A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini

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Abstract The phylogenetic relationships among the fishes in the perciform tribe Epinephelini (Serranidae) have long been poorly understood, in large part because of the numerous taxa that must be considered and the large, circumtropical distribution of the group. In this study, genetic data from two nuclear (Tmo-4C4 and histone H3) and two mitochondrial (16S and 12S) genes were gathered from 155 serranid and acanthomorph species as a means of developing a phylogenetic hypothesis using both maximum-likelihood and -parsimony criteria. The maximum-parsimony analysis recovered 675 most parsimonious trees of length 5703 steps (CI = 0.2523, HI = 0.7477, RI = 0.6582), and the maximum-likelihood analysis recovered 1 tree at –lnLikelihood = 28279.58341. These phylogenetic hypotheses are discussed in light of previous morphological evidence to evaluate the evolutionary history of the group and their implications for the currently recognized taxonomy. Our results question the monophyly of the Serranidae, as well as the genera *Cephalopholis, Epinephelus*, and *Mycteroperca* as currently defined. The Serranidae is monophyletic only with the exclusion of the genera *Acanthistius* and *Niphon.* We propose a revised classification of the tribe Epinephelini that reflects the hypothesized shared ancestry of the group and recognizes 11 genera: *Alphestes*, *Cephalopholis*, *Dermatolepis*, *Epinephelus*, *Gonioplectrus*, *Hyporthodus* (which is resurrected for 11 species of deep-bodied groupers), *Mycteroperca* (including 7 species heretofore allocated to *Epinephelus*), *Plectropomus*, *Saloptia*, *Triso*, and *Variola*.

Key words *Epinephelus* · *Cephalopholis* · *Mycteroperca* · Perciformes · Molecular phylogeny

The family Serranidae is a group of carnivorous marine fishes that inhabit tropical and subtropical waters worldwide. Although more-recent systematic treatments of the family have provided a reasonable classification, the family has traditionally been used as a convenient pigeonhole for lower percoid fishes whose affinities are unclear. Few studies exist that confidently place the Serranidae within the larger context of percoid relationships. Imamura and Yabe (2002) proposed a novel placement of the Serranidae within a new perciform suborder Scorpaenoidei that includes the Serranidae (as the Serranoidea) and the scorpaenoid lineage (as the Scorpaenoidea), thus separating the “scorpaenoid” and “cottoid” scorpaeniform lineages into two separate perciform suborders. Other recent studies (e.g., Dettai and Lecointre, 2004, 2005; Smith and Wheeler, 2004) were unable to demonstrate the monophyly of the Serranidae or confidently place it within the larger acanthomorph bush.

Our understanding of relationships within the Serranidae has been equally tenuous. Jordan and Eigenmann (1890) were the first to attempt to resolve the relationships within the Serranidae by defining six subfamilies: Serraninae, Epinephelinae, Anthiinae, Grammistinae, Latinae, and Percichthyinae. Katayama (1959) provided a thorough review of the Japanese serranids, recognizing 15 subfamilies and reorganizing the family, setting the stage for nearly all subsequent revisions. The first attempt to define a natural (phylogenetic) classification of the family came with Gosline (1966), who restricted the Serranidae to Jordan and Eigenmann’s (1890) Anthiinae, Epinephelinae, and Serraninae. Kendall (1976, 1979) agreed that Jordan and Eigenmann’s (1890) Serraninae, Epinephelinae, and Anthiinae were natural groups; however, he included the subfamily Grammistinae based on number and orientation of predorsal bones, which are similar to those of the Epinephelinae of Jordan and Eigenmann (1890). Within this group, Kendall (1976, 1979) included Jordan and Eigenmann’s (1890) liopropomines and grammistids. Gosline’s hypothesis of a restricted Serranidae was corroborated by Johnson (1983), who also placed Kendall’s Grammistinae into the Epinephelinae. Johnson (1983) diagnosed a monophyletic Epinephelinae based upon the derived feature of loss of an autogenous distal radial on the first dorsal-fin pterygiophore. In this diagnosis, Johnson also included the enigmatic

Niphon spinosus, which he hypothesized to be the sister-group of all other Epinephelinae. Johnson (1983, 1988) divided the Epinephelinae into the five tribes Niphonini, Epinephelini, Diploprionini, Liopropromini, and Grammistini, while Baldwin and Johnson (1993) proposed relationships among these tribes and demonstrated their monophyly.

The tribe Epinephelini (sensu Johnson, 1983) is one of the most speciose percoid assemblages, with hypothesized monophyly comprising more than 150 species (Nelson, 1994). Johnson's (1983) Epinephelini includes the genera *Aethaloperca*, *Alphestes*, *Anyperodon*, *Cephalopholis*, *Cromileptes*, *Dermatolepis*, *Epinephelus*, *Gonioplectrus*, *Gracila*, *Mycteroperca*, *Paranthias*, *Plectropomus*, *Saloptia*, *Triso*, and *Variola*. Johnson's Grammistini includes the genera *Aporops*, *Grammistes*, *Grammistops*, *Pogonoperca*, *Pseudogramma*, *Rypticus*, and *Suttonia*. Johnson (1983) also considered *Aulacocephalus, Belonoperca*, and *Diploprion* to be distinctive and allocated them to the tribe Diploprionini. Johnson's (1983) Liopropomini includes the genera *Liopropoma*, *Rainfordia*, and *Jeboehlkia*, while his Niphonini is monotypic and restricted to *N. spinosus*. Baldwin and Johnson (1993) reassigned *Jeboehlkia* from the Liopropomini to the Grammistini.

Since Johnson (1983, 1988) and Baldwin and Johnson (1993), few systematic studies have been undertaken to resolve the relationships or confirm the monophyly of the subfamily Epinephelinae or its included genera. Craig et al. (2001) presented the first molecular analysis of the group and provided evidence for a monophyletic Epinephelinae and a paraphyletic *Cephalopholis* and *Epinephelus*. That study, however, was a preliminary analysis and was based on a limited number of taxa. In the current study, we used DNA sequence data from two mitochondrial and two nuclear genes from 155 species of serranids and other acanthomorphs as a means of expanding the study of Craig et al. (2001). Herein, we (1) show that the Serranidae as currently defined are polyphyletic; (2) discuss the interrelationships of the various tribes within the subfamily Epinephelinae; (3) demonstrate the paraphyly of the genera *Cephalopholis*, *Epinephelus*, and *Mycteroperca* as currently defined; and (4) discuss the nomenclatural implications of these findings.

Materials and Methods

Specimens were collected in the field by various means including spear pole, hook-and-line, and anesthetic, or were purchased from fish markets at or near the collecting locality, or were purchased from the live aquarium trade. Fin clips, gill clips, and/or muscle tissue were removed from each individual and stored in either 5× net solution (Craig et al., 2001) or 70%–90% ethanol. When available, voucher specimens were deposited at the Scripps Institution of Oceanography Marine Vertebrate Collection (Appendix 1). Other tissues were obtained through various museum collections that maintain frozen or ethanol-preserved collections or from local contacts. Institutional abbreviations follow Leviton et al. (1985). When no voucher specimen was available, a photo voucher was retained by the author (M.T.C.) or the collector. One to 3 individuals per species were sequenced depending on availability to assess variability of the sequences within species. The individual sequences were inspected for significant differences and, if none or few were present, a consensus sequence was used in the final analysis. Overall, tissue samples were obtained for 155 species. Of these, we collected representatives of 24 of the 30 epinepheline genera and 24 species of acanthomorph outgroups (see Appendix 1). Within the tribe Epinephelini, these included 68 of 99 species of *Epinephelus*, 14 of 15 species of *Mycteroperca*, 16 of 22 species of *Cephalopholis*, 5 of 7 species of *Plectropomus*, all currently described species of *Alphestes*, *Dermatolepis*, *Paranthias*, and *Variola*, and the monotypic genera *Aethaloperca*, *Anyperodon*, *Cromileptes*, *Gracila*, *Saloptia*, and *Triso*. The Liopropomini was represented by 2 species of *Liopropoma*, the Diploprionini by *Diploprion bifasciatum* and *Belonoperca chabanaudi*, and the Grammistini by species in the genera *Aporops*, *Grammistes*, *Pogonoperca*, *Pseudogramma*, *Rypticus*, and *Suttonia*. The monotypic Niphonini was represented by *N. spinosus*. Several outgroups were selected from the Acanthomorpha as few molecular studies exist that confidently place the Serranidae within the larger context of the acanthomorph tree. The parsimony tree was rooted with the beryciform *Hoplostethus meditteraneus*.

Total DNA was isolated from tissues using the DNeasy nucleic acids isolation kit (Qiagen, Rockville, MD, USA) following the manufacturer's instructions. The polymerase chain reaction (PCR) was used to amplify portions of two mitochondrial (16S and 12S) and two nuclear (Tmo-4C4 and histone H3) genes (1838 bp). Primer pairs are listed in Table 1. PCR reactions using 25 µl were prepared following manufacturer's instructions included with the RedTaq Readymix (Sigma-Aldrich, St. Louis, MO, USA) with the addition of 10 pmol of each primer and 5–50 ng template DNA. Following an initial denaturation at 94ºC for 1 min, each reaction was subjected to 35 rounds of the following thermal cycling conditions: 94ºC for 30 s, 46ºC for 30 s, and 72ºC for 1 min. PCR products were "cleaned" using Millipore Montage PCR cleanup plates following manufacturer's protocols.

Sequence data were generated on a MegaBace 500 automated sequencer. Sequence reactions were prepared following manufacturer's instructions for the ET Terminator chemistry with the addition of 5 pmol primer [GE Healthcare (formerly Amersham-Biosciences), Buckinghamshire, UK]. Sequences were generated for both the forward and reverse directions. In the event of ambiguous base calls or heterozygosity in nuclear genes, bases were coded using IUPAC ambiguity codes in the final analysis. All sequences were deposited in GenBank, and the accession numbers are given in Appendix 1.

Sequence data were edited for miscalls and/or polymorphism using Sequencher version 4.2. Edited sequences were aligned using Clustal X with default settings (Thompson et al., 1997). The alignment was visually optimized using MacClade version 3.07 (Maddison and Maddison, 1997). A

Table 1. Sequencing and polymerase chain reaction (PCR) primers

Primer name	Gene	Sequence	Reference
16Sar-L	16S	5′-cgcctgtttatcaaaaacat-3′	Palumbi (1996)
16Sbr-H	16S	5′-ccggtctgaactcagatcacgt-3′	Palumbi (1996)
12Sa	12S	5′-aaactgggattatagaccccactat-3′	Palumbi (1996)
12Sb	12S	5′-gagggtgacgggcggtctct-3′	Palumbi (1996)
H3A-L	Histone III	5′-atggctcgtaccaagcagacvgc-3′	Colgan et al. (1998)
H3B	Histone III	5′-atatccttrggcatratrgtgac-3′	Colgan et al. (1998)
TMO-F1-5′	TMO4C4	5′-cctccggccttcctaaaacctctc-3′	Streelman and Karl (1997)
TMO-R1-5′	TMO4C4	5′-catcgtgctcctgggtgacaaagt-3′	Streelman and Karl (1997)

partition homogeneity test was used to determine the suitability of the four genes for use in a combined dataset. In some instances, PCR failed to amplify one or more genes for a particular taxon (see Appendix 1). In these instances, data were treated as missing ("?") in the final dataset.

Phylogenetic analyses were performed using PAUP* 4.0b10. Because of the large number of taxa and bases leading to computational constraints, the parsimony ratchet of Nixon (1999) was employed using the batch file created by PaupRat version 1b (Sikes and Lewis, 2001). Ten rounds of the ratchet were each performed using default settings (200 ratchets). All trees with the lowest tree score were retained from each ratchet. Each shortest tree was found to have identical length and topology; thus, one representative tree was submitted to PAUP*4.0b10 for a final round of branch swapping (TBR). Finally, a consensus of all most parsimonious trees was created in PAUP*4.0b10. Similarly, the likelihood ratchet was implemented in PAUP* using the batch file created by Vos (2003). The program Modeltest version 3.6 (Posada and Crandall, 1998) was used to determine which model of nucleotide substitution best explained the data using Aikake information criteria (AIC). Ten rounds of the likelihood ratchet were performed using default settings except that the HKY85+I+G substitution model was used as determined by Modeltest version 3.6. All trees with the best likelihood score were retained. For the parsimony analysis, gaps were treated as a "fifth base." Relative support at nodes was evaluated using the bootstrap as implemented in PAUP*4.0b10 using 1000 replicates and saving a maximum of 1000 trees per replicate for the parsimony analysis. Computational constraints prohibited bootstrapping of the likelihood dataset.

Results

Overall, 1900 bases were sequenced from the mitochondrial 16S, 12S, and the nuclear Tmo-4C4 and histone H3 genes. In nearly all cases, within-species variability was negligible (<0.5%). Sixty-two bases could not be aligned unambiguously and were deleted. Of the final 1838 bases, 1011 were constant, 176 were parsimony uninformative, and 651 were parsimony informative. The partition homogeneity test did not support the combination of the four gene datasets ($P = 0.01$); however, this test has been shown to produce inconsistent results when used with molecular data, particularly when variable rates of evolution among genes are apparent (Dolphin et al., 2000). As these nuclear and mtDNA genes are most certainly evolving at different rates, we chose to combine the datasets for the final analyses. The ten rounds of the parsimony ratchet algorithm found 7 trees of length 5703 steps [consistency index (CI) = 0.2523, homoplasy index (HI) = 0.7477, retention index (RI) = 0.6582]. These trees were identical, and a final round of branch swapping on 1 of them found 675 equally parsimonious trees. A strict consensus of these 675 trees is presented in Fig. 1. The maximum-likelihood (ML) algorithm found 1 tree with only minor differences in topology from the parsimony trees (–lnLikelihood = 28279.58341; Fig. 2).

Both tree construction methods found similar topologies with only minor differences at deeper nodes, most notably the placement of *Liopropoma* (see Discussion). Some differences were also apparent at tip clades, most of which reflected the increased resolution afforded by ML analyses. Both analyses supported a monophyletic Serranidae with the exclusion of the genera *Acanthistius* and *Niphon*, while the maximum-parsimony (MP) analysis supported serranid monophyly with the addition of *Cirrhitus* (Cirrhitidae). Both analyses also supported the monophyly of the Epinephelinae with the exclusion of *Niphon*. The genus *Epinephelus* formed two distinct clades in both ML and MP analyses. Separated by a clade containing the genus *Mycteroperca* and several species currently allocated to *Epinephelus*, the two main *Epinephelus* clades reflect a paraphyletic nature for the genus as currently diagnosed. The genus *Cephalopholis* also formed two distinct, monophyletic groups with the addition of species currently allocated to *Paranthias*, *Gracila*, and *Aethaloperca*. The genera *Alphestes* and *Dermatolepis* formed two clades that were sister to one another. *Saloptia* formed a sister relationship to a monophyletic *Plectropomus*. *Variola* was found to be monophyletic, while the monotypic *Triso* occupied a position that was sister to *Epinephelus* and *Mycteroperca* in the MP analysis, yet embedded within a basal grouper clade in the ML analysis.

Discussion

The genetic data gathered here from both nuclear and mitochondrial genes support the previously hypothesized paraphyly of the genera *Cephalopholis*, *Epinephelus*, and

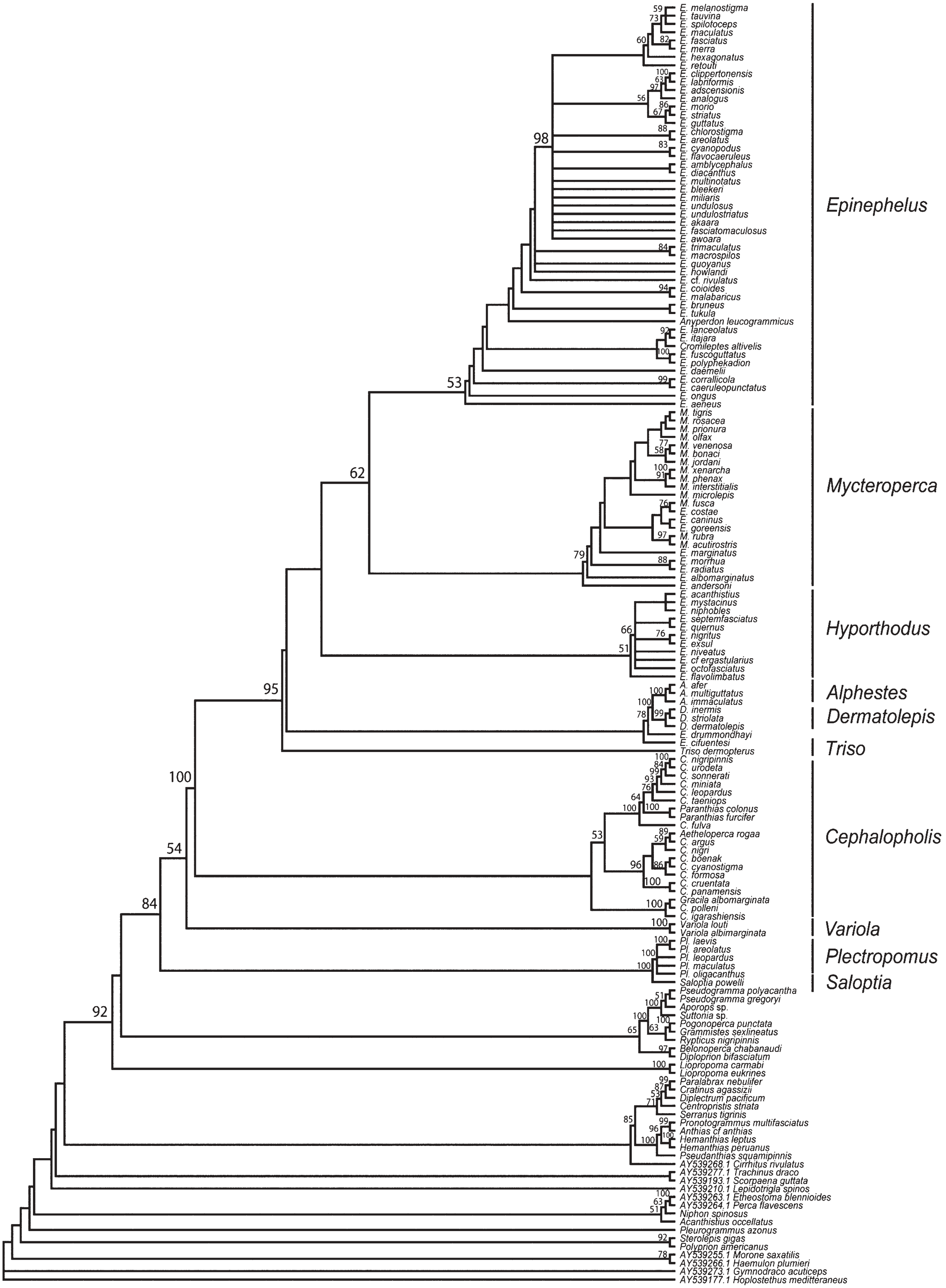

Fig. 1. Strict consensus of 675 most parsimonious trees of length 5703 steps (CI = 0.2523, HI = 0.7477, RI = 0.6582) for 155 species of acanthomorph fishes. *Numbers above nodes* are bootstrap values based on 1000 replicates. Proposed generic designations are shown *at right*

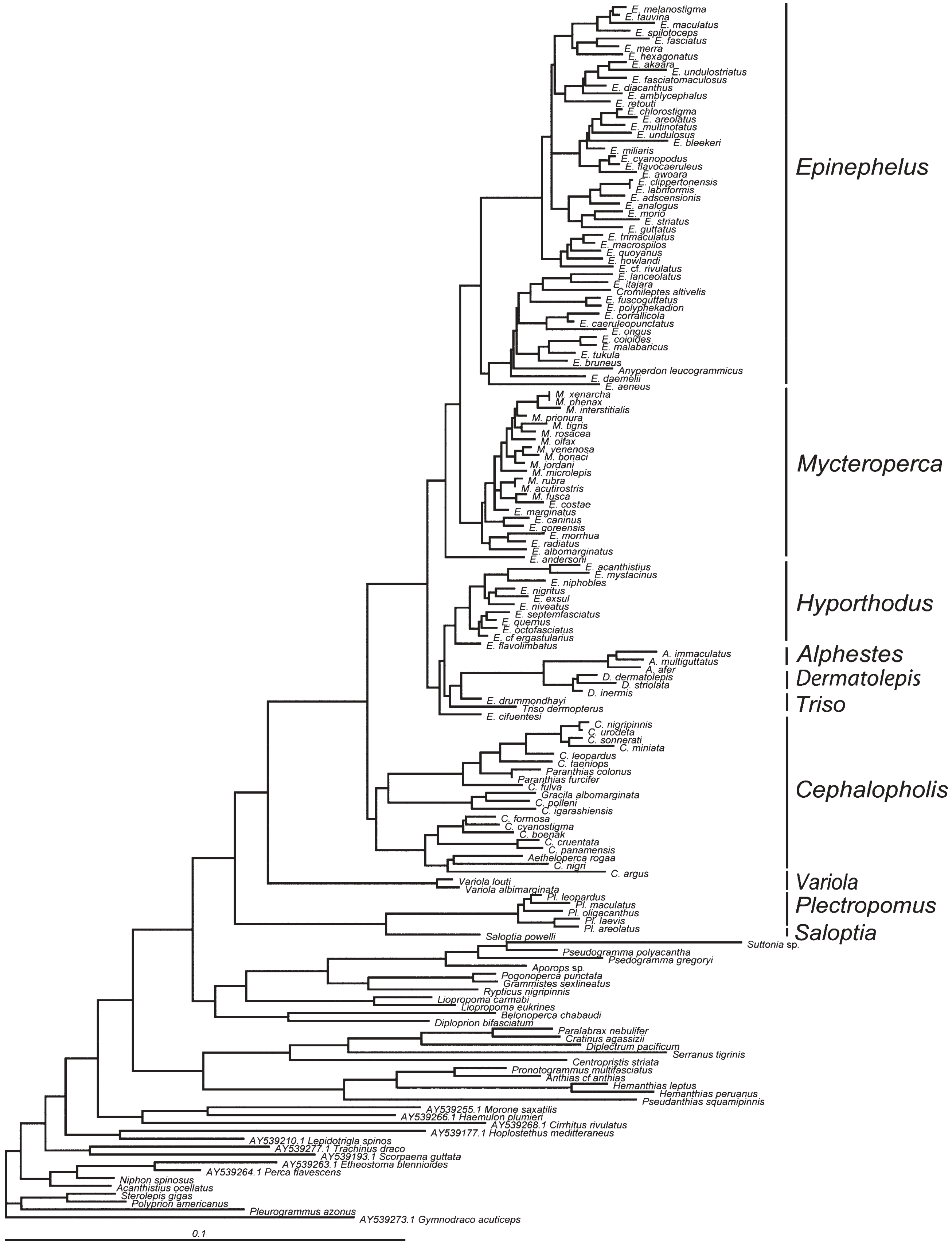

Fig. 2. Maximum-likelihood tree (–lnLikelihood = 28279.58341) for 155 species of acanthomorph fishes. Proposed generic designations are shown *at right*

Mycteroperca (Craig et al., 2001). The data also support a monophyletic Serranidae only with the exclusion of the genera *Niphon* and *Acanthistius*. Maximum-parsimony criteria yielded a monophyletic Serranidae with the inclusion of *Cirrhitus*, a result inconsistent with other recent molecular studies (e.g., Dettai and Lecointre, 2005; Smith and Wheeler, 2004) that was not recovered in our maximum-likelihood analysis. There is no other evidence to support the inclusion of *Cirrhitus* in the Serranidae, and we conclude that the maximum-parsimony result may be a consequence of long-branch attraction. Our results also suggest that the American groupers do not form a monophyletic group as hypothesized by Smith (1971), and that the subgenera of *Epinephelus* designated by him are not monophyletic.

Limits of the Serranidae. The Serranidae was defined and diagnosed by Johnson (1983) based on the presence of three reductive specializations (absence of a posterior uroneural, absence of the procurrent spur, and absence of a third preural cartilage) and one derived feature (presence of three opercular spines). Johnson (1983) also provided the first phylogenetic (cladistic) analysis aiming to determine relationships among serranid fishes including the Epinephelinae. In that study, Johnson (1983) presented morphological data supporting a monophyletic Serranidae and Epinephelinae. That study also placed the enigmatic *N. spinosus* as a primitive sister-group to all other epinephelines based on a single reductive character, loss of an autogenous distal radial in the first dorsal-fin pterygiophore. The presence of three opercular spines in *Niphon* added weight to its placement in the Serranidae. Further corroborative evidence came upon examination of the larvae of *Niphon*, which possess a modification of the dorsal-fin pterygiophores, similar to the condition seen in other epinephelines, which is presumably an aid in supporting the elongate larval dorsal-fin spine typical of larvae of the subfamily (Johnson, 1988). Before this, the relationships of *Niphon* were controversial. Jordan (1923) placed *Niphon* in a monotypic family, yet most subsequent authors treated *Niphon* as a serranid with uncertain affinities (e.g., Berg, 1940; Katayama, 1959; McCully, 1961; Norman, 1966; Greenwood et al., 1966). Gosline (1966), however, removed *Niphon* from the Serranidae and placed it within the Percichthyidae, based in part on the presence of a serrated lacrimal, which is not present in the Serranidae. Greenwood (1977) hypothesized that *Niphon* would eventually be placed into a group with close affinities to Gosline's (1966) Percichthyidae. Otero (2005) discussed morphological similarities between *Niphon* and members of the Latidae, presenting some evidence for the removal of this genus from the Serranidae.

Although the third opercular spine in *Niphon* and associated larval characters discussed by Johnson (1983, 1988) would seem to indicate a close affinity to the Serranidae (especially the Epinephelinae), other morphological evidence, combined with the genetic data herein, does not support its inclusion in the Serranidae. Although relatively uncommon among percoids, three opercular spines are present in some non-serranids, including the epigonid *Sphyraenops*, and two trachinids (*Echiichthys* and *Trachinus*; Johnson, 1983). Additionally, the three-spine condition in *Niphon* only superficially resembles that in serranids such as *Paralabrax*. In *Niphon*, the three spines are elongate and thin, forming distinct projections from the posterior margin of the opercle. In *Paralabrax* and other serranids, it is often difficult to establish the presence of all three spines, especially the ventralmost, as they more closely resemble broad flanges than distinct projections.

Other morphological characters distinguish *Niphon* from the Serranidae. The dorsal fin of serranids typically has fewer than 11 spinous rays; among Johnson's (1983) serranids, only *Niphon* and *Acanthistius* possess 13 dorsal-fin spines (*Acanthistius* may have 11–13 dorsal-fin spines; Heemstra and Heemstra, 2004). Although extremely variable in some percoids, vertebral number also sets *Niphon* apart from other serranids. Most serranids have 24 vertebrae (the subfamily Anthiinae and *Acanthistius* have 26; Nelson, 1994; Johnson, 1983); however, *Niphon* has 30. Last, Greenwood (1977) indicated that in *Niphon* the "caudal skeleton is virtually identical with that in the percichthyids." He based this conclusion on the presence of two uroneurals (serranids have only one, due to either a loss of one or a fusion of two elements). Although these uroneurals are fused in *Niphon* (Greenwood, 1977; Johnson, 1983), this condition may represent an autapomorphy if the typical serranid condition is indeed the result of a loss of the second element. Although we have not attempted to polarize the morphological characters just discussed, they may support exclusion of *Niphon* from the Serranidae upon further investigation.

Our genetic data place *Niphon* in a clade including *Acanthistius* and members of the Percidae (see Fig. 1). Although we do not propose a close relationship between *Niphon* and the percids, these results indicate that the genus should not be considered a serranid. It is likely that additional sampling of acanthomorphs will reveal the true affinities of *Niphon*. Indeed, additional genetic data (Smith and Craig, in preparation) place *Niphon* in a clade that includes relatively distant acanthomorphs.

The affinities of *Acanthistius* are even less clear. Placed in the Epinephelinae by Jordan and Eigenmann (1890), and later in the Serraninae (Johnson, 1983; Kendall, 1984), the genus has most recently been regarded as a member of the Anthiinae (Heemstra and Randall, 1986; Meisler, 1987; Heemstra and Heemstra, 2004). Although Meisler (1987) provided some morphological evidence for the placement of *Acanthistius* within the Anthiinae, he noted that its placement within the Serranidae remained tenuous. Members of this genus do possess three moderate opercular spines and some reductive specializations that characterize the Serranidae. However, they, similar to *Niphon*, have greater numbers of dorsal-fin spines (11–13) and vertebrae (26; Johnson, 1983; Nelson, 1994). Although an expanded morphological analysis of basal percomorphs is needed to establish the polarity of these morphological characters, results from our genetic analysis predict that further study will demonstrate that the affinities of *Acanthistius*, as well as those of *Niphon*, lie outside the Serranidae.

Relationships within the Serranidae. Beginning with Jordan and Eigenmann (1890), three subfamilies of serranid fishes have long been recognized: Anthiinae, Epinephelinae, and Serraninae. Our genetic data corroborate a monophyletic subfamily Epinephelinae (sensu lato) with the exclusion of *Niphon* and *Acanthistius* (see above). Although the anthiine and serranine representatives included in our analysis are both monophyletic, greater taxonomic sampling within these lineages is needed to adequately test their monophyly.

Relationships between the subfamilies of the Serranidae are not well corroborated. In their hypothesis based on morphology, Baldwin and Johnson (1993) recognized that their interrelationships were largely unresolved, yet presented some evidence that the Anthiinae are sister to the Epinephelinae and that the Serraninae are sister to these two. However, their hypothesis of interrelationships was based upon the supposition that *Acanthistius* and *Trachypoma* are primitive anthiines and that *Niphon* represents a primitive epinepheline. Our molecular analysis presents an alternative hypothesis of relationships among these subfamilies, suggesting that the Serraninae and Anthiinae have a sister-group relationship and that this clade is sister to the Epinephelinae (see Figs. 1, 2). The exclusion of *Acanthistius* and *Niphon* from the Serranidae (as indicated in the data presented here) necessitates a reinterpretation of Baldwin and Johnson's (1993) data, because the polarity of many characters would be based on genera outside the family. Our data, however, do corroborate a monophyletic subfamily Epinephelinae (sensu lato) with the exclusion of *Niphon* and *Acanthistius* (see foregoing discussion).

Relationships within the Epinephelinae. Recent authors have recognized four tribes within the Epinephelinae in addition to the Niphonini (discussed earlier). Our genetic data support the monophyly of the Epinephelini as well as that of the remaining tribes. Baldwin and Johnson (1993) evaluated relationships of the tribes within the Epinephelinae based on a cladistic analysis of morphological data. They hypothesized that the Grammistini are sister to the Liopropomini, the Diploprionini are sister to these two, and the Epinephelini are sister to all three. Our genetic data support their hypothesis, with the Epinephelini and Diploprionini + Grammistini + Liopropomini forming two distinct, monophyletic lineages in the ML analysis. A close relationship between the Liopropomini and the grammistin + diploprionin clades has been hypothesized based on morphological data (Kendall, 1979; Johnson, 1983). In our MP analysis, the Liopropomini is sister to the soapfish tribes Diploprionini, Grammistini, and Epinephelini, whereas in the ML analysis the Liopropomini are nested within the soapfishes. These alternative hypotheses for the placement of the Liopropomini are largely unresolveable in the current analyses yet support a close relationship among the Liopropmini, Grammistini, and Diploprionini.

The placement of the Liopropomini poses an interesting question regarding the evolution of the skin toxin grammistin, which is present in both soapfish tribes (Diplopronini and Grammistini). The chemical properties of this toxin have been discussed in detail (Randall et al., 1971; Oshima et al., 1974; Shiomi et al., 2000; Sugiyama et al., 2005). Baldwin and Johnson (1993) noted that those species traditionally called soapfishes (*Grammistes*, *Grammistops*, *Pogonoperca*, and *Rypticus*) not only have grammistin in epidermal cells, but also in specialized dermal glands, a feature unique to them. They hypothesized that the epidermal toxin was independently derived in the Grammistini and Diploprionini, with a subsequent loss within some members of the Grammistini (*Aporops*, *Pseudogramma*, and *Suttonia* lack the toxin). The presence of dermal toxin cells in the Grammistini is unique. Our ML data support this scenario. However, our MP analysis, in which *Liopropoma* occupies a sister relationship to all other epinepheline tribes, suggests that the skin toxin grammistin evolved in the ancestor of the liopropomins and the (grammistin + diploprionin) + epinephelin clade and was lost twice, once within the Grammistini and once in the ancestor of the Epinephelini. The inclusion of species and genera within the Liopropomini and Grammistini that were not represented in this study (*Jeboehlkia, Bathyanthias,* and *Rainfordia*) may serve to clarify the relationships within this tribe and thus the evolution of the skin toxin grammistin.

Relationships within the Epinephelini. To date, no hypothesis of relationships within the Epinephelini has been presented that adequately represents the large number of its included taxa. Craig et al. (2001) presented a preliminary analysis based on molecular data and hypothesized its paraphyly, and Maggio et al. (2005) provided a hypothesis of relationships for some eastern Atlantic species of *Epinephelus* and *Mycteroperca*. Those studies, however, severely undersampled the Epinephelini. Our analysis of molecular data supports a monophyletic tribe Epinephelini sensu Johnson (1983); however, it also supports a rearrangement of the taxonomy within this tribe.

Leis (1986) discussed the larval development of *Plectropomus* and attempted to assign character polarity for several features based on earlier studies of the ontogenetic development of other epinepheline larvae. In his conclusions, he indicated that the genus *Plectropomus* was most likely the sister-group of the remainder of the Epinephelini based (in no small part) on the development of the spination in the dorsal fin. Leis (1986) and Johnson (1988) concluded that the 8- or 9-spine condition is plesiomorphic within the Epinephelinae (thus, 10 or 11 spines are apomorphic). Leis (1986) also found that in *Cephalopholis* the first 8 spines are formed directly, while the 9th is formed indirectly by the transformation of the anteriormost dorsal soft ray. In grouper species with more than 9 spinous rays, the anteriormost 2 soft rays of the larvae develop into spines (Kendall, 1979). Leis (1986) concluded that the indirect transformation of soft rays into spines led to the increased number of spines seen in the genera *Alphestes*, *Anyperodon*, *Cromileptes*, *Epinephelus*, and *Dermatolepis*. Our molecular analysis supports the hypothesis that the 8- and/or 9-dorsal-fin spine configuration is indeed plesiomorphic within the Epinephelini, as all genera with 8 and 9 spines (*Aetheloperca*, *Cephalopholis*, *Gracila*, *Paranthias*, *Plectropomus*, *Saloptia*, and *Variola*) occupy basal positions in both the ML and MP analyses (see Figs. 1, 2). Our data also support the hypothesis of Leis (1986) that *Plectropomus*, along with its close ally *Saloptia*, is the sister-group to the remaining Epinephelini.

The placement of *Epinephelus acanthistius* of the eastern Pacific within *Cephalopholis* by earlier authors was based in large part on the presence of nine dorsal-fin spines in this species. Craig et al. (2001) demonstrated that this species clearly belongs within *Epinephelus*, implying a reversal of the fin-spine condition. The absence of the transformation of the anteriormost soft ray(s) apparently represents such a reversal in *Epinephelus acanthistius*. The transformation of the dorsal-fin ray series in species of *Epinephelus* with ten spines (*Epinephelus analogus*, *Epinephelus exsul*, *Epinephelus nigritus*) is unclear; however, these species are clearly nested within the *Epinephelus* lineage (Smith, 1971; Heemstra and Randall, 1993; Craig et al., 2001; see Figs. 1, 2) implying that this is a derived condition.

The nine-spined groupers in the genera *Aethaloperca, Cephalopholis,* and *Gracila* have long been assumed to be closely allied (Randall, 1964; Smith-Vaniz et al., 1988). Randall (1964) erected the genus *Gracila* for the species *Cephalopholis albomarginata* Fowler and Bean, 1930. In that study, Randall (1964) indicated that although there was a close relationship between *Gracila* and *Cephalopholis*, the species *albomarginata* did not belong in *Cephalopholis* based on its shorter head and semipelagic behavior. Smith (1954) elevated the subgenus *Aethaloperca* for the species *Perca rogaa*, to which he also allocated *albomarginata*. Randall (1964) removed *albomarginata* from Smith's *Aetheloperca* based on differences in the dorsal profile of the head (*Aethaloperca* having a much steeper profile) and proportional body depth (*Aethaloperca* being much deeper bodied). Katayama (1974) placed a second species, *Gracila okinawae* (= *polleni*) into *Gracila* based largely on its truncate caudal fin, a condition that is shared with *Gracila albomarginata*. Smith-Vaniz et al. (1988) provided a redescription of the species *albomarginata* and *polleni* and chose to follow Randall's (1964) allocation of *albomarginata* to *Gracila* while refuting Katayama's placement of *polleni* and placing it in *Cephalopholis*. Heemstra and Randall (1993) also reported that *Aethaloperca*, *Gracila*, *Cephalopholis*, and *Paranthias* share trisegmental pterygiophores, a character absent in many other serranid genera. Interestingly, our genetic analyses indicate a sister-species relationship between *Cephalopholis polleni* and *Gracila albomarginata*, supporting Katayama's (1974) hypothesis of relationships. However, his allocation of both species to *Gracila* may have been ill advised (see following). Additionally, the steeply sloping forehead of *Aethaloperca rogaa* is similar to that seen in *Cephalopholis igarashiensis* and all species of the somewhat distantly related genus *Dermatolepis*, indicating that this character is variable within the Epinephelinae and may not be a reliable indicator of relationships.

Our genetic analysis indicates a monophyletic lineage including *Aethaloperca*, *Cephalopholis*, *Gracila*, and *Paranthias*. The presence of nine spines in all four genera supports this relationship, and the development of these spines in larvae thus far examined indicates their homology (discussed in detail in Leis, 1986, and Craig et al., 2001). This result is not surprising as these genera share other morphological synapomorphies in addition to nine dorsal-fin spines. McCully (1961) surveyed the scalelets in the posterior field among members of the Epinephelinae. He found that in all genera with fewer than ten dorsal-fin spines (except *Plectropomus*), the scales have the first scalelet fused to the structures anterior to it. In genera with more than ten dorsal-fin spines (except *Alphestes* and *Dermatolepis*), the first scalelet is rarely fused to the main portion of the scale. Although *Cephalopholis* and *Aethaloperca* retain the plesiomorphic fused scalelet, *Gracila* exhibits the derived state of a free first scalelet (Smith-Vaniz et al., 1988). The remaining morphological characters that have been examined (neurocranial structure, morphometrics, robustness of fin spines, and shape of pectoral fin) appear either uninformative or represent autapomorphic states (e.g., the pectoral fin in *Aethaloperca* is uniquely asymmetrical) and thus may not be useful for establishing relationships. Our genetic data indicate that *A. rogaa* and *G. albomarginata* are nested well within *Cephalopholis* and consequently should be included in that genus. This finding implies that the unique morphology of these species was derived from an ancestor with a body form typical of species of *Cephalopholis*, but this hypothesis needs to be tested with a thorough analysis of additional morphological characters for these and related groupers.

Similarly, our genetic data indicate that both species of the genus *Paranthias* are nested within the *Cephalopholis* (sensu lato) clade, supporting previous hypotheses of a close relationship between these two genera (Smith, 1966; Craig et al., 2001). The unique, semipelagic lifestyle of *Paranthias* has led to several morphological innovations apparently convergent on those seen in the subfamily Anthiinae (and shared by *Gracila*) and has led to its recognition as a genus independent of *Cephalopholis*. Several morphological and ontogenetic characters (e.g., development of dorsal-fin spines, presence of epineural ribs on vertebrae 1–9) exist, however, that support the inclusion of *Paranthias* within *Cephalopholis*, and they have been discussed in detail elsewhere (Heemstra and Randall, 1993; Craig et al., 2001). Additionally, the ability of *Paranthias furcifer* to hybridize with *Cephalopholis fulva* may indicate a close relationship (Smith, 1966; Craig et al., 2001; Bostrom et al., 2002). Sibley (1957) argued that hybridization should indicate evolutionary relatedness; species should lose this ability as they diverge along evolutionary pathways. It is worth considering, however, that the ability to interbreed, if treated as a character in a phylogenetic (cladistic) framework, should represent a plesiomorphic state, and hence is phylogenetically uninformative until it is lost and is then treated as autapomorphy (Rosen, 1979). Nevertheless, we believe that the ability to interbreed indicates a close relationship between members of *Cephalopholis* and *Paranthias*, a conclusion consistent with our genetic data. It is therefore necessary to include the species *Paranthias colonus* and *Paranthias furcifer* with the remaining species of *Cephalopholis* to recognize only monophyletic taxa. Although it may be argued that to do this fails to recognize the remarkable evolutionary change associated with the semipelagic lifestyle of these two species, it provides a taxonomic scheme that reflects the shared ancestry of the group and fits well within a cladistic framework. In summary, we include the species *A. rogaa*, *G. albomarginata*, *P. colonus*, and *P. furcifer* within the genus *Cephalopholis*.

The only grouper species with a low number of dorsal-fin spines (eight) not included in our study is the Spanish Flag, *Gonioplectrus hispanus*. The relationships of *Gonioplectrus* within the Epinephelini remain unclear. Kendall and Fahay (1979) described the larvae of *Gonioplectrus,* and indicated its placement within the Epinephelinae, and Johnson (1983) placed it within the Epinephelini. The presence of a low dorsal-fin spine count and epineural ribs on vertebrae 1–9 would seem to indicate a close relationship to the genera *Plectropomus* or *Cephalopholis*. In the absence of comparative genetic material, we retain *Gonioplectrus* as a distinct genus within the Epinephelini.

This study confirms the monophyly of the genera *Alphestes* and *Dermatolepis* and their sister-group relationship (Craig et al., 2001, 2004). Smith-Vaniz et al. (1988) reported that the smooth scales of *Alphestes* and *Dermatolepis* are unique compared to those of all other epinephelines. Additionally, all species in these genera have a high dorsal profile of the head; however, this character occurs in other members of the subfamily (e.g., *Cephalopholis sonnerati*, *C. igarashiensis*, and *Cromileptes altivelis*). *Alphestes* spp. are unique in possessing a single, antrorse spine at the corner of the preopercle (also present in *Gonioplectrus*) and in having larvae with an extremely rugose neurocranium (Johnson and Keener, 1984; Heemstra and Randall, 1993). Although Smith (1971) demoted *Alphestes* and *Dermatolepis* to subgeneric status, subsequent treatments recognized these lineages at the generic level (Heemstra and Randall, 1993; Craig et al., 2001) consistent with results from this study. Craig et al. (2004) discussed their interrelationships in detail.

A surprising result of both the ML and MP analyses was the indication of a close relationship between *Epinephelus cifuentesi*, *Epinephelus drummondhayi*, *Triso dermopterus,* and the *Alphestes* + *Dermatolepis* clade. The affinities of *Triso* have been considered unclear (e.g., Heemstra and Randall, 1993). Our data clearly suggest that despite its morphological similarity to *Paranthias*, this genus is more closely allied with *Alphestes* and *Dermatolepis*. *Epinephelus cifuentesi* and *E. drummondhayi* appear to lie within *Epinephelus* (sensu lato) based on their overall morphology. However, in light of the molecular data here, it is necessary to either include them under one taxonomic unit encompassing the *Alphestes* + *Dermatolepis* clade and *Triso* or to treat them as independent taxonomic units. Given the placement of *Triso* in the parsimony analysis, we continue to recognize it as a monotypic genus. The situation is more complicated in *E. cifuentesi* and *E. drummondhayi*, and clearly more data are necessary, both molecular and morphological, to clarify these relationships. We therefore retain these species in *Epinephelus* pending further study.

In our genetic analysis, all species currently allocated to *Mycteroperca* are closely allied (see Figs. 1, 2). However, the presence of species currently placed in *Epinephelus* (*Epinephelus albomarginatus*, *Epinephelus caninus*, *Epinephelus costae*, *Epinephelus goreensis*, *Epinephelus marginatus*, *Epinephelus morrhua*, and *Epinephelus radiatus*) nested among traditional members of the genus renders *Mycteroperca* (sensu Heemstra and Randall, 1993) paraphyletic. Traditionally, *Mycteroperca* and *Epinephelus* are considered as closely related. Species within *Mycteroperca* are regarded as distinct from *Epinephelus* because of their elongate body form and the presence of 10–12 soft anal-fin rays (*Epinephelus* species typically have 8 or 9; Rosenblatt and Zahuranec, 1967; Smith 1971; Heemstra and Randall, 1993). Most of the species currently allocated to *Epinephelus* that form a clade with *Mycteroperca* species have 8–9 anal-fin rays, a character heretofore used to justify their placement within *Epinephelus*. Our analysis indicates that the number of anal-fin rays alone is not a reliable indicator of relationships.

No comprehensive phylogenetic treatment exists for the genus *Mycteroperca*. Cervigón and Velasquez (1966) examined the Venezuelan species, Rosenblatt and Zahuranec (1967) discussed the taxonomy of the eastern Pacific members, Smith (1971) treated the American species, and Heemstra (1991) discussed relationships among the *Mycteroperca rubra* species group. Maggio et al. (2005) discussed the relationships of *Mycteroperca fusca* and *M. rubra*, and Craig et al. (2001) discussed genetic relationships among 7 of 15 species within the genus based on molecular data. The present study thus represents the most thorough sampling of the genus to date. To retain a classification reflecting monophyly, we hereby consider the species *E. marginatus*, *E. costae*, *E. caninus*, *E. goreensis*, *E. albomarginata*, *E. morrhua*, and *E. radiatus* to be members of *Mycteroperca*. This placement, although not currently supported by morphological synapomorphies, provides the basis for a more detailed morphological study of *Mycteroperca*.

The remaining species currently in *Epinephelus* form two distinct clades. The first clade represents species that have previously been allocated to the *Epinephelus niveatus* species group (Smith, 1971). Smith (1971) hypothesized close relationships among the species *Epinephelus flavolimbatus*, *Epinephelus mystacinus*, *Epinephelus nigritus,* and *Epinephelus niveatus*, but did not examine the eastern Pacific species *Epinephelus exsul* and treated the eastern Pacific *Epinephelus niphobles* as a synonym of the western Atlantic *E. niveatus*. Heemstra and Randall (1993) recognized the specific status of the latter pair. Our genetic analysis supports the monophyly of the *niveatus* species group with the addition of the species *E. acanthistius* and *E. exsul* of the eastern Pacific, *Epinephelus ergastularias*, *Epinephelus octofasciatus*, and *Epinephelus septemfasciatus* of the Indo-Pacific, and *Epinephelus quernus* from the Hawaiian archipelago.

All species within the *niveatus* species group are characterized by having a much deeper body than the remaining *Epinephelus* species. This character is particularly evident in juveniles, which have a disk-shaped body (Fig. 3). Both juveniles and adults of the remaining species of *Epinephelus* and *Mycteroperca* have juveniles and adults with a much

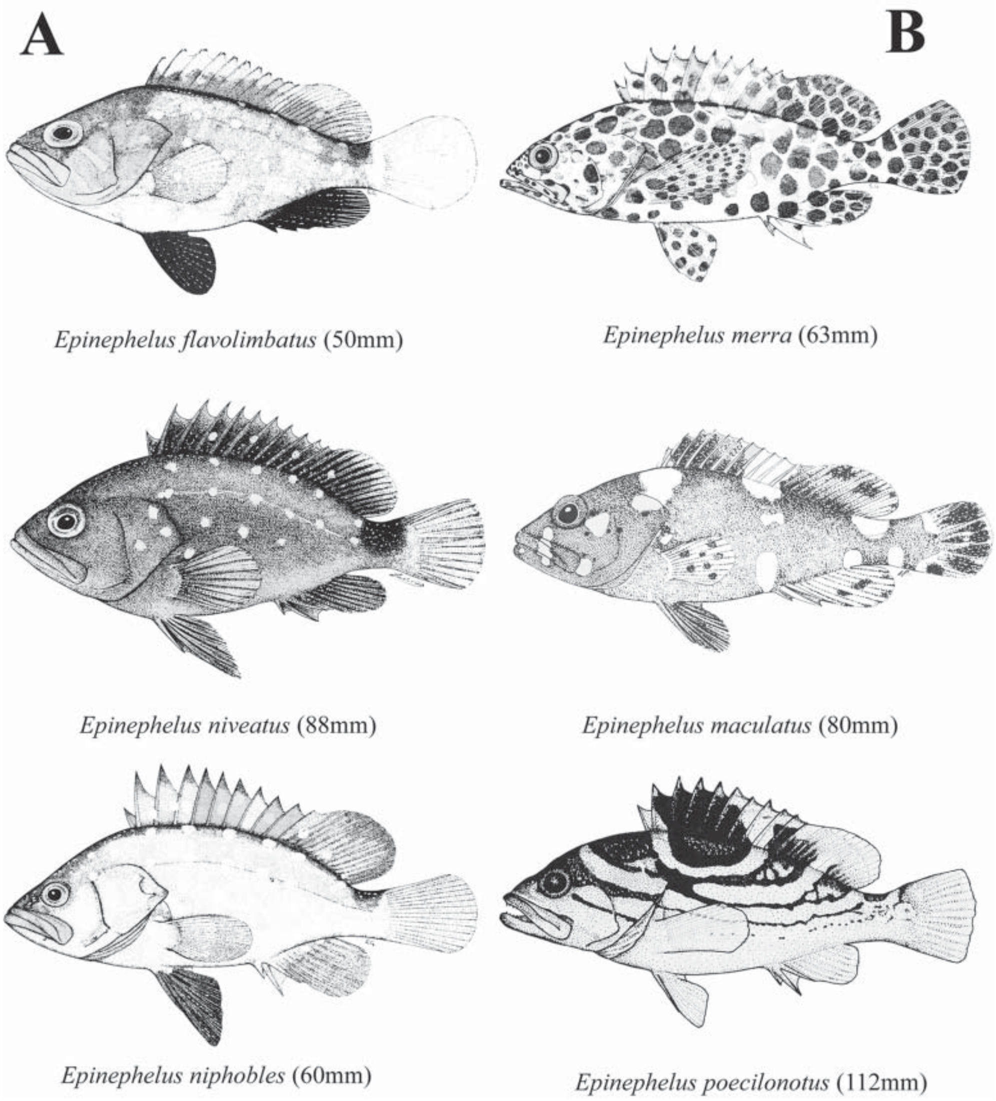

Fig. 3. Juvenile specimens of the *Epinephelus niveatus* species complex (**A**) and the *Epinephelus fasciatus* complex (**B**). [Pictures are reproduced by permission of the author (P.C.H.) from Heemstra and Randall (1993)]

more elongate body form (Fig. 3). Additionally, all species in the *niveatus* group share a characteristic drab brown or olive coloration that may or may not include several dark bars along the body. The *niveatus* species group is also characterized by having pelvic fins that insert immediately below or in front of the pectoral insertion, whereas the remaining *Epinephelus* species and all *Mycteroperca* species have pelvic fins that insert below or behind the pectoral insertion. In members of the *niveatus* species group, the articulation between the cleithrum and the coracoid forms an elongate, triangular foramen. In the remaining species of *Epinephelus* (sensu stricto) and *Mycteroperca*, this foramen is distinctly rounded at the same articulation in both adults and juveniles. In other species of the subfamily (e.g., *Cephalopholis* spp.) this articulation forms the circular foramen; thus, the elongate shape serves as a synapomorphy for those species in the *E. niveatus* clade.

The members of the *niveatus* species group thus represent a monophyletic lineage that is distinct from the remaining species of *Epinephelus*. In this light, it is apparent that the members of this complex should be considered as a unique genus. Consequently, we allocate the species within the clade to the oldest available generic name for one of its members, *Hyporthodus*.

One troublesome aspect of the phylogenetic hypothesis recovered in our analysis lies within the *niveatus* species group. The lack of a sister-group relationship between *E. niphobles* of the eastern Pacific and *E. niveatus* of the western Atlantic is surprising given that these two species, considered by some authors to be conspecific because of their extremely similar morphology, have long been considered as transisthmian geminates (Jordan, 1908; Smith, 1971; Heemstra and Randall, 1993). The *niveatus* lineage does include a confirmed geminate pair, *E. exsul* of the eastern

Pacific and *E. nigritus* of the western Atlantic. Our results may be confounded by the relatively small genetic distance between species in this clade, which may inhibit the ability of our analyses to resolve their relationships with the genetic markers herein employed.

The remaining species of *Epinephelus* form a monophyletic group designated the *E. fasciatus* species group (Craig et al., 2001), which also includes the monotypic genera *Anyperodon* and *Cromileptes*. This clade is characterized by the typically slender-bodied species of *Epinephelus* whose pelvic-fin insertion is below or behind the pectoral-fin insertion.

Within this clade, there are some monophyletic species groups whose affinities have been discussed based largely on color pattern (e.g., the reticulated groupers of Heemstra and Randall, 1993). The reticulated species examined here (*Epinephelus hexagonatus*, *Epinephelus macrospilos*, *Epinephelus maculatus*, *Epinephelus melanostigma*, *Epinephelus merra*, *Epinephelus spilotoceps*) form a clade along with *Epinephelus fasciatus*, *Epinephelus tauvina*, and *Epinephelus retouti*. Heemstra and Randall (1993) stated that the juveniles of *E. tauvina* are often confused with members of the reticulated groupers, and the color pattern of *E. tauvina*, along with the molecular data presented, clearly support its inclusion in the reticulated groupers. *Epinephelus fasciatus* is the type species for the genus *Epinephelus*, and although the color pattern of that species and of *E. retouti* do not clearly place it with the reticulated groupers, its inclusion in the clade is supported by high bootstrap support based on our genetic data.

The inclusion of the morphologically distinct *Anyperodon* and *Cromileptes* within the *fasciatus* species group was unexpected, although not surprising. The diagnoses of these genera reflect uniquely derived features, or autapomorphies, which are phylogenetically uninformative. In this light, it seems most prudent based on the genetic data to include these species within *Epinephelus*.

New Generic Classification for the Epinephelini

One of the central tenets of phylogenetic systematics is the designation of monophyletic groups and a nomenclatural system that reflects groups with shared ancestry (Forey et al., 1992). While basing nomenclatural decisions solely on molecular data is not ideal, we have highlighted previously described morphological characters and provided new characters where possible that may be phylogenetically informative when considered within the context of character states in appropriate outgroups. In light of the genetic and morphological data at hand, we herein present a reclassification for genera within the tribe Epinephelini that reflects a strict, cladistic interpretation of these data (Appendix 2). Several previously recognized genera were found to be monophyletic only with the addition of various morphologically distinct taxa that have been placed in monotypic genera. The genera *Alphestes*, *Dermatolepis*, *Gonioplectrus*, *Plectropomus*, *Saloptia*, and *Variola* remain as currently defined in Heemstra and Randall (1993). Appendix 2 provides a list of currently recognized species of epinepheline fishes. Unsampled species are referred to the most appropriate genus incertae sedis based on a qualitative assessment of their overall morphology and in accordance with previous classifications, especially those of Heemstra and Randall (1993). Although certain genera within this scheme may be considered undiagnosable based on the current knowledge of the group's morphology, it will undoubtedly provide a heretofore-unrecognized starting point to evaluate both previously discussed and new morphological characters. This revised taxonomy thus represents a framework that may be used to create a sensible taxonomic scheme which reflects the evolution of this diverse group of marine fishes.

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Appendix 1. Species included in this analysis, voucher specimen numbers, and GenBank accession numbers for data gathered in the current study

Species	*n*	Voucher number	16S	12S	TMO4C4	H III
Epinephelini						
Aethaloperca rogaa	2	SIO 02-138	AY947565	AY949367	AY949225	AY949552
Alphestes afer	2	SIO 03-49	AY314003	AY313982	AY313992	AY949455
A. immaculatus	1	SIO 00-92	AF297290	AY313980	AY313994	AY949456
A. multiguttatus	2	SIO 00-95	AF297305	AY313981	AY313991	
Anyperodon leucogrammicus	3	SIO 64-235	AF297306	AY949379		AY949577
Cephalopholis argus	2	PV, D.R. Robertson	AY947555	AY949357	AY949223	AY949472
C. boenak	2	SIO 02-138	AY947598	AY949325	AY949293	AY949520
C. cruentata	2	SIO 04-192	AF297323	AY949385	AY949266	AY949533
C. cyanostigma	1	SIO 04-191	AY947594	AY949389	AY949290	AY949517
C. formosa	1	SIO 04-191	AY947603	AY949370	AY949291	AY949588
C. fulva	2	SIO 00-146	AF297292	AY949395	AY949282	AY949589
C. igarashiensis	2	SIO 02-138	AY947599	AY949326	AY949292	AY949457
C. leopardus	1	PV, D.R. Robertson	AY947560	AY949327	AY949323	AY949473
C. miniata	1	SIO 64-235	AF297321	AY949400	AY949318	AY949523
C. nigri	1	SIO 04-39	AY947604	AY949451	AY949279	AY949581
C. nigripinnis	1	SIO 04-67	AY947605	AY949382	AY949280	AY949504
C. panamensis	3	SIO 00-92	AF297313	AY949396	AY949272	AY949531
C. polleni	1	SIO 04-191	AY947627	AY949371	AY949278	AY949553
C. sonnerati	2	SIO 64-235	AF297307	AY949404	AY949297	AY949534
C. taeniops	2	SIO 04-39	AY947589	AY949387		AY949498
C. urodeta	1	SIO 02-139	AF297325	AY949408	AY949277	AY949538
Cromileptes altivelis	3	SIO 02-141	AY947628	AY949328	AY949286	AY949500
Dermatolepis dermatolepis	2	SIO 64-235	AF297317	AY313984	AY313988	AY949536
D. inermis	1	PV, MTC	AY314005	AY313979	AY313987	AY949573
D. striolata	1	PV, D.R. Robertson	AY314004	AY313989	AY313989	AY949474
Epinephelus acanthistius	1	SIO 00-142	AF297318	AY949376		AY949590
E. adscencionis	2	SIO 00-145	AF297314	AY949381	AY949284	AY949487
E. aeneus	1	PV, P. Wirtz	AY947593	AY949441	AY949226	AY949476
E. akaara	1	R. Chapman	AY947600	AY949442		AY949569
E. albomarginata	1	PV, S. Fennesey	AY947590	AY949378	AY949298	AY949477
E. amblycephalus	1	SIO 64-228	AY731070	AY949434	AY949312	AY949513
E. analogus	1	SIO 00-185	AF297302	AY949330	AY949220	AY949499
E. andersoni	2	SIO 04-60	AY947592	AY949383	AY949315	AY949478
E. areolatus	1	SIO 00-235	AY731076	AY949391		AY949479
E. awoara	1	SIO 02-137	AY947558	AY949331	AY949227	AY949576
E. bleekeri	1	PV, MTC	AY947626	AY949366		AY949554
E. bruneus	1	PV, MTC	AY947562	AY949399	AY949228	AY949555
E. caeruleopunctatus	3	SIO 02-139	AY947563	AY949374	AY949229	AY949580
E. caninus	1	PV, E. Sala	AY947585	AY949428	AY949294	

Appendix 1. *Continued*

Species	*n*	Voucher number	16S	12S	TMO4C4	H III
E. chlorostigma	2	PV, D.R. Robertson	AY731075	AY949407	AY949231	AY949508
E. cifuentesi	2	SIO 00-138	AF297295	AY949397	AY949209	AY949480
E. clippertonensis	2	SIO 00-186	AY731077	AY949332	AY949304	AY949521
E. coioides	2	SIO 64-235	AY947608	AY949333	AY949295	AY949518
E. corrallicola	2	PV, MTC	AY947568	AY949334	AY949232	AY949459
E. costae	1	PV, E. Sala	AY947596	AY949368	AY949296	AY949506
E. cyanopodus	2	SIO 02-138, AMS I.39542007	AY731074	AY949335	AY949233	AY949460
E. daemelii	1	PV	AY947635	AY949453		AY949587
E. diacanthus	1	PV, MTC	AY947619	AY949406	AY949274	AY949549
E. drummondhayi	2	SIO 00-152	AF297317	AY313985	AY313993	AY949541
E. ergastularius	2	AMS I.39542007	AY947606	AY949432	AY949230	AY949575
E. exsul	2	SIO 02-21	AY947556	AY949358	AY949222	AY949461
E. fasciatomaculosus	2	PV, MTC	AY947622	AY949398	AY949324	AY949579
E. fasciatus	1	SIO 64-235	AF297319	AY949401		AY949524
E. flavocaeruleus	1	SIO 04-67	AY947607	AY949384	AY949316	AY949585
E. flavolimbatus	1	SIO 00-150	AF297293	AY949336	AY949269	AY949528
E. fuscogutattus	1	AMS I.42844005	AY947561	AY949415	AY949234	AY949510
E. guttatus	2	SIO 00-140	AF297299	AY949437	AY949281	AY949545
E. goreensis	1	PV, G. Menenzes	AY947621	AY949438	AY949305	AY949551
E. hexagonatus	2	AMNH 120080	AY947623	AY949380	AY949319	AY949462
E. howlandi	3	SIO 02-139	AY947620	AY949414	AY949317	AY949583
E. itajara	1	SIO 00-185	AF297294	AY949337	AY949235	AY949592
E. labriformis	3	SIO 00-137	AF297296	AY426252	AY949236	AY949566
E. lanceolatus	2	SIO 04-191	AY947588	AY949377	AY949237	AY949463
E. macrospilos	1	SIO 02-141	AY731072	AY949416	AY949238	AY949481
E. maculatus	1	SIO 02-138, AMS I.42844011	AY731068	AY949338	AY949313	AY949482
E. malabaricus	2	SIO 02-140	AY947609	AY949390	AY949275	AY949544
E. marginatus	2	SIO 04-62	AY947595	AY949369	AY949239	AY949483
E. melanostigma	2	SIO 02-138	AY947633	AY949339	AY949240	AY949591
E. merra	2	SIO 02-141	AY947629	AY949427	AY949288	AY949515
E. miliaris	1	PV, D.R. Robertson	AY947634	AY949418	AY949299	AY949516
E. morio	2	SIO 00-145	AF297324	AY949425	AY949322	AY949484
E. morrhua	2	SIO 02-137	AY947630	AY949340	AY949287	AY949464
E. multinotatus	2	PV, D.R. Robertson	AY428594	AY426252	AY425675	AY949567
E. mystacinus	2	SIO 00-138	AF297304	AY949341	AY949307	AY949485
E. nigritus	1	SIO	AF297297	AY949405	AY949309	AY949532
E. niphobles	1	SIO 64-235	AF297309	AY949342	AY949241	AY949584
E. niveatus	2	SIO 00-151	AF297310	AY949343	AY949262	AY949535
E. octofasciatus	2	SIO 02-138	AY947564	AY949388	AY949242	AY949501
E. ongus	3	SIO 02-138	AY947566	AY949344	AY949243	AY949496
E. polyphekadion	2	SIO 02-141	AY947569	AY949431	AY949244	AY949509
E. quernus	2	PV, M. Rivera	AY947570	AY949429	AY949245	AY949465
E. quoyanus	1	R. Chapman	AY731073	AY949394	AY949285	AY949502
E. radiatus	2	SIO 02-141	AY947602	AY949430	AY949301	AY949519
E. retouti	2	SIO 02-139	AY947625	AY949345	AY949246	AY949466
E. rivulatus	1	SIO 02-141	AY947586	AY949410	AY949224	AY949458
E. septemfasciatus	2	SIO 02-137	AY947559	AY949346	AY949247	AY949568
E. spilotoceps	1	PV, D.R. Robertson	AY731069	AY949440	AY949321	AY949564
E. striatus	2	SIO 00-146	AF297311	AY949433	AY949283	AY949539
E. tauvina	1	SIO 02-138	AY731067	AY949347	AY949248	AY949467
E. trimaculatus	2	R. Chapman	AY731071	AY949403	AY949264	AY949486
E. tukula	2	R. Chapman	AY947557	AY949443	AY949249	AY949507
E. undulosus	1	SIO 64-235	AF297326	AY949409	AY949302	AY949505
E. undulostriatus	1	PV, D.R. Robertson	AY947636	AY949454		AY949586
Gracila albomarginata	1	PV, MTC	AY947582	AY949348	AY949250	AY949574
Mycteroperca acutirostris	1	PV, R. Chapman	AY947591	AY949411	AY949251	AY949514
M. bonaci	1	SIO 00-145	AF297315	AY949449	AY949270	AY949546
M. fusca	2	PV, P. Wirtz	AY947597	AY949448	AY949252	AY949489

Appendix 1. *Continued*

Species	*n*	Voucher number	16S	12S	TMO4C4	H III
M. interstitialis	2	SIO	AY947632	AY949359	AY949221	AY949556
M. jordani	2	SIO 00-144	AF297329	AY949435	AY949303	AY949522
M. microlepis	2	SIO 00-148	AF297312	AY949373	AY949253	AY949490
M. olfax	2	SIO 00-89	AF317512	AY949360	AY949276	AY949537
M. phenax	2	SIO 00-145	AF297303	AY949450	AY949265	AY949548
M. prionura	1	PV, D. J. Pondella	AY947583	AY949361	AY949254	AY949557
M. rosacea	2	SIO 00-92	AF297300	AY949350	AY949268	AY949540
M. rubra	3	PV, T. Maggio	AY947587	AY949364	AY949255	AY949468
M. tigris	2	UKNHM-BRC T104	AY947574	AY949452	AY949217	AY949560
M. venenosa	2	SIO 00-147	AF297291	AY949419	AY949273	AY949527
M. xenarcha	1	SIO UN-CAT	AY947637	AY949445		AY949571
Paranthias colonus	1	SIO 00-89	AF297301	AY949351		AY949491
P. furcifur	2	SIO 00-125	AY947584	AY949372	AY949263	AY949595
Plectropomus areolatus	1	PV, MTC	AY947613	AY949447	AY949267	AY949565
P. laevis	1	SIO 64-236	AY947614	AY949444	AY949320	AY949542
P. leopardus	1	AMS I.42844017	AF297298	AY949352	AY949211	AY949525
P. maculatus	1	SIO 64-235	AF297320	AY949423		AY949570
P. oligocanthus	1	PV, MTC	AY947615	AY949386	AY949300	AY949547
Saloptia powelli	2	SIO 02-139	AY947631	AY949375		AY949578
Triso dermopterus	1	AMS I.41217002	AY947601	AY949365	AY949260	AY949469
Variola albimarginata	2	SIO 02-138	AY947567	AY949412	AY949261	AY949495
V. louti	2	SIO 04-191	AY947577	AY949363	AY949219	AY949494
Niphonini						
Niphon spinosus	2	SIO 00-174	AY947575	AY949420	AY949210	AY949596
Diploprionini						
Belonoperca chabanaudi	1	SIO 04-191	AY947580	AY949422		AY949561
Diploprion bifasciatum	2	SIO 04-191	AY947576	AY949329	AY949214	AY949475
Liopropomini						
Liopropoma eukrines	1	SIO 01-11	AY947581	AY949426	AY949208	AY949488
Liopropoma carmabi	1	PV, MTC	AY947579	AY949349	AY949310	AY949558
Grammistini						
Aporops sp.	1	UKNHM-BRC T804	AY947573	AY949356	AY949271	AY949471
Grammistes sexlineata	1	PV, MTC	AY539050	AY949413	AY539458.1	AY949572
Pseudogramma polyacantha	2	UKNHM-BRC T695, T696	AY947512	AY949362	AY949212	AY949493
Pseudogramma gregoryi	2	UKNHM-BRC T100, T155	AY947571	AY949417	AY949213	AY949492
Pogonoperca punctata	1	SIO 64-235	AF297322	AY949353	AY949218	AY949582
Rypticus nigripinnis	1	SIO 00-182	AY947578	AY949402	AY949258	AY949593
Suttonia sp.	1	UKNHM-BRC T805	AY947618	AY949355	AY949311	
Anthiine outgroups						
Anthias cf anthias	1	PV, G. Menezes	AY947617	AY949446		AY949550
Hemanthias leptus	1	MTC	AY947611	AY949392	AY539459.1	AY949512
Hemanthias peruanus	1	SIO 00-185	AY947610	AY949393	AY949306	AY949594
Pronotogrammus multifasciatus	2	SIO 00-139	AF297330	AY949354	AY949257	AY949511
Pseudanthias squamipinnis	2	SIO 04-51	AY947624	AY949436	AY949308	AY949543
Serranine outgroups						
Centropristes striata	1	UCLA W97-22	AY072667	AY072656.1	AY949216	AY949530
Cratinus agassizii	1	LACM 47328-1	AY072668	AY072647.1	AY949289	AY949526
Diplectrum pacificum	1	PV, D.J. Pondella	AY072669	AY072663	AY949215	AY949529
Paralabrax nebulifer	2	SIO 00-97	AF297328	AY072662	AY313990	AY949497
Serranus tigrinis	1	SIO 01-127	AY072688	AY072659.1	AY949259	AY949503
Serranidae *incertae sedis*						
Acanthistius ocellatus	1	AMS I.42844022	AY947612	AY949421	AY949314	AY949470
Other outgroups						
Cirrhitus rivulatus	1	Wm. L. Smith	AY539059.2	x	AY539467.1	AY539268.1
Etheostoma blennioides	1	Wm. L. Smith	AY539054.2	AY372771.1	AY539462.1	AY539263.1
Gymnodraco acuticeps	1	Wm. L. Smith	AY539064.2	U90413	AY539472.1	AY539273.1
Haemulon plumieri	1	Wm. L. Smith	AY539057.2	x	AY539465.1	AY539266
Hoplostethus medditeraneus	1	Wm. L. Smith	AY538968.2	AY141335	AY539384	AY539177

Appendix 1. *Continued*

Species	*n*	Voucher number	16S	12S	TMO4C4	H III
Lepidotrigla spinosa	1	Wm. L. Smith	AY539001.2	x		AY539210.1
Morone saxatilis	1	Wm. L. Smith	AY539046.2	x	AY539454.1	AY539255.1
Perca flavescens	1	Wm. L. Smith	AY539055.2	x	AY539463.1	AY539264.1
Pleurogrammos azonus	1	SIO 01-34	AY539012	AY949439	AY539424.1	AY949563
Polyprion americanus	1	AMS I.42844002	AY947616	AY949424	AY949256	AY949562
Scorpaena gutatta	1	Wm. L. Smith	AY538984.2	x	AY539400.1	AY539193.1
Stereolepis gigas	2	SIO 03-74	AY072683.1	AY072666		AY949559
Trachinus draco	1	Wm. L. Smith	AY539068.2	AY141378.1	AY539476.1	AY539277.1

x indicates sequence available but not yet deposited in GenBank; blanks indicate no sequence available; PV, photo voucher

Taxonomy follows traditional scheme (e.g., Heemstra and Randall, 1993); institutional abbreviations follow Leviton et al. (1985)

Appendix 2. Proposed classification for the fishes of the tribe Epinephelini based on molecular data. For a complete list of synonyms, see Heemstra and Randall (1993). Species not included in our genetic analysis are listed under insertae sedis within the most appropriate genus based on a qualitative assessment of their overall morphology and in accordance with previous classifications, especially Heemstra and Randall (1993).

Genus *Alphestes* Bloch and Schneider

Type species: *Epinephelus afer* Bloch (by subsequent designation of Jordan and Swain). Type locality: Guinea (Craig et al., 2007).

Included species: *A. afer* (Bloch), *A. immaculatus* Breder, *A. multiguttatus* (Günther).

Genus *Cephalopholis* Bloch and Schneider

Type species: *Cephalopholis argus* Bloch and Schneider. Type locality: East Indies.

Included species: *C. albomarginata* (Fowler and Bean), *C. argus* Bloch and Schneider, *C. boenak* (Bloch), *C. colonus* (Valenciennes), *C. cruentata* (Lacepéde), *C. cyanostigma* (Valenciennes), *C. formosa* (Shaw and Nodder), *C. fulva* (Linnaeus), *C. furcifer* (Valenciennes), *C. igarashiensis* Katayama, *C. leopardus* (Lacepéde), *C. miniata* (Forsskål), *C. nigri* (Günther), *C. nigripinnis* (Valenciennes *in* Cuvier and Valenciennes), *C. panamensis* (Steindachner), *C. polleni* (Bleeker), *C. rogaa* (Forsskål), *C. sonnerati* (Valenciennes), *C. taeniops* (Valenciennes), *C. urodeta* (Schneider).

Species incertae sedis: *C. aitha* Randall and Heemstra, *C. aurantia* (Valenciennes), *C. hemistiktos* (Rüppell), *C. microprion* (Bleeker), *C. oligosticta* Randall and Ben-Tuvia, *C. sexmaculata* (Rüppel), *C. spiloparaea* (Valenciennes).

Genus *Dermatolepis* Gill

Type species: *Dermatolepis punctatus* Gill (= *Epinephelus dermatolepis* Boulenger; replacement name for *D. punctatus* preoccupied in *Epinephelus* by *Holocentrus punctatus* Bloch). Type locality: Cape San Lucas, Baja California.

Included species: *D. dermatolepis* (Boulenger), *D. inermis* (Valenciennes), *D. striolata* (Playfair).

Genus *Epinephelus* Bloch

Type species: *Epinephelus marginalis* Bloch (= *E. fasciatus* (Forsskål) designated under the plenary powers of the IZCN, Opinion 93). Type locality: Red Sea.

Included species: *E. adscensionis* (Osbeck), *E. aeneus* (Geoffroy Saint-Hiliaire), *E. akaara* (Temminck and Schlegel), *E. altivelis* (Valenciennes), *E. amblycephalus* (Bleeker), *E. analogus* Gill, *E. areolatus* (Forsskål), *E. awoarra* (Temminck and Schlegel), *E. bleekeri* (Vaillant), *E. brunneus* Bloch, *E. caeruleopunctatus* (Bloch), *E. chabaudi* (Castlenau), *E. chlorostigma* (Valenciennes), *E. clippertonensis* Allen and Robertson, *E. coioides* (Hamilton), *E. corallicola* (Valenciennes), *E. cyanopodus* (Richardson), *E. daemelii* (Günther), *E. diacanthus* (Valenciennes), *E. fasciatomaculosus* (Peters), *E. fasciatus* (Forsskål), *E. flavocaeruleus* (Lacepéde), *E. fuscogutattus* (Forsskål), *E. guttatus* (Linnaeus), *E. hexagonatus* (Forster), *E. howlandi* (Günther), *E. itajara* (Lichtenstein), *E. labriformis* (Jenyns), *E. lanceolatus* (Bloch), *E. leucogrammicus* (Valenciennes), *E. macrospilos* (Bleeker), *E. maculatus* (Bloch), *E. malabaricus* (Bloch and Schneider), *E. melanostigma* Schultz, *E. merra* Bloch, *E. miliaris* (Valenciennes), *E. morio* (Valenciennes), *E. multinotattus* (Peters), *E. ongus* (Bloch), *E. polyphekadion* (Bleeker), *E. quoyanus* (Valenciennes), *E. retouti* Bleeker, *E. rivulatus* (Valenciennes), *E. spilotoceps* Schultz, *E. striatus* (Bloch), *E. tauvina* (Forsskål), *E. trimaculatus* (Valenciennes), *E. tukula* Morgans, *E. undulostriatus* (Peters), *E. undulosus* (Quoy and Gaimard).

Species incertae sedis: *E. andersoni* Boulenger, *E. bilobatus* Randall and Allen, *E. bontoides* (Bleeker), *E. chlorocephalus* (Valenciennes), *E. cifuentesi* Grove and Lavenberg in Heemstra and Randall, *E. drummondhayi* Goode and Bean, *E. epistictus* (Temminck and Schlegel), *E. erythrurus* (Valenciennes), *E. faveatus* (Valenciennes), *E. gabriellae* Randall and Heemstra, *E. heniochus* Fowler, *E. indistinctus* Randall and Heemstra, *E. irroratus* (Forster), *E. latifasciatus* (Temminck and Schlegel), *E. lebretonianus* (Hombron and Jacquinot), *E. longispinis* (Kner), *E. magniscuttis* Postel, Fourmanoir, and Guézé, *E. poecilonotus* (Temminck and Schlegel), *E. polylepis* Randall and Heemstra, *E. polystigma* (Bleeker), *E. posteli* Formanoir and Crosnier, *E. sexfasciatus* (Valenciennes), *E. socialis* (Günther), *E. stictus* Randall and Allen, *E. stolizkae* (Day), *E. suborbitalis* Amaoka and Randall, *E. summana* (Forsskål), *E. timorensis* Randall and Allen, *E. trophis* Randall and Allen, *E. tuamotoensis* Fourmanoir.

Genus *Gonioplectrus* Gill

Type species: *Plectropoma hispanum* Cuvier. Type locality: Martinique.

Included species: *G. hispanus* (Cuvier).

Genus *Hyporthodus* Gill

Type species: *Hyporthodus flavicauda* [=*Epinephelus niveatus* (Valenciennes *in* Cuvier and Valenciennes)] Type locality: Newport, Rhode Island.

Included species: *H. niveatus* (Valenciennes), *H. niphobles* (Gilbert and Starks), *H. exsul* (Fowler), *H. acanthistius* (Gilbert), *H. flavolimbatus* (Poey), *H. mystacinus* (Poey), *H. septemfasciatus* (Thunberg), *H. octofasciatus* (Griffin), *H. nigritus* (Holbrook), *H. ergastularias* (Whitley), *H. quernus* (Seale).

Species incertae sedis: *H. darwinensis* (Randall and Heemstra), *H. haifensis* (Ben-Tuvia), *H. perplexus* (Randall, Hoese, and Last).

Genus *Mycteroperca* Gill

Type species: *Serranus olfax* Jenyns (by subsequent designation of Gill, 1866). Type locality: Galápagos Islands.

Included species: *M. acutirostris* (Valenciennes), *M. albomarginata* (Boulenger), *M. bonaci* (Poey), *M. caninus* (Valenciennes), *M. cidi* Cervigón, *M. costae* (Steindachner), *M. fusca* (Lowe), *M. goreensis* (Valenciennes), *M. interstialis* (Poey), *M. jordani* (Jenkins and Evermann), *M. marginatus* (Lowe), *M. microlepis* (Goode and Bean), *M. morrhua* (Valenciennes), *M. olfax* (Jenyns), *M. phenax* Jordan and Swain, *M. prionura* Rosenblatt and Zahuranec, *M. radiatus* (Day), *M. rosacea* (Streets), *M. rubra* (Bloch), *M. tigris* (Valenciennes), *M. venenosa* (Linnaeus), *M. xenarcha* Jordan.

Genus *Plectropomus* Oken

Type species: *Bodianus maculatus* Bloch (by subsequent designation of Jordan, Tanaka, and Snyder). Type locality: Japan (probably erroneously reported for Java; Heemstra and Randall, 1993).

Included species: *P. areolatus* Rüppell, *P. laevis* (Lacepède), *P. leopardus* (Lacepède), *P. maculatus* (Bloch), *P. oligocanthus* Bleeker, *P. pessuliferus* Fowler, *P. punctatus* Quoy and Gaimard.

Genus *Saloptia* Smith

Type species: *Saloptia powelli* Smith. Type locality: Cook Islands.

Included species: *S. powelli* Smith.

Genus *Triso* Randall, Johnson, and Lowe

Type species: *Serranus dermopterus* Temminck and Schlegel. Type locality: Nagasaki, Japan.

Included species: *T. dermopterus* (Temminck and Schlegel).

Genus *Variola* Swainson

Type species: *Variola longipinna* Swainson (=*Perca louti* Forsskål by monotypy). Type locality: Indian Ocean.

Included species: *V. albimarginata* Baissac, *V. louti* (Forsskål)