Copeia, 2007(1), pp. 35–55

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

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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: *Niphon*, *Acanthistius*, Epinephelinae (less *Niphon*), 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 Percomorpha.

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 percid 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, percid, 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 morphological 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 C, denaturation for 30–60 sec at 94 C, annealing for 30–60 sec at 45–55 C, and extension for 1–2 min at 72 C, with an additional terminal extension at 72 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
BERYCIFORMES				
Berycidae				
Beryx splendens (ROOT)	DQ533161	DQ027918	DQ028088	DQ028177
Trachichthyidae				
Hoplostethus mediterraneus	AY362267, AY538864	AY539481	AY539073	AY538968
PERCOMORPHA				
ATHERINIFORMES				
Bedotiidae				
Rheocles wrightae	AY268896	AY266069	AY655558	AY655658
DACTYLOPTERIFORMES				
Dactylopteridae				
Dactylopterus volitans	AY538870, AY538974	AY539487	AY539183	AY539079
PERCIFORMES				
Anabantoidei				
Anabantidae				
Ctenopoma acutirostre	DQ533184	AY662702	AY662878	DQ533015
Anoplopomatoidei				
Anoplopomatidae				
Anoplopoma fimbria	AY538905, AY539522	AY539010	AY539219	AY539115
Blennioidei				
Blenniidae				
Salarias fasciatus	AY538965, AY539582	AY539070	AY539279	AY539174
Chaenopsidae				
Chaenopsis alepidota	DQ533171	DQ532850	DQ533347	DQ533005
Cottoidei				
Cottidae				
Cottus bairdi	AY538913, AY539530	AY539018	AY539227	AY539122
Cyclopteridae				
Cyclopterus lumpus	AY538938, AY539555	AY539043	AY539252	AY539147
Hexagrammidae				
Hexagrammos decagrammus	AY538906, AY539011	AY920475	AY539220	AY539116
Trichodontidae				
Trichodon trichodon	AY538961, AY539578	AY539066	AY539275	AY539170
Zaniolepididae				
Zaniolepis frenata	AY538908, AY539525	AY539013	AY539222	AY539118
Percoidei				
incertae sedis				
Acanthistius occelatus	DQ533146	DQ532831	DQ533328	DQ532986
Bathydraconidae				
Gymnodraco acuticeps	AY538959, AY539576	AY539064	AY539273	AY539168
Bembropidae				
Bembrops heterurus	DQ533159	DQ532842	DQ533339	DQ532997
Harpagiferidae				
Harpagifer kerguelensis	AY538958, AY539575	AY539063	AY539272	AY539167
Niphonidae				
Niphon spinosus	EF120786	AY947575	AY949596	EF120921
Percidae				
Etheostoma blennioides	AY538949, AY539566	AY539054	AY539263	AY539158
Etheostoma nigrum	EF120787	EF120839	EF120880	EF120922
Perca flavescens	AY538950, AY539567	AY539055	AY539264	AY539159
Percina caprodes	EF120788	EF120840	EF120881	EF120923
Sander vitreus	DQ533307	DQ532967	DQ533464	DQ533127
Zingel streber	EF120789	EF120841	EF120882	EF120924

TABLE 1. CONTINUED.

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

TABLE 1. CONTINUED.

TAXON	12S,tRNA-Val,16S	16S	Histone H3	28S
Trachyscorpia cristulata	AY538876, AY539493	AY538980	AY539189	AY539085
Serranidae - Anthiinae				
Hemanthias leptus	AY538946, AY539563	AY539051	AY539260	AY539155
Hemanthias signifer	EF120803	EF120848	EF120889	EF120938
Pronotogrammus multifasciatus	EF120804	EF120849	EF120890	EF120939
Luzonichthys waitei	EF120805	EF120850	EF120891	EF120940
Nemanthias carberryi	EF120806	EF120851	EF120892	EF120941
Plectranthias japonicus	EF120807	EF120852	EF120893	EF120942
Pseudanthias lori	EF120808	EF120853	EF120894	EF120943
Pseudanthias pleurotaenia	EF120809	EF120854	EF120895	EF120944
Pseudanthias squamipinnis	EF120810	EF120855	EF120896	EF120945
Tosana niwae	EF120811	EF120856	EF120897	EF120946
Serranidae - Serraninae				
Centropristis striata	EF120812	AY072656.1	AY949530	EF120947
Cratinus agassizii	EF120813	AY072647.1	AY949526	EF120948
Diplectrum formosum	AY538943, AY539560	AY539048	AY539257	AY539152
Hypoplectrus indigo	EF120814	EF120857	EF120898	EF120949
Hypoplectrus unicolor	EF120815	EF120858	EF120899	EF120950
Paralabrax maculatofasciatus	DQ533265	DQ532930	DQ533427	DQ533089
Serranus tigrinus	EF120816	AY072656.1	AY949530	EF120951
Zalanthias kelloggi	AY538947, AY539564	AY539052	AY539261	AY539156
Serranidae - Trachininae				
Trachinus collignoni	DQ533313	DQ532972	DQ533469	DQ533132
Trachinus draco	AY538963, AY539580	AY539068	AY539277	AY539172
Synanceiidae				
Inimicus sinensis	DQ533215	DQ532887	DQ533384	DQ533045
Synanceia verrucosa	AY538890, AY539507	AY538995	AY539204	AY539100
Tetrarogidae				
Ablabys taenionotus	AY538889, AY539506	AY538993	AY539202	AY539098
Centropogon australis	DQ533168	DQ532848	DQ533345	DQ533003
Gymnapistes marmoratus	DQ533207	AY538994	AY539203	AY539099
Triglidae				
Chelidonichthys lucernus	EF120817	EF120859	EF120900	EF120952
Lepidotrigla spinosa	AY538896, AY539513	AY539001	AY539210	AY539106
Peristedion miniatum	AY538899, AY539516	AY539004	AY539213	AY539109
Gasterosteoidei				
Aulorhynchidae				
Aulorhynchus flavidus	AY538866, AY539483	AY538970	AY539179	AY539075
Gasterosteidae				
Apeltes quadracus	AY538867, AY539484	AY538971	AY539180	AY539076
Icosteoidei				
Icosteidae				
Icosteus aenigmaticus	DQ533213	DQ532885	DQ533382	DQ533043
Kurtoidei				
Kurtidae				
Kurtus gulliveri	DQ533218	DQ532890	DQ533387	DQ533048
Labroidei				
Cichlidae				
Ptychochromis grandidieri	DQ533284	AY263811	AY662916	DQ533108
Labridae				
Lachnolaimus maximus	DQ533219	AY662709	AY662885	DQ533049
Moronoidei				
Acropomatidae				
Malakichthys griseus	DQ533236	DQ532903	DQ533400	DQ533062

TABLE 1. CONTINUED.

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

TABLE 1. CONTINUED.

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

TABLE 1. CONTINUED.

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

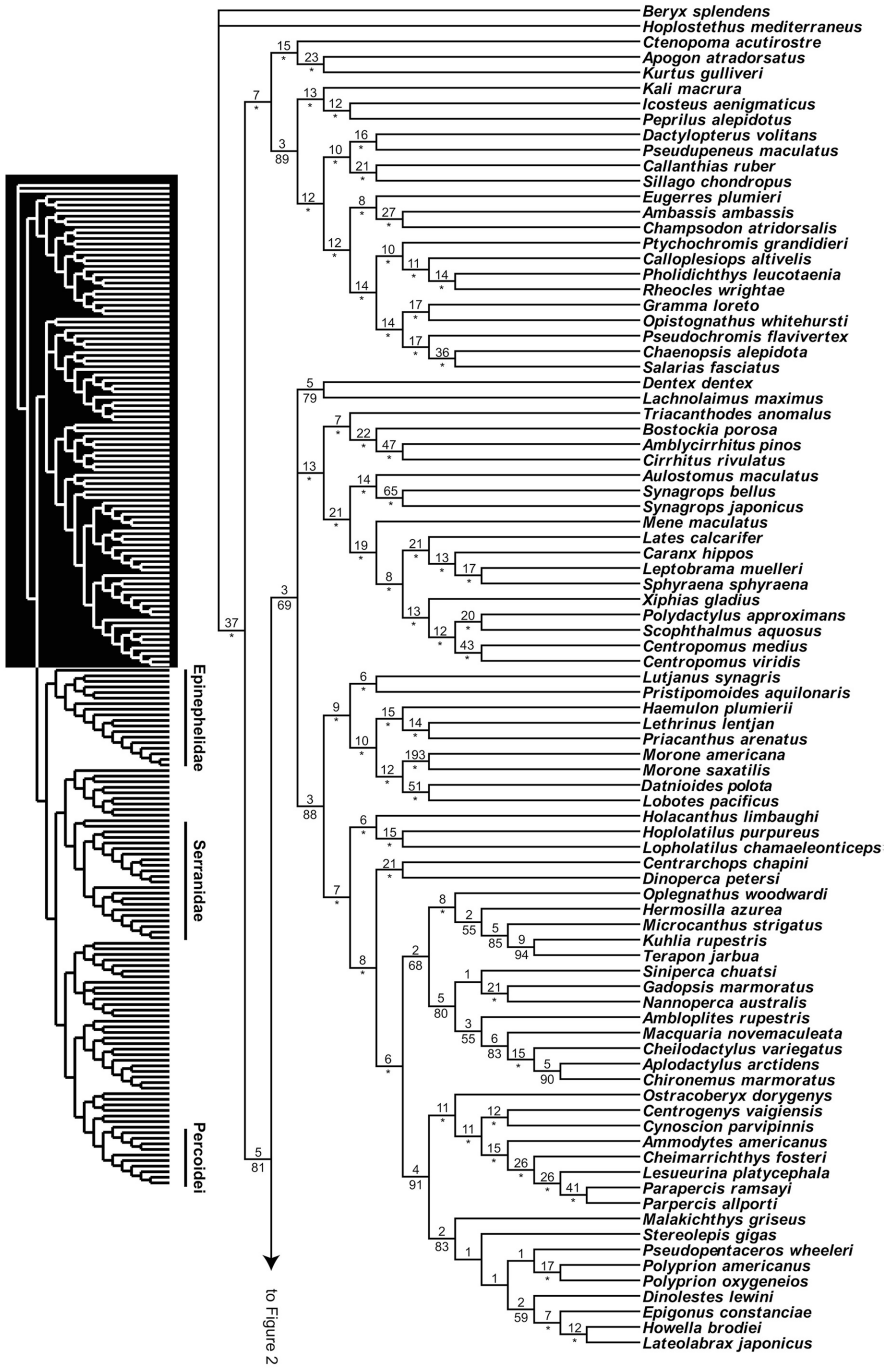

Fig. 1. Part I of the strict consensus of four equally most parsimonious trees recovered (tree length 18,577 steps) by direct optimization of the data set composed of 4,036 aligned base pairs. Numbers on branches represent Bremer support (above) and jackknife resampling values ≥ 50% (below). An ''*''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

nidae and Percidae. Our results corroborate the widespread idea that Percoidei is polyphyletic (Johnson, 1984). However, they also clearly refute the common belief (Nelson, 2006:341) that Percoidei represents ''the basal evolutionary group from which the other perciform groups and the remaining two orders [Pleuronectiformes and Tetraodontiformes] have been de-

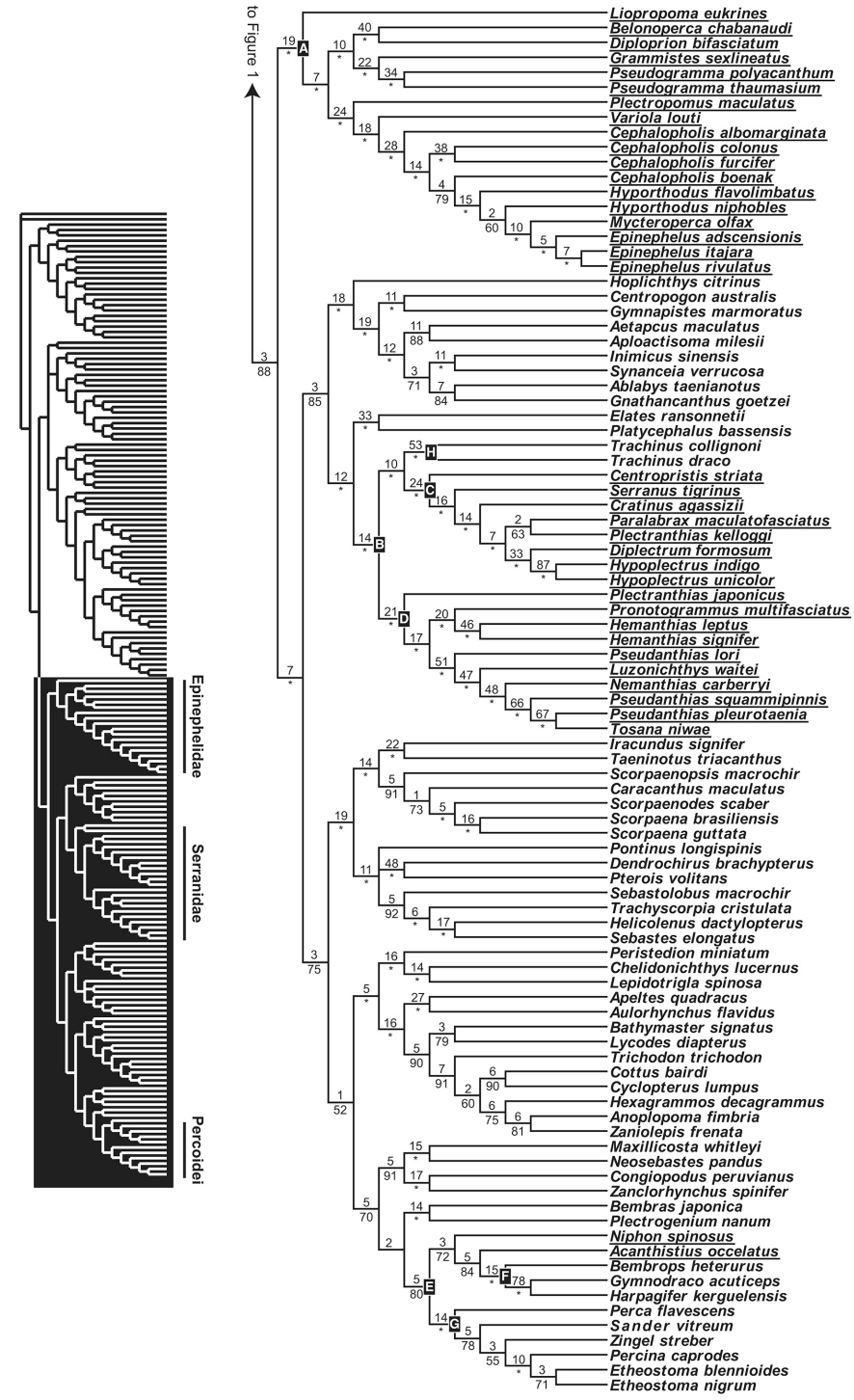

Fig. 2. Part II of the strict consensus of four equally most parsimonious trees presented in Figure 1. All traditionally recognized ''serranid'' taxa are underlined. Lettered clade designations are as follows: A—Epinephelidae; B—Serranidae; C—Serraninae; D—Anthiinae; E—Percoidei; F—Notothenioidea; G—Percidae; 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 *Niphon 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 *Niphon*, 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 *Niphon* 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, Niphon, 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 Niphonidae for *Niphon 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'' *Niphon spinosus* with which they share many characteristics (Baldwin and Johnson, 1993; Smith, 2005). The combined analysis of Smith (2005) found a *Niphon* 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 Cirrhitoidea.'' 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, gobiesocids, 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 Niphonidae, 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.

Acknowledgments

We are indebted to B. Erisman, J. Faivovich, T. Grant, P. Hastings, S. Schaefer, K. Smith, J. Sparks, and M. Stiassny for thoughtful discussions about the results of this project and/or making valuable suggestions on previous drafts. We thank D. Johnson for his time and willingness to discuss our results despite their disagreement with several of his studies. We thank W. Wheeler and N. Knowlton for providing lab space. We graciously thank the personnel of the AMNH, USNM, and Scripps Institution of Oceanography (SIO) Marine Vertebrates Collection for providing access to specimens housed in their collections, particularly D. Johnson for hosting WLS on multiple collection visits to the USNM. This work would not have been possible without the help of numerous friends and colleagues worldwide who provided tissue samples: P. Baverstock, M. Bell, A. Bentley, T. Bertozzi, B. Bowen, D. Bray, C. Burridge, K. Carpenter, A. Dettai, K. Donaldson, S. Donnellan, P. Doukakis, H. Endo, M. Fahay, H. Fock, the Gahan Family, A. Gill, A. Gosztonyi, V. Guida, D. Jerry, R. Hanel, P. Hastings, G. Hoffman, H. Larson, G. Lecointre, P. Loiselle, A. Mahon, J. Marliave, R. Mayden, R. McDowall, M. McGrouther, H. Mok, C. Nock, D. O'Meally, J. Orr, T. Pietsch, D. Pondella, J. Quattro, Reef and Fin (Stamford, CT), G. Sedberry, A. Simons, J. Sparks, C. Taylor, P. Unmack, J. Volff, H. Walker, W. Wakefield, E. Wiley, and Y. Yamanoue. This project was supported by funding from the AMNH, AMNH Lerner-Gray Program for Marine Research, ASIH Raney Fund, Columbia University, SIO Graduate Department, and NSF DEB-0405246 to M. Stiassny and WLS. This project would not have been possible without the computational resources at the AMNH, so we gratefully acknowledge all funding agencies, particularly NSF and NASA, and the personnel who have helped develop the AMNH parallel computing cluster.

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