summarizes that evidence and explores possible sister-group relationships with several percomorph groups. Johnson and Brothers (1993) present evidence that *Schindleria* (placed in a distinct suborder by G. et al.) is a paedomorphic gobioid and identify additional gobioid synapomorphies in the larvae. Hoese and Gill (1993) address relationships of eleotridids.

Ammodytoidei. — The Ammodytoidei of G. et al. included Ammodytidae and Hypotychidae. Ida (1976) showed that hypotychids are closely related to the

gasterosteiform aulorhynchids, an hypothesis further corroborated by Johnson and Patterson (1993). Pietsch and Zabetian (1989) proposed that ammodytids are the sister group of trachinids plus uranoscopids. As discussed below (see Trachinoidei), I believe that hypothesis should be tested with more detailed osteological data.

Kurtoidei. — G. et al. followed most previous classifications in allocating *Kurtus* to a separate suborder within the Perciformes. Some previous works (de Beaufort, 1914; Tominaga, 1968) have placed the Kurtoidei within or near the Beryciformes, interpreting a median ossification in the orbital roof of the neurocranium as an orbitosphenoid, which is lacking in all perciforms. My observations of developing *Kurtus* confirm the surmise of de Beaufort (1951) that this ossification is not an orbitosphenoid, but refute his identification of it as an ossified interorbital septum. Unlike the orbitosphenoid, this bone is a single median structure only in large specimens; it is composed of the bilaterally paired pterosphenoids that grow ventrally toward the orbital midline, where they eventually fuse. Although unusual in this feature and in the unique supraoccipital hook of the males, there is nothing in the osteology of *Kurtus* to exclude it from the suborder Percoidei. There is, in fact, evidence suggesting that *Kurtus* may be closely related to the Apogonidae. The configuration of the dorsal gill-arch elements is remarkably similar to that of the apogonids. Most notably, the second epibranchial has no direct articulation with the second pharyngobranchial, the articular head of the third pharyngobranchial is expanded and much broader than that of the fourth, and the fourth pharyngobranchial cartilage is absent. Another unusual feature shared by *Kurtus* and the apogonids is the presence of horizontal and vertical rows of sensory papillae on the head and body, frequently arranged in a grid-like pattern. Similar structures have been reported elsewhere among perciforms in gobioids, and they also occur in champsodontids (V. G. Springer, pers. comm.). More detailed comparison of the ultrastructure and innervation of sensory papillae will be necessary to evaluate their homology in these groups. Another test of the *Kurtus*-apogonid hypothesis is available through detailed comparison of the eggs, both of which bear filaments around the micropyle that serve to bind the eggs together into a mass which is brooded in the mouth of apogonids and carried on the supraoccipital hook in *Kurtus*. Preliminary examination by R. Mooi (pers. comm.) of the micropylar region in apogonid eggs using SEM suggests intriguing similarities to the configuration in *Kurtus* illustrated by Guitel (1913). More work is needed.

Acanthuroidei. — G. et al. included the Siganidae, Acanthuridae and Zanclidae (as acanthurids) in their Acanthuroidei, and following a convention widely accepted since Regan (1903), they treated the large oceanic fish, *Luvarus*, as a member of the Scombroidei. In a treatise on the morphology and relationships of *Luvarus*, Tyler et al. (1989) presented evidence from adults and larvae demonstrating that the louvar is actually a highly modified, pelagic acanthuroid, resurrecting an idea originally advocated by Regan (1902). Tyler et al. (1989) proposed the phyletic sequence Siganidae, Luvaridae, Zanclidae, Acanthuridae. The Scatophagidae and Ephippidae, respectively, were hypothesized to be the first and second outgroups for the Acanthuroidei and probably should be included within the suborder. The acanthuroids should prove an interesting group for molecular investigations, especially with regard to *Luvarus*, which has undergone extreme morphological and ecological divergence from other acanthuroids.

Scombroidei. — Two scombroid phylogenies (Collette et al., 1984; Johnson, 1986) have been advanced since G. et al., and the composition of the Scombroidei has

undergone some major changes. Both phylogenies excluded the Luvaridae and, as described above, *Luvarus* has been shown conclusively to be a pelagic acanthuroid (Tyler et al., 1989). Collette et al. (1984) included *Scombrolabrax* and *Gasterochisma* in their Scombroidei but did not list synapomorphies supporting the monophyly of the suborder. Johnson's (1986) diagnosis of the Scombroidei was based on six synapomorphies. He included the Sphyraenidae as the sister group of all other scombroids, excluded *Scombrolabrax,* discussed, but left unresolved, the affinities of *Gasterochisma,* and linked the scombroids to several percoid taxa in the ascending phyletic sequence Acropomatidae (in part), *Scombrolabrax, Scombrops, Pomatomus.* Johnson's phylogeny differed further from that of Collette et al. in that it demonstrated monophyly of the Gempylidae and placed the billfishes (Istiophoridae + Xiphiidae) within the family Scombridae as the sister group of *Acanthocybium.* The latter hypothesis remains controversial and is only slightly more parsimonious than that of Collette et al., which placed billfishes as the sister group of the Scombridae. Acceptance of the *Acanthocybium*-billfish hypothesis requires three hypothetical reversals—loss of the subocular shelf, loss of association of the fourth and fifth preural neural and haemal spines with the caudal-fin rays, and reemergence of a third epural. Rejection of the *Acanthocybium*-billfish hypothesis requires that three unique innovations (ontogenetic restructuring of the snout and upper jaw, fusion of the gill filament blades, and heavy investment of the latter with toothplates) have arisen independently twice in the evolution of scombroid fishes. Whatever their specific relationship to other scombroids, the evolutionary history of billfishes clearly reflects extensive morphological modification.

The morphological diversity exhibited within the Scombroidei makes this group a particularly interesting subject for molecular investigation. There has been some recent molecular work. Block (1991) referred to the mtDNA sequence data of Block and Stewart (1990 abstract) as being "used to clarify the relationships within scombroid fishes in an effort to determine how many times endothermy has evolved within teleost fishes," and presented the resultant cladogram based on a parsimony analysis of a 600 base pair region of the cytochrome b gene. That cladogram (Block, 1991, fig. 1) agrees in part with that of Collette et al. (1984) in placing billfishes as the sister group of the Scombridae (in which *Gasterochisma* is included). No details of the data or analysis (characters, consistency index, etc.) were given, so the validity of the conclusions cannot be evaluated. There are several obvious anomalies in the scheme, the most conspicuous being placement of the gempylid *Trichiurus* within the Scombridae as the sister group of *Acanthocybium* and placement of two species of *Scomberomorus* in different clades on the tree. Block's (1991) conclusion that "endothermy has evolved three separate times within the scombroid fishes" is also consistent with Johnson's (1986) alternative phylogeny.

Stromateoidei. —The composition of the Stromateoidei of G. et al. has been altered only by the addition of a previously unknown monotypic family, Amarsipidae (Haedrich, 1969), which lacks the pharyngeal sacs that characterize other stromateoids. Horn (1984) proposed a cladistic phylogeny of stromateoid genera based mainly on selected characters drawn from Haedrich (1967) and Ahlstrom et al. (1976). More detailed osteological work is needed. Haedrich (1967) suggested a possible relationship between stromateoids and several percoid families, including the Arripididae, Kuhliidae, Terapontidae, Scorpididae, Kyphosidae and Girellidae. Johnson and Fritzsche (1989) concurred, adding microcanthids and oplegnathids to this putative assemblage (see below).

Trachinoidei.—G. et al. included 16 families in their Trachinoidei: Trichodontidae, Opistognathidae, Bathymasteridae, Mugiloididae, Cheimarrichthyidae, Trachinidae, Percophididae, Trichonotidae, Creediidae, Limnichthyidae, Oxudercidae, Leptoscopidae, Dactyloscopidae, Uranoscopidae, Champsodontidae, and Chiasmodontidae. Johnson (1984) included opistognathids in his Percoidei but cited no evidence, Springer (1978) showed that *Oxuderces* is a gobioid, and Springer (1993) presents evidence that dactyloscopids are blennioids, as he proposed initially in Springer and Freihofer (1976). Pietsch (1990), in an attempt to establish outgroup relationships for his generic phylogeny of the Uranoscopidae, hypothesized cladistic affinity among certain of the trachinoid families, proposing the following phyletic sequence: Cheimarrichthyidae, Pinguipedidae (including Mugiloididae and Parapercidae), Percophididae-Creediidae (including Limnichthyidae) -Trichonotidae, Champsodontidae-Chiasmodontidae, Leptoscopidae, Trachinidae, Uranoscopidae. He listed and examined all families previously called "trachinoid," but did not discuss their possible affinities to the families for which he proposed a phylogeny; a subsequent paper (Pietsch and Zabetian, 1989) clarified that he considered the latter 10 families to "represent the core of, but not necessarily to delimit," the Trachinoidei.

Although Pietsch's (1990) uranoscopid phylogeny appears well-corroborated with many unique (and some complex) apomorphies, his familial trachinoid phylogeny needs reexamination. Because they represent formal, structured statements of relationship, published cladograms may become accepted uncritically in classifications. For that reason, I think it is important to take a critical look at Pietsch's trachinoid hypothesis.

The families united in Pietsch's core trachinoids are quite diverse in form and structure, and range in habitat from fast-flowing, freshwater streams to the bathypelagic realm of the open ocean. In light of that, I question the two synapomorphies (small, wide pectoral radials and a "pelvic spur") that purportedly unite the ten families as a monophyletic group (referred to hereafter as Pietsch's trachinoids). Among perciforms, neither of these is unique to this group nor consistently developed within it. There is, in fact, considerable variability in the size and shape of the pectoral radials among Pietsch's trachinoids (e.g., compare *Trichonotus, Bembrops,* and *Trachinus*), and I can identify no shared configuration that would clearly differentiate them from the similarly configured pectoral radials that characterize a number of other percomorph families, including some of those examined by Pietsch, e.g., Trichodontidae (see Starks, 1930, fig. 31), Bovichthyidae and Nototheniidae. As Pietsch noted, his hypothesis requires that the pectoral radials of champsodontids and chiasmodontids have reverted to a condition that is indistinguishable from that of most percoids. The pelvic spur is, likewise, quite variable among Pietsch's trachinoids (see Pietsch, 1990, fig. 3). At one extreme (e.g., *Bembrops, Champsodon*), it is a distinctive, elongate process, but at the other (e.g., *Hemerocoetes, Gnathagnus,* and the most primitive taxon *Cheimarrichthys*), it is little more than a bump or ridge, seemingly indistinguishable from that found in many percomorphs (some of which also have a very large spur). Perhaps Pietsch's trachinoids share a unique configuration of this pelvic spur, but I am unable to identify it.

A number of osteological complexes that have often been shown to be informative in higher-level phylogenies were not considered by Pietsch. Configurations of the dorsal gill-arch elements, median fin supports and supraneurals, ribs and intermuscular bones and caudal skeleton differ trenchantly among Pietsch's trachinoids, and their inclusion in the analysis would almost certainly result in a different hypothesis of relationships. Several characters used in the uranoscopid phylogeny

(e.g., reduced number of infraorbitals, ribs, predorsals and postcleithra) were not included in the familial (outgroup) phylogeny, even though the derived states characterize some of those families. Thus, for example, in Pietsch's data matrix, those uranoscopid genera with two postcleithra were coded as 0, and those with the derived condition of one or no postcleithrum were coded as 1, whereas all the outgroup families were coded as 0, despite the fact that percophidids, trichonotids, creediids, champsodontids, and leptoscopids have one or no postcleithrum (see Pietsch, 1990, tables 1, 2). The implication is that these characters are phylogenetically informative when they vary within, but not among, families.

Pietsch's (1990) treatment of the Percophididae, Trichonotidae, and Creediidae as a monophyletic group is not defended. He cited shared derived similarities in the pterygoid region of the suspensorium but stated that "this hypothesis of relationship needs further testing." Nelson (1986) described and illustrated this distinctive suspensorial configuration for *Trichonotus*, in which the ectopterygoid is rod-like and largely free from the endopterygoid, articulating only at its anterior tip with the palatine and movably with the quadrate at its posterior tip. Nelson noted that a similarly specialized suspensorium also characterizes *Hemerocoetes* and the creediids. As for the percophidids, I have observed it in all the *Pteropsaron*-related genera (*Spinapsaron, Osopsaron, Branchiposaron, Acanthophrites, Enigmapercis, Matsubaraea,* and *Squamicreedia*), but it does not characterize *Bembrops* or *Percophis,* and I find no other evidence to relate these two genera to the group with the specialized suspensorium. Trichonotids, creediids and the percophidid genera with the specialized suspensorium lack two of the five characters that would place them within Pietsch's trachinoids (these were treated as reversals on the cladogram). As discussed above two of the other characters are questionable. The only remaining character shared with some of Pietsch's trachinoids is cycloid scales, and this alone is unconvincing as evidence of close relationship. Pietsch and Zabetian (1989) added two synapomorphies to their matrix to "guarantee monophyly for the group containing the Percophididae, Trichonotidae and Creediidae," but they did not identify them, nor did they include them on their cladogram.

Another hypothesis advanced without character support by Pietsch is that champsodontids and chiasmodontids are sister groups. In the absence of any supporting evidence, such a relationship seems unlikely, given distinct differences in certain aspects of their osteology, such as the dorsal fin supports and gill arches. The spinous dorsal pterygiophores of chiasmodontids exhibit typical chain-link articulation, whereas those of champsodontids lack distal radials altogether. The pharyngobranchials of chiasmodontids are attenuate and horizontally oriented, whereas those of champsodontids are short and the second and third have dorsally directed columnar processes. I have found no evidence that champsodontids are closely related to chiasmodontids or any other of Pietsch's trachinoids, and certain features suggest that their relationships may lie elsewhere. They have free sensory papillae on the head and body (see Kurtoidei, above) and lack a neural spine on the first vertebra (see Blennioidei, above). Perhaps the most promising avenue of investigation (which I am currently pursuing with R. D. Mooi) is that of a possible relationship to scorpaeniforms. In champsodontids, Baudelot's ligament inserts on the first vertebra, rather than the occiput, an uncommon condition among percomorphs occurring elsewhere in some scorpaenoids, cottoids, and zoarcoids. The parietal bears a serrate ridge (ending in a spine) through which there is an opening for passage of the supratemporal sensory canal, a condition I have seen elsewhere only in scorpaeniform fishes (see above). Champsodontids have a dis-

continuous infraorbital series, and the absence of a third suborbital would explain their lack of a suborbital stay, despite an ancestral presence.

Pietsch and Zabetian (1989) argued that the Ammodytidae (treated as a separate suborder by G. et al.) are trachinoids, inserting them within the framework of Pietsch's (1990) phylogeny between leptoscopids and trachinids, as the sister group of trachinids plus uranoscopids. For some of the same reasons discussed above, I am not convinced that they are correct. They concluded that "While no one generally familiar with ammodytids, trachinids, and uranoscopids would ever suggest a common origin (ammodytids on one hand, and trachinoids and uranoscopids on the other, appear as very different kinds of fishes), the derived features shared among these taxa provide convincing evidence of monophyly." This is the strongest node on their cladogram (Pietsch and Zabetian, 1989, fig. 21), and the possibility of such a relationship should certainly be investigated further with additional character information from gill arches, median fin supports, supraneurals, intermusculars, caudal skeleton, etc. There is little else, however, to recommend placement of ammodytids within Pietsch's trachinoids. Ammodytids lack both synapomorphies of the entire group (unless one interprets the slight bump on the pelvic girdle of *Embolichthys,* Pietsch and Zabetian, 1989, fig. 16, as a pelvic spur) and both characters (rugose head bones and expanded infraorbitals) that purportedly unite champsodontids, chiasmodontids, leptoscopids, ammodytids, trachinids and uranoscopids. At the node comprising the latter four groups, six of the nine characters are not optimized correctly. The stated tree length of 46 is based on the correct optimization, but the character distribution shown gives a length of 52. The more parsimonious solution is that characters 10–14 and 16 arose independently in leptoscopids and uranoscopids. As a consequence, the monophyletic group comprising leptoscopids, ammodytids, trachinids and uranoscopids is supported by only three putative synapomorphies, lack of hypobranchial toothplates, adjacent scales with united epidermal covering, and pectoral radials sutured to scapula and coracoid, and the last of these is lacking in ammodytids.

Pietsch (1990) and Pietsch and Zabetian (1989) have provided much new and valuable character information about the fishes we now call trachinoids, but, as with so many perciform groups (e.g., scombroids), more work is needed before formal classificatory changes can be recommended.

Percoidei. — This largest and most diverse of the perciform suborders is undoubtedly polyphyletic. As with the order Perciformes, there has never been a serious attempt to diagnose a monophyletic Percoidei, nor to challenge its monophyly. Johnson (1984) modified the overall limits of the Percoidei only slightly from that of G. et al., whose familial classification is given in Table 2, wherein bold type designates those families for which new hypotheses about limits and/or relationship to other families have been proposed. Substantial progress has been made at one level, that is in the diagnosis of monophyletic families and the concomitant shuffling and reallocation of genera. A brief review follows.

Greenwood (1976) redefined the limits of the Centropomidae based on two synapomorphies, rejecting any close relationship to the Ambassidae, which were treated as a centropomid subfamily by G. et al. Greenwood (1977) refuted the previously overlooked phenetic hypothesis of Rivas and Cook (1968) that placed the enigmatic *Niphon* in the Centropomidae. The Serranidae of G. et al. (which included *Niphon*) was a non-monophyletic assemblage that included unrelated taxa and excluded some related ones (e.g., Grammistidae and Pseudogrammidae). Gosline (1966) redefined the Serranidae, placing *Niphon* and most of the other

excluded taxa (along with some not considered serranids by G. et al.) in a poly-phyletic Percichthyidae. Johnson (1983, 1988) refined Gosline's Serranidae, re-storing the genus *Niphon* to the family and confirming Kendall's (1976) inclusion of the pseudogrammids and grammistids. Johnson and Smith-Vaniz (1987) placed *Parasphyraenops*, previously associated with the Apogonidae or considered in-certae sedis (Fraser, 1972), in the serranid subfamily Serraninae. Baldwin and Johnson (1993) present an analysis of generic relationships within the serannid subfamily Epinephelinae, based on larval and adult morphology.

Johnson (1983) indicated that Gosline's (1966) Percichthyidae was not mono-phyletic, and Johnson (1984), based on only a brief diagnosis, restricted the family to fresh and brackish water genera of Australia and South America, adding three genera, *Nannoperca, Edelia* and *Nannatherina*, that previously had been included in the Kuhliidae and one, *Gadopsis*, that had been treated variously as a separate order (Scott, 1962), a percoid family (G. et al.), an ophidioid (Gosline, 1968), or a trachinoid or blennioid (Rosen and Patterson, 1969). The integrity of Johnson's (1984) Percichthyidae has not been challenged; an in depth, critical examination is needed.

Of the genera excluded from Gosline's Percichthyidae, Johnson (1984) allocated most of the "oceanic" forms to the family Acropomatidae, and suggested that *Symphysanodon*, removed from the Lutjanidae to incertae sedis by Johnson (1981), might be related to them. However, no evidence supporting monophyly of this group has been identified. Johnson (1986) noted that some of these genera share dentition characters that suggest the possibility of an outgroup relationship to scombroids, but there is no other corroborating evidence.

The composition of the Grammatidae of G. et al. was unclear. Nelson (1974) listed eight genera, and Springer (1982) noted that two of those are plesiopids and one is a cichlid, and found little evidence to unite the remaining five. Johnson (1984) treated two of those, *Callanthias* and *Grammatonotus*, as a distinct family Callanthiidae, and suggested that *Stigmatonotus* is probably a larval or juvenile serranid. Johnson's (1984) Grammatidae comprised, by default, the remaining genera, *Gramma* and *Lipogramma*. Gill and Mooi (1993) present evidence for monophyly of Johnson's Callanthiidae and Grammatidae.

Springer et al. (1977) demonstrated that the Anisochromidae, Pseudoplesiop-idae and Pseudochromidae (separate families in G. et al.) form a monophyletic group and synonymized them under the family name Pseudochromidae. Godkin and Winterbottom (1985) demonstrated that the Pseudochromidae of Springer et al. (1977) was paraphyletic without the inclusion of the Congrogadidae, which were included in the Blennioidei by G. et al. Godkin and Winterbottom (1985) identified 13 synapomorphies of congrogadines and anisochromines and relegated the former to subfamilial status within the Pseudochromidae.

G. et al. treated the Plesiopidae and Acanthoclinidae as separate families. Mooi (1993) demonstrates that the Plesiopidae are paraphyletic without inclusion of the Acanthoclinidae and accordingly synonymizes the two (Plesiopidae). Gill and Mooi (1993) present evidence to support the suggestion of Smith-Vaniz and Johnson (1990) that notograptids are related to acanthoclinine plesiopids, but elect not to alter the classification to reflect this hypothesis, pending additional corroborative evidence.

G. et al. recognized the family Gregoryinidae, but noted that it may be based on a juvenile cheilodactylid. Randall (1983) confirmed their surmise and syn-onymized the two (Cheilodactylidae).

In a comparative study of the acoustico-lateralis system of the Centrarchidae, Branson and Moore (1962) placed the pigmy sunfish, *Elassoma*, in a separate

family, based on more than 20 mostly reductive features in which it differs from centrarchids, but still considered the two groups related. G. et al. included *Elassoma* in their Centrarchidae. Johnson (1984) rejected the hypothesis of close phylogenetic relationship between the two, adding eight reductive features of the skeleton of *Elassoma* to the many differences enumerated by Branson and Moore, and pointing out that no apomorphies shared by *Elassoma* and centrarchids have been identified. He also described several features of *Elassoma* that he suggested cast doubt on its affinities with the Percoidei. Some of these are reductive in nature and (as with many of the characters in which *Elassoma* differs from centrarchids) could be interpreted as the result of developmental truncation in the diminutive *Elassoma* and thus invalid indicators of phylogenetic relationship. Others, however, represent character states that do not appear in any stage of development in other percoids. These include the presence of a full neural spine on the second preural centrum, fused haemal spines on the second and third preural centra, a fused neural spine on the first centrum (which also bears strong parapophyses), and a mesethmoid comprising two discoidal ossifications. The latter two features also characterize atherinomorphs.

The relationships of *Elassoma* remain obscure, and I am not optimistic about the potential for a clear resolution of this problem based on morphological data alone. One osteological feature not considered previously suggests another possible line of investigation, although I hold little hope that it will be a fruitful one, as the relationship seems unlikely. One of the more unusual features of the laterosensory-canal system of *Elassoma* described by Branson and Moore (1962) is the complete dissociation of the posttemporal canal from the posttemporal proper. An alternative intepretation of the condition is that the posttemporal canal is absent and the posterior extrascapular is posteriorly displaced. I had thought this condition unique to *Elassoma* but have found that a similar condition characterizes the Mugilidae (Stiassny, 1993, fig. 7D). In both groups, the posttemporal does not bear a bony canal, and a trough-like or tubular ossification lies in the skin, well lateral and partially anterior to the posttemporal. Although such an arrangement may occur elsewhere in fishes, I am unaware of it, and it does not occur among percoids, nor can it be viewed as paedomorphic, because the posttemporal canal typically develops as an integral part of the posttemporal (i.e., it does not ossify separately and later fuse) and the posterior extrascapular develops anterior, not lateral, to the posttemporal. *Elassoma* and mugilids are also remarkably similar (and unlike percoids) in having strong, laterally directed parapophyses beginning on the first vertebra, with pleural ribs sometimes beginning anterior to the third vertebra. With these features in mind it is worth enumerating the additional possibly apomorphic (based only on the common percoid state) characters shared by *Elassoma* and mugilids, remembering that no synapomorphies are known for *Elassoma* and centrarchids. These include a posterior origin of the spinous dorsal fin (sixth or seventh interneural space) with the neural spines anterior to the fin broader than those posterior to it, first neural spine fused to centrum, lack of articulation of the pelvic girdle with the cleithra, low number of principal caudal-fin rays (14–15), absence of a lateral line on the body, open preopercular canal, reduced infraorbital series, and widely separated exoccipital condyles.

Although a sister-group relationship between *Elassoma* and the mugilids seems implausible, there are enough similarities to warrant some further investigation involving additional morphological complexes or molecular data. My exploration of the osteology has been relatively superficial, and there is much that should be done relative to questions of character homology, including examining them from

a developmental perspective. For now, the osteological data are ambiguous. Many of the characters shared by *Elassoma* and mugilids can also be found among atherinomorphs. As discussed above, Stiassny (1990) proposed that mugilids are the sister group of atherinomorphs based on four putative synapomorphies, but noted also that the mugilid pelvic girdle exhibits the derived percomorph configuration, as does that of *Elassoma*. One of Stiassny's mugilid-atherinomorph synapomorphies, expanded anterior neural arches, is weakly developed in *Elassoma*, wherein the anterior spines, though not really expanded, are clearly more robust and longer than the posterior ones. The remaining three synapomorphies, all involving the branchial musculature, are lacking in *Elassoma*; however, as I noted above, I also found two of them lacking in the primitive mugilid *Agonostomus*. My "second look" at *Elassoma* served to further convince me that it has no relationship to the Centrarchidae or other lower percoids, but did not lead me to a satisfactory resolution of its true affinities. Johnson and Patterson (1993) explore the problem further and propose a new percomorph assemblage that includes, among others, the three groups mentioned above.

The Apogonidae of G. et al. included the Epigonidae and Dinolestidae. Fraser (1971) convincingly rejected a close relationship between *Dinolestes* and the apogonids, but he (1972a) continued to treat epigonids (*Epigonus, Florenciella* and *Brinkmannella*) as an apogonid subfamily. Fraser's (1972a) work stands as one of the most comprehensive osteological treatises on a percoid family, but he did not attempt to cladistically diagnose the Apogonidae or its component subfamilies. Johnson (1984) cited several osteological specializations that he believed united Fraser's epigonines, along with *Sphyraenops* and *Brinkmanella*, as a monophyletic group, which he elevated to family. He observed that the two anal spines of apogonids and epigonids, usually cited as evidence of their close relationship, are not the same serial elements; in apogonids one spine is serially associated with the first pterygiophore and the other is supernumerary, whereas in epigonids both spines are supernumerary.

Further investigation has failed to produce evidence supporting an apogonid-epigonid relationship and has revealed three autapomorphies of the Apogonidae. Among percoids with separation between the spinous and soft portions of the dorsal fin, only apogonids have an extremely short distal radial associated with the last spine, so that the serially associated proximal-middle element almost contacts the base of the spine. In other groups with separate fins (including epigonids) the distal radial of the last spine is notably elongate, so that the proximal-middle element is well anterior to its serial spine. The configuration of the dorsal gill-arch elements of apogonids is distinctive in having no articulation between the second epibranchial and second pharyngobranchial, expanded third and narrow fourth epibranchials and a relatively small fourth upper pharyngeal toothplate lacking a fourth pharyngobranchial cartilage. As I noted above, this configuration is quite similar to that of *Kurtus*. I have observed lack of articulation between the second epibranchial and pharyngobranchial elsewhere among percoids only in *Pempheris* and *Glaucosoma*, both of which lack the other distinctive gill-arch features of apogonids (see below). A third apomorphy of apogonids (also present in *Kurtus*) is the presence of horizontal and vertical rows of sensory papillae on the head and body. These papillae previously have been said to characterize only pseudamine apogonids, but I find that they characterize most apogonine genera as well. Among percomorphs, only gobioids and champsodontids are known to have apparently similar structures. A detailed comparative study of the ultrastructure and innervation of these sensory papillae is needed.

The Pempherididae of G. et al. included *Leptobrama*. However, Tominaga

(1965) demonstrated that the only character used to unite the two groups, a single short dorsal fin, is invalid, because the elements comprising the dorsal fin in each group are not topographically homologous. Accordingly, he placed *Leptobrama* in a distinct family where it has remained in most subsequent classifications (Nelson, 1976; Springer, 1982). Tominaga (1968) presented clear evidence for monophyly of the Pempherididae, comprising *Pempheris* and *Parapriacanthus*. Tominaga (1986) called attention to the proposal of Katayama (1954) that *Glaucosoma* is similar to *Pempheris* in certain features of the cranium and swimbladder, and hypothesized that *Glaucosoma* is closely related to the pempheridids. I agree with Tominaga (1986) that the distinctive and complex swimbladder arrangement in these fishes appears structurally homologous. Haemapophyses of several anterior vertebrae are modified to form flat plates that are bound to the sclerotic cover of the swimbladder. In addition, a cylindrical muscle extends from the pterotic to insert on the dorsal surface of the swimbladder beneath the free anterior margin of the sclerotic cover. A pempherid-*Glaucosoma* relationship is also suggested by the similar configuration of the dorsal gill-arch elements, wherein there is no direct articulation between the second epibranchial and pharyngobranchial (not true for *Parapriacanthus*) and the fourth upper pharyngeal toothplate is wider than long and extends medially well beyond the margin of the third pharyngobranchial. I recommend that *Glaucosoma* be included as a subfamily within the Pempherididae.

Several changes in the classification of "carangoid" fishes have been proposed since G. et al. In a comparative osteology of *Nematistius*, Rosenblatt and Bell (1976) removed the genus from the Carangidae, although they regarded it as closely related to them. Freihofer (1978) noted that the Nematistiidae, Carangidae, Coryphaenidae, Rachycentridae and Echeneididae share a unique specialization in the lateralis system on the snout—an anterior extension of the anterior nasal canal surrounded by one or two tubular ossifications. Smith-Vaniz (1984) and Johnson (1984) cited this, together with the presence of small, adherent, cycloid scales, as evidence that these five families constitute a monophyletic group and hypothesized relationships among them based on additional synapomorphies. I recommend that this group be recognized as the suborder Carangoidei. Johnson (1984) also presented evidence for a monophyletic group (superfamily Echeneoidea) comprising echeneidids, *Rachycentron* and *Coryphaena* and described a complex specialization of the epithelium in the larvae of the latter two that supports a previously unproposed sister-group relationship between them. Smith-Vaniz (1984) hypothesized the phyletic sequence Nematistiidae, echeneoids, Carangidae and proposed tribal relationships within the Carangidae. He included in his carangid tribe Carangini the genus *Parastromateus*, treated as a separate family (Formionidae) by G. et al.

G. et al. followed Schultz's (1945) concept of the Emmelichthyidae, a polyphyletic assemblage of planktivorous fishes that included taxa from five unrelated lineages. Heemstra and Randall (1977) and Johnson (1981) demonstrated that the superficially similar highly protrusible jaw mechanisms differ trenchantly and used this and other evidence to restrict the Emmelichthyidae to three genera, *Emmelichthys, Plagiogenion* and *Erythrocles*. Of the excluded genera, *Dipterygonotus* was shown to be a caesionid, *Inermia* and *Emmelichthyops* were placed in a family Inermiidae, *Labracoglossa* in a family Labracoglossidae and the remaining genera in the family Centracanthidae. Johnson (1981) presented evidence to link caesionids to the Lutjanidae, inermiids to the Haemulidae and centracanthids to the Sparidae. Johnson (1981) did not consider *Labracoglossa* but later (1984) included it in the Scorpididae based on similarities in osteology and scale

morphology and one specialized feature observed elsewhere only in *Scorpis*, a small slip of muscle extending from the basioccipital to the first vertebra.

Johnson's (1981) treatment of the Caesionidae as a separate family renders the Lutjanidae paraphyletic, as there is definitive evidence in jaw muscles (Johnson, 1981) and larval morphology (Leis and Rennis, 1983; Johnson, 1984) that the lutjanid subfamily, Lutjaninae, is the sister group of the caesionids. Carpenter (1990) followed Johnson's classification, but I would now recommend treating caesionines as a subfamily of the Lutjanidae.

G. et al. treated the Nemipteridae, Pentapodidae, Lethrinidae and Sparidae as separate families, including the Paradicichthyidae in the latter family. Akazaki (1962) considered these four families to be closely related (his spariform fishes). Based on specializations of the suspensorium and other features, Johnson (1981) supported monophyly of Akazaki's spariform fishes with the inclusion of the Centracanthidae, which he believed to be the sister group of the Sparidae based on a specialized maxillary-premaxillary articulation. Johnson (1981) removed the Paradicichthyidae from the Sparidae and demonstrated its correct placement as a subfamily (comprising the genera *Symphorichthys* and *Symphorus*) of the Lutjanidae. He also corroborated the monophyly of Akazaki's Nemipteridae, which included pentapodids, based on loss of a supraneural and specializations of the rostral ligaments and adductor mandibulae. However, he disagreed with Akazaki's phyletic sequence Nemipteridae, Sparidae, Lethrinidae, arguing that the lethrinid, *Gnathodentex*, and the nemipterid, *Scolopsis*, may share certain specializations of the other family. This suggests that a more rigorous cladistic analysis could demonstrate paraphyly for one or both families.

The Kyphosidae of G. et al. included scorpidids, girellids and parascorpidids. Johnson (1984) recognized four separate families and included the Labracoglossidae of G. et al. in his Scorpididae, but not the Microcanthidae, which had been included by Springer (1982). Johnson and Fritzsche (1989) identified six synapomorphies of *Graus* and *Girella* (their Girellidae), the most distinctive being insertion of the A_2 division of the adductor mandibulae on the lateral surface of the coronoid process of the dentary. For purposes of outgroup comparison, they tentatively accepted a close relationship between the Kyphosidae, Scorpididae, and Girellidae based on the overall similarity of their larvae and the putative synapomorphy of progenic serial tooth replacement, uncommon among perciforms, but not unique to those three families. They further proposed that these families may be part of a larger monophyletic assemblage that includes arripidids, kuhliids, microcanthids, oplegnathids, terapontids, and stromateoids, based on the common possession of Freihofer's (1963) pattern 10 of the ramus lateralis accessorius. Johnson and Fritzsche provisionally included *Neoscorpis* in their Kyphosidae, but to date no evidence has been found to relate *Parascorpis* to any specific percoid family.

G. et al. included *Drepane* in their Ephippidae and treated *Rhinoprenes* as a separate family. Based on specializations of the gill arches, Johnson (1984) proposed that a monophyletic Ephippidae comprises the following genera: *Chaetodipterus, Ephippus, Parapsettus, Platax, Proteracanthus, Rhinoprenes* and *Tripterodon*. He found no evidence to relate *Drepane* to the ephippids, and Tyler et al. (1989) hypothesized that it is the sister group of chaetodontids and pomacanthids based on a shared modification of the mesethmoid. However, Blum (unpubl. Ph.D. diss.), using additional characters, found placement of *Drepane* as the sister group of ephippids more parsimonious.

Okada and Suzuki (1956) presented osteological evidence for a close relationship between the Cepolidae and Owstoniidae. G. et al. treated them as separate families;

however, Springer et al. (1977) identified additional specializations shared by the two families and synonymized them under the Cepolidae. Gill and Mooi (1993) agree with Springer et al. (1977) and identify a unique specialization in the gill arches of cepolids.

Monophyly for several percoid families, as classified by G. et al., has been demonstrated. Vari (1978) defined the Terapontidae based on apomorphies of the swimbladder and associated extrinsic muscles, urohyal and third pharyngo-branchial, rejecting Fowler's (1931) inclusion of *Datnioides* and *Pseudohelotes,* but he was unable to identify the sister group of the terapontids. *Datnioides* is usually included in the Lobotidae (Nelson, 1984), but there is no explicit evidence supporting that relationship, and Johnson (1984) left *Datnioides* incertae sedis. Starnes (1988) identified three synapomorphies of the Priacanthidae, distinctive spinulose scales, form of the first epibranchial and absence of an interarcual cartilage, and a single postcleithrum, but also was unable to determine their relationship to other percoids. Sasaki (1989) identified 21 synapomorphies of the Sciaenidae (many of which are not unique among percoids to sciaenids) but again was unable to identify their sister group. As I suggested above, I believe the Polynemidae are the closest relatives of the Sciaenidae.

DISCUSSION

The period since the mid 1960's has been an exciting time of discovery in systematic ichthyology. Refinement of techniques for enzyme clearing and staining of whole specimens for bone (Taylor, 1967) and cartilage (Dingerkus and Uhler, 1977) sparked renewed interest in the detailed study of fish skeletons. These preparations greatly facilitated examination of complexes such as gill arches and median fin supports, whose intricacies are much less accessible in dry skeletons, and provided an important breakthrough for the study of the developing skeleton, still far from fully exploited. Our knowledge of the comparative osteology of fishes has increased dramatically, and this, combined with cladistic methodology, has markedly advanced our understanding of phylogenetic relationships.

No other vertebrate group, and perhaps no other group of animals, has seen classificatory modifications over the past 25 years equivalent in scope to those in teleost fishes, particularly the Percomorpha. New hypotheses of limits and/or interrelationships proposed since G. et al. have classificatory implications for almost every percomorph order, all but two or three suborders of the Perciformes and about two-thirds of the 70 families of the Percoidei.

Within percoids, the major strides have been definition of monophyletic families and the concomitant shuffling of genera. On that level, we have made substantial progress, and we have been able to define some larger monophyletic groups. By and large, however, relationships above the family level have remained elusive. There has been no overall or partial phylogeny proposed for the Percoidei, and we have no evidence that it is a monophyletic assemblage. The same can be said for the order Perciformes; limits and monophyly of many of the suborders have been established, but their interrelationships remain obscure and there is no evidence that perciforms are monophyletic. Some progress has been made in elucidating relationships among percomorph orders, but there are several conflicting hypotheses and no consensus about the composition of the Percomorpha.

A major question before us now is how best to approach the seemingly intractable problems of higher level relationships within the Percomorpha. Undoubtedly, many of these problems will be addressed with molecular data in the near future. These analyses will be important and provocative as tests of existing

hypotheses of relationship. Whether they will provide convincing resolutions to problems where morphology has not remains to be seen. Regardless, morphological studies will continue; molecular data is of little interest without them. I suspect that myology and neuroanatomy will be studied more extensively, and in these areas broad character surveys are needed. Gill-arch musculature, for example, offers a wealth of largely unexplored information, difficult to evaluate until we have a better appreciation of the variability at various taxonomic levels (see my discussion above under Labroidei). The use of comparative neuroanatomy in phylogenetic studies of teleosts has not progressed beyond the seminal work of Freihofer (1963, 1970, 1972, 1978), largely because the time and painstaking effort required in nerve preparation and dissection overwhelms most of us, and again because we are unable to confidently evaluate the character information that exists. That prospect is further aggravated by the realization that correct identification of individual nerves may require experimental work (Song and Northcutt, 1991; Song and Boord, 1993). Daunting though it may be, a better understanding of innervation patterns of percomorph fishes will undoubtedly offer new and substantive phylogenetic insight.

Although I am optimistic about future progress based on osteological investigations, I think it is unlikely that the conventional approach will continue to provide the same degree of phylogenetic revelation that we have experienced over the last three decades. While there is still much to be learned, we now have a basic descriptive knowledge of most aspects of the adult skeleton of all major percomorph groups. With this has come an inevitable awakening to the rampant homoplasy that has characterized percomorph evolution, particularly at the higher levels. Each new study produces yet another conflicting hypothesis (see, for example, Parenti, 1993; Stiassny, 1993; Moore, 1993; Winterbottom, 1993; Johnson and Patterson, 1993), and parsimony solutions are unconvincing in the absence of corroboration by uniquely shared apomorphies. Progress, I believe, will require not simply more characters and better algorithms, but a more thorough exploration of the morphology associated with each character. At these higher levels critical evaluation of structural homology is imperative, demanding meticulous scrutiny not only of adult structures, but also of their ontogeny.

In 1983, the Ahlstrom Memorial Symposium, "Ontogeny and Systematics of Fishes," promised new impetus for developmental studies. Almost 10 years after its publication the historical separation between studies of early life history stages and "mainstream" systematic ichthyology appears only slightly diminished. Most comparative osteological and phylogenetic studies of fishes do not incorporate development and thus ignore both the potential for additional suites of characters and for testing homology.

One aspect of ontogenetic information, specialized larval characters, has been successfully explored and utilized, perhaps because it is the most accessible and does not require exhaustive studies of complete developmental series. There are numerous examples of the utility of such characters, some of the most notable being the convincing evidence they provide for monophyly and intrarelationships of the Acanthuroidei (Johnson and Washington, 1987; Tyler et al., 1989) and of the serranid subfamilies Anthiinae (Baldwin, 1990), and Epinephelinae (Johnson, 1988; Baldwin and Johnson, 1993). Within percomorphs these highly adaptive specializations appear to be most informative at the family level and below (with a few exceptions), and I doubt that they will be much help in resolving relationships above that level.

Another aspect of ontogeny that intuitively would seem less subject to selection and thus perhaps better reflect phyletic history is the pattern and sequence of

chondrification and ossification of skeletal elements. Developmental patterns of the vertebral column and median fin supports have been described and compared among scombroid families (Potthoff et al., 1986) and a few percoids (Potthoff et al., 1984, 1988). Johnson and Brothers (1993) found diagnostic patterns of development in the pectoral, caudal and vertebral skeletons of gobioids. Because skeletal development proceeds rapidly over a small size range, accurate documentation of pattern and sequence requires large numbers of specimens representing the complete developmental series and is labor intensive. As a consequence, this type of information, which may hold important clues to phylogenetic relationships, is largely unknown for most percomorphs.

Finally, and perhaps most importantly, I would emphasize the power of ontogeny for testing homology of osteological characters. My work on the monophyly of several eutelostean clades (Johnson, 1992) convinced me that there is enormous unrealized potential here. In that study, relatively simple observations of developing gill arches contributed to the resolution of a longstanding problem of identity of the fifth upper pharyngeal toothplate in non-ctenosquamates, and a synapomorphy was identified in the pelvic fin of eurypterygians that is recognizable in higher acanthomorphs only with an ontogenetic perspective. Consider then, studies like Winterbottom's (1993) search for the gobioid sister group, which is confounded by his discovery that gobioids share different sets of putatively homologous characters with several diverse perciform groups. Careful scrutiny of the development of such characters (e.g., similarly configured pelvic girdles) could potentially shed light, one way or another, on the conjecture of homology and thus reduce the level of apparent homoplasy that confounds the problem. The same would apply to many of the papers in this volume with equally unsettling levels of homoplasy (Johnson and Patterson, 1993). Acquisition of this ontogenetic data is admittedly laborious, and we cannot expect that it will always, or even most of the time, be enlightening. Nonetheless if it is accessible, the inconvenience associated with obtaining it seems inadequate justification for ignoring such a potentially illuminating aspect of character information. I believe it will be a critical key to our continued progress in elucidating the complex phyletic history of percomorph fishes.

Literature Cited

Ahlstrom, E. H., J. L. Butler and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26: 285–402.

Akazaki, M. 1962. Studies on the spariform fishes—anatomy, phylogeny, ecology, and taxonomy. Osaka, Japan, 8 Kosugi Co. Ltd., 368 pp. (In Japanese, English summary)

Baldwin, C. 1990. Morphology of the larvae of American Anthiinae (Teleostei: Serranidae), with comments on relationships within the subfamily. Copeia 1990: 913–955.

——— and G. D. Johnson. 1993. Phylogeny of the Epinephelinae (Teleostei: Serranidae). Bull. Mar. Sci. 52: 240–283.

Banister, K. 1970. The anatomy and taxonomy of *Indostomus paradoxus* Prashad and Mukerji. Bull. Brit. Mus. Nat. Hist. (Zool.) 19: 179–209.

Birdsong, R. S. 1975. The osteology of *Microgobius signatus* Poey (Pisces: Gobiidae), with comments on other gobioid fishes. Bull. Fla. St. Mus., Biol. Sci. 19: 135–187.

———, E. O. Murdy and F. L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships. Bull. Mar. Sci. 42: 174–214.

Block, B. A. 1991. Evolutionary novelties: how fish have built a heater out of muscle. Amer. Zool. 31: 726–742.

———— and A. F. R. Stewart. 1990. Evolution of endothermy in scombroid fishes: systematic rela-
    tionships examined with direct sequencing of mitochondrial DNA. Amer. Zool. 30: 72A.
Branson, B. A. and G. A. Moore. 1962. The lateralis components of the acoustico-lateralis system
    in the sunfish family Centrarchidae. Copeia 1962: 399–422.
Carpenter, K. E. 1990. A phylogenetic analysis of the Caesionidae (Perciformes: Lutjanoidea). Copeia
    1990: 692–717.
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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.
de Beaufort, L. F. de. 1914. Die anatomie und systematische stellung des genus Kurtus Bloch.
    Morphol. Jahrb. 48: 391–410.
————. 1951. Suborder Kurtoidea. Pages 82–85 in L. F. de Beaufort and W. M. Chapman (eds.).
    The fishes of the Indo-Australian Archipelago, Vol. 9. E. J. Brill, Leiden.
de Sylva, D. P. 1984. Polynemoidei: development and relationships. Pages 540–541 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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.
Dingerkus, G. and L. D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates
    for demonstration of cartilage. Stain Technol. 52: 229–232.
Fowler, H. W. 1931. The fishes of the families Pseudochromidae, Lobotidae, Pempheridae, Pria-
    canthidae, Lutjanidae, Pomadasyidae and Teraponidae, collected by the United States Bureau of
    Fisheries Steamer "Albatross," chiefly in Philippine seas and adjacent waters. Bull. U.S. Natl.
    Mus. vol. 100, 388 pp.
Fraser, T. H. 1971. The fish Dinolestes lewini with comments on its osteology and relationships.
    Jap. J. Ichthyol. 18: 157–163.
————. 1972a. Comparative osteology of the shallow water cardinal fishes (Perciformes: Apogonidae)
    with reference to the systematics and evolution of the family. Ichthyol. Bull. Rhodes Univ. 34:
    1–105.
————. 1972b. Some thoughts about the teleostean fish concept—the Paracanthopterygii. Jap. J.
    Ichthyol. 19: 232–242.
Freihofer, W. C. 1963. Patterns of the ramus lateralis accessorius and their systematic significance
    in teleostean fishes. Stan. Ichthyol. Bull. 8: 80–189.
————. 1970. Some nerve patterns and their systematic significance in paracanthopterygian, sal-
    moniform, gobioid, and apogonid fishes. Proc. Calif. Acad. Sci., ser. 4, 38: 215–264.
————. 1972. Trunk lateral line nerves, hyoid arch gill rakers, and olfactory bulb location in ath-
    eriniform, mugilid, and percoid fishes. Occas. Pap. Calif. Acad. Sci. 95: 1–31.
————. 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. Nat. Sci. 128: 1–78.
George, A. and V. G. Springer. 1980. Revision of the clinid fish tribe Ophiclinini, including five
    new species, and definition of the family Clinidae. Smiths. Contrib. Zool. 307: 1–31.
Gill, A. C. and R. D. Mooi. 1993. Monophyly of the Grammatidae and of the Notograptidae, with
    evidence for their phylogenetic positions among perciforms. Bull. Mar. Sci. 52: 327–350.
Godkin, C. M. and R. Winterbottom. 1985. Phylogeny of the family Congrogadidae (Pisces: Per-
    ciformes) and its placement as a subfamily of the Pseudochromidae. Bull. Mar. Sci. 36: 633–671.
Gosline, W. A. 1962. Systematic position and relationships of the percesocine fishes. Pac. Sci. 16:
    207–217.
————. 1966. The limits of the fish family Serranidae, with notes on other lower percoids. Proc.
    Cal. Acad. Sci. 33: 91–111.
————. 1968. The suborders of perciform fishes. Proc. U.S. Natl. Mus. 124(3647): 1–78.
————. 1970. A reinterpretation of the teleostean fish order Gobiesociformes. Proc. Cal. Acad. Sci.
    38: 363–382.
————. 1971. Functional morphology and classification of teleostean fishes. Univ. Press Hawaii,
    Honolulu. 208 pp.
Greenwood, P. H. 1976. A review of the family Centropomidae (Pisces, Perciformes). Bull. Brit.
    Mus. (Nat. Hist.) Zool. 29: 1–81.
————. 1977. A review of the family Centropomidae (Pisces, Perciformes): an appendix. Bull. Brit.
    Mus. (Nat. Hist.) Zool. 31: 297–301.
————. 1978. A review of the Pharyngeal âpophysis and its significance in the classification of
    African cichlid fishes. Bull. Brit. Mus. Nat. Hist. (Zool.) 33: 297–323.

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

Guitel, F. 1913. L'appareil fixateur de l'ouef du *Kurtus gulliveri*. Arch. de Zool. Exp. et Gen. 52: 1–11.

Haedrich, R. L. 1967. The stromateoid fishes: systematics and a classification. Bull. Mus. Comp. Zool. Harv. Univ. 135: 31–39.

————. 1969. A new family of stromateoid fishes from the equatorial Indo-Pacific. Dana-Rep. Carlsberg Found. 76: 1–13.

Heemstra, P. C. and J. E. Randall. 1977. A revision of the Emmelichthyidae (Pisces: Perciformes). Aust. J. Mar. Freshwater Res. 28: 361–396.

Hoese, D. F. 1984. Gobioidei: relationships. Pages 588–591 *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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

———— and A. C. Gill. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). Bull. Mar. Sci. 52: 415–440.

Horn, M. H. 1984. Stromateoidei: development and relationships. Pages 620–628 *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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

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

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

————. 1981. The limits and relationships of the Lutjanidae and associated families. Bull. Scripps Inst. Oceanog. 24 (for 1980): 1–114.

————. 1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae. Copeia 1983: 777–787.

————. 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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

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

————. 1988. *Niphon spinosus*, a primitive epinepheline serranid: corroborative evidence from the larvae. Jap. J. Ichthyol. 35: 7–18.

————. 1992. Monophyly of the euteleostean clades Neotelostei, Eurypterygii and Ctenosquamata. Copeia 1992: 8–25.

———— and E. B. Brothers. 1993. *Schindleria*: a paedomorphic goby (Teleostei: Gobioidei). Bull. Mar. Sci. 52: 441–471.

———— and R. A. Fritzsche. 1989. *Graus nigra*, an omnivorous girellid, with a comparative osteology and comments on relationships of the Girellidae (Pisces: Perciformes). Proc. Acad. Nat. Sci. Phil. 141: 1–27.

———— and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bull. Mar. Sci. 52: 554–626.

———— and W. F. Smith-Vaniz. 1987. Redescription and relationships of *Parasphyraenops atrimanus* Bean (Pisces; Serranidae), with discussion of other Bermudian fishes known only from stomach contents. Bull. Mar. Sci. 40: 48–58.

———— 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.

Jollie, M. T. 1954. The general anatomy of *Lampanyctus leucopsarus* (Eigenmann and Eigenmann). Unpubl. Ph.D. Dissertation, Univ. Microfilms, 239 pp.

Jungerson, H. F. E. 1915. Some facts regarding the anatomy of the genus *Pegasus*. Rept. 84th Brit. Assoc. Adv. Sci. 1914, Trans. Sec. D. 6: 420–422.

Katayama, M. 1954. Taxonomic position of the genus *Glaucosoma*. Bull. Fac. Educ. Yamaguchi Univ. 4: 23–29.

Kaufman, L. S. and K. F. Liem. 1982. Fishes of the suborder Labroidei (Pisces; Perciformes): phylogeny, ecology, and evolutionary significance. Breviora 472: 1–19.

Kendall, A. W., Jr. 1976. Predorsal and associated bones in serranid and grammistid fishes. Bull. Mar. Sci. 26: 585–592.

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. and D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Sydney.

Liem, K. F. and P. H. Greenwood. 1981. A functional approach to the phylogeny of the pharyngognath teleosts. Amer. Zool. 21: 83–101.

Miller, P. J. 1973. The osteology and adaptive features of *Rhyacichtyhs aspro* (Teleostei: Gobiodei) and the classification of gobioid fishes. J. Zool. (London) 171: 397–434.

Mooi, R. D. 1993. Phylogeny of the Pleisiopidae (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.

Nelson, G. 1967. Gill arches of some teleostean fishes of the families Girellidae, Pomacentridae, Embiotocidae, Labridae, and Scaridae. J. Nat. Hist. 1: 289–293.

Nelson, J. S. 1974. Fishes of the world. John Wiley and Sons, New York. 416 pp.

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

———. 1986. Some characters of Trichonotidae, with emphasis to those distinguishing it from Creediidae (Perciformes: Trachinoidei). Jap. J. Ichthyol. 33: 1–6.

Okada, Y. and K. Suzuki. 1956. On the similarity of the osteological characters found between Owstoniidae and Cepolidae. Rep. Fac. Fish., Pref. Univ. Mie. 2: 185–194.

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

Parenti, L. R. 1993. Relationships of atherinomorph fishes (Teleostei). Bull. Mar. Sci. 52: 170–196.

Patterson, C. 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. L.A. County Sci. Ser., No. 32.

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

———. 1990. Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). Copeia 1990: 78–100.

——— and C. P. Zabetian. 1989. Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989: 253–303.

Potthoff, T., S. Kelley and L. A. Collins. 1988. Osteological development of the red snapper, *Lutjanus campechanus* (Lutjanidae). Bull. Mar. Sci. 43: 1–40.

———, ——— and J. C. Javech. 1986. Cartilage and bone development in scombroid fishes. Fish. Bull. U.S. 84: 647–678.

———, ———, M. Moe and F. Young. 1984. Description of porkfish larvae and their osteological development. Bull. Mar. Sci. 34: 21–59.

Randall, J. E. 1983. A review of the fishes of the subgenus *Goniistius* genus *Cheilodactylus*, with description of a new species from Easter Island and Rapa. Occ. Pap. Bishop Mus. 25(7): 1–24.

Regan, C. T. 1902. On the systematic position of *Luvarus imperialis* Rafinesque. Ann. Mag. Nat. Hist., ser. 7, 10: 278–281.

———. 1903. On the skeleton and systematic position of *Luvarus imperialis*. Ann. Mag. Nat. Hist., ser. 7, 11: 372–374.

Rivas, L. R. and B. A. Cook. 1968. Relationships of the western Pacific "percichthyid" fish *Niphon spinosus*, with the family Centropomidae. Wassman J. Biol. 26: 201–208.

Roberts, C. D. 1993. 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. Contrib. 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. Amer. Mus. Nat. Hist. 127(5): 217–268.

———. 1973. Interrelationships of higher euteleostean fishes. Pages 397–513 *in* P. H. Greenwood, R. S. Miles and C. Patterson, eds. J. Linn. Soc. (Zool.) 53, suppl. 1.

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

———. 1985. An essay on euteleostean classification. Am. Mus. Novit. 2827: 1–45.

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

——— 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.

Rosenblatt, R. H. and M. A. Bell. 1976. Osteology and relationships of the roosterfish *Nematistius pectoralis* Gill. Contrib. Sci. (Los Ang.) 279: 1–23.

Sasaki, K. 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). Mem. Fac. Fish. Hokkaido Univ. 36: 1–137.

Scott, T. D. 1962. The marine and freshwater fishes of South Australia. W. L. Harves, Gov. Printer, Adelaide.

Schultz, L. P. 1945. *Emmelichthyops atlanticus,* a new genus and species of fish (family Emmelichthyidae) from the Bahamas, with a key to related genera. J. Wash. Acad. Sci. 35: 132–136.

Smith-Vaniz, W. F. 1984. Carangidae: relationships. Pages 522–530 *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. Amer. Soc. Ich. and Herp., Spec. Publ. 1.

——— and G. D. Johnson. 1990. Two new species of Acanthoclininae (Pisces: Plesiopidae) with a synopsis and phylogeny of the subfamily. Proc. Acad. Nat. Sci. Phil. 142: 211–260.

Song, J. and R. L. Boord. In press. Motor components of the trigeminal nerve and the organization of mandibular arch muscles: a phylogenetic conservative pattern and its ontogenetic base. Brain Behav. Evol.

——— and R. G. Northcutt. 1991. The morphology, distribution and innervation of the lateral line receptors of the Florida Gar, *Lepisosteus platyrhincus.* Brain Behav. Evol. 37: 10–37.

Springer, V. G. 1978. Synonymization of the family Oxudercidae, with comments on the identity of *Apocryptes cantoris* Day (Pisces: Gobiidae). Smiths. Contrib. Zool. 270: 1–14.

———. 1982. Pacific plate biogeography, with special reference to shorefishes. Smiths. Contrib. Zool. 367: 1–181.

———. 1983. *Tyson belos,* new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. Smiths. Contrib. Zool. 390: 1–40.

———. 1993. Definition of the suborder Blennioidei and its included families (Pisces: Perciformes). Bull. Mar. Sci. 52: 472–495.

——— and T. H. Fraser. 1976. Synonymy of the fish families Cheilobranchidae (=Alabetidae) and Gobiesocidae, with descriptions of two new species of *Alabes.* Smiths. Contrib. Zool. 234: 1–23.

——— and W. C. Freihofer. 1976. Study of the monotypic fish family Pholidichthyidae (Perciformes). Smiths. Contrib. Zool. 216: 1–43.

———, C. L. Smith and T. H. Fraser. 1977. New species of protogynous hermaphroditic fish and synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae. Smiths. Contrib. Zool. 252: 1–15.

Starks, E. C. 1930. The primary shoulder girdle of bonyfishes. Stanford Univ. Publ., Univ. Ser., Biol. Sci 6: 149–239.

Starnes, W. C. 1988. Revision, phylogeny, and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae. Bull. Mar. Sci. 43: 117–203.

Stiassny, M. L. J. 1986. The limits and relationships of the acanthomorph teleosts. J. Zool., London (B) (1986) 1: 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). Amer. Mus. Novit. 2979: 1–33.

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

——— and J. S. Jensen. 1987. Labroid intrarelationships revisited: morphology, complexity, key innovations, and the study of comparative diversity. Bull. Mus. Comp. Zool. 151(5): 269–319.

——— 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.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Nat. Mus. 122: 1–17.

Tominaga, Y. 1965. The internal morphology and systematic position of *Leptobrama mulleri,* formerly included in the family Pempheridae. Jap. J. Ichthyol. 12: 33–56.

———. 1968. Internal morphology, mutual relationships and systematic position of the fishes belonging to the family Pempherididae. Jap. J. Ichthyol. 15: 43–95.

———. 1986. The relationships of the families Glaucosomatidae and Pempherididae. Pages 594–599 *in* T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura. Indo-Pacific fish biology. Ichthyol. Soc. Jap., Tokyo.

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. Brit. Mus. Nat. Hist. (Zool.) 46: 1–133.

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

Tyler, J. C. 1980. Osteology, phylogeny, and higher classification of the fishes of the order Plectognathi (Tetraodontiformes). NOAA Tech. Rept. NMFS Circ. 434: 1–422.

———, G. D. Johnson, I. Nakamura and B. B. Collette. 1989. Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). Smiths. Contrib. Zool. 485: 1–77.

Vari, R. P. 1978. The terapon perches (Percoidei: Teraponidae). A cladistic analysis and taxonomic
    revision. Bull. Amer. Mus. Nat. Hist. 159: 177–340.
Washington, B. B., W. N. Eschmeyer and K. M. Howe. 1984. Scorpaeniformes: relationships. Pages
    438–447 *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. Amer. Soc. Ich. and Herp., Spec.
    Publ. 1.
Winterbottom, R. 1974. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces)
    as evidenced by their comparative myology. Smiths. Contrib. Zool. 155: 1–201.
————. 1993. Search for the gobioid sister group (Actinopterygii: Percomorpha). Bull. Mar. Sci. 52:
    395–414.
Zehren, S. J. 1979. The comparative osteology and phylogeny of the Beryciformes (Pisces: Teleostei).
    Evol. Monog. (Univ. Chicago) 1: 1–389.

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