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Casting the Percomorph Net Widely: The Importance of Broad Taxonomic Sampling in the Search for the Placement of Serranid and Percid Fishes

WM. LEO SMITH AND MATTHEW T. CRAIG

The limits and relationships of serranid and percid fishes, in the context of the percomorph radiation, were resolved using 4036 aligned base pairs of mitochondrial and nuclear DNA sequence data for 180 acanthomorph species. Representatives of all major serranid and percid lineages were analyzed along with 91 additional families from six acanthomorph orders and 25 suborders. Percidae was recovered as monophyletic, and the traditional Serranidae was recovered as polyphyletic, forming five clades: *Nippon*, *Acanthistius*, Epinephelinae (less *Nippon*), Anthiinae (less *Acanthistius* and *Zalanthias kelloggi* [formerly included in *Plectranthias*]), Serraninae (including *Zalanthias kelloggi*). These traditional “percoid” families were separated from all other “percoid” taxa and recovered within a clade composed of the mail-cheeked fishes and their allies. Based on the evidence provided in this molecular study and prior morphological studies, we recommend taxonomic changes to the Perciformes, Percoidei, Trachinoidei, and Serranidae, we resurrect the Epinephelidae and Niphonidae, and we create a new group, the Moronoidei, to reflect our recovered relationships.

THE hallmark of percomorph systematics, particularly within the species-rich Percoidei, is a large number of families that typically have some evidence of their monophyly, but little or no evidence for their interrelationships. It is for this reason that Gary Nelson (1989) described the vast percomorph assemblage as the unresolved bush at the top of the teleostean tree. Clearly, the situation is not as dire as a completely unresolved bush because numerous clades have been identified and diagnosed. Unfortunately, recent studies have also demonstrated that several of these traditional percomorph assemblages are para- or polyphyletic (e.g., Gasterosteiformes, Perciformes, Scorpaeniformes; Imamura and Yabe, 2002; Miya et al., 2003; Smith and Wheeler, 2006).

As noted by Stiassny et al. (2004), the morphological revival in teleostean systematics was brought on by the nearly simultaneous development of phylogenetic systematics, improvements in skeletal preparations, and the publication of the revised classification of teleosts by Greenwood et al. (1966). A comparison between the classifications and supporting evidence presented in Greenwood et al. (1966) and Nelson (2006) will illustrate the advances that morphological studies have made toward the resolution of teleostean relationships, but they will also highlight the limited progress that has been made on the intrarelationships of Percomorphia.

As discussed by Miya et al. (2003), molecular studies have also been slow to provide significant insights into the higher-level relationships of

teleosts. This slow progress may be due, in part, to inadequate taxon sampling. Fortunately, recent technological improvements in DNA sequencing technology and the increased availability of tissue samples now allow for the examination of sufficient numbers of taxa to explore ordinal and subordinal relationships, which can then be compared (Near et al., 2004; Smith and Wheeler, 2004; Holcroft, 2005) or combined (Tang et al., 1999; Lovejoy, 2000; Sparks and Smith, 2004a) with explicit morphological analyses to better understand percomorph relationships. Most of these higher-level molecular studies have recovered the traditionally recognized assemblage under investigation as monophyletic; however, notable exceptions include Perciformes (Chen et al., 2003; Miya et al., 2003; Smith and Wheeler, 2006), Scorpaeniformes (Smith and Wheeler, 2004), Labroidei (Streelman and Karl, 1997; Sparks and Smith, 2004b; Westneat and Alfaro, 2005), and Percoidei (Chen et al., 2003; Dettai and Lecointre, 2004, 2005; Smith and Wheeler, 2004, 2006). Although valuable, those studies that have resulted in para- or polyphyletic assemblages have only included enough taxa to highlight the inadequacy of the current classification; they have not included sufficient taxon sampling to resolve the placement of the problematic taxa.

“*The percomorph problem*.”—It is clear that the difficulty surrounding the resolution of Nelson’s (1989) percomorph bush revolves around two issues: inadequate taxon sampling and dogmatic thinking. As Patterson noted in the foreword to Rosen and Patterson (1990:2), Rosen believed

that studies of percomorph groups “tended to be too narrowly focused in their view of a problem and not ready enough to cast the net of investigation more widely.” Unfortunately, these narrow limits were usually borne out of necessity. It is time consuming and difficult to examine and individuate homologous morphological characters across a diversity of teleostean exemplars. Despite this complexity, it is surprising that no studies have ever broadly examined Percomorpha with multiple character systems, given that other large teleostean assemblages have been explicitly examined (e.g., Fink and Fink, 1981; Johnson and Patterson, 1996).

When Rosen (1973:508) identified the Percomorpha, he was unable to diagnose it. Rosen noted that the existing percomorph taxonomy consisted of “grade classifications adopted as temporary expedients.” He continued that the relationships within this assemblage would never be resolved “unless we are prepared also to adopt an uncompromisingly cladistic approach”. Following Rosen (1973), there have been numerous studies of smaller percomorph groups or single character complexes across the Percomorpha (reviewed in Johnson [1993] and Stiassny et al. [2004]). Unfortunately, there have not been any explicit, “uncompromisingly cladistic” studies of this entire group that drew upon multiple character systems; therefore, we still retain the historic grade classifications within Percomorpha. The only morphological study to look broadly at the Percomorpha was Johnson and Patterson (1993). These authors were finally able to provide synapomorphies for the Percomorpha, but only after removing the Polymixiiformes, Lampriformes, Zeiformes, Beryciformes, and Stephanoberyciformes and including the Atherinomorpha. However, unlike Rosen’s “uncompromisingly cladistic approach,” Johnson and Patterson (1993:555) chose to analyze a restricted number of characters. They argued, “any tree can be justified by special pleading, by insisting that certain characters are uniquely derived but others are more labile or plastic . . . [they are convinced that] very few of the characters found among percomorphs and their relatives are uniquely derived, and progress will not be made without some special pleading.” This “special pleading” obviously introduces bias into the results (Fink, 1985), and it makes it difficult to avoid dogmatic thinking. Only recently have molecular studies been able to broadly examine percomorph relationships. Beginning with Miya et al. (2001), and continuing with Chen et al. (2003), Dettai and Lecointre (2004, 2005), Miya et al. (2003, 2005), and Smith and Wheeler (2004, 2006), molecular studies

have begun to look broadly at the limits and relationships of the Percomorpha. The results of these large-scale studies have highlighted numerous problems with the current taxonomy, but they lacked sufficient sampling to resolve the vast majority of outstanding phylogenetic questions within the Percomorpha. We believe that the lack of progress on the percomorph problem stems more from the inappropriate approaches (molecular or morphological) used to examine its intrarelationships than any inherent difficulties with the group itself. We believe that Rosen was correct that only an “uncompromisingly cladistic approach” that “casts the net of investigation widely” will provide resolution of the percomorph problem, generally, and the interrelationships of its constituent families.

For this study, we have taken Rosen’s advice for broad taxonomic sampling during this more thorough examination of the interrelationships of Percidae and Serranidae. Our previous analyses (Smith and Wheeler, 2004; Craig, 2005; Smith, 2005) suggested that serranids and “scorpaeniforms” were not monophyletic and that these two assemblages shared a complicated evolutionary history with each other (also see Imamura and Yabe, 2002) and several other percomorph groups. In particular, it was clear from Smith and Wheeler (2004) that one other percoid family, Percidae, was also involved, so we expanded the taxon sampling to more thoroughly examine its placement as well. Therefore, the interrelationships of the serranids and percids are being examined together in this study because of their separation from all other percoids and, more importantly, their recurrent placement among the so-called mail-cheeked fishes and allies in our preliminary studies and several recent molecular studies (Chen et al., 2003; Dettai and Lecointre, 2004; Smith and Wheeler, 2006). Below, we will briefly review the relevant phylogenetic history of both of these families and provide references for those interested in more detailed information on their intrarelationships.

Serranid relationships.—The intrarelationships of Serranidae have received substantial attention from morphologists. In the early 20th century, serranids served as the “wastebasket” for generalized perciform fishes. The number of families into which this diversity of fishes were classified ranged anywhere from one (McCully, 1961) to ten (Jordan, 1923). In 1966, this situation changed dramatically with Gosline’s critical review of the serranids and “lower” percoids. Gosline restricted the composition of Serranidae (and its “offshoot” Grammistidae) to a subset of

the former assemblage that shared a third opercular spine. Gosline (1966) noted that this feature was also found in *Niphon spinosus*. Despite some overall similarities, he excluded *Niphon* from his Serranidae–Grammistidae on the basis of differences in several morphological features. Thus, Gosline retained a Serranidae–Grammistidae composed of three “groupings” that largely correlated with the historical Anthiinae, Epinephelinae (including “Grammistidae”), and Serraninae (c.f. Jordan and Eigenmann, 1890; Smith, 1965). Subsequent to Gosline (1966), Smith and Atz (1969), Randall et al. (1971), and Kendall (1976) disagreed over the classification of several genera, primarily *Pseudogramma*, on the basis of gonad morphology, presence/absence of the skin toxin grammistin, and configuration of the supraneurals. Kendall (1976) specifically argued that four serranid subfamilies should be recognized, thus relegating the former grammistids (*Grammistes*, *Liopropoma*, *Pseudogramma*, *Rainfordia*, and *Rypticus*) to the serranid subfamily Grammistinae. Johnson (1983) revisited serranid monophyly and intrarelationships. He diagnosed the family on the basis of three reductive specializations (absence of posterior uroneural, procurrent spur, and third preural radial cartilage) and the third opercular spine highlighted by Gosline (1966). Johnson (1983) retained the Anthiinae and Serraninae of Gosline (1966), but he made several changes to the taxonomy of the Epinephelinae, including the incorporation of Kendall’s (1976) grammistines and the enigmatic *Niphon spinosus*. The evidence for epinepheline monophyly and the incorporation of *Niphon* into the subfamily was drawn principally from their shared modification of a first dorsal-fin pterygiophore that lacks an autogenous distal element (Johnson, 1983:fig. 7). Since Johnson (1983), the composition of Serranidae and its subfamilies has remained essentially unchanged.

Subsequent to Johnson (1983), many morphological studies have focused on the limits and relationships of the three serranid subfamilies (Meisler, 1987; Baldwin, 1990; Baldwin and Johnson, 1993). Several recent molecular studies have also examined serranid subfamilial intrarelationships (Craig et al., 2001; Pondella et al., 2003; Craig and Hastings, in press); a comparison of the results of serranid morphological and molecular studies suggests considerable areas of agreement (e.g., a close relationship between the soapfishes [Grammistini and Diploprionini] and the liopropomins) and disagreement (e.g., relationships of *Cephalopholis* [= *Gracila*] *albomarginata*). Despite numerous studies examining serranid intrarelationships, comparatively little attention has been given to the phylogenetic

placement of Serranidae in Percomorpha since the dramatic restriction of the family by Gosline (1966). However, one recent study (Imamura and Yabe, 2002) has suggested a novel relationship between serranids and scorpionfishes (broadly defined) in a new perciform suborder, Scorpaenoidei, based on the shared presence of a backwardly directed opercular spine that extends beyond the subopercle and an *adductor dorsalis* (see also Smith and Wheeler, 2004; Smith, 2005). Neither large-scale (Chen et al., 2003; Dettai and Lecointre, 2004, 2005; Smith and Wheeler, 2006) nor focused molecular studies (Smith and Wheeler, 2004; Craig and Hastings, in press) have broadly sampled serranids in the context of resolving their interrelationships, but they have provided some agreement with Imamura and Yabe’s (2002) Scorpaenoidei hypothesis. Furthermore, these molecular studies have not only challenged a percoid placement for Serranidae, but they have also refuted its monophyly, suggesting a variety of serranid sister-groups ranging from trachinids to lampriforms. Clearly, the limits and relationships of serranid fishes remain unsettled.

Percid relationships.—The intrarelationships of Percidae have been examined using both phenotypic (Page, 1985; Wiley, 1992) and genotypic data (Near, 2000; Sloss et al., 2004). Despite a wealth of information regarding percid intrarelationships, morphological hypotheses for their interrelationships have remained surprisingly limited. The most explicit statement comes from an abstract (McCully, 1962) that suggested that although percid scales share some similarities to *Niphon*, *Stereolepis*, *Centrogenys*, and *Doderleinia*, a moronid sister group was preferred. Unfortunately, this reference does not provide the evidential basis for these hypotheses. The most recent review and molecular phylogeny of percids (Sloss et al., 2004) does not discuss percid interrelationships; instead, this analysis included only a centrarchid, lutjanid, moronid, and sciaenid as outgroups without justification or discussion.

Molecular data (Chen et al., 2003; Dettai and Lecointre, 2004, 2005; Smith and Wheeler, 2004, 2006) have begun to weigh in on percid interrelationships with surprising results. These molecular phylogenies have not agreed entirely on the sister-group itself, but the results of all explicit studies clearly indicate a non-percoid sister-group for the Percidae, an ironic and troubling result for the prevailing taxonomy. Chen et al. (2003) and Dettai and Lecointre (2004, 2005) recovered a notothenioid sister-group for Percidae, whereas Smith and Wheeler

(2004, 2006) have suggested potential relationships with various scorpaenoid groups. Given these non-percoid sister-group hypotheses for Percidae, it is clear that broad taxonomic sampling from across Percomorpha will be necessary to adequately resolve percoid interrelationships.

Given the lack of morphological or molecular evidence for the placement of Serranidae and Percidae with other so-called "lower" percoids and their apparent close relationship to each other and mail-cheeked fishes and their allies, we present the results of a molecular analysis designed specifically to address the limits and relationships of these two important "percoid" families. Our analysis includes representatives from all major lineages within these two families as well as all groups previously conjectured to be related to these families in the extensive morphological studies of Katayama (1959), Gosline (1966), Johnson (1983), the character surveys of Freihofer (1963), Mooi and Gill (1995), and Springer and Orrell (2004), and the molecular studies of Chen et al. (2003), Dettai and Lecointre (2004, 2005), and Smith and Wheeler (2004, 2006). Furthermore, we have included scores of additional percomorphs to ensure that Rosen's net is cast sufficiently wide to resolve the placement of these families. The resulting hypothesis of relationships is based upon the simultaneous analysis of nucleotide characters from three mitochondrial loci: the small ribosomal subunit (12S), the complete tRNA-Val, and the large ribosomal subunit (16S), and two nuclear loci: the large ribosomal subunit (28S) and histone H3. The objectives of this study are to use these nucleotide characters to test the monophyly of Serranidae and Percidae, hypothesize the interrelationships (i.e., sister groups) for both of these families or their constituent clades if polyphyletic, and make the necessary taxonomic changes to reflect a monophyletic classification.

MATERIALS AND METHODS

Taxon sampling.—The phylogenetic analysis was rooted using *Beryx splendens*. Beryciforms have been recovered consistently as the sister-group to Percomorpha (Johnson and Patterson, 1993; Smith and Wheeler, 2006). The 180 taxa sequenced in this study include representatives of all major serranid, percoid, and "scorpaeniform" lineages. Furthermore, we have included (Table 1) a broad diversity of perciform, primarily percoid, taxa that have previously been suggested to be possible allies with Percidae and Serranidae in recent molecular and mor-

phological studies. In total, 93 families, 25 suborders, and six acanthomorph orders were sampled following the classification of Nelson (2006).

Acquisition of nucleotide sequences.—Fish tissues were preserved in either a 5X net solution (Craig et al., 2001), 70–95% ethanol, or stored frozen at -70°C prior to extraction of DNA. Nuclear and mitochondrial DNA was extracted from muscle or fin clips using a DNeasy Tissue Extraction Kit (Qiagen). The polymerase chain reaction (PCR) was used to amplify four segments, representing five loci. Double-stranded amplifications were performed in a 25- μL volume containing either one Ready-To-Go PCR bead (GE Healthcare), 1.25 μL (10 pmol) of each primer, and 2–5 μL of DNA or RedTaq Readymix (Sigma-Aldrich) with the addition of 10 pmol of each primer and 5–50 ng of DNA.

We used the following primer pairs for DNA amplification and sequencing (primer sequences can be found in Smith and Wheeler, 2004): 12SL13-L and TitusI-H (12S, tRNA-Val, 16S fragment); 16S ar-L and 16S br-H (remaining 16S fragment); 28SV and 28SJJ (28S large ribosomal subunit fragment); H3a-L and H3b-H 5 (histone H3 fragment). Amplifications for all fragments were carried out in 30–40 cycles using the following temperature profile: initial denaturation for 6 min at 94 $^{\circ}\text{C}$, denaturation for 30–60 sec at 94 $^{\circ}\text{C}$, annealing for 30–60 sec at 45–55 $^{\circ}\text{C}$, and extension for 1–2 min at 72 $^{\circ}\text{C}$, with an additional terminal extension at 72 $^{\circ}\text{C}$ for 6 min. The double-stranded amplification products were desalted and concentrated using an ArrayIt PCR Product Purification Kit (TeleChem International Inc.) on a Beckman BIOMEK 2000 laboratory automated pipetting workstation with minor modifications to the manufacturer's protocol or using AMPure (Agencourt Biosciences). Both strands of the purified PCR fragments were used as templates and directly cycle-sequenced using the original amplification primers and a Prism Dye Terminator Reaction Kit Version 1.1 (Applied Biosystems) or an ET Terminator Kit (GE Healthcare) with minor modifications to the manufacturer's protocols. The sequencing reactions were cleaned and desalted using standard isopropanol–ethanol precipitation or using cleanSEQ (Agencourt Biosciences). The nucleotides were sequenced on an ABI 3700, ABI3730XL, or a Megabace 500 automated DNA sequencer. Contigs were built in Sequencher (Gene Codes) using DNA sequences from the complementary heavy and light strands. Sequences were edited in Sequencher and Bioedit (Hall, 1999). All novel sequences (Table 1) were

TABLE 1. CLASSIFICATION OF INCLUDED SPECIES WITH GENBANK ACCESSION NUMBERS.

| TAXON | 12S,tRNA-Val,16S | 16S | Histone H3 | 28S |
|-----------------------------------|--------------------|----------|------------|----------|
| <u>BERYCIFORMES</u> | | | | |
| Berycidae | | | | |
| <i>Beryx splendens</i> (ROOT) | DQ533161 | DQ027918 | DQ028088 | DQ028177 |
| Trachichthyidae | | | | |
| <i>Hoplostethus mediterraneus</i> | AY362267, AY538864 | AY539481 | AY539073 | AY538968 |
| <u>PERCOMORPHA</u> | | | | |
| <u>ATHERINIFORMES</u> | | | | |
| Bedotiidae | | | | |
| <i>Rheocles wrightae</i> | AY268896 | AY266069 | AY655558 | AY655658 |
| <u>DACTYLOPTERIFORMES</u> | | | | |
| Dactylopteridae | | | | |
| <i>Dactylopterus volitans</i> | AY538870, AY538974 | AY539487 | AY539183 | AY539079 |
| <u>PERCIFORMES</u> | | | | |
| <u>Anabantoidei</u> | | | | |
| Anabantidae | | | | |
| <i>Ctenopoma acutirostre</i> | DQ533184 | AY662702 | AY662878 | DQ533015 |
| <u>Anoplopomatoidei</u> | | | | |
| Anoplopomatidae | | | | |
| <i>Anoplopoma fimbria</i> | AY538905, AY539522 | AY539010 | AY539219 | AY539115 |
| <u>Blennioidei</u> | | | | |
| Blenniidae | | | | |
| <i>Salarias fasciatus</i> | AY538965, AY539582 | AY539070 | AY539279 | AY539174 |
| Chaenopsidae | | | | |
| <i>Chaenopsis alepidota</i> | DQ533171 | DQ532850 | DQ533347 | DQ533005 |
| <u>Cottoidei</u> | | | | |
| Cottidae | | | | |
| <i>Cottus bairdi</i> | AY538913, AY539530 | AY539018 | AY539227 | AY539122 |
| Cyclopteridae | | | | |
| <i>Cyclopterus lumpus</i> | AY538938, AY539555 | AY539043 | AY539252 | AY539147 |
| Hexagrammidae | | | | |
| <i>Hexagrammos decagrammus</i> | AY538906, AY539011 | AY920475 | AY539220 | AY539116 |
| Trichodontidae | | | | |
| <i>Trichodon trichodon</i> | AY538961, AY539578 | AY539066 | AY539275 | AY539170 |
| Zaniolepididae | | | | |
| <i>Zaniolepis frenata</i> | AY538908, AY539525 | AY539013 | AY539222 | AY539118 |
| <u>Percoidei</u> | | | | |
| <i>incertae sedis</i> | | | | |
| <i>Acanthistius ocellatus</i> | DQ533146 | DQ532831 | DQ533328 | DQ532986 |
| Bathdraconidae | | | | |
| <i>Gymnodraco acuticeps</i> | AY538959, AY539576 | AY539064 | AY539273 | AY539168 |
| Bembropidae | | | | |
| <i>Bembrops heterurus</i> | DQ533159 | DQ532842 | DQ533339 | DQ532997 |
| Harpagiferidae | | | | |
| <i>Harpagifer kerguelensis</i> | AY538958, AY539575 | AY539063 | AY539272 | AY539167 |
| Niphonidae | | | | |
| <i>Niphon spinosus</i> | EF120786 | AY947575 | AY949596 | EF120921 |
| Percidae | | | | |
| <i>Etheostoma blennioides</i> | AY538949, AY539566 | AY539054 | AY539263 | AY539158 |
| <i>Etheostoma nigrum</i> | EF120787 | EF120839 | EF120880 | EF120922 |
| <i>Perca flavescens</i> | AY538950, AY539567 | AY539055 | AY539264 | AY539159 |
| <i>Percina caprodes</i> | EF120788 | EF120840 | EF120881 | EF120923 |
| <i>Sander vitreus</i> | DQ533307 | DQ532967 | DQ533464 | DQ533127 |
| <i>Zingel streber</i> | EF120789 | EF120841 | EF120882 | EF120924 |

TABLE 1. CONTINUED.

| TAXON | 12S,tRNA-Val,16S | 16S | Histone H3 | 28S |
|------------------------------------|--------------------|----------|------------|----------|
| Scorpaenoidei | | | | |
| Aploactinidae | | | | |
| <i>Aploactisoma milesii</i> | AY538891, AY539508 | AY538996 | AY539205 | AY539101 |
| Bembridae | | | | |
| <i>Bembras japonica</i> | AY538901, AY539518 | AY539006 | AY539215 | AY539111 |
| Congiopodidae | | | | |
| <i>Congiopodus peruvianus</i> | AY538893, AY539510 | AY538998 | AY539207 | AY539103 |
| <i>Zanclorhynchus spinifer</i> | AY538894, AY539511 | AY538999 | AY539208 | AY539104 |
| Epinephelidae | | | | |
| <i>Belonoperca chabanaudi</i> | EF120790 | AY949422 | AY949561 | EF120925 |
| <i>Cephalopholis albomarginata</i> | EF120791 | EF120842 | EF120883 | EF120926 |
| <i>Cephalopholis boenak</i> | EF120792 | EF120843 | EF120884 | EF120927 |
| <i>Diploprion bifasciatum</i> | EF120793 | AY949329 | AY949475 | EF120928 |
| <i>Epinephelus adscensionis</i> | AY538944, AY539561 | AY539049 | AY539258 | AY539153 |
| <i>Epinephelus itajara</i> | EF120794 | EF120844 | EF120885 | EF120929 |
| <i>Epinephelus rivulatus</i> | EF120795 | EF120845 | EF120886 | EF120930 |
| <i>Grammistes sexlineatus</i> | AY538945, AY539562 | AY539050 | AY539259 | AY539154 |
| <i>Hyporthodus flavolimbatu</i> | EF120796 | AY949336 | AY949528 | EF120931 |
| <i>Hyporthodus niphobles</i> | EF120797 | AY949342 | AY949584 | EF120932 |
| <i>Liopropoma eukrines</i> | EF120798 | EF120846 | EF120887 | EF120933 |
| <i>Mycteroperca olfax</i> | EF120799 | EF120847 | EF120888 | EF120934 |
| <i>Paranthias colonus</i> | EF120800 | AY949351 | AY949491 | EF120935 |
| <i>Paranthias furcifer</i> | EF120801 | AY949372 | AY949595 | EF120936 |
| <i>Plectropomus maculatus</i> | EF120802 | AY949423 | AY949570 | EF120937 |
| <i>Pseudogramma polyacanthum</i> | DQ533282 | DQ532947 | DQ533444 | DQ533106 |
| <i>Pseudogramma thaumasium</i> | AY538897, AY539514 | AY539002 | AY539211 | AY539107 |
| <i>Variola louti</i> | DQ533322 | DQ532981 | DQ533478 | DQ533141 |
| Gnathanacanthidae | | | | |
| <i>Gnathanacanthus goetzei</i> | DQ533205 | DQ532879 | DQ533376 | DQ533036 |
| Hoplichthyidae | | | | |
| <i>Hoplichthys citrinus</i> | AY538904, AY539521 | AY539009 | AY539218 | AY539114 |
| Neosebastidae | | | | |
| <i>Maxillicosta whitleyi</i> | AY538874, AY539491 | AY538978 | AY539187 | AY539083 |
| <i>Neosebastes pandus</i> | DQ533252 | DQ532917 | DQ533414 | DQ533076 |
| Pataecidae | | | | |
| <i>Aetapcus maculates</i> | AY538892, AY539509 | AY538997 | AY539206 | AY539102 |
| Platycephalidae | | | | |
| <i>Elates ransonnetii</i> | AY538902, AY539519 | AY539007 | AY539216 | AY539112 |
| <i>Platycephalus bassensis</i> | AY538903, AY539520 | AY539008 | AY539217 | AY539113 |
| Plectrogeniidae | | | | |
| <i>Plectrogenium nanum</i> | AY538900, AY539517 | AY539005 | AY539214 | AY539110 |
| Scorpaenidae | | | | |
| <i>Caracanthus maculates</i> | AY538895, AY539512 | AY539000 | AY539209 | AY539105 |
| <i>Dendrochirus brachypterus</i> | AY538886, AY539503 | AY538990 | AY539199 | AY539095 |
| <i>Helicolenus dactylopterus</i> | AY538871, AY539488 | AY538975 | AY539184 | AY539080 |
| <i>Iracundus signifer</i> | AY538877, AY539494 | AY538981 | AY539190 | AY539086 |
| <i>Pontinus longispinis</i> | AY538878, AY539495 | AY538982 | AY539191 | AY539087 |
| <i>Pterois volitans</i> | AY538887, AY539504 | AY538991 | AY539200 | AY539096 |
| <i>Scorpaena brasiliensis</i> | AY538879, AY539496 | AY538983 | AY539192 | AY539088 |
| <i>Scorpaena guttata</i> | AY538880, AY539497 | AY538984 | AY539193 | AY539089 |
| <i>Scorpaenodes scaber</i> | AY538882, AY539499 | AY538986 | AY539195 | AY539091 |
| <i>Scorpaenopsis macrochir</i> | AY538883, AY539500 | AY538987 | AY539196 | AY539092 |
| <i>Sebastes elongatus</i> | AY538872, AY539489 | AY538976 | AY539185 | AY539081 |
| <i>Sebastolobus macrochir</i> | AY538875, AY539492 | AY538979 | AY539188 | AY539084 |
| <i>Taenianotus triacanthus</i> | AY538884, AY539501 | AY538988 | AY539197 | AY539093 |

TABLE I. CONTINUED.

| TAXON | 12S,tRNA-Val,16S | 16S | Histone H3 | 28S |
|--------------------------------------|--------------------|------------|------------|----------|
| <i>Trachyscorpia cristulata</i> | AY538876, AY539493 | AY538980 | AY539189 | AY539085 |
| Serranidae - Anthiinae | | | | |
| <i>Hemanthias leptus</i> | AY538946, AY539563 | AY539051 | AY539260 | AY539155 |
| <i>Hemanthias signifer</i> | EF120803 | EF120848 | EF120889 | EF120938 |
| <i>Pronotogrammus multifasciatus</i> | EF120804 | EF120849 | EF120890 | EF120939 |
| <i>Luzonichthys waitei</i> | EF120805 | EF120850 | EF120891 | EF120940 |
| <i>Nemanthias carberryi</i> | EF120806 | EF120851 | EF120892 | EF120941 |
| <i>Plectranthias japonicus</i> | EF120807 | EF120852 | EF120893 | EF120942 |
| <i>Pseudanthias lori</i> | EF120808 | EF120853 | EF120894 | EF120943 |
| <i>Pseudanthias pleurotaenia</i> | EF120809 | EF120854 | EF120895 | EF120944 |
| <i>Pseudanthias squamipinnis</i> | EF120810 | EF120855 | EF120896 | EF120945 |
| <i>Tosana niwae</i> | EF120811 | EF120856 | EF120897 | EF120946 |
| Serranidae - Serraninae | | | | |
| <i>Centropristis striata</i> | EF120812 | AY072656.1 | AY949530 | EF120947 |
| <i>Cratinus agassizii</i> | EF120813 | AY072647.1 | AY949526 | EF120948 |
| <i>Diplectrum formosum</i> | AY538943, AY539560 | AY539048 | AY539257 | AY539152 |
| <i>Hypoplectrus indigo</i> | EF120814 | EF120857 | EF120898 | EF120949 |
| <i>Hypoplectrus unicolor</i> | EF120815 | EF120858 | EF120899 | EF120950 |
| <i>Paralabrax maculatofasciatus</i> | DQ533265 | DQ532930 | DQ533427 | DQ533089 |
| <i>Serranus tigrinus</i> | EF120816 | AY072656.1 | AY949530 | EF120951 |
| <i>Zalanthias kelloggi</i> | AY538947, AY539564 | AY539052 | AY539261 | AY539156 |
| Serranidae - Trachininae | | | | |
| <i>Trachinus collignoni</i> | DQ533313 | DQ532972 | DQ533469 | DQ533132 |
| <i>Trachinus draco</i> | AY538963, AY539580 | AY539068 | AY539277 | AY539172 |
| Synanceiidae | | | | |
| <i>Inimicus sinensis</i> | DQ533215 | DQ532887 | DQ533384 | DQ533045 |
| <i>Synanceia verrucosa</i> | AY538890, AY539507 | AY538995 | AY539204 | AY539100 |
| Tetrarogidae | | | | |
| <i>Ablabys taenionotus</i> | AY538889, AY539506 | AY538993 | AY539202 | AY539098 |
| <i>Centropogon australis</i> | DQ533168 | DQ532848 | DQ533345 | DQ533003 |
| <i>Gymnapistes marmoratus</i> | DQ533207 | AY538994 | AY539203 | AY539099 |
| Triglidae | | | | |
| <i>Chelidomichthys lucernus</i> | EF120817 | EF120859 | EF120900 | EF120952 |
| <i>Lepidotrigla spinosa</i> | AY538896, AY539513 | AY539001 | AY539210 | AY539106 |
| <i>Peristedion miniatum</i> | AY538899, AY539516 | AY539004 | AY539213 | AY539109 |
| Gasterosteidae | | | | |
| Gasterosteidae | | | | |
| <i>Apeltes quadracus</i> | AY538867, AY539484 | AY538971 | AY539180 | AY539076 |
| Icosteidae | | | | |
| Icosteidae | | | | |
| <i>Icosteus aenigmaticus</i> | DQ533213 | DQ532885 | DQ533382 | DQ533043 |
| Kurtoidei | | | | |
| Kurtidae | | | | |
| <i>Kurtus gulliveri</i> | DQ533218 | DQ532890 | DQ533387 | DQ533048 |
| Labroidei | | | | |
| Cichlidae | | | | |
| <i>Ptychochromis grandidieri</i> | DQ533284 | AY263811 | AY662916 | DQ533108 |
| Labridae | | | | |
| <i>Lachnolaimus maximus</i> | DQ533219 | AY662709 | AY662885 | DQ533049 |
| Moronoidei | | | | |
| Acropomatidae | | | | |
| <i>Malakichthys griseus</i> | DQ533236 | DQ532903 | DQ533400 | DQ533062 |

TABLE 1. CONTINUED.

| TAXON | 12S,rRNA-Val,16S | 16S | Histone H3 | 28S |
|----------------------------------|--------------------|----------|------------|----------|
| <i>Synagrops bellus</i> | EF120818 | EF120860 | EF120901 | EF120953 |
| <i>Synagrops japonicus</i> | EF120819 | EF120861 | EF120902 | EF120954 |
| Ambassidae | | | | |
| <i>Ambassis ambassis</i> | DQ533151 | DQ532836 | DQ533333 | DQ532991 |
| Ammodytidae | | | | |
| <i>Ammodytes americanus</i> | DQ533154 | DQ532839 | DQ533336 | DQ532994 |
| Aplodactylidae | | | | |
| <i>Aplodactylus arctidens</i> | EF120820 | EF120862 | EF120903 | EF120955 |
| Apogonidae | | | | |
| <i>Apogon atradorsatus</i> | DQ533157 | DQ532840 | DQ533337 | DQ532995 |
| Callanthiidae | | | | |
| <i>Callanthias ruber</i> | EF120821 | EF120863 | EF120904 | EF120956 |
| Carangidae | | | | |
| <i>Caranx hippos</i> | DQ533167 | DQ532847 | DQ533344 | DQ533002 |
| Centrarchidae | | | | |
| <i>Ambloplites rupestris</i> | DQ533152 | DQ532837 | DQ533334 | DQ532992 |
| Centrogeniidae | | | | |
| <i>Centrogenys vaigiensis</i> | AY538942, AY539559 | AY539047 | AY539256 | AY539151 |
| Centropomidae | | | | |
| <i>Centropomus medius</i> | EF120822 | EF120864 | EF120905 | EF120957 |
| <i>Centropomus viridis</i> | DQ533169 | DQ532849 | DQ533346 | DQ533004 |
| Champsodontidae | | | | |
| <i>Champsodon atridorsalis</i> | AY538960, AY539577 | AY539065 | AY539274 | AY539169 |
| Cheilodactylidae | | | | |
| <i>Cheilodactylus variegatus</i> | AY538955, AY539572 | AY539060 | AY539269 | AY539164 |
| Cheimarrichthyidae | | | | |
| <i>Cheimarrichthys fosteri</i> | DQ533176 | DQ532855 | DQ533352 | DQ533010 |
| Chiasmodontidae | | | | |
| <i>Kali macrura</i> | DQ533217 | DQ532889 | DQ533386 | DQ533047 |
| Chironemidae | | | | |
| <i>Chironemus marmoratus</i> | DQ533177 | DQ532856 | DQ533353 | EF120958 |
| Cirrhitidae | | | | |
| <i>Amblycirrhitus pinos</i> | DQ533153 | DQ532838 | DQ533335 | DQ532993 |
| <i>Cirrhitus rivulatus</i> | AY538954, AY539571 | AY539059 | AY539268 | AY539163 |
| Dinolestidae | | | | |
| <i>Dinolestes lewini</i> | DQ533191 | DQ532866 | DQ533363 | DQ533022 |
| Dinopercidae | | | | |
| <i>Centrarchops chapini</i> | EF120823 | EF120865 | EF120906 | EF120959 |
| <i>Dinoperca petersi</i> | EF120824 | EF120866 | EF120907 | EF120960 |
| Epigonidae | | | | |
| <i>Epigonus constanciae</i> | EF120825 | EF120867 | EF120908 | EF120961 |
| Gerreidae | | | | |
| <i>Eugerres plumieri</i> | DQ533201 | DQ532875 | DQ533372 | DQ533032 |
| Grammatidae | | | | |
| <i>Gamma loreto</i> | AY538948, AY539565 | AY539053 | AY539262 | AY539157 |
| Haemulidae | | | | |
| <i>Haemulon plumieri</i> | AY538952, AY539569 | AY539057 | AY539266 | AY539161 |
| Kuhliidae | | | | |
| <i>Kuhlia rupestris</i> | AY538953, AY539570 | AY539058 | AY539267 | AY539162 |
| Kyphosidae | | | | |
| <i>Hermosilla azurea</i> | DQ533209 | AY662703 | AY662879 | DQ533039 |
| Lateolabracidae | | | | |
| <i>Lateolabrax japonicus</i> | DQ533221 | DQ532891 | DQ533388 | DQ533050 |
| Latidae | | | | |
| <i>Lates calcarifer</i> | DQ533222 | DQ532892 | DQ533389 | DQ533051 |
| Leptobramidae | | | | |
| <i>Leptobrama muelleri</i> | DQ533226 | DQ532894 | DQ533391 | DQ533053 |

TABLE I. CONTINUED.

| TAXON | 12S,tRNA-Val,16S | 16S | Histone H3 | 28S |
|--------------------------------------|--------------------|----------|------------|----------|
| Leptoscopidae | | | | |
| <i>Lesueurina platycephala</i> | DQ533227 | DQ532895 | DQ533392 | DQ533054 |
| Lethrinidae | | | | |
| <i>Lethrinus lentjan</i> | DQ533228 | DQ532896 | DQ533393 | DQ533055 |
| Lobotidae | | | | |
| <i>Datnioides polota</i> | EF120826 | EF120868 | EF120909 | EF120962 |
| <i>Lobotes pacificus</i> | EF120827 | EF120869 | EF120910 | EF120963 |
| Lutjanidae | | | | |
| <i>Lutjanus synagris</i> | DQ533234 | DQ532901 | DQ533398 | DQ533060 |
| <i>Pristipomoides aquilonaris</i> | DQ533278 | DQ532943 | DQ533440 | DQ533102 |
| Malacanthidae | | | | |
| <i>Hoplostiltilus purpureus</i> | AY538951, AY539568 | AY539056 | AY539265 | AY539160 |
| <i>Lopholatilus chamaeleonticeps</i> | DQ533232 | DQ532900 | DQ533397 | DQ533059 |
| Menidae | | | | |
| <i>Mene maculatus</i> | DQ533242 | DQ027927 | DQ028099 | DQ028189 |
| Microcanthidae | | | | |
| <i>Microcanthus strigatus</i> | DQ533244 | DQ532910 | DQ533407 | DQ533069 |
| Moronidae | | | | |
| <i>Morone americana</i> | EF120828 | EF120870 | EF120911 | EF120964 |
| <i>Morone saxatilis</i> | AY538941, AY539558 | AY539046 | AY539255 | AY539150 |
| Mullidae | | | | |
| <i>Pseudupeneus maculatus</i> | DQ533283 | DQ532948 | DQ533445 | DQ533107 |
| Opistognathidae | | | | |
| <i>Opistognathus whitehursti</i> | DQ533258 | DQ532923 | DQ533420 | DQ533082 |
| Oplegnathidae | | | | |
| <i>Oplegnathus woodwardi</i> | DQ533259 | DQ532924 | DQ533421 | DQ533083 |
| Ostracoberycidae | | | | |
| <i>Ostracoberyx dorygenys</i> | EF120829 | EF120871 | EF120912 | EF120965 |
| Pentacerotidae | | | | |
| <i>Pseudopentaceros wheeleri</i> | DQ533267 | DQ532932 | DQ533429 | DQ533091 |
| Percichthyidae | | | | |
| <i>Bostockia porosa</i> | DQ533162 | DQ532844 | DQ533341 | DQ532999 |
| <i>Gadopsis marmoratus</i> | EF120830 | EF120872 | EF120913 | EF120966 |
| <i>Howella brodiei</i> | DQ533211 | DQ532883 | DQ533380 | DQ533041 |
| <i>Macquaria novemaculeata</i> | EF120831 | EF120873 | EF120914 | EF120967 |
| <i>Nannoperca australis</i> | EF120832 | EF120874 | EF120915 | EF120968 |
| Pholidichthyidae | | | | |
| <i>Pholidichthys leucotaenia</i> | DQ533271 | DQ532936 | DQ533433 | DQ533095 |
| Pinguipedidae | | | | |
| <i>Parapercis ramsayi</i> | AY538962, AY539579 | AY539067 | AY539276 | AY539171 |
| <i>Parapercis allporti</i> | EF120833 | EF120875 | EF120916 | EF120969 |
| Plesiopidae | | | | |
| <i>Calloplesiops altivelis</i> | EF120834 | AY662701 | AY662877 | EF120970 |
| Polynemidae | | | | |
| <i>Polydactylus approximans</i> | DQ533273 | DQ532938 | DQ533435 | DQ533097 |
| Polyprionidae | | | | |
| <i>Polyprion americanus</i> | DQ533275 | DQ532940 | DQ533437 | DQ533099 |
| <i>Polyprion oxygeneios</i> | EF120835 | EF120876 | EF120917 | EF120971 |
| <i>Stereolepis gigas</i> | DQ533306 | DQ532966 | DQ533463 | DQ533126 |
| Pomacanthidae | | | | |
| <i>Holacanthus limbaughi</i> | DQ533210 | DQ532882 | DQ533379 | DQ533040 |
| Priacanthidae | | | | |
| <i>Priacanthus arenatus</i> | EF120836 | EF120877 | EF120918 | EF120972 |
| Pseudochromidae | | | | |
| <i>Pseudochromis flavivertex</i> | DQ533281 | DQ532946 | DQ533443 | DQ533105 |

TABLE 1. CONTINUED.

| TAXON | 12S,tRNA-Val,16S | 16S | Histone H3 | 28S |
|-------------------------------|--------------------|----------|------------|----------|
| Sciaenidae | | | | |
| <i>Cynoscion parvipinnis</i> | DQ533185 | DQ532860 | DQ533357 | DQ533016 |
| Sillaginidae | | | | |
| <i>Sillago chondropus</i> | EF120837 | EF120878 | EF120919 | EF120973 |
| Sinipercidae | | | | |
| <i>Siniperca chuatsi</i> | EF120838 | EF120879 | EF120920 | EF120974 |
| Sparidae | | | | |
| <i>Dentex dentex</i> | DQ533188 | DQ532863 | DQ533360 | DQ533019 |
| Sphyraenidae | | | | |
| <i>Sphyraena sphyraena</i> | DQ533304 | DQ532964 | DQ533461 | DQ533124 |
| Terapontidae | | | | |
| <i>Terapon jarbua</i> | DQ533310 | DQ532970 | DQ533467 | DQ533130 |
| Scombroidei | | | | |
| Xiphiidae | | | | |
| <i>Xiphias gladius</i> | DQ533324 | DQ532983 | DQ533480 | DQ533143 |
| Stromateoidei | | | | |
| Stromateidae | | | | |
| <i>Peprilus alepidotus</i> | DQ533269 | DQ532934 | DQ533431 | DQ533093 |
| Zoarcoidei | | | | |
| Bathymasteridae | | | | |
| <i>Bathymaster signatus</i> | AY538956, AY539573 | AY539061 | AY539270 | AY539165 |
| Zoarcidae | | | | |
| <i>Lycodes diapterus</i> | AY538957, AY539574 | AY539062 | AY539271 | AY539166 |
| PLEURONECTIFORMES | | | | |
| Scophthalmidae | | | | |
| <i>Scophthalmus aquosus</i> | DQ533296 | DQ532957 | DQ533454 | DQ533117 |
| SYGNATHIFORMES | | | | |
| Aulostomidae | | | | |
| <i>Aulostomus maculatus</i> | AY538869, AY539486 | AY538973 | AY539182 | AY539078 |
| TETRAODONTIFORMES | | | | |
| Triacanthodidae | | | | |
| <i>Triacanthodes anomalus</i> | DQ533314 | DQ532973 | DQ533470 | DQ533133 |

submitted to GenBank and assigned accession numbers EF120786-EF120974.

Phylogenetic analyses.—A total of 4036 base pairs (as inferred from the resulting implied alignment; Wheeler, 2003a) from the five loci were simultaneously analyzed under the optimality criterion of parsimony with equal weights (i.e., insertions, deletions, transitions, and transversions all given a weight of one). The parsimony analysis was conducted using direct optimization (Wheeler, 1996) and iterative pass (Wheeler, 2003b) as implemented in the program POY (vers. 3.0.12a, W. C. Wheeler, D. S. Gladstein, and J. De Laet, American Museum of Natural History, New York, NY, 2004) and run on the American Museum of Natural History Parallel Computing Cluster.

Because of the large size of the data set, an extensive and thorough search strategy was necessary (Faivovich et al., 2005). The 180-terminal analysis began by generating three random addition sequences (RAS) with subtree pruning and regrafting (SPR) branch swapping. This procedure was repeated 100 times. The results of these 100 analyses (consisting of a total of 300 RAS with SPR branch swapping) were used to make an 85% majority-rule consensus tree. This 85% majority-rule tree was used to quickly estimate the groups present in the consensus of large data sets (Goloboff and Farris, 2001). The idea behind this “quick consensus” is that groups that were consistently recovered in these rapid analyses were likely to be retained in subsequent analyses. The quick-consensus tree was then submitted to jack2hen

(W. C. Wheeler, American Museum of Natural History, New York, NY) to generate a group-inclusion matrix (Farris, 1973). The resulting matrix was then submitted to POY as a constraint file such that all nodes present in the 85% majority-rule consensus tree were constrained (i.e., assumed to be correct and not swapped) for the next round in the analyses to greatly speed up the searches. This next round in the analysis consisted of ten independent runs that each had 50 RAS, 50 TBR-ratchet replicates (Nixon, 1999), tree fusing (Goloboff, 1999), and TBR branch swapping. The best trees resulting from these ten constrained runs were then submitted to POY, without the constraint file (so that all branches were free to swap), for TBR branch swapping, 100 TBR-ratchet replicates, and tree fusing. Following the methods in previous studies (Smith and Wheeler, 2004; Sparks and Smith, 2004a, 2004b), the single resulting tree from this analysis was submitted to POY for further tree searching using the commands iterative pass (Wheeler, 2003b) and exact (Wheeler et al., 2006), which reduce heuristics. This second step of the analysis began with 20 rounds of TBR ratcheting (ratchetpercent 20, ratchetseverity two or five) followed by tree fusing and TBR branch swapping. This step was repeated five times for a total of 100 rounds of TBR ratcheting with tree fusing. The three unique trees resulting from these five rounds of TBR ratcheting and fusing under iterative pass were submitted to a final round of tree fusing and TBR branch swapping. Following this search, a variety of different methods were employed for ten days in an attempt to continue to find shorter trees using the optimal trees as a starting point (e.g., drifting [Goloboff, 1999], manual rearrangements, fusing, and TBR branch swapping). None of these methods for breaking islands were successful in reducing tree length further, so the analysis was stopped.

The length of the resulting implied alignment (Wheeler, 2003a) was verified in PAUP* (vers. 4.0b8, D. L. Swofford, PAUP*: phylogenetic analysis using parsimony [*and other methods], Sinauer, Sunderland, MA, 2002). To estimate the "robustness" of the clades recovered in the phylogenetic hypotheses, Bremer supports (Bremer, 1995) and jackknife percentages (200 replications, five random addition sequences per replicate, holding a maximum of 500 trees per replication) were calculated in PAUP* (in conjunction with TreeRot [vers. 2c, M. D. Sorenson, Boston University, Boston, MA, 1999] for Bremer supports) based on the resulting implied alignment.

RESULTS

The combined analysis of the five gene fragments resulted in four equally most parsimonious trees that each had a length of 18,577 steps. The implied alignment of 4,036 base pairs had a consistency index (CI, Kluge and Farris, 1969) of 0.25 and a retention index (RI, Farris, 1989) of 0.47 when uninformative characters were retained. The resulting strict-consensus cladogram is split between Figures 1 and 2. Most of the 177 nodes remaining in the strict consensus from this analysis were well supported, with 147 nodes (83%) having a Bremer support ≥ 5 and 107 nodes (60%) having a Bremer support ≥ 10 . Additionally, 158 nodes (89%) were supported by a jackknife value ≥ 70 and 126 nodes (71%) had a jackknife value ≥ 95 .

Most families that were represented by multiple species were recovered as monophyletic; however, several families were recovered as para- or polyphyletic (Table 1). These families include: Acropomatidae, Percichthyidae, Polyprionidae, and most importantly Serranidae (species included in the family by Johnson [1983] are underlined in Figure 2). The resulting phylogeny suggested that the former Serranidae should be separated into five clades: Epinephelinae (less *Nippon spinosus*; Fig. 2: clade A), Serraninae (including *Zalanthias kelloggi* [formerly placed in *Plectranthias*]; Fig. 2: clade C), Anthiinae (less *Zalanthias kelloggi* and *Acanthistius ocellatus*; Fig. 2: clade D), *Acanthistius ocellatus* (Fig. 2), and *Nippon spinosus* (Fig. 2). Therefore, the traditionally recognized serranid subfamilies were generally recovered, despite the polyphyly of Serranidae. The least inclusive clade that includes all former serranid taxa also involves the traditional Bembropidae, Gasterosteioidei, Notothenioidei, Percidae, Scorpaeniformes (less Dactylopteridae), Trachinidae, and Zoarcoidei, so it is clear that taxonomic changes among the groupers and seabasses are necessary. The percids, on the other hand, were recovered as monophyletic and sister to a clade composed of *Nippon spinosus*, *Acanthistius ocellatus*, Bembropidae, and the traditional Notothenioidei. As was recovered in prior molecular studies, the included constituents of this clade were deeply nested within an assemblage composed primarily of mail-cheeked fishes, so it is also clear that significant restructuring of perciform taxonomy is warranted.

DISCUSSION

This study was designed specifically to look at the limits and relationships of so-called "lower" percoids, in particular, the placement of Serra-

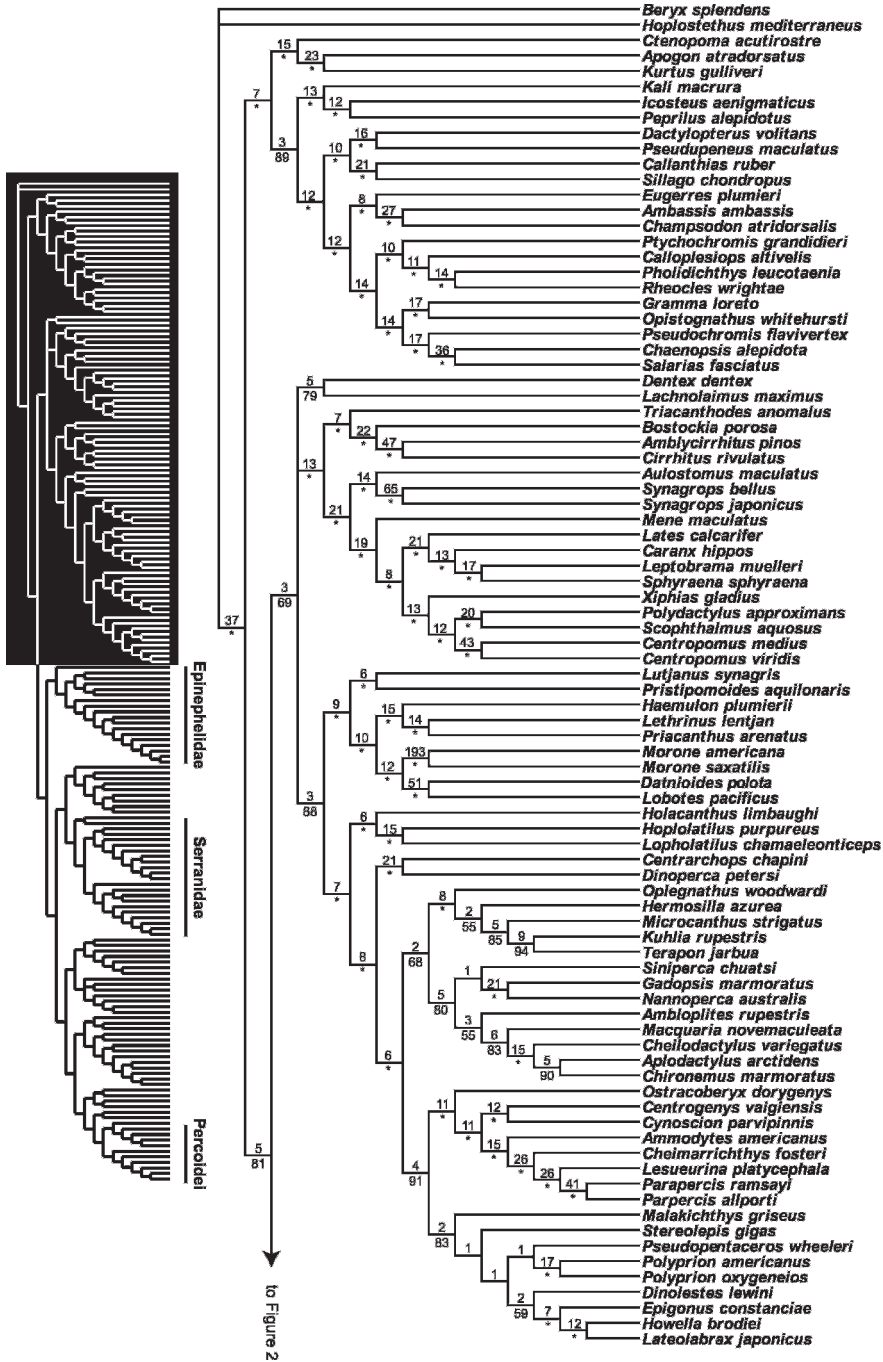


Fig. 1. Part I of the strict consensus of four equally most parsimonious trees recovered (tree length 18,577 steps) by direct optimization of the data set composed of 4,036 aligned base pairs. Numbers on branches represent Bremer support (above) and jackknife resampling values $\geq 50\%$ (below). An “*” represents a jackknife resampling value of 95% or higher.

nidae and Percidae. Our results corroborate the widespread idea that Percoidae is polyphyletic (Johnson, 1984). However, they also clearly refute the common belief (Nelson, 2006:341)

that Percoidae represents “the basal evolutionary group from which the other perciform groups and the remaining two orders [Pleuronectiformes and Tetraodontiformes] have been de-

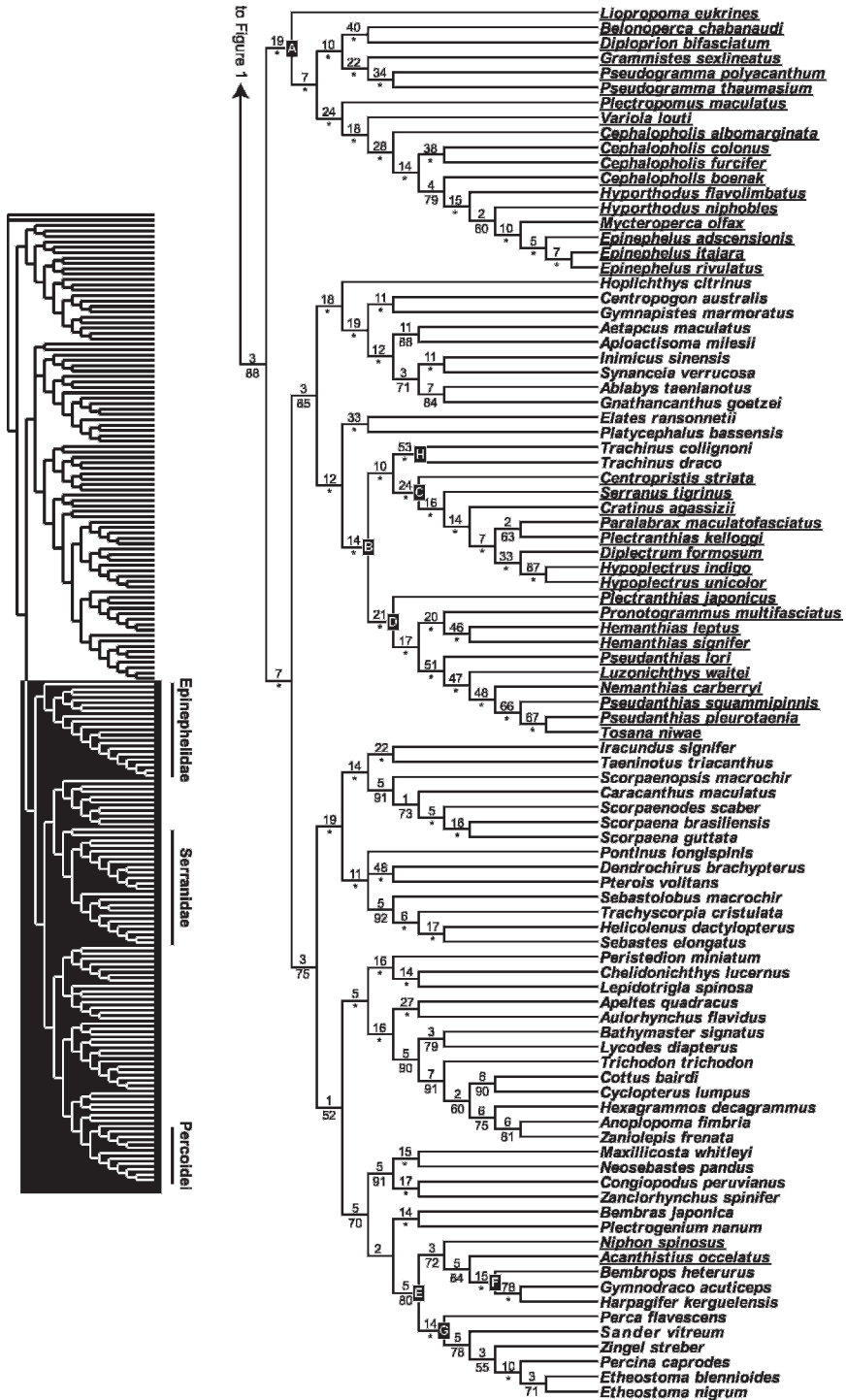


Fig. 2. Part II of the strict consensus of four equally most parsimonious trees presented in Figure 1. All traditionally recognized "serranid" taxa are underlined. Lettered clade designations are as follows: A—Epinephelidae; B—Serranidae; C—Serraninae; D—Anthiinae; E—Percoidei; F—Notothenioidea; G—Percidae; H—Trachininae.

rived.” In our results, the various percoid lineages were distributed throughout the various perciform, pleuronectiform, and tetraodontiform clades, but there were also representatives found among the traditional Atheriniformes, Gasterosteiformes, and Scorpaeniformes. Therefore, Nelson’s (2006) retention of a narrowly defined Percomorpha, despite all evidence to the contrary (Johnson and Patterson, 1993; Miya et al., 2003; Smith and Wheeler, 2004), must be expanded or significantly restructured to maintain any semblance of a cladistic classification.

The results clearly illustrate that it is time to stop viewing percomorph assemblages as either pre-perciform (e.g., Gasterosteiformes, Scorpaeniformes) or post-perciform (e.g., Tetraodontiformes, Pleuronectiformes). This study and many others (Chen et al., 2003; Miya et al., 2005; Smith and Wheeler, 2006) highlight that there is no phylogenetic difference between the Percoidei, Perciformes, and Percomorpha (*sensu* Johnson and Patterson, 1993) because “percoids” are spread throughout the entire Percomorpha.

We assign ranks to all novel or revised names in accordance with the International Code of Zoological Nomenclature; however, individual researchers are welcome to apply these names at the assigned rank or without ranks according to their own nomenclatural orientation. For researchers who prefer an unranked taxonomy, node-based definitions are also provided.

Limits and relationships of “serranid” fishes.—As noted above, the relationships resolved in our analysis did not recover a monophyletic Serranidae or a placement of *Nippon spinosus* or *Acanthistius* with any of the three “serranid” subfamilies. Therefore, we recommend several taxonomic changes for the former Serranidae, and we provide morphological features to diagnose the various clades that we recognize formally in the revised classification.

The first change that we recommend is elevating the groupers to familial status. This elevated Epinephelidae (Fig. 2: clade A; clade stemming from the most recent common ancestor [MRCA] of *Diploprion*, *Epinephelus*, *Grammistes*, and *Liopropoma*) now comprises all epinepheline genera noted in Baldwin and Johnson (1993) except *Nippon*, which we have shown herein and elsewhere (Craig, 2005; Smith, 2005; Craig and Hastings, in press) to be distantly related to the groupers. The monophyly of this revised Epinephelidae is also supported by one morphological character noted by Baldwin and Johnson (1993): the spine serially associated with the first dorsal-fin pterygiophore in larval epinephelids is elongate and encased in a fleshy sheath. Baldwin and Johnson (1993) used two additional features

involving the spine(s) associated with first dorsal-fin pterygiophore and supraneurals to diagnose this clade. These two features, in the absence of a *Nippon* sister group and a polyphyletic Serranidae, do not optimize on this node due to their widespread distribution among closely allied “scorpaenoids” (Ishida, 1994; Imamura, 1996; Smith, 2005). This clade would also be diagnosed by the presence of three opercular spines (Gosline, 1966; Johnson, 1983).

The bulk of the remaining “serranids” (Anthiinae and Serraninae less *Acanthistius*) remain in a restricted Serranidae (Fig. 2: clade B; clade stemming from the MRCA of *Anthias*, *Plectranthias*, *Serranus*, and *Trachinus*). Among taxa classified in the Serranidae by Johnson (1983), the Anthiinae and Serraninae can be united, to the exclusion of all other “serranids” and “scorpaeniforms,” by *ramus lateralis accessorius* (RLA) pattern nine (Freihofer, 1963) and group-III scales (McCully, 1961). Furthermore, recent work on gonad morphology among “serranids” supports the close relationship between anthiines and serranines and the separation of these groups from the epinephelids (P. Hastings, B. Erisman, and M. Craig, unpubl. data). To this revised Serranidae we add *Trachinus* and *Echiinichthys*. As noted by Johnson (1983), the weeverfishes share all of his “serranid” synapomorphies. Johnson (1983) chose to exclude trachinids from the serranids at that time, but he suggested that they might be closely related. Given that the three reductive features Johnson (1983) used to diagnose the former Serranidae are found among a diversity of scorpaenoids, these cannot be used to diagnose this restricted Serranidae (Shinohara, 1994; Imamura, 1996; Smith, 2005). However, this revised Serranidae can be diagnosed by the presence of three opercular spines and group-III scale morphology.

Within this revised Serranidae, we recommend the recognition of three subfamilies: Trachininae (= former Trachinidae), Anthiinae (= former Anthiinae less *Zalanthias kelloggi* and *Acanthistius*), and Serraninae (= former Serraninae including *Zalanthias kelloggi*). Trachininae (clade stemming from the MRCA of *Trachinus* and *Echiinichthys*) can be diagnosed by several features, but most notably by its elongate opercular spine and associated venom gland (Smith and Wheeler, 2006). The monophyly of Anthiinae (Fig. 2: clade D; clade stemming from the MRCA of *Anthias*, *Hemanthias*, *Plectranthias*, and *Pseudanthias*) has not been examined in detail, but Baldwin (1990) suggested that the absence of a toothplate on epibranchial two might unite this clade. She reported that this feature was not found in her examined epinephelid and serranin

taxa. Smith (2005) reported that his examined trachinins and platycephalids have a toothplate on epibranchial two, so there is corroborative evidence that this feature diagnoses Anthiinae in light of our resulting phylogenetic hypothesis. Additionally, Anderson et al. (1990) suggested that the presence of 26 vertebrae might diagnose the Anthiinae. Finally, the evidence for the monophyly of Serraninae (Fig. 2: clade C; clade stemming from the MRCA of *Centropristis*, *Chelidoperca*, *Diplectrum*, and *Serranus*) was provided by Meisler (1987) who diagnosed this clade by the loss of the supramaxillae and the lateral position of the second infraorbital with respect to the posterior portion of the lachrymal. The absence of supramaxillae is shared with trachinins, platycephalids, and scorpaenoids (Imamura, 1996; Smith, 2005), so it cannot be used to unite the Serraninae; however, its presence in Epinephelidae and most anthiines may provide additional support for the monophyly of those two clades.

As noted above, we have placed *Zalanthias kelloggi* (formerly in *Plectranthias*) in Serraninae, which was previously suggested by McCully (1961) who placed his *Zalanthias azumanus* (a junior synonym of *Z. kelloggi*) into Anthiinae based on *Zalanthias* sharing a derived scale morphology with other anthiines. This addition of *Z. kelloggi* is the only alteration to Serraninae that we propose. It is also noteworthy that McCully (1961) also suggested that *Caprodon* should be moved to Serraninae on the basis of scale morphology. Therefore, we retain its current placement in Anthiinae, but the possibility that it belongs with the serranins demands further study. Although not identical in taxon sampling, the relationships recovered by both Meisler (1987) and Pondella et al. (2003) are largely congruent with the relationships that we recovered within Serraninae. A revised placement for the historically problematic *Acanthistius* and *Niphon* will be discussed below in the context of a revised Percoidei.

Limits and relationships of Percidae.—As noted above, Percidae (Fig. 2: clade G; clade stemming from the MRCA of *Etheostoma*, *Perca*, and *Sander*) was recovered as monophyletic in our analyses. Our results are congruent with the hypothesis presented by Page (1985) and corroborate those of Wiley (1992). Our results differed from Collette and Banarescu (1977); they suggested a more terminal placement for *Perca* and a closer relationship between *Sander* and *Zingel*. Our results differed from those of Song et al. (1998) and Near (2000) in that we recovered pectinate relationships for *Perca*, *Sander*, and *Zingel* leading

toward the Etheostomatinae, whereas the results of these other studies recovered all non-etheostomatine percids as a clade. Similarly, our pectinate relationships among the non-etheostomatine percids differed from the trees presented by Sloss et al. (2004). Essentially, all studies have recovered a monophyletic Etheostomatinae, but relationships among the various genera remain controversial.

As noted above, the interrelationships of the percids have not been the focus of any morphological cladistic investigation. Most previous studies have compared percids to other North American freshwater groups (e.g., centrarchids, moronids). McCully (1962) made the most specific comments on percid interrelationships, but he did not provide the evidence in support of these comments. Wiley (1992) made the most explicit statements of percid monophyly, offering two potential synapomorphies for Percidae: reduction in the number of supraneurals and two anal spines. He did not propose a specific sister-group in his analysis. In the only study to combine morphological and molecular data on percid interrelationships (in the context of mail-cheeked fish relationships), Smith (2005) diagnosed the Percidae by the transformation from three to two anal spines. Smith (2005) recovered a clade composed of the enigmatic “serranids,” *Acanthistius* and *Niphon*, sister to Percidae.

Molecular studies of percids have never thoroughly examined percid interrelationships, so most information on their likely relatives has been derived from higher-level acanthomorph studies. The first study to examine percid interrelationships, in the context of Gnathostomata, was Le et al. (1993), who recovered a triglid-percid sister group (also recovered in Holcroft’s [2004] tetraodontiform study). Chen et al. (2003) and Dettai and Lecointre (2004, 2005) have consistently recovered notothenioids as the sister-group of the percids. Smith and Wheeler (2004, 2006) recovered a large clade of scorpionfishes and *Acanthistius*, when included, sister to the Percidae. Finally, Craig and Hastings (in press) recovered the putative grouper *Niphon spinosus* as the sister-group of *Perca*. As noted above, our results recovered a clade sister to Percidae that not only included the notothenioids (as suggested first by Chen et al. [2003]), but also the Bembropidae (allied with the notothenioids in Smith [2005] and Smith and Wheeler [2006]) and the enigmatic “serranids” *Acanthistius* and *Niphon* (as suggested in all studies that included these taxa [i.e., Craig, 2005; Smith, 2005; Smith and Wheeler, 2006]). Given the consistent recovery of the constituent members of this clade in all previous analyses

and the presence of several diagnostic morphological features, we believe that there is more than sufficient evidence to make the necessary changes to the taxonomy of Percoidei and Perciformes that we recommend below.

Revised percoid taxonomy.—The results of our analysis pose many problems for the current percoid taxonomy (Nelson, 2006). We recognize that there may be some resistance to the monophyletic taxonomy being proposed herein, but we view these taxonomic changes as the critical first steps toward the resolution of the “percomorph problem.”

Our results separate two of the name-bearing families from the bulk of their respective perciform suborders due to rampant subordinal polyphyly: Percidae from Percoidei and Trachinidae from Trachinoidei. Because of the consistent placement of Percidae with non-percoid clades in either molecular or combined analyses (Chen et al., 2003; Dettai and Lecointre, 2004, 2005; Smith, 2005; Smith and Wheeler, 2006; this study), we believe that the evidence is clearly sufficient to make the difficult taxonomic change to reduce the taxonomic scope of Percoidei to the clade stemming from the MRCA of *Acanthistius*, *Bembrops*, *Bovichtus*, *Etheostoma*, *Harpagifer*, *Nippon*, *Notothenia*, *Perca*, and *Sander* (Fig. 2: clade E). Smith (2005) diagnosed this clade by the loss of the suborbital stay, the presence of a caudal-fin hypurapophysis, and a post-pelvic process that was expanded laterally and flattened posteriorly. This latter pelvic-girdle character (Katayama, 1959:fig. 32D; Smith, 2005:fig. 36) had not been utilized in previous studies and was unique and unreversed among the taxa he examined. Furthermore, we recommend that the former notothenioids and their sister-group Bembropidae be recognized as the superfamily Notothenioidea (clade stemming from the MRCA of *Bembrops*, *Bovichtus*, *Harpagifer*, and *Notothenia*). Smith (2005) diagnosed this Notothenioidea (his Notothenioidei) by the loss of one pectoral radial (three distinct radials present vs. four) and the rostral displacement of the pelvic fins such that they originate anteriorly to the pectoral fins. We recommend the resurrection of the family name Nipponidae for *Nippon spinosus*. The diagnosis for this family is contingent upon the eventual placement of *Acanthistius*; however, it can be diagnosed, at present, by several characters noted by Baldwin and Johnson (1993): pattern of supraneurals, anterior dorsal-fin pterygiophores, and neural spines; 30 vertebrae; preopercle with enlarged spine at angle. The classification of *Acanthistius* within the Percoidei (*sensu stricto*) is less clear, and it has never been used as the

name-bearing type of a family. This enigmatic genus had bounced from “serranid” subfamily to subfamily in traditional morphological studies and has often been allied with *Trachypoma*. Baldwin and Johnson (1993) most recently argued that *Acanthistius* and *Trachypoma* represented the “basal” anthiines. These researchers were apparently misled by similarities between these two taxa and what they believed to be the “basal epinepheline” *Nippon spinosus* with which they share many characteristics (Baldwin and Johnson, 1993; Smith, 2005). The combined analysis of Smith (2005) found a *Nippon* sister-group for *Acanthistius*. Molecular studies have allied this genus with various scorpionfish, percid, or notothenioid groups. We recommend the classification of *Acanthistius* be left as *incertae sedis* in the Percoidei until corroborative evidence for its placement can be provided by the additional data, particularly additional sampling of *Acanthistius* species and/or *Trachypoma*.

As noted by Gosline (1966), restricting “wastebasket” groups creates the problem of what to do with the groups usually classified in these revised clades. For the taxa herein excluded from the Percoidei, we recommend the use of the name Moronoidei for this assemblage. Moronoidei can be treated as a node-based definition of the clade stemming from the MRCA of *Morone* and *Polyprion*. We have chosen Moronidae as the root for this new subordinal name because of several factors: the present analysis, the morphological studies of Johnson (1983), Wiley (1992), and Baldwin and Johnson (1993), and the combined analysis of Smith (2005) included *Morone*; the results of recent molecular analyses (Smith and Wheeler, 2004, 2006; Dettai and Lecointre, 2005; this study) suggest that moronids do not associate closely with taxa that are classified in existing perciform suborders (to reduce the chances of future synonymy with older subordinal names); moronids are consistently included among any discussion of the “lower percoids”.

In addition to the taxonomic changes required by this placement for Percidae, it is also necessary to make changes to the taxonomy of Trachinoidei because Trachininae was reclassified in Serranidae. Although some semblance of a Trachinoidei dates back well over 100 years, the monophyly and composition of the group has been challenged and/or discussed in recent studies (Johnson, 1993; Mooi and Johnson, 1997; Dettai and Lecointre, 2005). Therefore, we recommend that all of Nelson’s (2006) trachinoids except Trachinidae, Trichodontidae (see Smith and Wheeler, 2004), and Bembropidae also be classified in the Moronoidei, particularly in light of our results that suggest that at

least some traditional trachinoid groups (e.g., Cheimarrichthyidae, Leptoscopidae, Pinguipedidae) are relatively closely related to *Morone*.

Outgroup relationships.—Now that we have restricted Percoidei to a monophyletic assemblage, more attention needs to be focused on the inter- and intrarelationships of moronoid taxa. The revised Moronoidei, like its percoid predecessor, is still a demonstrably polyphyletic assemblage.

Our results suggest several interesting relationships for moronoid groups traditionally allied with serranid fishes (Fig. 1). In many cases, the results complicate our understanding of the former “lower percoids” because several families were recovered as polyphyletic, but there are notable results that are congruent with traditional hypotheses. Our results corroborate the widespread, but unsubstantiated, view that the “triple-fins” (Lobotidae: *Datnioides* and *Lobotes*) form a clade, distinct from any “serranid” or other moronoid clade. Our results suggest that this family should be recognized and that these taxa may be closely related to *Morone*. Additionally, the analyses of our data support the proposition of Heemstra and Hecht (1986) that the dinopercids (*Centrarchops* and *Dinoperca*) are monophyletic, distinct, and unrelated to “serranid” fishes.

In addition to these findings that corroborate recent morphological hypotheses, our results are at odds with recent hypotheses for several moronoid groups that have been historically allied with the serranid fishes. In particular, we will discuss our relationships for the moronids, polyprionids, percichthyids, and the so-called “pseudochromoids” in the context of recent molecular and morphological studies.

As has been recovered in some previous analyses (Orrell and Carpenter, 2004), we have a separation of *Morone* from *Lateolabrax*. However, other large-scale molecular analyses (Dettai and Lecointre, 2005) that have included multiple moronid genera (i.e., *Dicentrarchus* and *Lateolabrax*) have recovered moronids as a clade. To date, there have not been any large-scale molecular percomorph studies that have included all moronid genera. Our results contradict some previous morphological studies (Waldman, 1986), but are not inconsistent with the treatment of *Lateolabrax* as a distinct family by Springer and Johnson (2004). Similarly, we resolved the Polyprionidae (*Stereolepis* and *Polyprion*) as polyphyletic. The limits and relationships of the Polyprionidae have not been studied in detail, so additional study is needed; however, our results suggest that their previous grouping with some of the “oceanic percichthyids” (e.g.,

Howella) may have merit. Additionally, the more restrictive Percichthyidae (*sensu* Nelson, 2006) remains polyphyletic. First, the oceanic *Howella* is widely separated from the freshwater “percichthyids;” instead, *Howella* was recovered sister to *Lateolabrax* and closely allied to the deepwater epigonids. In addition to the separation of *Howella* from the freshwater percichthyids, we also recovered a polyphyletic Australian Percichthyidae. Our results separate the *Nannoperca*–*Gadopsis* group from the *Bostockia* group from the *Macquaria* group. Although not monophyletic, the *Macquaria*, *Gadopsis*, and *Nannoperca* percichthyids were recovered in a clade along with the freshwater percoids *Siniperca* and *Centrarchidae* as well as the marine “non-cirrhitid Cirrhitidae.” This percichthyid–centrarchid relationship was also suggested by McCully (1962) and Chang (1988) on morphological grounds.

Our final classical “serranid” assemblage that we will discuss is the so-called “disjunct lateral-line serranoids” (Böhlke, 1960) or “pseudochromoids” (Leis and Carson-Ewart, 2000). Much has been written about this assemblage of fishes, noting that they are the only percoids that have adhesive eggs with chorionic filaments (Johnson, 1984; Mooi et al., 1990), which has been the primary evidence for uniting them. This study, like Smith and Wheeler (2004, 2006), recovered these “pseudochromoid” taxa with blennioids, cichlids, pholidichthyids, and atheriniforms. As noted by Smith and Wheeler (2004), this historically diverse group, taxonomically speaking, is united by this unusual egg characteristic that they also share (at least superficially) with apogonids, gobioidids, gobioids, kurtids, and pomacentrids. Furthermore, Springer and Orrell (2004) recovered many of these groups in their “Clade A.” It is clear that there is mounting morphological and molecular evidence to suggest that these groups that have been spread across several orders and perciform suborders may actually be closely related.

Finally, given the placement of the former serranid fishes among various mail-cheeked fish clades, we follow Imamura and Yabe (2002) in classifying the revised Serranidae and Epinephelidae in the Scorpaenoidei. In many respects, our resulting mail-cheeked fish phylogeny matches previously published molecular studies (Smith and Wheeler, 2004, 2006); however, there are some areas of disagreement. The largest differences between our results and the results of Smith and Wheeler (2004) stem from the incorporation of the former serranid fishes within the mail-cheeked fishes (Smith and Wheeler, 2004: clade S) and the interrelationships of the Bembridae, Congiopodidae, Neose-

bastidae, Percidae, and Plectrogeniidae. These changes appear to be due to the incorporation of additional serranid and epinephelid taxa because our results are more similar to Smith and Wheeler (2006), which had a substantially larger sampling of serranid and percid fishes.

In this study, we have built upon recent large-scale molecular analyses (Dettai and Lecointre, 2004; Miya et al., 2005; Smith and Wheeler, 2006) and focused studies on the "serranids" and "scorpaeniforms" (Smith and Wheeler, 2004; Craig, 2005; Smith, 2005; Craig and Hastings, in press) to resolve the placement of the former serranid and percid fishes. By sampling broadly across Percomorpha, the "serranids," and Percidae, we have provided strong evidence that these two classic "percoid" families are separated from most "percoid" taxa and actually belong among the mail-cheeked fishes and their allies. We make taxonomic changes to the Perciformes, Percoidei, Trachinoidei, and Serranidae, we resurrect the Epinephelidae and Niponidae, and we create a new group, the Moronoidei, to reflect our recovered relationships. We provide corroborative morphological evidence or highlight studies that provide corroborative morphological evidence to support the taxonomic changes that we recommend. In doing this, we have followed the lead of other studies (Gosline, 1966; Rosen, 1973; Johnson, 1984) by identifying and naming acanthopterygian clades in hopes that it will encourage others to take Rosen's "uncompromisingly cladistic approach" to resolve percomorph relationships.

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