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Molecular Phylogenetics of Perciform Fishes Using the Nuclear Recombination Activating Gene 1

Andrew R. Mahon
Old Dominion University

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MOLECULAR PHYLOGENETICS OF PERCIFORM FISHES USING THE NUCLEAR RECOMBINATION ACTIVATING GENE 1

by

Andrew R. Mahon

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Approved by:

Kent E. Carpenter (Director)

John R. Holsinger (Member)

Guillermo Orti (Member)

ABSTRACT

MOLECULAR PHYLOGENETICS OF PERCIFORM FISHES USING THE NUCLEAR RECOMBINATION ACTIVATING GENE 1

Andrew R. Mahon
Old Dominion University, 2007
Director: Dr. Kent E. Carpenter

The order Perciformes contains one-third of all extant fishes in twenty different suborders and over 10,000 species. Few systematic investigations have been performed on this large group of fishes at the suborder level and their evolutionary history is widely recognized as problematic. This dissertation presents three studies: a molecular phylogenetic analysis of the putative suborders of the order Perciformes, an analysis of interrelationships of the families of the perciform suborder Percoidei, and a multi-gene investigation of the percoid superfamily Sparoidea.

The taxa sampled in this dissertation represent one of the most inclusive molecular datasets, to date, testing the monophyly of the Perciformes and relationships of its suborders, including the Percoidei. Analyses are performed using a 1425-1431 base fragment of exon three of the single copy, nuclear recombination activating gene 1 (RAG1). Results of these tests reject the monophyly of the Perciformes and of its largest suborder, the Percoidei. However, this study does support some previous relationships at the suborder and family level for these groups and also presents novel interpretations of many groups. A lack of nodal support is seen for mid-level clades in these analyses. Genetic bias, such as high GC content and low effective number of codons, in some taxa, is hypothesized to be one of the causes for some of the unexpected relationships found in this work.

A multi-gene approach was taken to test the monophyly of the superfamily Sparoidea and its families. Analyses of RAG1, cytochrome b (cytB), and combined RAG1 + cytB datasets reject a monophyletic Sparoidea but find the Nemipteridae, Sparidae plus Centracanthidae, and Lethrinidae to be individually monophyletic. The one exception to this is in the cytB maximum likelihood phylogeny, which fails to resolve a monophyletic Lethrinidae.

The phylogenetic hypotheses discussed in this dissertation are an important step toward an understanding of perciform, percoid, and sparoid relationships and deserve further testing. The high level of taxon sampling presented here should be replicated and expanded using other molecular markers to help resolve the bush at the top of the teleostean tree.

This dissertation is dedicated to my wife, Heidi K. Mahon, without whom this work would not have been possible.

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CHAPTER I

GENERAL INTRODUCTION

The order Perciformes contains over 10,000 species, representing one-third of all extant fishes in twenty different suborders (Nelson, 2006). Few systematic investigations have been performed on this large group of fishes at the suborder level, and the order's limits as well as its evolutionary relationships are widely recognized as problematic. The largest of these suborders is the Percoidei, which contains 78 families and approximately 3,000 species (Nelson, 2006). Morphological characters have been successful for determining the limits of individual families within the group, but have not been successful in defining the monophyly of the suborder or for determining broad interfamilial relationships within the suborder (Johnson, 1993; Johnson and Patterson, 1993). Johnson (1984) stated that the percoids exemplify the inadequacies inherent in perciform classification.

Aside from morphological characters, many current research studies are utilizing molecular information such as DNA sequence data to infer phylogenetic relationships among organisms. The phylogenetic resolution that DNA sequences provide depends on the gene used and the taxonomic level in question. Differences in levels of saturation, rate of variation between lineages, and compositional biases can result in the inefficiency of a gene or gene fragment to elucidate deeper levels of phylogenetic relationships (Meyer, 1994; Brocchieri, 2001).

The journal model chosen for this dissertation is Molecular Phylogenetics and Evolution (Elsevier, Inc.).

Many studies have relied on mitochondrial gene sequences to infer phylogenetic inference. However, rates of change in mitochondrial DNA may be too rapid to resolve higher level relationships, including those at interfamiliar levels, the suborder level, and higher (Hillis and Huelsenbeck, 1992; Lydeard and Roe, 1997; Orrell and Carpenter, 2004). To resolve relationships of higher taxonomic groups (i.e. deeper phylogenetic levels), slower evolving, nuclear exons hold promise (Groth and Barrowclough, 1999).

The single copy, nuclear recombinase activating gene 1 (RAG1) is found in all vertebrates. Along with the closely related RAG2 gene, RAG1 aids in the production of immunoglobins and T-cell receptors (Groth and Barrowclough, 1999; Greenhalgh and Steiner, 1995). Previous systematic studies have utilized the RAG1 gene because of its rarity of insertions and deletions (indels), its slow evolutionary rate, and its minimal saturation of transition changes at third position codons (Groth and Barrowclough, 1999). In a study of the rainbow trout (*Oncorhynchis mykiss*), Hansen and Kaattari (1995) proposed that the slow evolutionary change in the RAG1 gene may be useful for vertebrate systematic analyses. Holcroft (2004) used the RAG1 gene to elucidate sister-group relationships for the order Tetraodontiformes. The RAG1 gene was also utilized to develop a phylogeny of the Esociformes (Lopez et al., 2004). The conserved nature of the RAG1 gene makes it potentially useful for testing relationships within the largest order of vertebrates, the Perciformes, and the largest suborder of perciforms, the Percoidei.

In this dissertation, I present an analysis of perciform suborder relationships, with a focus on interfamilial relationships within the suborder Percoidei. This work includes representatives from all twenty putative suborders of the Perciformes and from seventy of the seventy-eight families included in the Percoidei (sensu Nelson, 2006). Also included are representatives of putative outgroups and sister groups of the Perciformes, including members of the orders Zeiformes, Beryciformes, Atheriniformes, Mugiliformes, Beloniformes, Synbranchiformes, Gasterosteiformes, Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes. In total, 279 RAG1 nucleotide sequences from percomorph fishes are presented in this investigation.

To test the relationships within this diverse group of fishes, I use a 1431 base coding region of the nuclear RAG1 gene to complete the data analyses. Total and individual codon position mutational site saturation, GC nucleotide content, base compositional stationarity, and synonymous codon usage were analyzed. Maximum parsimony analyses using the parsimony ratchet method and maximum likelihood analyses using the GARLI algorithm (Zwickl, 2006) were performed to investigate phylogenetic relationships. The maximum parsimony analyses included calculations of both bootstrap and jackknife nodal support. These calculations estimate levels of phylogenetic support at each node.

Maximum parsimony analyses function by selection of trees with the shortest length, i.e. those with the least number of evolutionary steps required to explain the dataset (Swofford et al., 1996). Neighbor-joining methods calculate phylogenetic trees by comparing pairwise evolutionary distances in related taxa (Gascuel and Steel, 2006). At slower rates of evolution, maximum parsimony algorithms outperform neighbor-joining calculations, whereas at faster rates, this is not always the case (Rosenberg and Kumar, 2001; Kuhner and Felsenstein, 1994). The RAG1 gene was selected for this study because of its slow evolutionary rate and therefore, maximum parsimony analyses are more appropriate than neighbor joining.

Minimum evolution methods estimate branch lengths of a tree using algorithms from pairwise distance data and the sum of branch lengths are then computed for possible tree topologies (Nei, 1996). The topology that has the smallest sum of branch lengths is the most "likely" tree (Nei, 1996). Minimum evolution methods were not chosen as a method of analysis because they calculate tree score from pairwise distances and not directly from the observed data which can cause a loss of information (Swofford et al., 1996). Distance methods can also be potentially misleading because they output a single final tree, eliminating the possibility to examine conflicting tree topologies (Harrison and Langdale, 2006).

Maximum likelihood methods for phylogenetic analyses were first developed by Felsenstein (1981) and are based on models of nucleotide substitution (Nei, 1996). Although computationally intensive, maximum likelihood methods are considered extremely robust for data analysis of this type (e.g. Kuhner and Felsenstein, 1994; Rosenberg and Kumar, 2001). Likelihood analyses often yield lower variances due to sampling error and they tend to outperform alternative methods such as maximum parsimony (Kunher and Felsenstein, 1994; Swofford et al., 1996).

The first chapter of this dissertation tests the monophyly of the order Perciformes and investigates the relationships among perciform suborders and their relationships to putative outgroups. Johnson (1993) hypothesized that the Perciformes is polyphyletic and provides morphological evidence for relationships between some of the putative suborders of this group. However, to date, very few efforts have been made to derive a phylogeny from molecular datasets that include representatives of all putative suborders proposed by Nelson (2006).

The second chapter of this dissertation investigates interfamilial relationships within the perciform suborder Percoidei. The suborder is undoubtedly polyphyletic (e.g. Johnson, 1993) and, therefore, other perciform groups are included in analyses to test alternative percoid affinities. Taxon sampling includes representatives of seventy of the seventy-eight families percoid proposed by Nelson (2006).

The third chapter of this dissertation uses RAG1 nucleotide data in combination with a mitochondrial gene, cytochrome B (cytB), to investigate relationships between families included in the putative superfamily Sparoidea and the monophyly of these families amongst numerous percoid outgroups. The superfamily Sparoidea consists of the families Nemipteridae, Lethrinidae, Sparidae and Centracanthidae (Carpenter and Johnson, 2002). Morphological evidence has given the phyletic sequence of Nemipteridae, Lethrinidae, Sparidae + Centracanthidae (Carpenter and Johnson, 2002). However, the previous study utilized only five outgroup taxa from three percoid families does not provide characterization of the superfamily within the context of extensive percoid outgroups.

The focus of this dissertation is to infer a phylogeny of putative percoid families within the Perciformes. This is accomplished by: a) providing a framework for relationships among suborders of the Perciformes, b) an investigation of interfamilial relationships among the numerous families of the Percoidei within the context of the Perciformes and its putative outgroups, and c) testing the evolutionary hypotheses of the superfamily Sparoidea using molecular data. The lack of any existing phylogenetic hypothesis for families within the suborder Percoidei and other perciform suborders is the most significant reason for completion of this work. A molecular approach using the RAG1 gene will provide a working hypothesis that tests the relationships of this large group of fishes. This work also helps test the phylogenetic applicability of the RAG1 gene for analyses at suborder and familial taxonomic levels. Levels of resolution found in this work test the limits of this gene for phylogenetic analyses and provide a framework and direction for future systematic investigations using this molecular marker.

CHAPTER II

A MOLECULAR ANALYSIS OF THE SUBORDERS OF THE PERCIFORMES

Introduction

Perciformes is the largest order of vertebrates with over 10,000 species (Nelson, 2006). These fishes are the dominant vertebrate group in the oceans as well as in many tropical and subtropical freshwater systems; they inhabit nearly every aquatic habitat on the planet (Nelson, 2006). This diverse group is classified within 160 families and 20 suborders and only limited attempts have been made to hypothesize their phylogenetic relationships, or the relationship of the order and its putative sister groups.

To investigate phylogenetic relationships within the Perciformes, the order must be studied within the context of the larger taxonomic groups in which it is placed. The order Perciformes has traditionally been classified within the Series Percomorpha and this Series is placed within the Acanthomorpha (e.g. Johnson and Patterson, 1993; Nelson, 2006). Rosen (1973) noted that the acanthomorph fishes were comprised of two major groups, the Superorder Paracanthopterygii and the Superorder Acanthopterygii. This relationship was supported by the morphological investigation of Stiassny (1986). Johnson and Patterson (1993) characterized the acanthomorpha as those fishes with the following characteristics: dorsal and anal fin-spines, rostral cartilage, the absence of median caudal cartilages, separate anterior and medial infracarinales, the dorsal limb of the posttemporal bound to the epioccipital, a distally ossified medial pelvic process, and the first centrum with anterior surface bearing distinct facets that articulate with the exoccipital condyles. This included the Lampriformes, Polymixiiformes, and the Superorder Acanthopterygii (Johnson and Patterson, 1993; Figure 1).

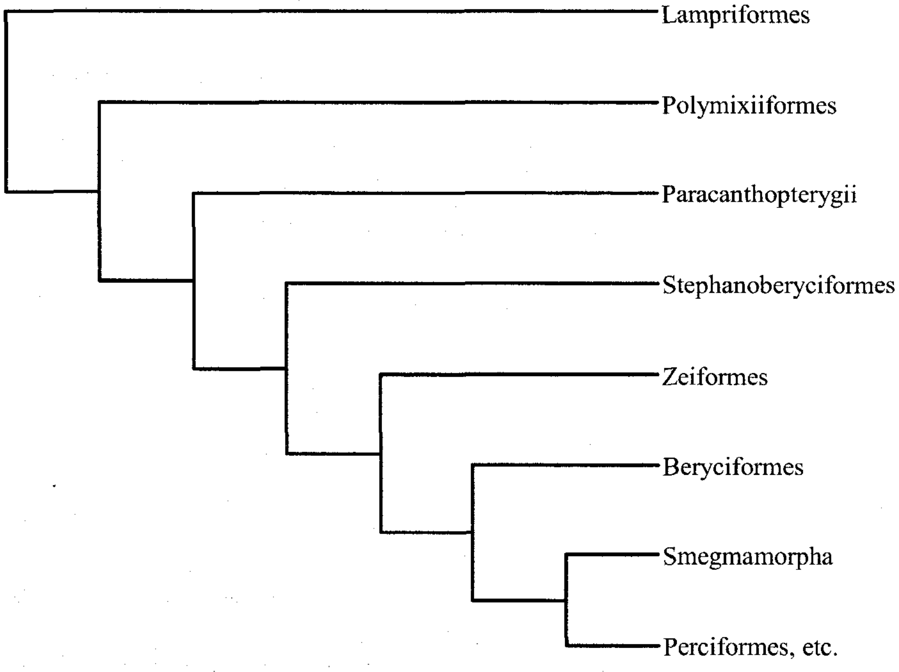


Fig. 1. Summary of acanthomorph interrelationships. Adapted from Johnson and Patterson (1993). Johnson and Patterson's (1993) "Perciformes, etc." included the Perciformes, Scorpaeniformes, and Pleuronectiformes. They did not discuss the Tetraodontiformes.

Series Percomorpha

The superorder Acanthopterygii may be divided into three Series of fishes, the Mugilomorpha, Atherinimorpha, and Percomorpha, for which different classifications have been proposed (Nelson, 2006). Of these groups, the Percomorpha are thought to be the most derived (Johnson and Patterson, 1993). Rosen (1973) proposed that the percomorphs comprise all members of the superorder Acanthopterygii except the series Atherinimorpha. This left his Percomorpha containing the beryciform fishes (Berycidae, Stephanoberycidae, Trachyichthyidae, etc.), Perciformes (including the Mugiloidei), Zeiformes, Lampridiformes, Gasterosteiformes, Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes. However, this classification did not provide any character-based evidence to distinguish the group from other members of the Acanthopterygii (Johnson and Patterson, 1993).

Lauder and Liem (1983) called Rosen's (1973) Percomorpha "ill-defined". Their subsequent revision of the Series utilizes over forty morphological characters, although they considered some to be poorly informative. Similar to Rosen's (1973) description of the Series, Lauder and Liem (1983) included all members of the Acanthopterygii minus the Atherinimorpha within the Percomorpha (Figure 2). They argued for future studies to clarify the relationships within this Series and stated that large weaknesses exist in the knowledge of relationships among members of the Percomorpha.

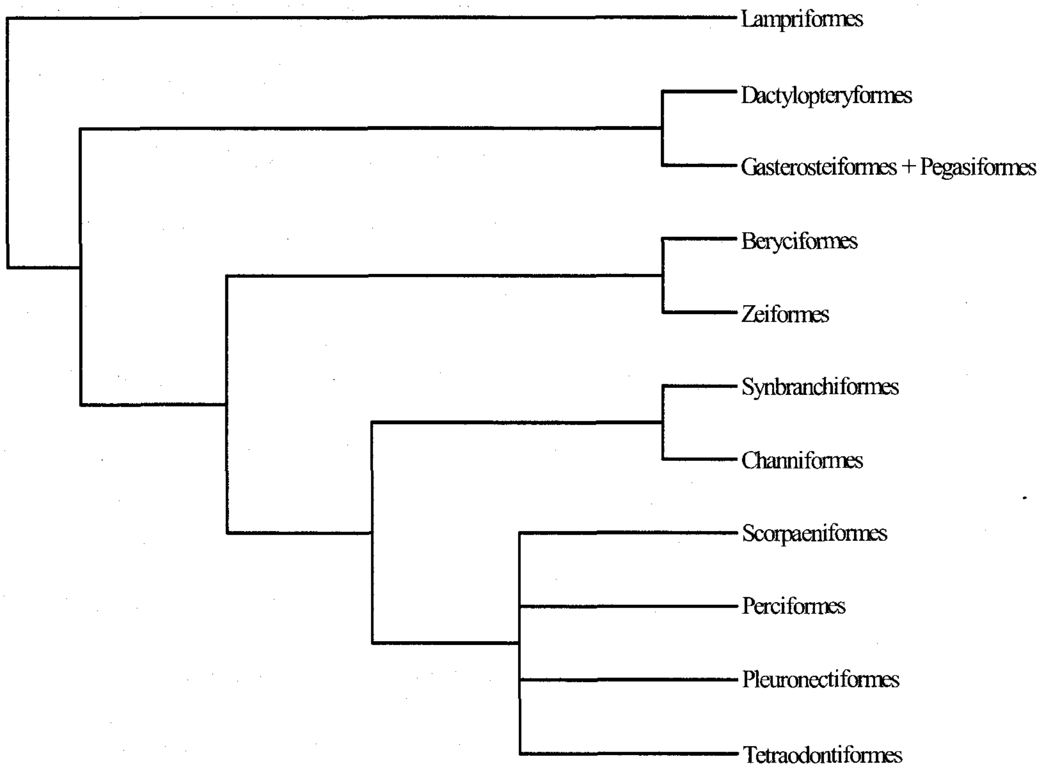


Fig. 2. Interrelationships of the percomorph Acanthopterygii. Adapted from Lauder and Liem (1983).

In an investigation of the pelvic girdle of acanthomorph fishes, Stiassny and Moore (1992) proposed alternative hypotheses that differ in what groups are placed within the Percomorpha. Their first hypothesis stated that the Percomorpha includes the Trachichthyiformes, Berycidae, Holocentridae, Zeiformes, Scorpaeniformes, and the Perciformes (Stiassny and Moore, 1992). Alternatively, they proposed that the percomorphs could include the Trachichthyiformes, Lampridiformes, Berycidae, Holocentridae, Zeiformes, Scorpaeniformes, and the Perciformes. Stiassny and Moore (1992) also noted that the characteristic pelvic girdle plan in "higher percomorphs" is consistent and is evidence for the monophyly of the group. They proposed that the Holocentridae be placed as the sister group to the higher percomorphs, which includes Zeiformes + Scorpaeniformes + Perciformes (Stiassny and Moore, 1992). They did not include the Synbranchiformes, Dactylopteriformes, Pleuronectiformes, and the Gasterosteiformes in their investigation because of the high level of specialization of pelvic girdle structure. Their dataset also does not include the Tetraodontiformes, but note in passing that they have a state III articulation of the pelvic girdle and thus infer they are "higher percomorphs."

Patterson (1964) used otolith morphology to describe a sister group relationship between the Zeiformes and Beryciformes. These taxa are considered the putative sister groups to the Perciformes and Patterson (1964) noted that perciform origins should be found among the Beryciformes. Lauder and Liem (1983) included the Perciformes, Scorpaeaniformes, Tetraodontiformes, Pleuronectiformes, Channiformes, and Synbranchiformes in the sister group to the Zeiform-Beryciform clade (Figure 2).

Springer and Orrell (2004) analyzed a morphological dataset of dorsal gill-arch muscles and skeletal components from over 200 species of fishes and found the Zeiformes as sister to the scorpaeniform family Rhamphocottidae and the trachinoid family Uranoscopidae. Johnson and Patterson (1993) found that the Zeiformes (minus the caproids) were not percomorphs, but they did form a monophyletic group. Previous work using the recombination activating gene 1 (RAG1) has shown the Zeiformes to be related to a group containing gadiform and percopsiform taxa, although the data had neither bootstrap nor Bremer support for this relationship (Holcroft, 2004). The relationship between gadiform and zeiform taxa is also seen in other molecular and total evidence studies (Chen et al., 2003; Wiley et al., 2000).

From their majority rule consensus tree, Springer and Orrell (2004) found a relationship between the beryciform family Holocentridae and the gadiform Ranicipitidae within a larger clade that includes Ophidiiformes, Stephanoberyciformes, and the Polymixiformes. Johnson and Patterson (1993) did not find support for a zeiform-beryciform relationship (e.g. Lauder and Liem, 1983), but instead proposed that the Zeiformes were the basal group of the Acanthopterygii and the beryciform fishes were sister to their redefined Percomorpha (Figure 1).

Johnson and Patterson (1993) redefined the Percomorpha to include the Perciformes and their immediate relatives (the Scorpaeniformes, Dactylopteriformes, Pleuronectiformes, and Tetraodontiformes) plus a newly described group, the Smegmamorpha, which includes the Synbranchiformes, Gasterosteiformes, Mugiloidei, Atherinomorpha, and *Elassoma*. Their Percomorpha is based on eight morphological characters: 1) possession of rod-like interarcual cartilage, 2) absence of the second ural centrum, 3) five or fewer hypurals, 4) pelvic fins with fewer than six soft rays, 5) transforming ctenoid scales, 6) absence of free pelvic radials, 7) point of origin of all but the first two epineurals ventrally, and 8) seventeen principal caudal-fin rays in a I,8,8,I pattern. The defining character that separates the Smegmamorpha from the remainder of the Percomorpha is that their first epineural originates on a transverse parapophysis (Johnson and Patterson, 1993). However, recent morphological and molecular studies describe evidence against the monophyly of the Smegmamorpha. Springer and Orrell (2004) found that 56 muscular and skeletal characters from 168 taxonomic groups of acanthomorph fishes did not support a monophyletic Smegmamorpha. Molecular and combined morphological and molecular studies also refute the monophyly of the Smegmamorpha (Miya et al., 2003; Chen et al., 2003; Wiley et al., 2000). Therefore, the relationship of the Perciformes to these taxa remains unresolved.

Nelson (2006) presented a different classification scheme for the Percomorpha. He included the Stephanoberyciformes, Beryciformes, Zeiformes, Gasterosteiformes, Synbranchiformes, Scorpaeniformes, Perciformes, Pleuronectiformes, and Tetraodontiformes in the Percomorpha, whereas Johnson and Patterson (1993) did not include the first three orders in their Percomorpha. Smith and Craig (2007) found that Nelson's (2006) definition of the Percomorpha was too narrowly defined and that it must be expanded or restructured for the group to maintain cladistic significance. More specifically, they note a need for broad taxonomic sampling among acanthomorph lineages and comprehensive datasets to resolve percomorph relationships. The remainder of this dissertation will use the definition provided by Johnson and Patterson (1993) when describing the Series Percomorpha.

Order Perciformes

The largest order in the Series Percomorpha is the Perciformes, which contains one-third of all extant fishes in 20 different suborders (Nelson, 2006). Few systematic investigations have been performed on this large group of fishes at the suborder level and its limits and evolutionary relationships are poorly understood. Lauder and Liem (1983) described the order as polyphyletic and an "unnatural assemblage". Johnson and Patterson (1993) noted that the Scorpaeniformes and Pleuronectiformes may be nested within the Perciformes. Nelson (2006) noted that the Scorpaeniformes, Pleuronectiformes, and Tetraodontiformes might be derivatives of the Perciformes. Smith and Craig (2007) found that there was no phylogenetic difference between the Percoidei, the Perciformes, and the Percomorpha (sensu Johnson and Patterson) because their results show that the largest suborder of the Perciformes, the Percoidei, was polyphyletic and found throughout other Percomorph lineages.

The evolutionary relationships of the suborders of the Perciformes are poorly understood. Each of the twenty putative suborders proposed by Nelson (2006) and others proposed in the literature will be described in the following paragraphs (Table 1).

The largest of the perciform suborders is the Percoidei, containing 79 families, 549 genera, and over 3,100 species (Nelson, 2006). Johnson (1984, 1993) called this suborder undoubtedly polyphyletic and stated that there have been no serious attempts to diagnose or refute its monophyly. This suborder will be examined in detail in the second chapter of this dissertation.

Johnson (1993) proposed recognition of the suborder Carangoidei that contained the families Nematistiidae, Carangidae, Coryphaenidae, Rachycentridae, and

Table 1
Putative suborders of perciform fishes. Adapted from Nelson (2006) and Johnson (1993)

Perciform suborder
Percoidei
Carangoidei
Elassomatoidei
Labroidei
Zoarcoidei
Notothenioidei
Trachinoidei
Pholidichthyoidei
Blennioidei
Icosteoidei
Gobiesocoidei
Callionymoidei
Gobioidei
Kurtoidei
Acanthuroidei
Scombrolabracoidei
Scombroidei
Stromateoidei
Anabantoidei
Channoidei
Caproidei

Echeneidae. These families, noted by others to be in the Suborder Percoidei (e.g. Nelson, 2006), all possess an anterior extension of the anterior nasal canal surrounded by one or two tubular ossifications (Johnson, 1993). Since Nelson (2006) classified these families as members of the suborder Percoidei, they will be discussed in the next chapter of this dissertation.

The Elassomatoidei (pygmy sunfishes) is a problematic suborder sometimes placed within the Perciformes (Nelson, 2006). Previous studies have placed it in or closely related to the percoid family Centrarchidae (e.g. Nelson, 1984), while others have placed the Elassomatoidei as sister to the Gasterosteidae (sticklebacks and tubesnouts; Johnson and Springer, 1997; Springer and Orrell, 2004). Johnson and Patterson (1993) removed the elassomatoids from the Perciformes and included them in the Smegmamorpha. Wiley et al. (2000) did not clarify the precise placement of *Elassoma*, although it is presented in an unresolved clade that contains the percoid family Centrarchidae and other percomorph taxa. These authors stated that although their research failed to resolve the position of the Elassomatoidei among the percomorphs, they suggested that *Elassoma* are not centrarchids. Recent molecular data places the elassomatoids as sister to a group containing both tetraodontiform and perciform taxa (Holcroft, 2004). Smith and Wheeler (2006) suggested the Elassomatoidei were sister to two synbranchiform taxa.

The suborder Labroidei contains six families of fishes, including the cichlids, damselfishes, surfperches, wrasses, and parrotfishes. This large suborder represents approximately fifteen percent of all extant fishes (Streelman and Karl, 1997; Nelson, 2006). Stiassny and Jensen (1987) supported "beyond any reasonable doubt" the monophyly of this suborder based on their analysis of the labroid pharyngeal jaw apparatus. Johonson (1993) stated that other skeletal elements provide no support for the monophyly of the Labroidei with the exception of the pharyngeal jaw apparatus. Streelman and Karl (1997) presented molecular evidence questioning the monophyly of the suborder and noted that the pharyngeal jaw apparatus modifications may have evolved independently multiple times, making it a poor evolutionary marker for this group. Clements et al. (2004) described the labrid tribe Odacini and also questioned the monophyly of the Labroidei as defined by Stiassny and Jensen (1987). Springer and Orrell (2004) postulated that the Labroidei are paraphyletic without the inclusion of the Pholidichthyidae. Smith and Craig (2007) find the Labroidei to be polyphyletic in their molecular analysis, although their investigation included only two taxa from two families of the suborder.

The Zoarcoidei includes nine families of marine fishes and lacks diagnostic characters to isolate it from other blennioid perciforms, leaving its monophyly uncertain (Nelson, 2006). Proposed sister groups to this suborder include the Cottoidei (Chen et al., 2003) and the Notothenioidei (Nelson, 2006). Springer and Orrell (2004) found this suborder to be polyphyletic and proposed its members to have affinities to a number of acanthomorph taxa. Smith and Wheeler (2006) grouped the Zoarcoidei within a clade of scorpaeniform, gasterosteiform, and trachinoid taxa. Smith and Craig (2007) find a monophyletic Zoarcoidei sister to a clade containing trachinoid and scorpaeniform taxa.

The members of the suborder Notothenioidei are the predominant fishes of the Southern Ocean and Antarctic waters (Near et al., 2004). The suborder is comprised of six families of fishes most of which are confined to depths of less than 1000 meters and have evolved physiological mechanisms to adapt to subzero (to -2°C) temperatures of their environment (Lecointre et al., 1997). Recent studies using mitochondrial DNA sequence data corroborate morphological data demonstrating the monophyly of this suborder (Near et al., 2004). However, other investigations have shown no support for a monophyletic Notothenioidei (Lecointre et al., 1997). Potential sister groups include the Blennioidei (Gosline, 1968), the Zoarcoidei, Trachinoidei, or Callionymoidei (Springer and Orrell, 2004; Nelson, 2006) and the percoid family Percidae (Chen et al., 2003).

The suborder Trachinoidei contains twelve families of marine fishes including the stargazers and sandperches (Nelson, 2006). Pietsch (1989) and Pietsch and Zabetian (1990) found support for the monophyly of the Trachinoidei. However, Johnson (1993) and Mooi and Johnson (1997) refuted the monophyly of the suborder. Chen et al. (2003) found the Trachinoidei to be polyphyletic using mitochondrial and nuclear gene evidence and stated that future work is needed to define the relationships of this suborder. Smith and Wheeler (2006) also described the Trachinoidei as polyphyletic. Smith and Craig (2007) found a polyphyletic Trachinoidei and propose reclassification of the group since the Trachininae were nested within the family Serranidae.

The suborder Pholidichthyoidei is enigmatic in its placement among the perciform suborders. It is comprised of two species in a single genus and family (Nelson, 2006). These fishes have previously been placed in the Trachinoidei (Nelson, 1994). The suborder has also been associated with the Blennioidei and the Labroidei in recent investigations (Springer and Johnson, 2004; Springer and Orrell, 2004). Springer and Orrell (2004) suggested that the Labroidei would be a monophyletic group with the inclusion of the Pholidichthyoidei. Smith and Wheeler (2006) found this group as sister to the sygnathiform *Aulostomus maculatus*. Smith and Craig (2007) place the Pholidichthyoidei sister to the atheriniform *Rheocles wrightae* and these sister to the percoid family Plesiopidae.

The blennies, suborder Blennioidei, are hypothesized to be a monophyletic group that includes six families of marine fishes that are circumglobally distributed in temperate and tropical systems (Springer, 1993). Previous studies have used osteological evidence to define the group and the lack of a neural spine on the first few vertebrae supports the monophyly of the suborder (Springer, 1993; Johnson, 1993). Springer and Orrell (2004) found the Blennioidei to be monophyletic and sister to the perciform suborder Gobiesocoidei. Other potential sister groups of the Blennioidei are the percoid families Opistognathidae, Pseudochromidae, and Grammatidae (Smith and Wheeler, 2006; Smith and Craig, 2007).

The monotypic suborder Icosteoidei contains the ragfish, *Icosteus aenigmaticus* (Nelson, 2006). This fish inhabits the waters of the North Pacific, lacks pelvic fins as an adult, and has a largely uncalcified cartilaginous skeleton (Nelson, 2006). Some ichthyologists (e.g. Gosline, 1971) have suggested this fish be placed in its own order. Springer and Johnson (2004) were inconclusive in the placement of this fish (see Nelson, 2006), leaving it as either a pre-percomorph or a perciform suborder. Springer and Orrell (2004) described this fish in their pre-perciform group, sister to a group that contains, among others, four of the five stephanoberyciform fishes in their study and other taxa. Smith and Wheeler (2006) found the Icosteoidei sister to a group that contains stromateoid, trachinoid, percoid and scombroid taxa. Smith and Craig (2007) placed the Icosteoidei sister to the Stromateoidei.

The placement of the clingfishes, suborder Gobiesocoidei, within the Perciformes remains uncertain. Mattei (1991) proposed that the gobiesocoids were similar to the Batrachoidiformes based on the structure of their spermatozoa. Springer and Orrell (2004) and Nelson (2006) proposed that the gobiesocoids are a sister group to the Callionymoidei. Springer and Orrell (2004) also postulated a relationship between the Gobiesocoidei, the Callionymoidei, the Dactylopteridae, and the Blennioidei, calling this assemblage the Benthomorpha, although they questioned the inclusion of the Dactylopteridae in this group. Another potential sister group is the labroid Pomacentridae (Smith and Wheeler, 2006).

The suborder Callionymoidei contains two families, the Callionymidae and the Draconettidae (Nelson, 2006). Diferent hypotheses exist on their relationships to other groups of fishes. Potential sister groups of the callionymoids include the Gobiesocoidei and the Notothenioidei (Springer and Orrell, 2004; Nelson, 2006). Other possibilities include the blennies or gobies (Lauder and Liem, 1983; Winterbottom, 1993). Smith and Wheeler's (2006) results showed that this group is paraphyletic without the inclusion of the Batrachoidiformes.

The Gobioidei are recognized to contain nine families of marine fishes and over 2,200 species (Nelson, 2006). Relationships to other groups are poorly understood. However, some evidence supports an affinity with callionymoids, trachinoids, or the scorpaeniform hoplichthyids (Nelson, 2006; Winterbottom, 1993). Smith and Wheeler (2006) presented evidence that the sister group of the Gobioidei is the percoid family Apogonidae.

The nurseryfishes, suborder Kurtoidei, are comprised of two anatomically unique species in a single genus (Nelson, 2006). These fishes inhabit fresh and estuarine waters in the Australian and Indo-Malay regions (Berra, 2001; Nelson, 2006). Male nurseryfishes possess a hook extending from their supraoccipital crest that is reported to carry eggs (Berra and Neira, 2003; Berra, 2003). Nurseryfish were thought to be related to the Beryciformes because of a median ossification of the orbital roof that was interpreted as an orbitosphenoid (Tominaga, 1968). This bone is absent in all members of the Perciformes. Tominaga (1968) also hypothesized the kurtids were related to the percoid family Pempheridae. Johnson (1993) rejected the identity of Tominaga's "orbitosphenoid", noting that it is an ossified interorbital septum and that nothing about the Kurtoidei prevents it from being included in the suborder Percoidei. Johnson (1993) further hypothesized a kurtid relationship to the family Apogonidae (suborder Percoidei) based on gill arch configurations and possession of sensory papillae on the head and body. Springer and Orrell (2004) showed the Kurtoidei as sister to a large group of percomorph fishes (see clade C, node 52; pg. 246). Smith and Wheeler (2006) grouped the Kurtoidei sister to a clade containing the Apogonidae and the Gobioidei. Smith and Craig (2007) found the Kurtoidei sister to a clade containing the percoid family Apogonidae.

The Acanthuroidei includes approximately 125 species of primarily marine tropical and subtropical fishes (Tang et al., 1999). Morphological studies have included the Siganidae, Zanclidae, Acanthuridae, Ephippidae, Scatophagidae, and the Luvaridae in this suborder (Tyler et al., 1989; Johnson and Washington, 1987; Winterbottom, 1993; Tang et al., 1999). Molecular evidence that included mitochondrial 12S and 16S

DNA sequences also placed the Louvaridae in the Acanthuroidei (Tang et al., 1999). The Tetraodontiformes are a possible sister group to the acanthuroids, making them a possible link between the Perciformes and the Tetraodontiformes (Lauder and Liem, 1983; Holcroft, 2004). Another proposed sister group to the acanthuroids is the percoid family Leiognathidae (Springer and Orrell, 2004). Smith and Wheeler (2006) found the suborder Acanthuroidei to be polyphyletic.

The suborder Scombrolabracoidei contains a single species, *Scombrolabrax heterolepis*. Sister groups of this fish are unclear, but some suggest it is a primitive sister species to the Scombroidei (Johnson, 1986; Nelson, 2006). Springer and Orrell (2004) did not find the Scombrolabracoidei sister to the scombroid taxa and *Scombrolabrax* was grouped in a polytomy with other percoids including serranids, bathyclupeids, and sciaenids. Smith and Wheeler (2006) described *Scombrolabrax* in a clade sister to the stromateoid *Peprilus alepidotus*.

The Scombroidei consists of six families of marine families, including the barracudas, tunas, and billfishes (Nelson, 2006). Johnson (1986) excluded the Scombrolabracoidei from this suborder, but placed it as a primitive sister group. He also included the Sphyraenidae in the Scombroidei as a sister to all other scombroid families. Other scombroid affinities include the billfishes (Collette et al., 1984; Block, 1991). Recent molecular evidence excluded the Sphyraenidae from this suborder and placed the barracudas with other percomorph taxa including the carangids, echeneids, menids, polynemids, centropomids, and pleuronectiforms (Chen et al., 2003). Springer and Orrell (2004) found the Scombridae sister to a group containing, among others, the Sphyraenidae and the percoid Polynemidae. Smith and Wheeler (2006) presented evidence that the Scombroidei, as defined by Nelson (2006), was a polyphyletic assemblage, with the billfishes and barracudas nested in a completely different clade than the remaining scombroid groups.

The Stromateoidei includes six families of fishes from warm temperate and tropical marine waters (Nelson, 2006). Lauder and Liem (1983) considered the group unquestionably monophyletic. Proposed relationships of this suborder include a number of percoid families (Haedrich, 1967; Johnson and Fritzsche, 1989; Johnson, 1993). In a morphological investigation, this suborder was found to be polyphyletic and sister to various acanthomorph groups, including the percoid Ambassidae (Springer and Orrell, 2004). Chen et al. (2003) showed this suborder in differing relationships with their separate and combined datasets, although all analyses confirmed an affinity to scombroid and trachinoid taxa. Smith and Wheeler (2006) also showed this suborder to have an affinity with scombroid taxa, but also included a relationship with trachinoids, arripids, and pomatomids. Smith and Craig (2007) included a single stromateoid in their molecular investigation and found it sister to the monotypic suborder Icosteoidei.

Members of the Anabantoidei include three families (Helostomatidae, Osphronemidae, Anabantidae) and approximately 140 species of fishes, all of which possess a suprabranchial organ (Nelson, 2006; Ruber et al., 2004b; Ruber et al., 2006). The anabantoids primarily inhabit the freshwater regions of Africa and southern Asia (Berra, 2001). Lauder and Liem (1983) noted that the families in this suborder comprise a monophyletic group. Potential sister groups to the anabantoids include the snakeheads (suborder Channoidei) and the percoid families Nandidae and Badidae (Springer and Orrell, 2004). Britz (2003) noted that the closest relatives appear to be the channoids and these two groups form a larger assemblage with the badids and nandids. Springer and Orrell (2004) also suggested that the anabantomorphs are polyphyletic without the inclusion of the Percesoces (atherinomorphs + mugilomorphs), although they have no suggestions as to the group's (including the percoid families Nandidae and Badidae) nearest relatives. Smith and Wheeler (2006) showed the anabantoids as sister to the suborder Channoidei. Smith and Craig (2007) found the Anabantoidei sister to the clade containing the Apogonidae and Kurtoidei.

The suborder Channoidei includes a single family (Channidae) and its constituents inhabit freshwater regions of Africa and southern Asia (Nelson, 2006). Lauder and Liem (1983) proposed that the Channoidei is a separate order, a primitive sister to the Synbranchiformes. Other potential sister groups of the snakeheads are the suborder Anabantoidei and the percoid family Nandidae (Badinae + Nandinae; Nelson, 2006; Chen et al., 2003; Springer and Orrell, 2004; Smith and Wheeler, 2006).

The suborder Caproidei is also problematic among acanthomorph taxa. Johnson and Patterson (1993) placed it in the Percomorpha and noted that it was not related to the Zeiformes. Bannikov (1991) proposed that the group was related to the Acanthuroidei. Stiassny and Moore (1992) showed that *Capros* was sister to perciform taxa, separated from the Zeiformes by all beryciform taxa included in their investigation. Holcroft (2004) found *Antigonia capros* sister to a group containing the acanthuroid *Siganus* and the lophiuroid *Lophius*. Springer and Orrell (2004) found the Caproidei to be polyphyletic, with *Capros* sister to acanthuroids and *Antigonia* sister to the tetraodontiform family Triacanthodidae. Smith and Wheeler (2006) found the Caproidei as sister to the percoid family Sparidae.

The goal of this study is to investigate the phylogenetic relationships of the suborders placed within the Perciformes using a molecular genetic dataset. The level of phylogenetic resolution that DNA sequence data can provide depends on the molecular markers chosen to reconstruct relationships and the level of taxonomic resolution desired. For example, studies investigating Order level relationships should not necessarily use the same molecular markers as species or population level studies. Differences in levels of saturation, rate of variation between lineages, and compositional biases can result in the inefficiency of a gene to determine deeper level phylogenetic relationships (Meyer, 1994; Brocchieri, 2001). Many studies have relied on mitochondrial gene sequences for phylogenetic inference. However, rates of change in mitochondrial DNA may be too rapid to determine higher level relationships (eg. Hillis and Huelsenbeck, 1992; Lydeard and Roe, 1997; Orrell and Carpenter, 2004). To elucidate relationships at deeper phylogenetic levels, slower evolving nuclear exons hold promise (Groth and Barrowclough, 1999).

Materials and Methods

Taxon Sampling

In order to investigate suborder level relationships of the Perciformes a broad sampling of members of the series Percomorpha and its outgroups was necessary. Therefore, this study included representatives of each putative perciform suborder (sensu Nelson, 2006), and members of the Orders Scorpaeniformes, Pleuronectiformes, Tetraodontiformes, Beloniformes, Atheriniformes, Mugiliformes, Gasterosteiformes, Synbranchiformes, Zeiformes, and Beryciformes (Table 2).

Table 2
Taxa examined in this investigation following the classification of Nelson (2006). RAG-Megadataset sequences courtesy of Dr. Guillermo Orti

Order	Suborder	Family	Genus-species	Voucher Info
Zeiformes	Cyttoidei	Cyttidae	*Cyttus traversi*	AY308779
	Zeioidei	Grammicolepididae	*Grammicolepis brachiusculus*	AY308780
		Oreosomatidae	*Allocyttus verrucosus*	AY308781
		Zeidae	*Zenopsis conchifera*	AY308778
Beryciformes	Holocentroidei	Holocentridae	*Sargocentron vexillarium*	AY308770
		Holocentridae	*Sargocentron punctatissimum*	AY430223
		Holocentridae	*Sargocentron cornutum*	FMNH-BUS03-010
Mugiliformes	Mugiloidei	Mugilidae	*Mugil curema*	AY308783
Atheriniformes	Atherinoidei	Atherinidae	*Menidia menidia*	AY430225
Beloniformes	Belonoidei	Scomberesocidae	*Scomberesox saurus*	AY308771
Gasterosteiformes	Gasterosteoidei	Gasterosteidae	*Gasterosteus aculeatus*	RAG-Megadataset
		Gasterosteidae	*Spinachia spinachia*	RAG-Megadataset
Synbranchiformes	Mastacembeloidei	Mastecembelidae	*Mastacembelus armatus*	RAG-Megadataset
	Synbranchoidei	Synbranchidae	*Monopterus albus*	RAG-Megadataset
Scorpaeniformes	Platycephaloidei	Platycephalidae	*Grammoplites scaber*	ODU-3116
	Scorpaenoidei	Scorpaenidae	*Pterois lunulata*	No voucher
		Triglidae	*Peristedion miniatum*	AY308774
Perciformes	Anabantoidei	Helostomatidae	*Helostoma temminkii*	ODU-3185
		Helostomatidae	*Helostoma temminkii*	AY763779
		Osphronemidae	*Trichogaster trichopterus*	ODU-3186
		Osphronemidae	*Betta splendens*	AF519728
		Osphronemidae	*Trichogaster leerii*	AF519734
		Osphronemidae	*Trichogaster chuna*	AF519735
		Osphronemidae	*Trichopsis vittata*	AF519736
		Osphronemidae	*Macropodus opercularis*	AF519737
		Osphronemidae	*Pseudosphromenus cupanus*	AF519738
		Osphronemidae	*Malpulutta kretseri*	AF519739
		Osphronemidae	*Parosphromenus deissneri*	AF519740
	Blennioidei	Blenniidae	*Blennius normani*	ODU-3170

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Tripterygiidae	*Helcogramma sp.*	FMNH-BUS03-312
	Callionymoidei	Callionymidae	*Synchiropus ocellatus*	AMNH, not processed yet
		Callionymidae	*Callionymus sp.*	FMNH-BUS03-285
	Channoidei	Channidae	*Channa marulia*	AY763787
		Channidae	*Parachanna obscura*	AY763788
		Channidae	*Channa sp.*	FMNH-BUS03-290
		Channidae	*Channa sp.*	FMNH-BUS03-290
	Elassomatoidei	Elassomatidae	*Elassoma evergladei*	AY308784
		Elassomatidae	*Elassoma zonatum*	RAG-Megadataset
	Gobiesocoidei	Gobiesocidae	*Gobiesox strumosus*	RAG-Megadataset
		Gobiesocidae	*Discotrema crinophilia*	FMNH-BUS03-313
	Gobioidei	Gobiidae	*Amblygobius hectori*	FMNH-BUS03-143
		Microdesmidae	*Ptereleotris zebra*	ODU-3187
	Icosteoidei	Icosteidae	*Icosteus aenigmaticus*	SIO-99-95
	Kurtoidei	Kurtidae	*Kurtus gulliveri*	ODU-3167
	Labroidei	Cichlidae	*Amphilophus rhytisma*	AY208616
		Embiotocidae	*Embiotoca lateralis*	AY208615
		Labridae	*Coris julis*	ODU-3171
		Labridae	*Halichoeres melanurus*	AY208617
		Pomacentridae	*Chromis atripes*	AY208633
		Pomacentridae	*Chrysiptera annulata*	AY208645
		Pomacentridae	*Parma oligolepis*	AY208662
		Pomacentridae	*Plectroglyphidodon dickii*	AY208663
		Pomacentridae	*Pomacentrus nigromanus*	AY208671
		Pomacentridae	*Stegastes planifrons*	AY208673
	Notothenioidei	Nototheniidae	*Notothenia coriiceps*	C. Amsler, collector/ voucher
	Percoidei	Acropomatidae	*Synagrops bellus*	SIO-01-131
		Ambassidae	*Ambassis agrammus*	ODU-3177
		Ambassidae	*Denariusa bandata*	ODU-3179

Table 2 (*continued*)

Order	Suborder	Family	Genus-species	Voucher Info
		Ambassidae	*Ambassis macleayi*	P.J. Unmack, collector/ voucher
		Aplodactylidae	*Aplodactylus arctidens*	C.P. Burridge, collector/ voucher
		Apogonidae	*Glossamia aprion*	RAG-Megadataset
		Apogonidae	*Cheilodipterus macrodon*	No voucher
		Apogonidae	*Apogon aureus*	ODU-3084
		Arripidae	*Arripis trutta*	CSIRO-H-3856-01
		Arripidae	*Arripis truttacea*	CSIRO-H-4388-03
		Banjosidae	*Banjos banjos*	MUFS-23047
		Bramidae	*Brama orcini*	FMNH-BUS03-299
		Caesionidae	*Gymnocaesio gymnoptera*	ODU-3046
		Caesionidae	*Caesio lunaris*	ODU-3084
		Callanthiidae	*Callanthias australis*	AMS I.43550003
		Carangidae	*Alectis alexandrinus*	ODU-3168
		Carangidae	*Caranx hippos*	ODU-3169
		Carangidae	*Decapterus macrosoma*	Photo voucher, KEC
		Caristiidae	*Caristius sp.*	NMV A 22138
		Centracanthidae	*Spicara alta*	ODU-2811
		Centracanthidae	*Centracanthus cirrus*	ODU-3133
		Centracanthidae	*Spicara maena*	ODU-3134
		Centracanthidae	*Spicara flexuosa*	ODU-3148
		Centrarchidae	*Lepomis macrochirus*	ODU-3180
		Centrarchidae	*Micropterus salmoides*	ODU-3181
		Centrarchidae	*Lepomis cyanellus*	RAG-Megadataset
		Centropomidae	*Centropomus viridus*	SIO-01-37
		Cepolidae	*Acanthocepola krustensternii*	ODU-3088
		Cepolidae	*Cepola macrophthalma*	Mahon, photo voucher
		Chaetodontidae	*Chaetodon striatus*	AY308775
		Chaetodontidae	*Hemitaurichtys polylepis*	FMNH-BUS03-282
		Cheilodactylidae	*Nemadactylus monodactylus*	ODU-3200

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Cheilodactylidae	*Chirodactylus grandis*	ODU-3199
		Chironemidae	*Chironemus marmoratus*	AMS I.41268.001
		Cirrhitidae	*Cirrhitus pinnulatus*	FMNH-BUS03-192
		Coryphaenidae	*Coryphaena hippurus*	D. Reed, collector/ voucher
		Coryphaenidae	*Coryphaena sp*	RAG-Megadataset
		Dichistiidae	*Dichistius capensis*	Alan Connell, collector/ voucher
		Dinolestidae	*Dinolestes lewini*	I.41084034
		Dinopercidae	*Dinoperca petersi*	RAG-Megadataset
		Drepaneidae	*Drepane punctata*	AY308772
		Echeneidae	*Echeneis naucrates*	ODU-3184
		Echeneidae	*Remora australis*	No voucher
		Emmelichthyidae	*Erythrocles monodi*	ODU-3023
		Enoplosidae	*Enoplosus armatus*	NMV A 25195-001
		Epigonidae	*Epigonus telescopus*	NMV A 25142-009
		Gerreidae	*Gerres argyreus*	ODU-3120
		Gerreidae	*Diapterus auratus*	RAG-Megadataset
		Gerreidae	*Eucinostomus gula*	RAG-Megadataset
		Centracanthidae	*Centracanthus cirrus*	ODU-3133
		Centracanthidae	*Spicara maena*	ODU-3134
		Centracanthidae	*Spicara flexuosa*	ODU-3148
		Centrarchidae	*Lepomis macrochirus*	ODU-3180
		Centrarchidae	*Micropterus salmoides*	ODU-3181
		Centrarchidae	*Lepomis cyanellus*	RAG-Megadataset
		Centropomidae	*Centropomus viridus*	SIO-01-37
		Cepolidae	*Acanthocepola krustensternii*	ODU-3088
		Cepolidae	*Cepola macrophthalma*	Mahon, photo voucher
		Chaetodontidae	*Chaetodon striatus*	AY308775
		Chaetodontidae	*Hemitaurichtys polylepis*	FMNH-BUS03-282

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Cheilodactylidae	*Nemadactylus monodactylus*	ODU-3200
		Cheilodactylidae	*Chirodactylus grandis*	ODU-3199
		Chironemidae	*Chironemus marmoratus*	AMS I.41268.001
		Cirrhitidae	*Paracirrhites arcatus*	ODU-3189
		Cirrhitidae	*Cirrhitus pinnulatus*	FMNH-BUS03-192
		Coryphaenidae	*Coryphaena hippurus*	D. Reed, collector/ voucher
		Coryphaenidae	*Coryphaena sp*	RAG-Megadataset
		Dichistiidae	*Dichistius capensis*	Alan Connell, collector/ voucher
		Dinolestidae	*Dinolestes lewini*	I.41084034
		Dinopercidae	*Dinoperca petersi*	RAG-Megadataset
		Drepaneidae	*Drepane punctata*	AY308772
		Echeneidae	*Echeneis naucrates*	ODU-3184
		Echeneidae	*Remora australis*	No voucher
		Emmelichthyidae	*Erythrocles monodi*	ODU-3023
		Enoplosidae	*Enoplosus armatus*	NMV A 25195-001
		Epigonidae	*Epigonus telescopus*	NMV A 25142-009
		Gerreidae	*Gerres argyreus*	ODU-3120
		Gerreidae	*Diapterus auratus*	RAG-Megadataset
		Gerreidae	*Eucinostomus gula*	RAG-Megadataset
		Gerreidae	*Diapterus peruvianus*	No voucher
		Glaucosomatidae	*Glaucosoma herbriacum*	AMNH, not processed yet
		Glaucosomatidae	*Glaucosoma buergeri*	ODU-3192
		Grammatidae	*Gramma loreto*	USNM-Saba
		Haemulidae	*Anisotremus virginicus*	ODU-2893
		Haemulidae	*Brachydeuterus auritus*	ODU-3198
		Haemulidae	*Haemulon aurolineatum*	RAG-Megadataset

Table 2 (*continued*)

Order	Suborder	Family	Genus-species	Voucher Info
		Haemulidae	*Haemulon plumerii*	RAG-Megadataset
		Haemulidae	*Plectorhinchus macrolepis*	Mahon, photo voucher
		Inermiidae	*Inermia vittata*	KU T-329
		Kuhliidae	*Kuhlia mugil*	USNM 336646
		Kuhliidae	*Kuhlia rupestris*	P.J. Unmack, collector/ voucher
		Kyphosidae	*Kyphosis incisor*	KU T-81
		Kyphosidae	*Microcanthus strigatus*	AMS I.41265.002
		Kyphosidae	*Neoscorpis lithophilus*	Alan Connell, collector/ voucher
		Kyphosidae	*Neoscorpis lithophilus*	Alan Connell, collector/ voucher
		Latidae	*Lates calcarifer*	ODU-3197
		Latridae	*Latridopsis forsteri*	CSIRO-H-3774-01
		Latridae	*Latris lineata*	CSIRO-H-4944-01
		Leiognathidae	*Gazza minuta*	ODU-3094
		Leiognathidae	*Leiognathus stercorarius*	ODU-3103
		Leiognathidae	*Leiognathus stercorarius*	ODU-3103
		Leiognathidae	*Leiognathus sp.*	FMNH-BUS03-215
		Lethrinidae	*Lethrinus harak*	ODU-3042
		Lethrinidae	*Lethrinus obsoletus*	ODU-3043
		Lethrinidae	*Lethrinus lentjan*	ODU-3060
		Lethrinidae	*Lethrinus olivaceus*	ODU-3190
		Lethrinidae	*Gymnocranius elongatus*	ODU-3202
		Lethrinidae	*Lethrinus xanthochilus*	USNM 349306
		Lethrinidae	*Gnathodentex aureolineatus*	FMNH-BUS03-040
		Haemulidae	*Plectorhinchus macrolepis*	Mahon, photo voucher
		Inermiidae	*Inermia vittata*	KU T-329
		Kuhliidae	*Kuhlia mugil*	USNM 336646
		Kuhliidae	*Kuhlia rupestris*	P.J. Unmack, collector/ voucher
		Kyphosidae	*Kyphosis incisor*	KU T-81
		Kyphosidae	*Microcanthus strigatus*	AMS I.41265.002

Table 2 (*continued*)

Order	Suborder	Family	Genus-species	Voucher Info
		Kyphosidae	*Neoscorpis lithophilus*	Alan Connell, collector/ voucher
		Kyphosidae	*Neoscorpis lithophilus*	Alan Connell, collector/ voucher
		Latidae	*Lates calcarifer*	ODU-3197
		Latridae	*Latridopsis forsteri*	CSIRO-H-3774-01
		Lethrinidae	*Gnathodentex aureolineatus*	FMNH-BUS03-056
		Lethrinidae	*Lethrinus atkinsoni*	FMNH-BUS03-170
		Lethrinidae	*Lethrinus atlanticus*	ODU-3204
		Lethrinidae	*Lethrinus haematopterus*	USNM 006364
		Lethrinidae	*Monotaxis grandoculis*	MIN0017-8
		Lobotidae	*Datnioides microlepis*	RAG-Megadataset
		Lobotidae	*Datnioides quadrifasciatus*	RAG-Megadataset
		Lutjanidae	*Pinjalo pinjalo*	ODU-3072
		Lutjanidae	*Lutjanus analis*	RAG-Megadataset
		Lutjanidae	*Lutjanus dentatus*	Gulf of Guinea photo voucher
		Lutjanidae	*Symphorus nematophorus*	No voucher
		Malacanthidae	*Lophilatilus chamaeleonticeps*	19-FFM-4-10-31-03
		Malacanthidae	*Caulolatilus microps*	24-ISLA-1-8-19-03
		Malacanthidae	*Branchiostegus semifasciatus*	Gulf of Guinea, photo voucher
		Menidae	*Mene maculata*	ODU-3069
		Monodactylidae	*Schuettea scalaripinnis*	I.41266027
		Moronidae	*Morone chrysops*	AY308767
		Moronidae	*Dicentrarchus labrax*	P.J. Unmack, collector/ voucher
		Moronidae	*Dicentrarchus punctatus*	ODU-3201
		Mullidae	*Upeneus sulphureus*	ODU-3125
		Mullidae	*Upeneus mollucensis*	ODU 3126
		Mullidae	*Mullus surmuletus*	RAG-Megadataset

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Nandidae	*Badis assamensis*	AY330966
		Nandidae	*Badis corycaeus*	AY330969
		Nandidae	*Badis kanabos*	AY330970
		Nandidae	*Badis siamensis*	AY330975
		Nandidae	*Dario dario*	AY330977
		Nandidae	*Dario hysginon*	AY330978
		Nandidae	*Nandus nandus*	AY330979
		Nematistiidae	*Nematistius pectoralis*	ODU-3004
		Nematistiidae	*Nematistius pectoralis*	ODU-3004
		Nemipteridae	*Scolopsis affinis*	ODU-3030
		Nemipteridae	*Scolopsis vosmeri*	ODU 2827
		Nemipteridae	*Scolopsis ciliata*	FMNH-BUS03-230
		Nemipteridae	*Pentapodus setosus*	FMNH-BUS03-256
		Nemipteridae	*Parascolopsis eriomma*	FMNH-BUS03-307
		Nemipteridae	*Scolopsis ciliata*	ODU-3049
		Nemipteridae	*Pentapodus bifasciatus*	ODU-3031
		Nemipteridae	*Scolopsis taenioptera*	ODU-3091
		Nemipteridae	*Nemipterus marginatus*	ODU-3104
		Nemipteridae	*Nemipterus japonicus*	ODU-3163
		Opistognathidae	*Opistognathus aurifrons*	USNM-Saba
		Oplegnathidae	*Oplegnathus punctatus*	mvfs 21469
		Oplegnathidae	*Oplegnathus punctatus*	mvfs 21469
		Ostracoberycidae	*Ostracoberyx dorygenys*	NMV A 251030-007
		Pempheridae	*Pempheris oualensis*	FMNH-BUS03-193
		Pempheridae	*Parapriacanthus ransonneti*	min0022-4 22-5
		Pentacerotidae	*Pseudopentaceros richardsoni*	I.41420-001

Table 2 (*continued*)

Order	Suborder	Family	Genus-species	Voucher Info
		Percichthyidae	*Bostockia porosa*	P.J. Unmack, collector/ voucher
		Percichthyidae	*Gadopsis marmoratus*	P.J. Unmack, collector/ voucher
		Percidae	*Perca flavescens*	AY308768
		Percidae	*Etheostoma caeruleum*	AY430226
		Plesiopidae	*Trachinops taeniatus*	I.41084015
		Plesiopidae	*Plesiops cephalotaenia*	FMNH-BUS03-031
		Polynemidae	*Polydactylus macrochir*	Berra 1-18-01
		Polynemidae	*Pentanemus quinquarius*	Mahon, photo voucher
		Polyprionidae	*Polyprion americanus*	P.J. Unmack, collector/ voucher
		Polyprionidae	*Stereolepis gigas*	RAG-Megadataset
		Pomacanthidae	*Pygoplites diacanthus*	FMNH-BUS03-013
		Pomacanthidae	*Genicanthus melanospilos*	FMNH-BUS03-279
		Pomacanthidae	*Pomacanthus maculosus*	No voucher
		Pomatomidae	*Pomatomus saltatrix*	No voucher
		Pomatomidae	*Pomatomus saltatrix*	RAG-Megadataset
		Priacanthidae	*Priacanthus tayenus*	ODU-3129
		Priacanthidae	*Priacanthus hamrur*	MIN0017-7
		Pseudochromidae	*Pseudochromis sp*	FMNH-BUS03-026
		Pseudochromidae	*Pseudochromis bitaenatus*	FMNH-BUS03-117
		Rachycentridae	*Rachycentron canadum*	ODU-3193
		Sciaenidae	*Leiostomus xanthurus*	ODU-3176
		Sciaenidae	*Micropogonias undulatus*	ODU-3182
		Serranidae	*Epinephelus tauvina*	P.J. Unmack, collector/ voucher
		Serranidae	*Rypticus subbifrenatus*	USNM 327568
		Serranidae	*Cromileptes altivelis*	FMNH-BUS03-233

Table 2 (*continued*)

Order	Suborder	Family	Genus-species	Voucher Info
		Sillaginidae	*Sillago sihama*	ODU-3124
		Sillaginidae	*Sillago aeolus*	ODU-3191
		Sparidae	*Boopsoidea inornata*	ODU-2791
		Sparidae	*Argyrops spinifer*	ODU-2814
		Sparidae	*Diplodus bermudensis*	ODU-2815
		Sparidae	*Pagellus erythrinus*	ODU-2841
		Sparidae	*Boops boops*	ODU-2912
		Sparidae	*Cheimerius nufar*	ODU-2933
		Sparidae	*Pagrus caerulostictus*	ODU-3027
		Sparidae	*Lagodon rhomboides*	ODU-3175
		Sparidae	*Pagrus pagrus*	ODU-3188
		Sparidae	*Sarpa salpa*	ODU-3203
		Sparidae	*Pagrus auriga*	ODU-2786
		Sparidae	*Lithognathus mormyrus*	ODU-2784
		Sparidae	*Calamus calamus*	BCA-0032
		Sparidae	*Sparus aurata*	RAG-Megadataset
		Sparidae	*Viridentex acromegalus*	17-02-04 (016)
		Sparidae	*Rhabdosargus holubi*	No voucher
		Sparidae	*Pagrus pagrus*	ODU-3188
		Sparidae	*Oblada melanura*	No voucher
		Sparidae	*Stenotomus chrysops*	VIMS VA1-00057
		Sparidae	*Chrysoblephus anglicus*	No voucher
		Sparidae	*Pachymetopon grande*	ODU-2909
		Teraponidae	*Mesopristes argenteus*	P.J. Unmack, collector/ voucher
		Teraponidae	*Terapon theraps*	ODU-3038
		Toxotidae	*Toxotes lorentzi*	ODU-3178
		Toxotidae	*Toxotes chatareus*	ODU-3196
	Scombroidei	Istiophoridae	*Makaira nigricans*	VIMS CM03 19-08-03
		Scombridae	*Rastrelliger brachysoma*	ODU-3106
		Scombridae	*Scomber scombrus*	RAG-Megadataset
		Scombridae	*Acanthocybium solandri*	RAG-Megadataset
		Scombridae	*Scomberomorus sp.*	NMFS-0195
		Sphyraenidae	*Sphyraena guachancho*	ODU-3174

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Sphyraenidae	*Sphyraena sphyraena*	RAG-Megadataset
		Trichiuridae	*Trichiurus lepturus*	ODU-3172
		Trichiuridae	*Trichiurus lepturus*	RAG-Megadataset
		Xiphiidae	*Xiphias gladias*	RAG-Megadataset
	Scombrolabracoidei	Scombrolabracidae	*Scombrolabrax heterolepis*	NMFS-U3-F0412
	Stromateoidei	Ariommatidae	*Ariomma bondi*	ODU-3173
		Nomeidae	*Psenes maculatus*	AMNH, not processed yet
		Stromateidae	*Stromateus fiatola*	Mahon, photo voucher
	Trachinoidei	Pinguipedidae	*Parapercis cylindrica*	FMNH-BUS03-275
		Uranoscopidae	*Uranoscopus albesca*	Mahon, photo voucher
	Pholidichthyioidei	Pholidicthyidae	*Pholidichthys leucotaenia*	ODU-3183
	Zoarcoidei	Pholidae	*Pholis ornata*	LMB-200301-3-1
		Zoarcidae	*Lycodes brevipes*	LMB-200301-3-2
	Acanthuroidei	Acanthuridae	*Zebrasoma scopas*	AY308776
		Acanthuridae	*Acanthurus guttatus*	RAG-Megadataset
		Ephippidae	*Chaetodipterus faber*	AY308773
		Scatophagidae	*Scatophagus argus*	RAG-Megadataset
		Scatophagidae	*Selenotoca multifasciata*	RAG-Megadataset
		Siganidae	*Siganus doliatus*	AY308777
		Siganidae	*Siganus sp.*	RAG-Megadataset
	Caproidei	Caproidae	*Antigonia capros*	AY308785
Pleuronectiformes	Pleuronectoidei	Achiridae	*Trinectes maculatus*	AY430224
		Bothidae	*Bothus lunatus*	AY308769
		Bothidae	*Arnoglossus blochei*	RAG-Megadataset
		Bothidae	*Arnoglossus imperialis*	RAG-Megadataset
		Citharidae	*Citharus lingnatula*	RAG-Megadataset
		Cynoglossidae	*Symphurus plagiusa*	RAG-Megadataset

Table 2 (*continued*)

Order	**Suborder**	**Family**	**Genus-species**	**Voucher Info**
		Pleuronectidae	*Hippoglossus hippoglossus*	AY454396
		Pleuronectidae	*Pleuronectes platessus*	RAG-Megadataset
		Scophthalmidae	*Scophthalmus maximus*	RAG-Megadataset
		Soleidae	*Solea solea*	RAG-Megadataset
Tetraodontiformes	Tetraodontoidei	Diodontidae	*Diodon hystrix*	AY308791
		Molidae	*Masturus lanceolatus*	AY308792
		Monacanthidae	*Amanses scopas*	AY308793
		Tetraodontidae	*Takifugu rubripes*	AF108420
		Tetraodontidae	*Sphoeroides dorsalis*	AY308795
	Triacanthoidei	Triacanthodidae	*Triacanthodes anomalus*	AY308788

This taxon sampling consists of representatives of all orders included in Johnson and Patterson's (1993) Percomorpha and its immediate outgroups (the Beryciformes and Zeiformes). This study included members (number of sequences of each group in parentheses) of the Zeiformes (4), Atheriniformes (1), Mugiliformes (1), Pleuronectiformes (10), Beryciformes (3), Scorpaeniformes (3), Beloniformes (1), Synbranchiformes (2), Gasterosteiformes (2), Perciformes (246), and Tetraodontiformes (6) (Table 2). In all analyses, the Zeiformes (*Zenopsis conchifera, Cyttus traversi, Grammicolepis brachiusculus* and *Allocyttus verrucosus*) were treated as the outgroup taxa.

DNA Extraction

Genomic DNA was extracted from approximately 0.25 cm^3 of muscle, gill, or fin tissues of taxa included in this investigation using a Qiagen DNEasy tissue extraction kit (Qiagen Inc., Valencia, CA). Methods described by the manufacturer were followed except that the final elution was done with a single 125 uL aliquot. This process was done to increase the final concentration of DNA in the sample to aid in amplification procedures.

For those samples where DNA was difficult to extract or where the extraction kit was unable to extract DNA in sufficient quantities, a phenol-chloroform extraction method, modified from Hillis et al. (1996), was employed. Tissue extracted in this fashion were added to 100 uL of STE (0.1 M NaCl, 0.05 M Tris-HCl pH 7.5, 0.001 M EDTA disodium), 7.5 uL SDS (20% w/v in water), and 7.5 uL PK (10 mg/mL proteinase K in STE) and incubated for 10 hours at 37°C, or for 2 hours at 58°C. One hundred microliters of PCI (phenol:chloroform:isoamyl alcohol, 25:24:1) was added and the sample vortexed. The sample was incubated for five minutes and vortexed again prior to spinning five minutes at 14,000 rpm. The aqueous phase was removed and added to 100 uL of CI (chloroform:isoamyl alcohol, 24:1). The sample was vortexed and spun for five minutes at 14,000 rpm. The resulting aqueous layer was again removed, added to 10 uL of 3 M sodium acetate (1/10th original volume) and 250 uL 100% ethanol (2.5 times original volume), and placed at -20°C for two hours. Samples were centrifuged at 14,000 rpm for five minutes and drained. Four hundred and fifty microliters of 70% ethanol was added, vortexed and incubated at room temperature for 20 minutes. The samples were centrifuged for five minutes at 14,000 rpm, drained, and dried at 58°C for 20-60 minutes. Between 20 and 100 uL of water was added to the extracts, depending on pellet size.

Polymerase Chain Reaction (PCR)

PCR was used to isolate a 1545 base pair segment of the RAG1 gene from the genomic DNA extracts. Reactions were performed using Takara ExTaq polymerase (Takara Mirus Bio, Madison, WI) and two external primers (Table 3). Initial reactions were run at 25 uL volumes to prevent waste of materials. The successful reactions were run again at 100 uL for purification and sequencing. One hundred microliter reactions were performed using approximately 400 nanograms of genomic DNA, 1X ExTaq Buffer (supplied by manufacturer, 1.6 mM $MgCl_2$ final concentration), 0.5 uM each primer, 200 uM dNTPs, and 2.5 units of ExTaq polymerase. Concentrations and volumes were optimized accordingly to ensure success of reactions. Amplification consisted of the following thermal program: 95°C for 1 minute; 15 cycles of 95°C for one minute, 53°C for 45 seconds, 72°C for 1 minute 30 seconds; 15 additional cycles of 95°C for 45 seconds, 51°C for 45 seconds, and 72°C for 1 minute 30 seconds; 72°C for seven minutes; 4°C incubation.

Table 3
Oligonucleotide primer list for sequencing reactions of the RAG1 gene for this investigation. * indicate primers obtained with permission from the lab of Dr. G. Orti at the University of Nebraska-Lincoln.

Primer Name	DNA Primer Sequence
RAG1 2533F*	5' CTG AGC TGC AGT CAG TAC CAT AAG ATG T 3'
RAG1 2800F	5' CGG CGS TTT CGC TAT GAT GT 3'
RAG1 3032F*	5' AAA CTC AGA ACT GTC CTG 3'
RAG1 3500F	5' AGA GTC AAA GGN GST CNG C 3'
RAG1 4078R*	5' TGA GCC TCC ATG AAC TTC TGA AGR TAY TT 3'

Resulting PCR reactions were run on a 1% agarose gel, visualized, and purified with the Qiagen Qiaquick gel extraction kit (Qiagen Inc., Valencia, CA). Manufacturer's recommendations were followed with the exception of the final elution being done with 32 uL of double distilled water to ensure the amount of resulting product was enough for sequencing.

Cloning

Those samples that were unable to be sequenced directly were cloned using the Promega pGEM-T Easy vector system (Promega Co., Madison, WI). The vector system includes a blue-white colony screening procedure and the vector system included EcoRI restriction enzyme cut sites at -49 and 70 bases from the site of insertion. Ligations were performed using 5 uL of 2X Rapid Ligation Buffer, 1uL of T4 DNA ligase, 1 uL of pGEM-T Easy vector, and 3 uL of PCR product. Ligations were transformed into JM109 high efficiency competent cells. Transformations were plated on agar plates containing ampicillin, X-gal (5-bromo-4-chloro-3-indolyl-beta-D-galactopyranoside) and IPTG (isopropyl-beta-D-thiogalactopyranoside) as recommended by the manufacturer. Those colonies that screened positively through both PCR and restriction enzyme analysis were grown in an overnight culture (up to 20 hours) of LB broth and ampicillin. Overnight cultures were isolated with the Wizard Miniprep DNA purification system (Promega Co., Madison, WI) and sequencing reactions were then performed on the isolated plasmid DNA.

Sequencing

Products from both purified PCR and cloning products were sequenced on either an ABI 310 or ABI 3100 capillary sequencer (Applied Biosystems, Foster City, CA). External PCR primers were used to sequence approximately 1431 bases (1425-1431, with insertions and deletions) of the RAG1 gene and internal primers were used as necessary to aid in completion of each sequence (Table 3). Sequencing reactions each contained approximately 3.2 pM primer (2 uL), 2.6 uL BigDye (Applied Biosystems, Foster City, CA), 2.0 uL 5X Sequencing Buffer (Applied Biosystems, Foster City, CA), 10-40 ng (~10-13 uL) DNA, and distilled, deionized water to a total volume of 20 uL. The sequencing reactions were run using the following thermal program: 25 cycles of 96°C for 30 seconds, 50°C for 15 seconds, and 60°C for 4 minutes. Following this, 50 uL of 100% ethanol, 2uL of 3M sodium acetate, and 2 uL of 125 mM EDTA were added to each reaction and incubated for 20 minutes at room temperature. The reactions were centrifuged for 20 minutes at 14,000 rpm. The liquid was carefully removed from the samples and replaced with 70 uL of 70% ethanol for 5 minutes. Samples were again centrifuged for 5 minutes at 14,000 rpm. The liquid was removed and the samples were dried for 1 minute at 90°C. Samples were denatured by adding 16 uL of ABI Hi-Di Formamide or TSR (Applied Biosystems, Foster City, CA) and incubated for 2 minutes at 95°C. Following incubation, the samples were immediately placed on ice until they could be sequenced.

Data Analysis

Sequences were screened in Genbank (www.ncbi.nlm.nih.gov) to ensure they matched existing RAG1 vertebrate sequences prior to their compilation. They were checked using the freeware program Chromas v.1.45 (www.technlysium.com.au/chromas) for base call ambiguities. Sequences were compiled using two internet sources. The Baylor College of Medicine's website (http://searchlauncher.bcm.tmc.edu/seq-util/seq-util.html) was used to generate reverse complements to sequences generated with reverse PCR primers. The reverse complement sequences were then added to the forward sequences using the National Center for Biotechnology Information's (NCBI) Basic Local Alignment Search Tool (BLAST). The BLAST2Seqs function on the NCBI website (http://www.ncbi.nlm.nih.gov/blast) easily allows the forward and reverse sequences to be added together following another careful screening of all base calls in the overlapping regions.

Once sequences were compiled, they were compared to previously published sequences to screen for errors such as gaps and ambiguous base calls not seen in the earlier screenings using Bioedit v7.0x (Hall, 1999). Any errors found (gaps, etc.) were screened and the corresponding chromatograms were checked to ensure base continuity. Once all errors were fixed, the sequence file was cropped as a whole so as to keep the dataset "in-frame" (i.e. the translation would give the correct protein sequence and not include any stop codons). This was also done using the Bioedit v7.0x (Hall, 1999) program. After the data were compiled and screened, an alignment was performed using the ClustalW attachment in BioEdit v7.0x (Hall, 1999). The complete, aligned dataset was saved in the FASTA file format for further study. This dataset was converted to the NEXUS format using either CluxtalX (Thompson et al, 1997) or SeqVerter 2.0x (www.genestudio.com).

Mutational site saturation for the RAG1 gene in the compiled dataset was examined both as a whole and at each of the three codon positions in PAUP*4.0b10 (Swofford, 2003). The output was logged and the "pairdiff" command in the short format was employed. After completion, the datafile was edited and graphs were generated to compare transitions and transversions vs. sequence divergence in a spreadsheet program. To analyze for each codon position, the data were defined using the following commands:

```
charset 1st = 1-./3;
charset 2nd = 2-./3;
charset 3rd = 3-./3;
```

Positions could be excluded using the "exclude" command so that each position could be analyzed independently. Graphs for each position comparing transitions and transversions vs. sequence divergence were prepared.

Base compositional stationarity was also calculated in PAUP*4.0b10 (Swofford, 2003). Using the base composition function found in the data menu (or simply the "basefreq" command), a chi squared value was computed for the dataset. This value tests whether the base composition of the dataset is equivalent throughout the dataset.

Next, using the program Mega 3.1 (Kumar et al., 2004), the nucleotide composition of the data was calculated. This calcuation was done by opening the data file with the program and converted to the Mega format (*.meg). Under the statistics menu of the program, the nucleotide composition was calculated and the resulting datafile was opened in Microsoft Excel for formatting and calculation of GC content at all positions.

Wright's effective number of codons was calculated for each sequence to investigate synonymous codon usage (codon bias). Using the Mega 3.1 program (Kumar et al., 2004) codon usage was calculated for each individual sequence and the data compiled into a spreadsheet (created from the formulas of Wright (1990)). Codon bias values (the effective number of codons) can range from 20 (high bias) to 61 (no bias).

Phylogenetic analyses were performed using a modified maximum parsimony analysis on the dataset. Again, because of the large size of the dataset (279 sequences) it was necessary to employ the Parsimony Ratchet method using the PAUPRat program (Nixon, 1999; Sikes and Lewis, 2001). This method finds the shortest, most parsimonious trees for larger datasets (i.e. those too large for traditional heuristic methods). It works by sacrificing the thoroughness of individual island searching in order to increase the total number of islands visited during a heuristic search, thus keeping the search from getting stuck in a local maxima. PAUPRat was run ten times, each run consisting of 200 iterations. The shortest, most parsimonious trees from each run were combined and a consensus tree was calculated. Evaluation of each internode was done by calculation of both bootstrap and jackknife supports in PAUP*4.0b10 (Swofford, 2003). Again, because of the large size of the dataset, both jackknife and bootstrap evaluations were limited in their number of rearrangements (per addition sequence replicate) to 25,000,000.

In order to determine the appropriate model of substitution for likelihood analyses, MrModeltest (v2.2; Nylander, 2004) was used. The coding block for this calculation was downloaded from http://www.csit.fsu.edu/~nylander/MrModelblock and was placed at the end of the nexus datafile. The dataset was then executed in PAUP*4.0b10 (Swofford, 2003). The resulting 'mrmodel.scores' file was then executed in the MrModeltest2 program (Nylander, 2004). The output file contained the most appropriate model of substitution for the dataset (Ronquist and Huelsenbeck 2003). Maximum likelihood analyses were run using the GARLI program (version 0.94; Zwickl, 2006). This program uses the General Time Reversable (GTR) model of nucleotide substitution with gamma distributed rate heterogeneity and an estimated proportion of invariable sites (GTR+I+G). In order to ensure the best log likelihood (lnL) values were obtained, 10 independent runs of the likelihood analysis were performed. Following the recommendation of the author (Zwickl, 2006), a starting topology was used because of the large size of the dataset.

Results

The final dataset included 1431 characters of the RAG1 gene, of which 1085 were parsimony informative (novel sequences, Appendix I). Site saturation was not evident for the total analysis, nor was it evident at the first, second, or third positions independently (Figure 3a-b). Base composition across did not deviate from stationarity ($\chi^2 = 855.73$; df=834; $P = 0.2933$). Average GC content of all sequences was 53.8% (Table 4). GC content was a minimum in the gobiesocoid *Discotrema crinophila* at 47.7% and a maximum in the anabantoid *Trichogaster chuna* at 61.8%. Average GC content at first position codons was 54.6%; at second position codons, 42.2%; and at third position codons, 64.8%. Most taxa had a GC content greater than 60% at the third position codon (224 out of 279 sequences). In the third codon position, the lowest GC content was seen in *Discotrema crinophila* (47.3%) and the highest in *Trichogaster chuna* (86.9%). The highest codon bias, seen by the lowest value of effective number of

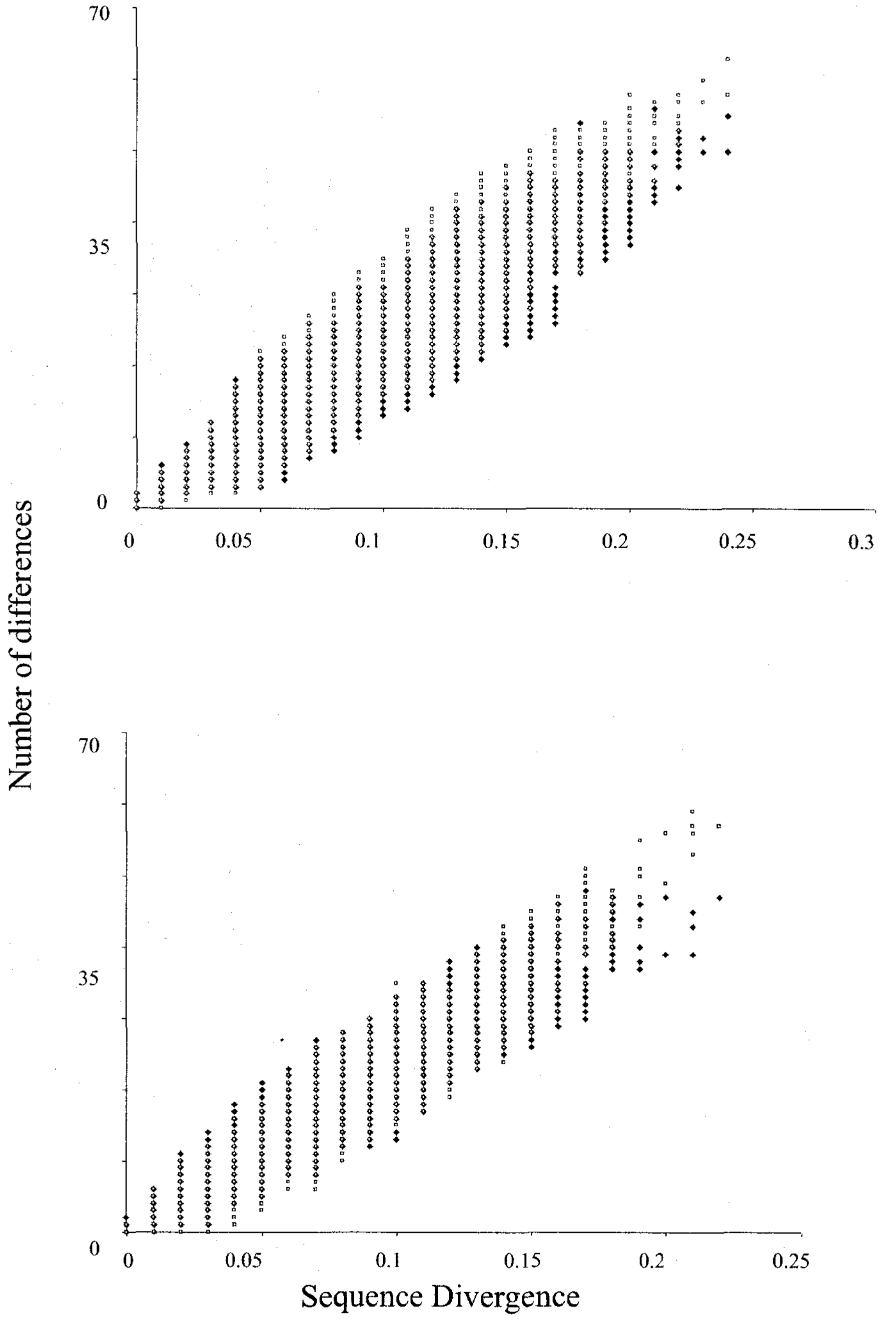


Fig. 3a. Saturation curves for the first and second codon positions of the RAG1 gene. Number of transition and transversion substitutions vs. the sequence divergence for RAG1 for the first codon position (top) and second codon position (bottom) bases. Transitions are shown with the dark background symbols, transversions are shown with the white background symbols.

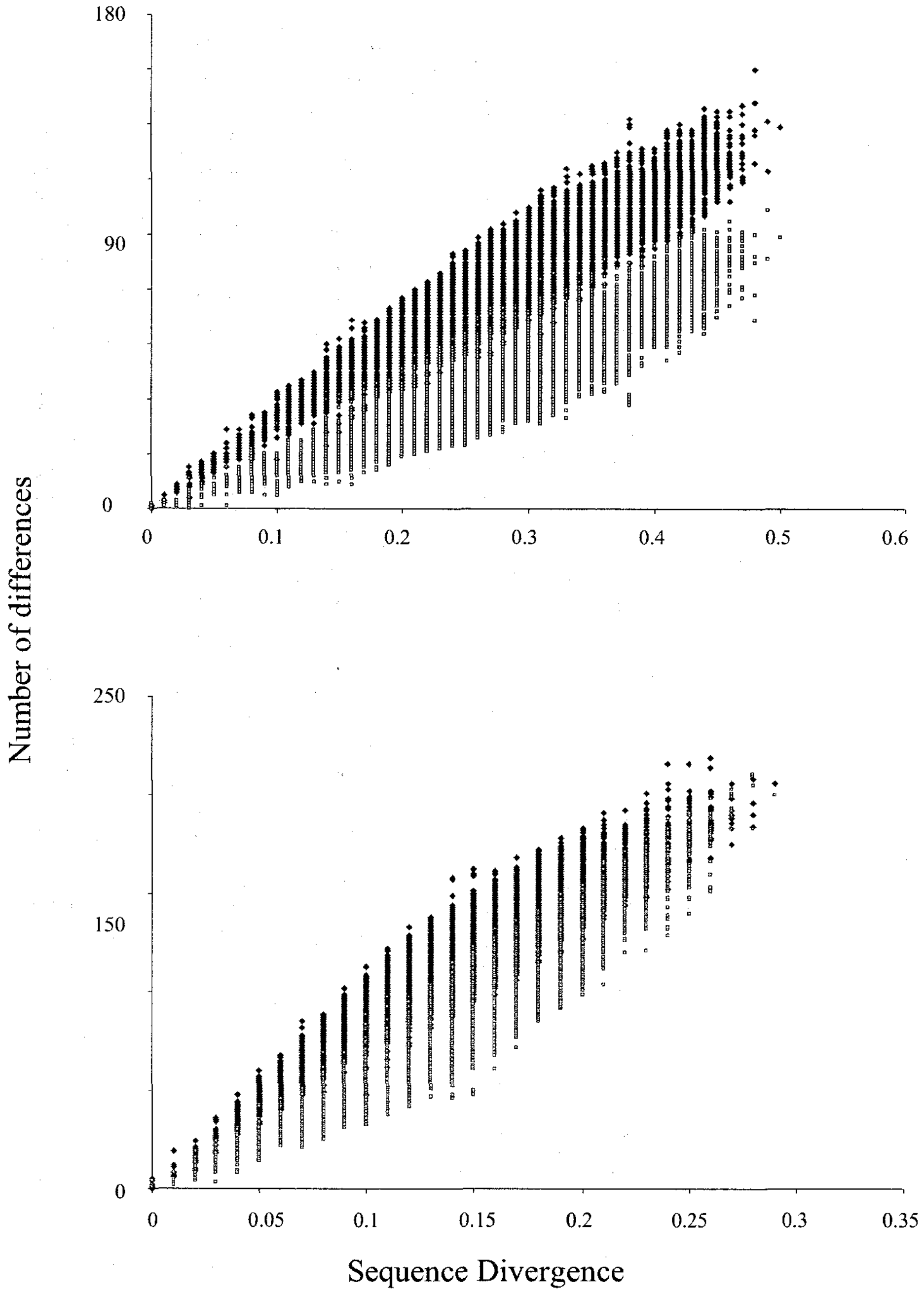


Fig. 3b. Saturation curves for the third codon position bases and all codon positions. Number of transition and transversion substitutions vs. the sequence divergence for RAG1 for the third codon position bases (top) and all codon positions (bottom). Transitions are shown with the dark background symbols, transversions are shown with the white background symbols.

Table 4
Base composition for all three codon positions and codon bias data for all species included in the current study.

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Acanthocepola krustensternii	54.4	42.9	65.7	54.4	50.9
Acanthocybium solandri	54.8	42.2	59.7	52.2	54.6
Acanthurus guttatus	55.1	42.6	57.1	51.6	54.3
Alectis alexandrinus	53.7	42.7	60.9	52.4	53.8
Allocyttus verrucosus	54.9	43.0	67.7	55.2	51.1
Amanses scopas	55.3	41.6	73.4	56.8	45.6
Ambassis agrammus	54.2	41.6	56.3	50.7	54.1
Ambassis macleayi	54.5	41.7	56.8	51.0	53.3
Amblygobius hectori	54.6	42.7	61.4	52.9	54.7
Amphilophus rhytisma	54.9	41.8	57.0	51.2	52.8
Anisotremus virginicus	54.8	42.2	61.1	52.7	55.0
Antigonia capros	54.8	42.2	60.9	52.6	53.3
Aplodactylus arctidens	55.3	42.9	66.2	54.7	51.2
Apogon aureus	53.9	42.4	56.7	51.0	55.8
Argyrops spinifer	55.8	42.9	70.4	56.3	47.3
Ariomma bondi	53.8	42.1	58.6	51.5	52.9
Arnoglossus blochei	56.3	43.1	83.6	61.0	38.6
Arnoglossus imperialis	55.1	42.9	85.7	61.2	37.9
Arripis trutta	56.3	42.7	64.3	54.4	49.7
Arripis truttacea	55.9	42.7	64.5	54.3	49.8
Badis assamensis	53.5	41.7	56.8	50.6	53.7
Badis corycaeus	53.7	41.5	56.4	50.5	54.2
Badis kanabos	53.5	41.7	56.4	50.5	53.5
Badis siamensis	54.1	41.7	56.2	50.7	53.9
Banjos banjos	55.0	42.5	63.8	53.8	51.9
Betta splendens	55.2	42.0	77.3	58.2	42.8
Blennius normani	56.3	42.0	58.6	52.4	55.0
Boops boops	55.0	42.7	69.1	55.6	47.5
Boopsoidea inornata	55.8	41.8	67.0	54.9	51.3
Bostockia porosa	54.8	41.8	59.0	51.9	54.2
Bothus lunatus	55.4	42.7	77.4	58.5	43.1
Brachydeuterus auritus	54.4	42.2	62.0	52.9	52.7
Brama orcini	54.6	41.6	61.6	52.6	53.3
Branchiostegus semifasciatus	53.6	42.7	62.0	52.8	54.5
Caesio lunaris	55.0	41.6	68.7	55.1	50.0
Calamus calamus	55.3	42.2	72.1	56.5	46.7
Callanthias australis	55.2	44.3	70.6	56.7	47.5
Callionymus sp.	53.8	42.4	58.4	51.5	54.5
Caranx hippos	53.5	43.2	63.6	53.4	51.7
Caristius sp.	54.4	42.1	60.3	52.2	54.1
Caulolatilus microps	54.2	42.6	61.5	52.8	55.0
Centracanthus cirrus	54.8	42.4	78.1	58.5	43.1

Table 4 (*continued*)

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Centropomus viridis	55.3	41.9	68.7	55.4	49.8
Cepola macrophthalma	53.4	39.9	65.6	53.0	51.6
Chaetodipterus faber	54.5	41.6	59.8	52.0	52.3
Chaetodon striatus	54.0	42.8	60.1	52.3	53.4
Channa marulia	53.8	42.0	61.3	52.4	52.0
Channa sp 1	54.6	43.1	63.0	53.6	50.9
Channa sp 2	54.2	42.9	63.1	53.3	50.7
Cheilodipterus macrodon	52.7	41.9	54.7	49.7	53.8
Cheimerius nufar	55.2	42.0	68.7	55.3	48.8
Chirodactylus grandis	55.9	42.0	68.1	55.4	48.7
Nemadactylus monodactylus	54.7	42.8	67.4	55.0	49.6
Chironemus marmoratus	55.8	42.6	68.9	55.8	50.2
Chromis atripes	54.8	41.3	68.1	54.8	49.9
Chrysiptera annulata	54.4	42.5	71.4	56.1	47.3
Chrysoblephus anglicus	55.5	41.8	68.7	55.4	48.1
Cirrhitus pinnulatus	54.4	42.7	69.9	55.7	47.8
Citharus lingnatula	55.5	42.7	73.6	57.3	48.1
Coris julis	54.6	42.4	62.1	53.0	53.6
Coryphaena hippurus	53.6	42.0	59.1	51.5	54.1
Coryphaena sp	53.4	42.3	59.3	51.6	54.5
Cromileptes altivelis	54.8	41.6	65.1	53.8	50.8
Cyttus traversi	55.0	42.3	62.4	53.2	51.2
Dario dario	54.3	41.9	59.3	51.9	54.9
Dario hysginon	54.3	41.7	58.1	51.3	54.7
Datnioides microlepis	54.2	42.4	58.0	51.5	54.2
Datnioides quadrifasciatus	54.6	42.9	58.6	52.0	54.1
Decapterus macrosoma	52.5	41.9	62.5	52.3	53.5
Denariusa bandata	54.2	42.2	60.5	52.3	55.5
Diapterus auratus	54.9	41.6	64.2	53.5	49.7
Diapterus peruvianus	54.0	41.6	65.6	53.8	49.6
Dicentrarchus labrax	54.9	41.5	59.3	51.9	52.4
Dicentrarchus punctatus	54.6	41.4	60.1	52.0	52.9
Dichistius capensis	55.9	41.6	68.3	55.2	47.9
Dichistius capensis B	55.1	41.5	67.1	54.6	48.7
Dinolestes lewini	51.9	42.0	60.5	51.5	54.2
Dinoperca petersi	54.9	42.2	62.6	53.2	53.9
Diodon hystrix	52.5	40.7	53.1	48.8	54.9
Diplodus bermudensis	55.9	42.5	71.0	56.5	47.8
Discotrema crinophila	54.6	41.3	47.3	47.7	56.3
Drepane punctata	55.0	41.5	60.7	52.5	51.9
Echeneis naucrates	53.6	43.9	64.7	54.0	50.2
Elassoma evergladei	53.8	41.6	59.2	51.5	55.2
Elassoma zonatum	53.6	41.6	61.2	52.1	54.4
Embiotoca lateralis	54.4	41.8	61.5	52.6	51.8

Table 4 (*continued*)

Species	Position 1 %GC	Position 2 %GC	Position 3 %GC	All positions %GC	ENC
Enoplosus armatus	54.2	42.1	61.5	52.6	54.9
Epigonus telescopus	53.8	42.0	62.4	52.8	53.8
Epinephelus tauvina	55.8	41.4	67.2	54.8	49.9
Erythrocles monodi	55.0	42.2	63.0	53.5	52.6
Etheostoma caeruleum	54.4	42.0	63.9	53.4	50.6
Eucinostomus gula	53.3	42.5	61.7	52.6	53.5
Gadopsis marmoratus	55.5	42.2	60.4	52.7	53.5
Gasterosteus aculeatus	54.1	42.7	73.9	56.9	47.7
Gazza minuta	54.7	42.3	62.1	53.1	53.2
Genicanthus melanospilos	55.2	42.3	67.2	54.9	50.4
Gerres argyreus	54.6	41.6	66.4	54.2	48.7
Glaucosoma buergeri	54.4	40.3	62.4	52.4	49.2
Glaucosoma herbraicum	54.6	41.0	61.6	52.4	51.5
Glossamia aprion	52.9	42.0	57.5	50.8	54.9
Gnathodentex aureolineatus	55.0	43.1	63.9	54.0	48.6
Gnathodentex aureolineatus B	54.8	41.8	64.7	53.8	52.8
Gobiesox strumosus	55.5	40.7	59.1	51.7	56.4
Gramma loreto	55.7	40.9	60.9	52.5	50.5
Grammicolepis brachiusculus	55.2	42.3	65.1	54.2	51.7
Gymnocaesio gymnoptera	54.1	42.4	67.7	54.7	50.2
Gymnocranius elongatus	55.0	42.3	65.2	54.2	48.9
Haemulon aurolineatum	54.8	42.2	62.5	53.2	53.4
Haemulon plumierii	55.2	42.2	63.2	53.5	53.2
Halichoeres melanurus	54.9	41.8	62.8	53.2	53.7
Helcogramma sp	55.6	42.5	65.1	54.4	52.8
Helostoma temminckii B	54.4	41.3	59.4	51.8	54.6
Helostoma temminckii	54.4	41.3	59.4	51.8	54.6
Hemitaurichtys polylepis	54.4	42.7	64.5	53.9	51.6
Hippoglossus hippoglossus	55.0	42.9	70.6	56.2	49.5
Icosteus aenigmaticus	55.0	41.8	60.5	52.5	53.7
Inermia vittata	55.5	43.1	66.4	55.0	51.7
Kuhlia mugil	55.1	42.2	64.2	53.8	52.4
Kuhlia rupestris	55.3	42.2	63.4	53.6	51.7
Kurtus gulliveri	53.2	42.2	58.4	51.3	56.0
Kyphosus incisor	56.4	42.4	62.8	53.8	50.3
Lagodon rhomboides	55.4	42.6	80.6	59.6	40.7
Lates calcarifer	54.8	42.7	68.0	55.2	48.4
Latridopsis forsteri	54.2	41.8	64.0	53.4	52.3
Latris lineata	53.6	42.3	63.0	53.0	53.2
Leiognathus sp	54.2	42.0	67.0	54.4	49.4
Leiognathus stereorarus	54.1	42.1	61.9	52.7	54.6
Leiognathus stereorarus B	53.5	42.3	62.5	52.8	53.6
Leiostomus xanthurus	54.2	42.0	59.7	52.0	52.9
Lepomis cyanellus	54.7	41.9	59.4	52.0	54.3

Table 4 (*continued*)

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Lepomis macrochirus	54.8	42.0	59.8	52.2	53.4
Lethrinus atkinsoni	54.7	43.7	64.0	54.1	51.8
Lethrinus atlanticus	54.8	42.1	64.5	53.8	51.5
Lethrinus haematopterus	54.8	42.0	65.6	54.1	52.7
Lethrinus harak	54.4	42.0	64.3	53.6	53.9
Lethrinus lentjan	55.2	42.4	64.3	54.0	52.7
Lethrinus obsoletus	54.2	41.8	64.5	53.5	53.0
Lethrinus olivaceus	54.2	42.3	63.6	53.4	51.5
Lethrinus xanthochilus	54.4	41.8	65.2	53.8	52.3
Lithognathus mormyrus	53.4	42.2	66.8	54.2	49.3
Lopholatilus chamaeleonticeps	53.9	42.7	61.6	52.8	54.9
Lutjanus analis	54.8	42.2	65.3	54.1	52.7
Lutjanus dentatus	54.8	42.0	66.8	54.5	50.7
Lycodes brevipes	53.8	41.7	62.2	52.5	51.2
Macropodus opercularis	55.2	41.8	72.2	56.4	46.7
Makaira nigricans	54.3	42.1	62.1	52.9	50.2
Malpulutta kretseri	55.7	41.6	73.9	57.1	45.5
Mastacembelus armatus	54.2	42.0	56.5	50.9	55.4
Masturus lanceolatus	54.8	41.6	61.6	52.7	51.4
Mene maculata	55.0	42.7	64.1	54.0	51.7
Menidia menidia	54.1	40.9	61.8	52.3	51.2
Mesopristes argenteus	54.5	42.1	63.7	53.5	54.1
Microcanthus strigatus	55.9	42.4	64.2	54.2	51.5
Micropogonias undulatus	53.8	42.3	59.7	51.9	54.3
Micropterus salmoides	54.4	41.6	60.3	52.1	52.3
Monopterus albus	54.4	42.0	58.0	51.4	56.4
Monotaxis grandoculis	54.6	42.7	65.8	54.4	49.9
Morone chrysops	54.8	41.6	59.9	52.1	53.4
Mugil curema	55.4	41.6	64.4	53.8	52.6
Mullus surmuletus	55.0	42.5	69.0	55.4	50.6
Nandus nandus	53.5	42.5	56.2	50.7	55.5
Nematistius pectoralis	54.8	42.1	69.9	55.5	49.8
Nematistius pectoralis B	54.7	41.9	69.5	55.3	50.2
Nemipterus japonicus	54.8	42.9	72.3	56.7	49.1
Nemipterus marginatus	53.6	43.7	70.8	56.0	49.8
Neoscorpis lithophilus	55.5	42.4	64.7	54.3	49.3
Neoscorpis lithophilus B	55.5	42.4	64.3	54.1	49.2
Notothenia coriiceps	54.2	42.0	63.2	53.2	54.0
Oblada melanura	54.8	43.0	68.3	55.4	47.2
Opistognathus aurifrons	54.2	42.7	61.3	52.7	53.0
Oplegnathus punctatus	55.0	42.0	61.7	53.0	52.5
Oplegnathus punctatus B	55.3	42.0	61.7	53.1	52.6
Ostracoberyx dorygenys	54.9	43.1	63.9	53.9	51.1
Pachymetopon grande	55.6	42.6	69.5	56.0	46.5

Table 4 (*continued*)

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Pagrus caeruleostictus	54.8	42.2	67.4	54.2	50.8
Pagellus erythrinus	53.8	42.7	66.8	54.6	50.1
Pagrus auriga	53.6	41.3	66.3	54.3	50.0
Pagrus pagrus	55.0	42.1	79.0	58.7	46.7
Pagrus pagrus	54.8	42.2	74.8	57.3	43.7
Parachanna obscura	54.6	42.3	56.5	51.1	55.7
Paracirrhites arcatus	55.3	44.5	69.7	56.6	48.9
Parapercis cylindrica	54.0	43.1	65.3	54.2	52.8
Parapriacanthus ransonneti	55.5	41.8	61.4	52.8	53.7
Parascolopsis eriomma	53.4	42.9	71.0	55.8	48.4
Parma oligolepis	53.4	41.6	68.9	54.6	48.5
Parosphromenus deissneri	54.3	42.5	68.8	55.2	49.5
Pempheris oualensis	55.7	42.0	62.6	53.4	53.1
Pentanemus quinquarius	54.6	40.9	60.5	52.0	55.6
Pentapodus bifasciatus	53.6	42.0	70.8	55.5	48.1
Pentapodus setosus	54.7	42.2	71.2	56.0	48.3
Perca flavescens	54.4	42.1	63.8	53.4	52.1
Peristedion miniatum	54.9	41.6	68.7	55.1	49.0
Pholidichthys leucotaenia	54.8	41.8	66.8	54.4	48.5
Pholis ornata	54.2	42.9	62.6	53.2	50.9
Pinjalo pinjalo	54.6	41.5	66.6	54.2	52.8
Grammoplites scaber	52.7	43.0	56.1	50.6	56.6
Plectorhinchus macrolepis	55.3	41.6	64.1	53.7	52.1
Plectroglyphidodon dickii	54.6	41.8	66.6	54.3	50.0
Plesiops cephalotaenia	53.8	41.7	63.7	53.1	53.8
Pleuronectes platessus	54.4	42.0	71.9	56.1	47.5
Polydactylus macrochir	55.2	40.9	61.3	52.5	55.2
Polyprion americanus	55.3	42.2	62.4	53.3	52.4
Pomacanthus maculosus	55.9	42.4	65.2	54.4	51.3
Pomacentrus nigromanus	53.8	42.3	68.9	55.0	50.4
Pomatomus saltatrix	54.8	42.3	62.9	53.4	52.8
Pomatomus saltatrix B	54.8	42.1	62.6	53.2	53.3
Priacanthus hamrur	53.5	41.1	64.5	53.0	52.2
Priacanthus tayenus	53.7	41.6	64.9	53.4	51.5
Psenes maculatus	54.0	42.5	62.0	52.8	53.5
Pseudochromis sp.	55.3	41.4	69.1	55.3	49.0
Pseudopentaceros richardsoni	55.7	41.6	63.7	53.7	52.6
Pseudosphromenus cupanus	55.4	41.8	74.4	57.2	46.1
Psuedochromis bitaeniatus	55.7	41.1	68.7	55.2	49.0
Ptereleotris zebra	54.7	43.0	62.0	53.2	52.5
Pterois lunulata	53.0	42.0	56.9	50.6	56.5
Pygoplites diacanthus	54.0	43.1	67.4	54.8	51.5
Rachycentron canadum	52.5	42.0	62.6	52.4	52.3
Rastrelliger brachysoma	53.8	42.5	57.1	51.2	54.9

Table 4 (*continued*)

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Remora australis	53.2	43.9	65.1	54.0	51.3
Rhabdosargus holubi	55.3	41.4	72.3	56.3	46.6
Rypticus subbifrenatus	55.3	42.0	64.6	53.9	50.7
Sargocentron cornutum	55.8	41.5	65.5	54.3	50.3
Sargocentron punctatissimum	55.1	41.1	61.9	52.7	52.0
Sargocentron vexillarium	56.2	41.1	64.6	53.9	50.3
Sarpa salpa	54.6	42.9	69.1	55.6	48.5
Scatophagus argus	52.9	42.1	56.6	50.5	54.7
Schuettea scalaripinnis	55.0	42.5	61.8	53.1	52.9
Scolopsis affinis	55.5	43.2	73.9	57.5	47.8
Scolopsis ciliata 2	54.6	42.9	74.1	57.2	47.1
Scolopsis ciliata	54.6	42.7	73.7	57.0	46.8
Scolopsis taenioptera	54.6	43.3	72.9	56.9	47.3
Scolopsis vosmeri	54.8	42.4	73.9	57.1	47.0
Scomber scombrus	54.3	41.8	58.7	51.7	54.6
Scomberesox saurus	54.5	41.2	58.1	51.2	53.8
Scomberomorous sp.	53.2	42.9	58.2	51.4	54.1
Scombrolabrax heterolepis	54.6	42.3	61.7	52.8	53.0
Scophthalmus maximus	54.8	41.1	62.3	52.8	53.1
Selenotoca multifasciata	52.7	42.1	56.8	50.5	55.3
Siganus doliatus	54.2	42.3	59.4	51.9	55.0
Siganus sp.	53.7	42.0	58.7	51.4	55.3
Sillago aeolus	53.5	42.6	65.8	54.0	50.2
Sillago sihama	53.4	42.0	65.5	53.6	49.9
Solea solea	52.5	41.4	58.3	50.7	56.0
Sparus aurata	55.7	42.0	77.1	58.2	42.8
Sphoeroides dorsalis	52.6	42.7	66.5	54.0	51.8
Sphyraena guachancho	55.4	42.4	67.4	55.1	49.5
Sphyraena sphyraena	55.1	42.4	67.4	55.0	51.0
Spicara alta	55.0	42.7	73.1	56.9	47.1
Spicara flexuosa	54.9	42.9	72.7	56.8	45.8
Spicara maena	54.8	42.0	72.7	56.6	46.3
Spinachia spinachia	54.6	42.5	67.2	54.8	53.2
Stegastes planifrons	55.4	42.1	71.7	56.4	48.0
Stenotomus chrysops	56.3	42.4	77.1	58.6	45.4
Stereolepis gigas	55.4	41.9	63.7	53.6	53.2
Stromateus fiatola	54.0	43.1	60.5	52.6	53.3
Symphorus nematophorus	55.3	42.0	73.3	56.9	47.6
Symphurus plagiusa	55.5	42.3	72.8	56.8	43.6
Synagrops bellus	55.7	41.7	70.1	55.8	48.7
Synchiropus ocellatus	52.8	42.7	67.9	54.4	49.2
Takifugu rubripes	52.6	41.5	59.6	51.2	52.7
Terapon theraps	55.5	42.1	62.0	53.2	53.6
Toxotes chatareus	54.6	42.4	63.2	53.5	52.0

Table 4 (*continued*)

Species	**Position 1 %GC**	**Position 2 %GC**	**Position 3 %GC**	**All positions %GC**	**ENC**
Toxotes lorentzi	54.9	42.0	63.9	53.5	50.9
Trachinops taeniatus	54.7	41.8	66.8	54.4	49.7
Triacanthodes anomalus	53.9	41.7	61.4	52.3	52.4
Trichiurus lepturus	52.6	42.2	59.3	51.4	54.0
Trichiurus lepturus	53.0	42.4	59.3	51.6	53.1
Trichogaster chuna	55.5	43.1	86.9	61.8	36.5
Trichogaster leerii	55.1	43.0	70.4	56.2	47.6
Trichogaster trichopterus	54.9	43.1	76.0	58.0	45.2
Trichopsis vittata	54.8	42.5	77.3	58.2	42.4
Trinectes maculatus	54.8	42.4	65.6	54.3	50.5
Upeneus moluccensis	55.4	41.3	69.0	55.3	48.4
Upeneus sulphureus	56.6	41.9	78.1	58.9	44.1
Uranoscopus albesca	54.1	40.9	61.6	52.2	52.6
Virididentex acromegalus	55.1	41.6	67.0	54.6	50.6
Xiphias gladius	55.4	42.3	62.0	53.2	54.2
Zebrasoma scopas	55.5	41.8	54.4	50.5	53.8
Zenopsis conchifera	56.4	42.1	71.2	56.6	49.5
Mean	54.6	42.2	64.8	53.9	51.2
Minimum	51.9	39.9	47.3	47.7	36.5
Maximum	56.6	44.5	86.9	61.8	56.6

codons (ENC), was found in *Trichogaster chuna* (ENC = 36.5) and the lowest codon bias was found in *Plectorhinchus macrolepis* (ENC = 56.6). The mean ENC value for the dataset was 51.2 (Table 4).

Insertions and deletions, although not common, were found in the dataset. Both species of Lobotidae (*Datnioides microlepis* and *Datnioides quadrifasciatus*) had a three base insertion approximately 400 bases into the sequenced region of the RAG1 gene. One codon (3 base) deletions were found in the same region in *Plesiops cephalotaenia*, *Diodon hystrix*, *Takifugu rubripes*, *Sphoeroides dorsalis*, *Parosphromenus deissneri*, *Makaira nigricans*, *Uranoscopus albesca*, and in all taxa from the families Apogonidae, Holocentridae, Carangidae, Nandidae, Leiognathidae, Nematistiidae, and Mullidae. Two codon deletions were seen in all three species of the anabantoid genus *Trichogaster*.

The maximum parsimony analysis using the parsimony ratchet method in PAUPRat (Nixon, 1999; Sikes and Lewis, 2001) resulted in 167 most parsimonious trees, each of which had a total length of 16,443 steps (CI=0.170; HI=0.830; RI=0.532; RC=0.091). Both bootstrap and jackknife supports have been plotted on the 50% majority rule consensus tree created from the most parsimonious tree set (Figures 4-8, 9a-d, 10). Bootstrap and jackknife supports below 50% were omitted. Those terminal groups with labels in bold text include multiple taxa.

The general, time reversible plus proportion invariant with gamma distribution (GTR+I+G) model of evolution was found to be the best substitution model for the dataset using MrModeltest v2.2 (Nylander, 2004). This made modifications to the GARLI likelihood algorhithm setup files unnecessary, as the default model of substitution of the program is the same (Zwickl, 2006). The maximum likelihood analyses resulted in a best log likelihood value of -81469.25958 after 10 runs (Figures 11-16).

Discussion

Maximum parsimony and maximum likelihood analyses find the Zeiformes (100% bootstrap, 100% jackknife in parsimony) to be the sister group to the Beryciformes + Percomorpha (sensu Johnson and Patterson, 1993; Figures 4, 12). The relationship of the Zeiformes to the ingroup taxa (Beryciformes + Percomorpha) has 100% nodal support in the maximum parsimony analysis. The monophyly of the percomorph ingroup is also found in both analyses and again has 100% bootstrap and jackknife support in the parsimony analysis (Figures 4, 12). This investigation agrees with the results of Smith and Craig (2007), finding that perciform lineages are scattered among scorpaeniform, pleuronectiform, gasterosteiform, tetraodontiform, and atheriniform lineages.

The Smegmamorpha of Johnson and Patterson (1993) is polyphyletic in both parsimony and likelihood analyses. Both parsimony and likelihood place the Atheriniformes sister to the Beloniformes with strong nodal support (bootstrap 92%, jackknife 85%) and the Mugiliformes sister to the labroid family Pomacentridae with weak nodal support seen in the parsimony analysis (bootstrap 57%, jackknife 58%) (Figure 9d, Figure 15). The Synbranchiformes and Gasterosteiformes do not form a natural group in these analyses although both groups are individually monophyletic with strong (100% bootstrap, 100% jackknife) and moderate (82% bootstrap, 79% jackknife)

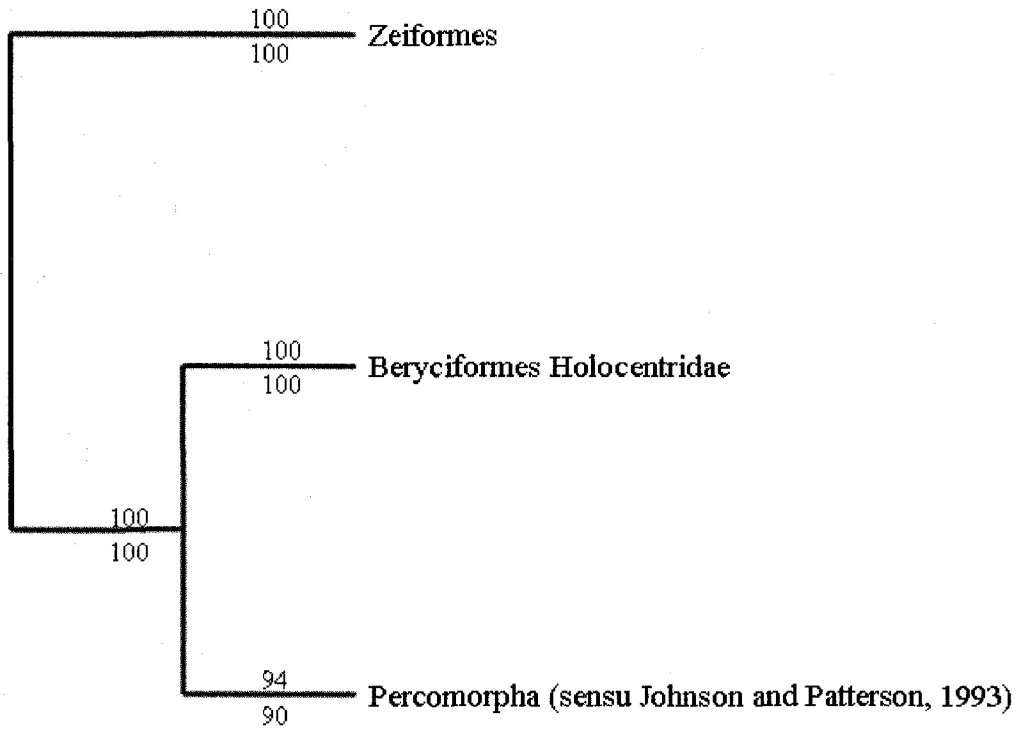


Fig. 4. Tree resulting from the majority rule consensus (50%) of 167 most parsimonious trees in the maximum parsimony analysis. Total length = 16,443 steps, CI=0.170, HI=0.830, RI=0.532 RC=0.091. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inference values. The Percomorpha (sensu Johnson and Patterson) includes all taxa in the study except the Zeiformes and Beryciformes (Holocentridae) in a well supported, monophyletic group.

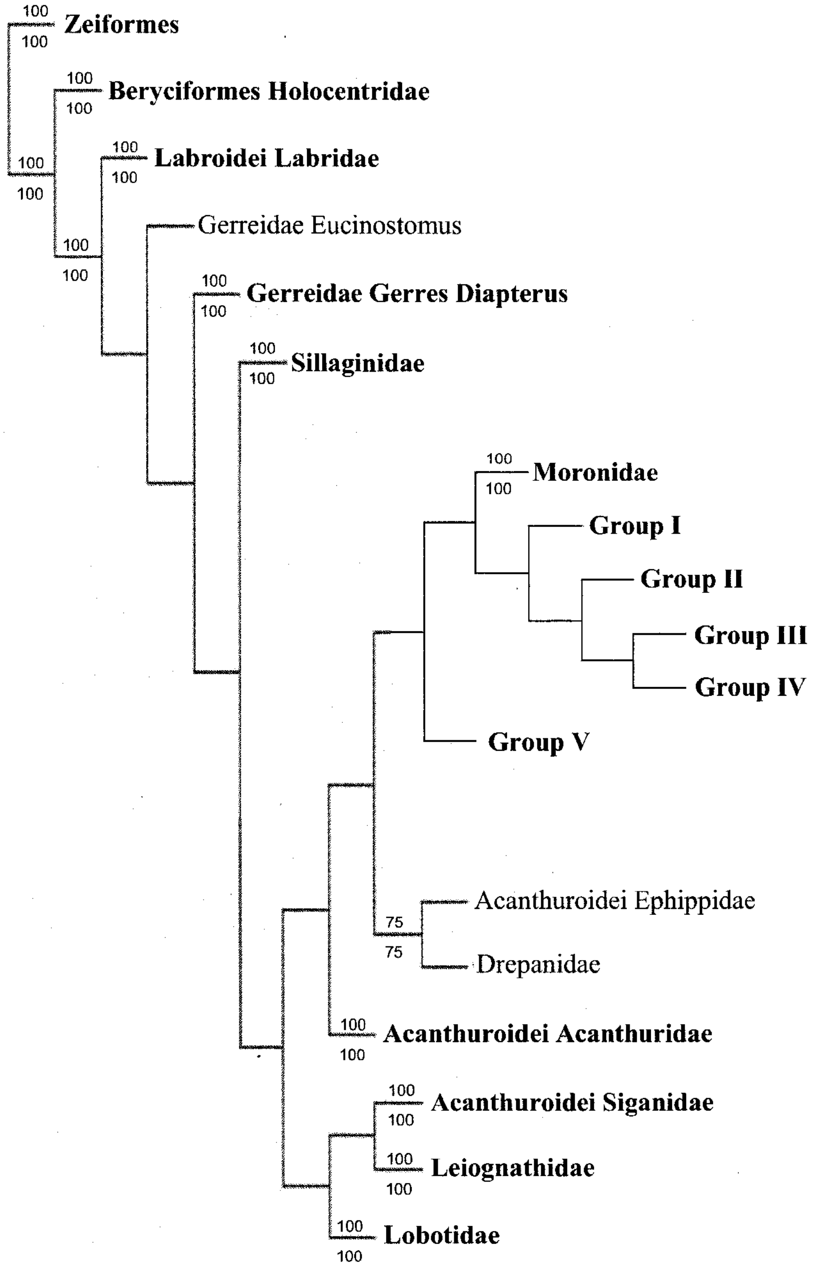


Fig. 5. Maximum parsimony majority rule consensus tree, expanded, detailing ingroup taxa used in the current investigation. Statistics include: total length = 16,443 steps, CI=0.170, HI=0.830, RI=0.532, and RC=0.091. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed. Groups I-V will be described in the following figures.

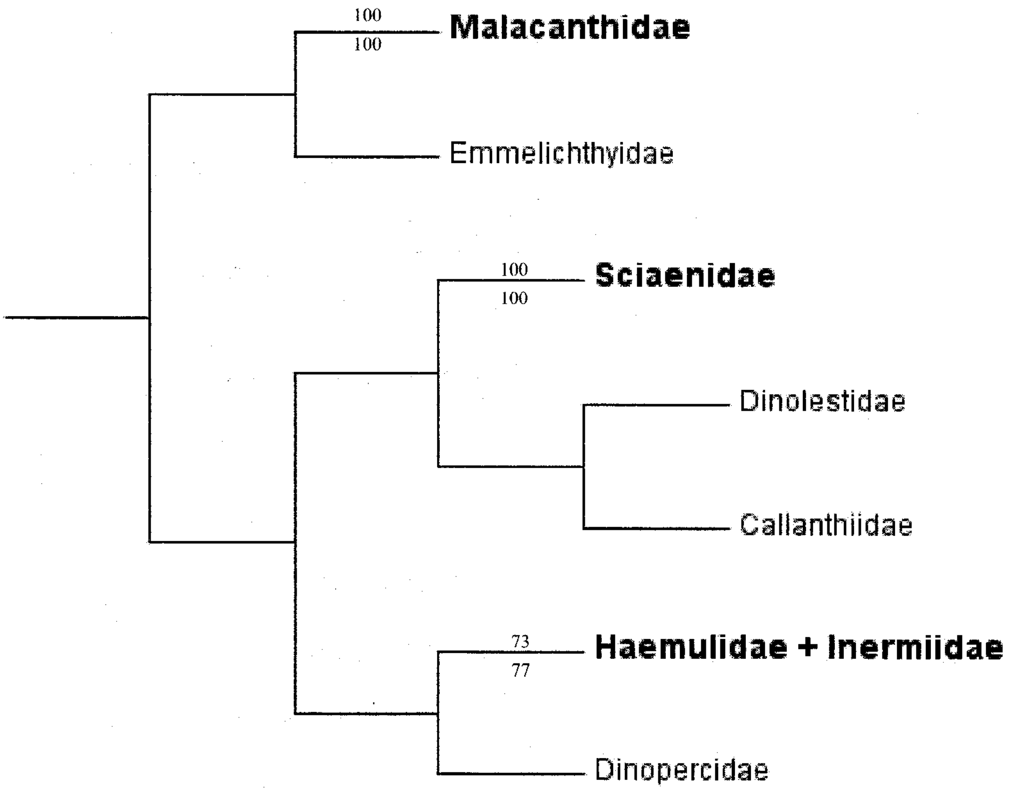


Fig. 6. Group I. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

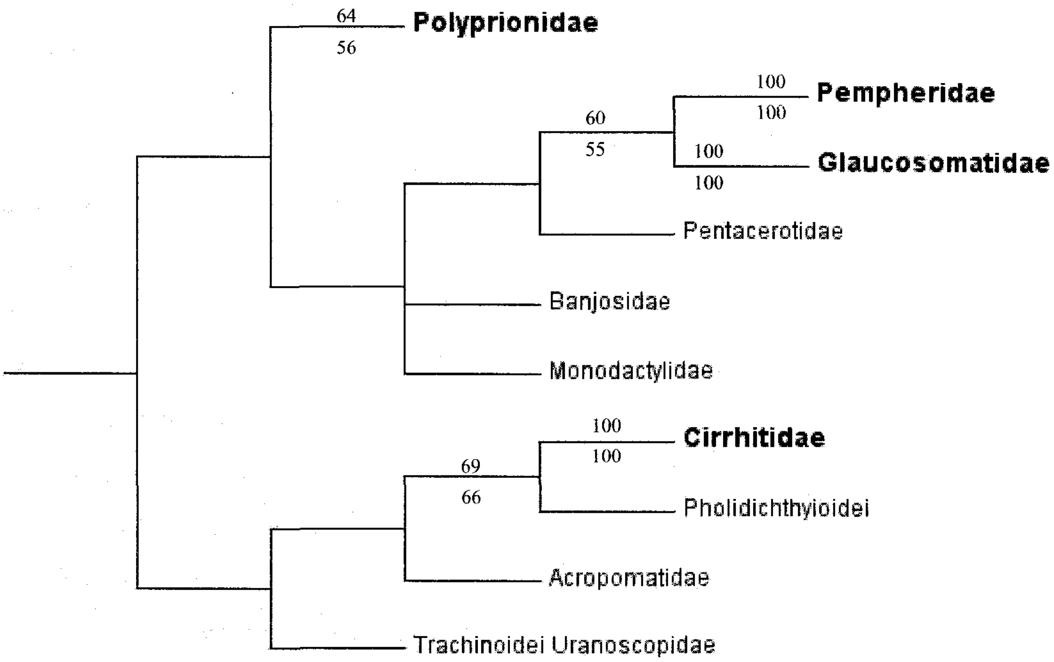


Fig. 7. Group II. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

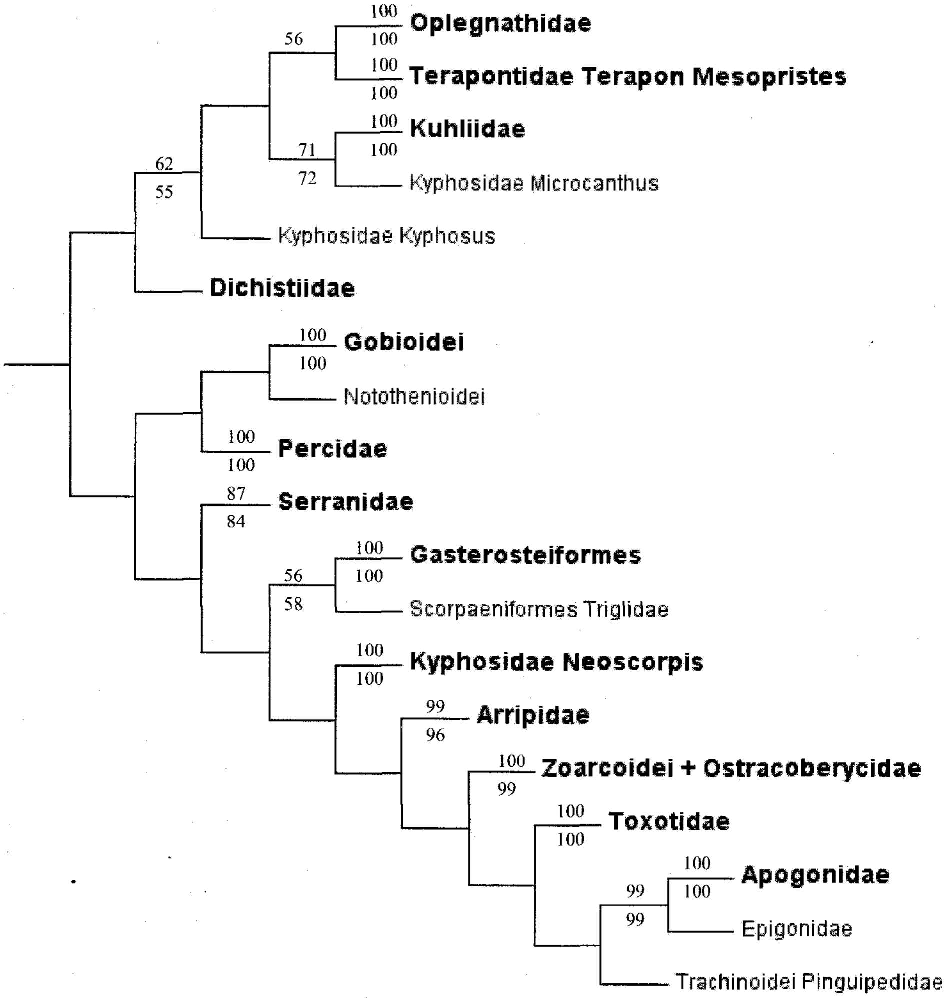


Fig. 8. Group III. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

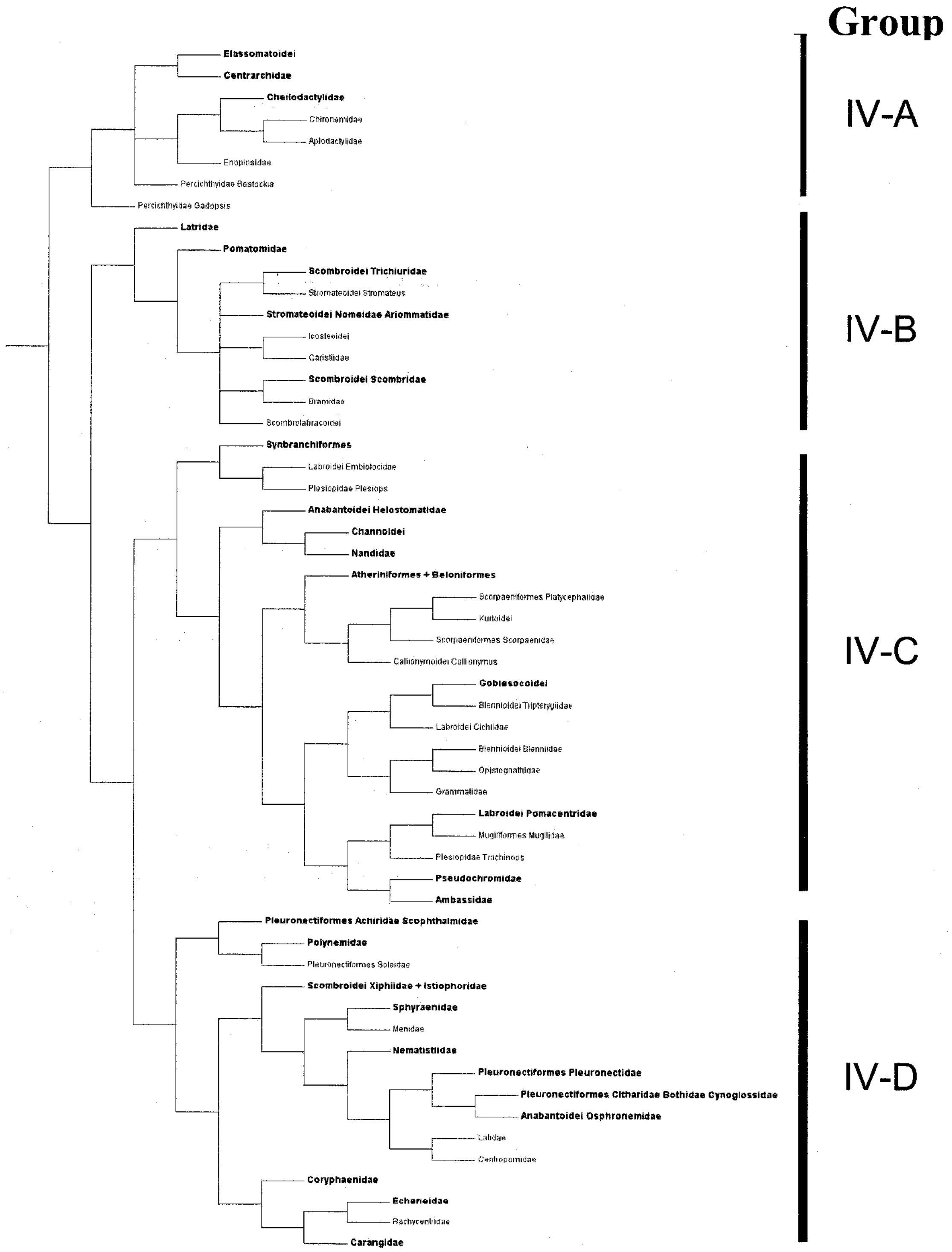


Fig. 9a. Group IV. Bold labels indicate multiple taxa are included in that group and have been collapsed. Figures 9b-e include nodal supports for clades. Unreadable taxa can be seen in the following figures (9b-e).

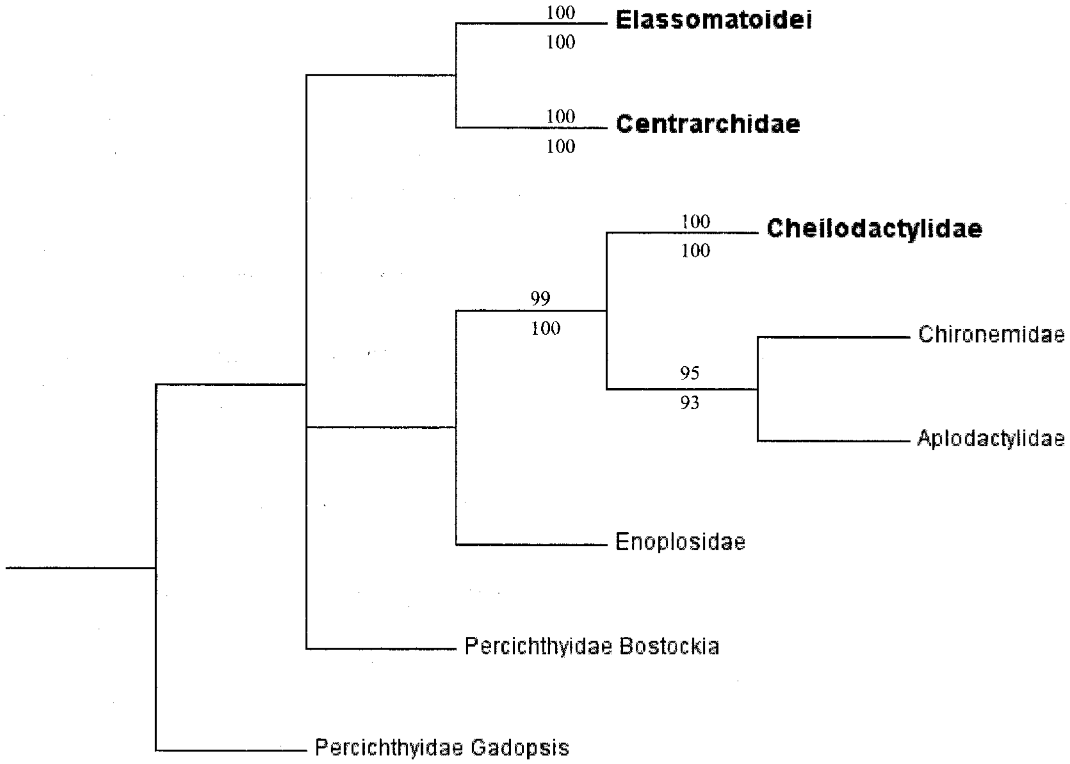


Fig. 9b. Group IV-A. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

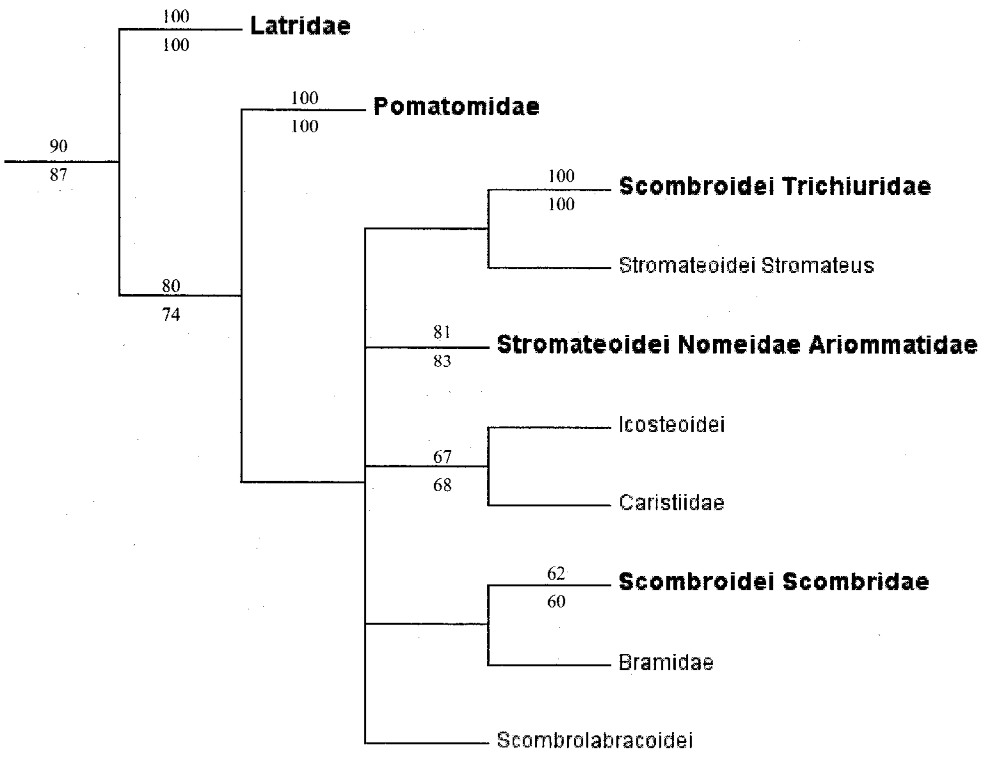


Fig. 9c. Group IV-B. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

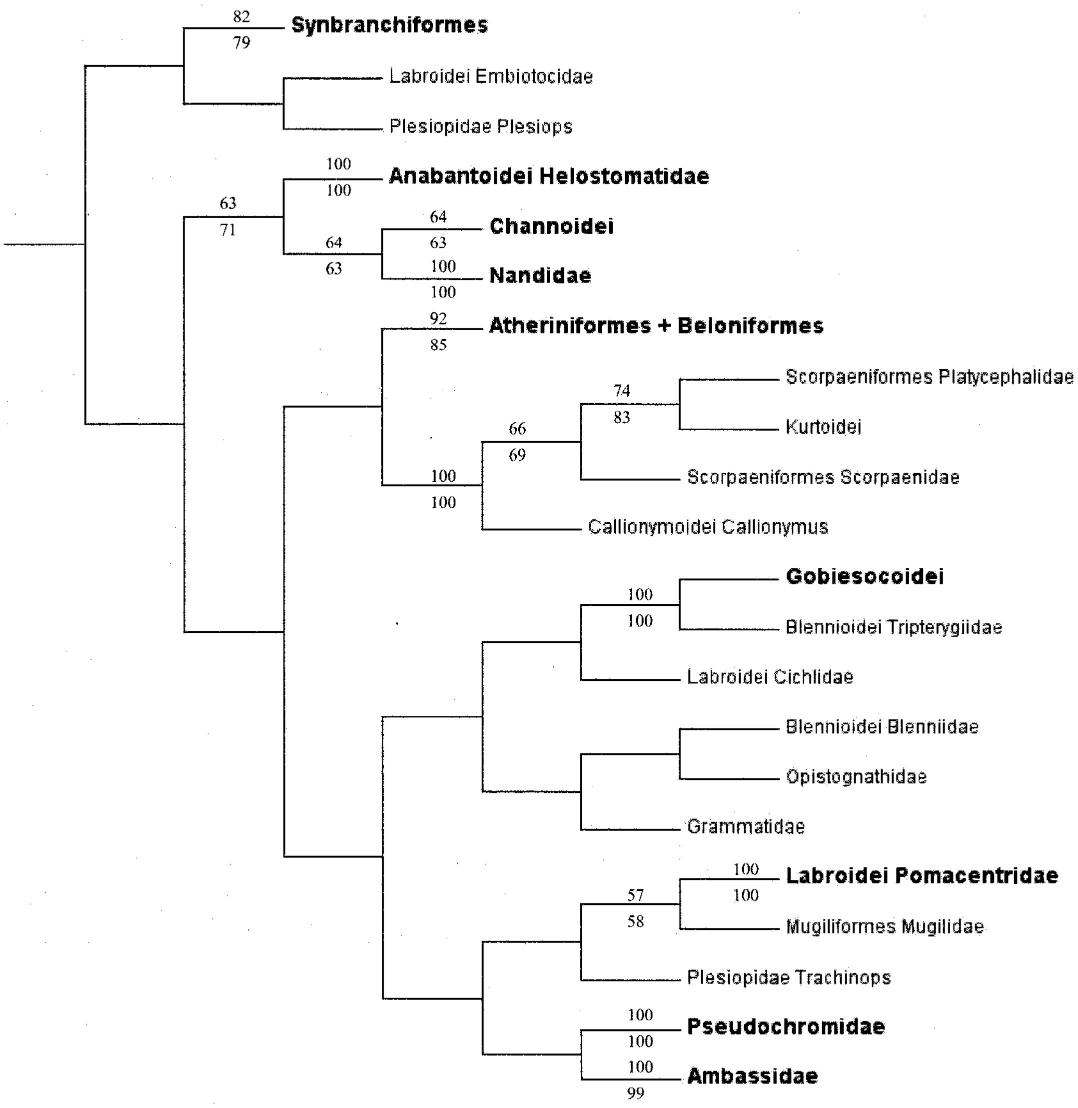


Fig. 9d. Group IV-C. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

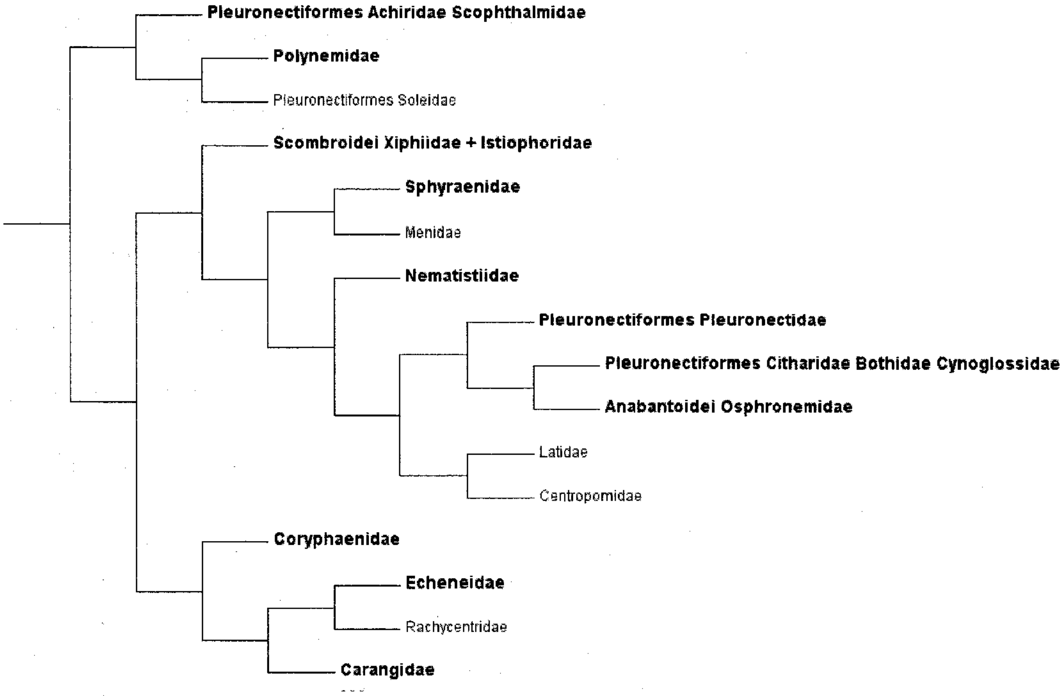


Fig. 9e. Group IV-D. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

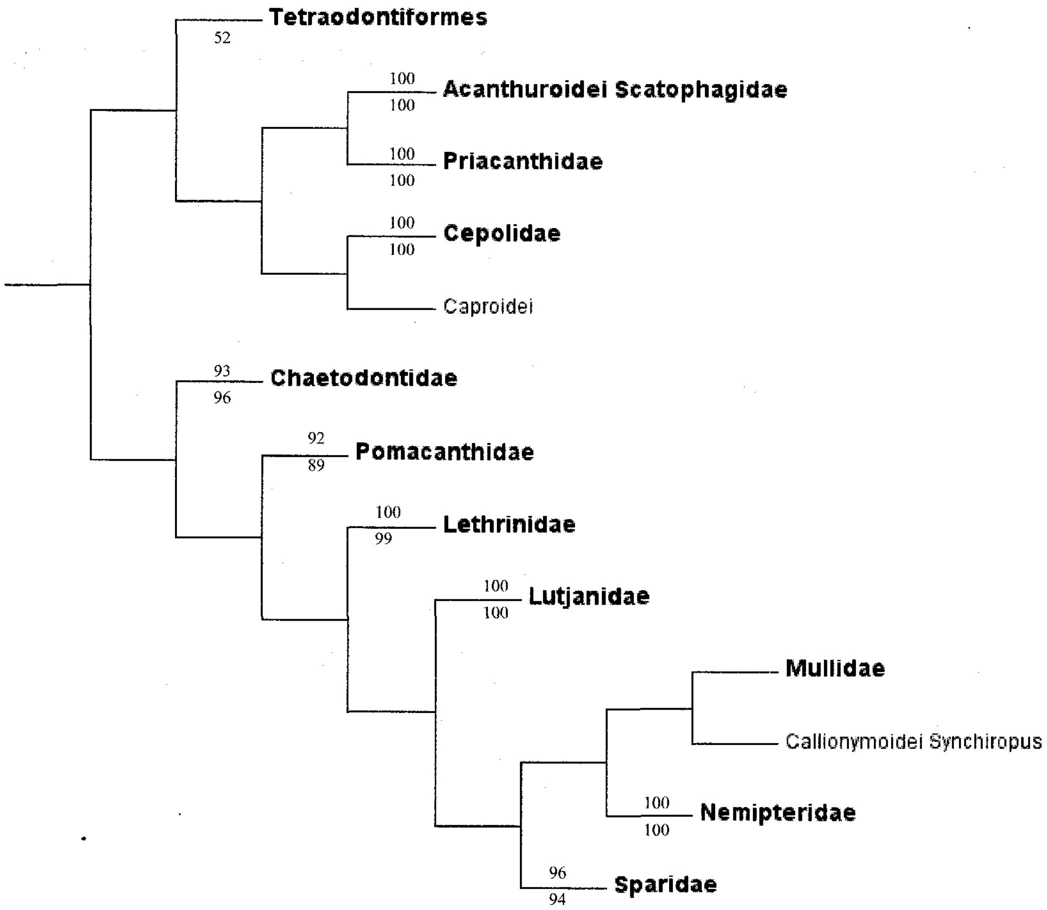


Fig. 10. Group V. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

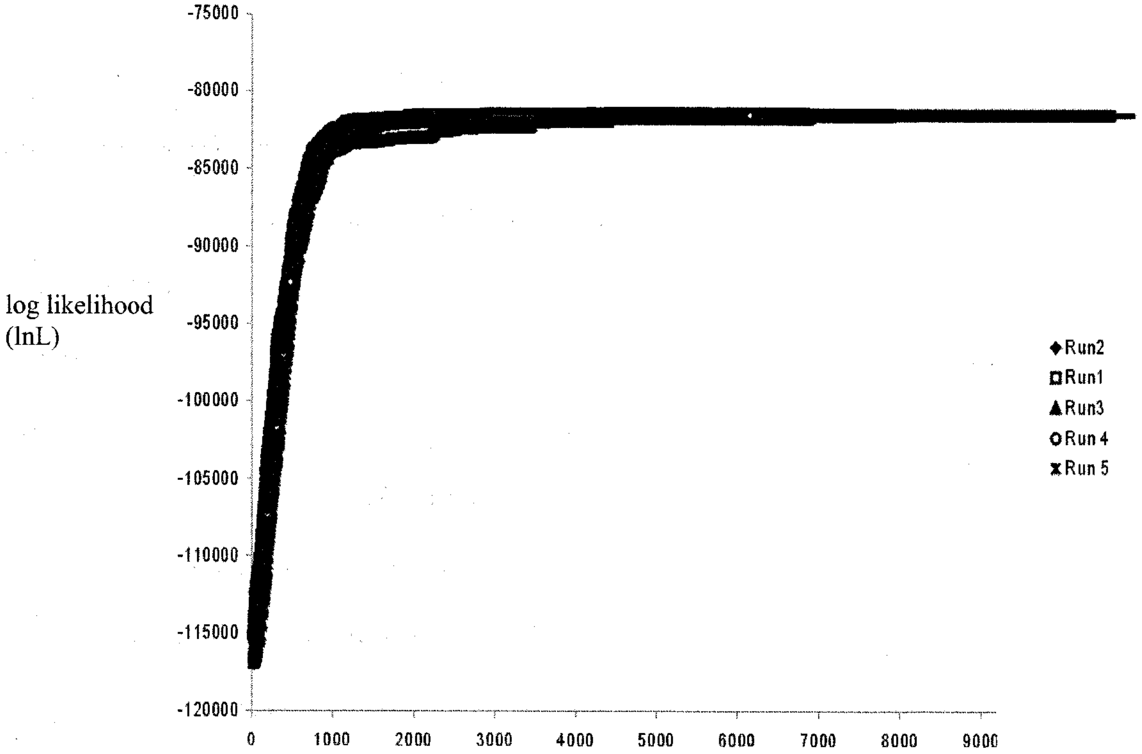


Fig 11. Plot of time (s) vs. log likelihood (lnL) values calculated in the maximum likelihood analysis by the program GARLI. Each run approaches approximately -80,000 and the best score, that with the lowest log likelihood value was lnL = -81469.25958 (Run #8).

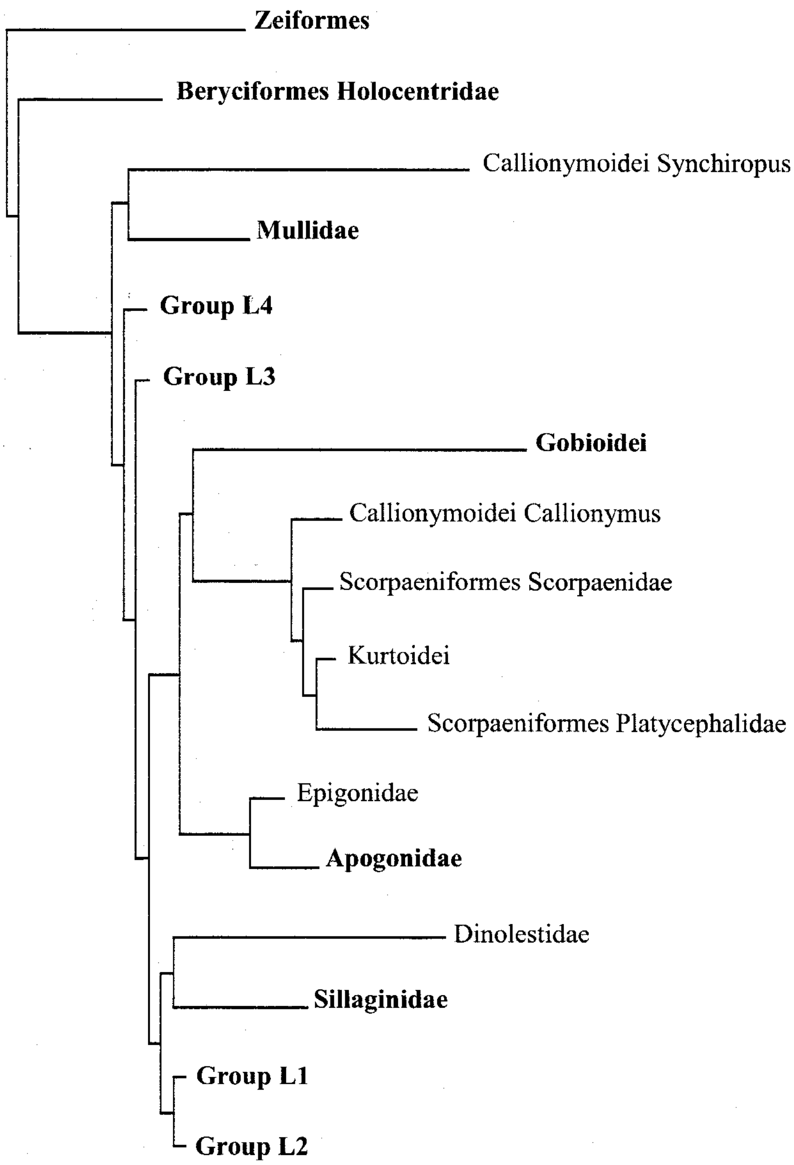


Fig. 12. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

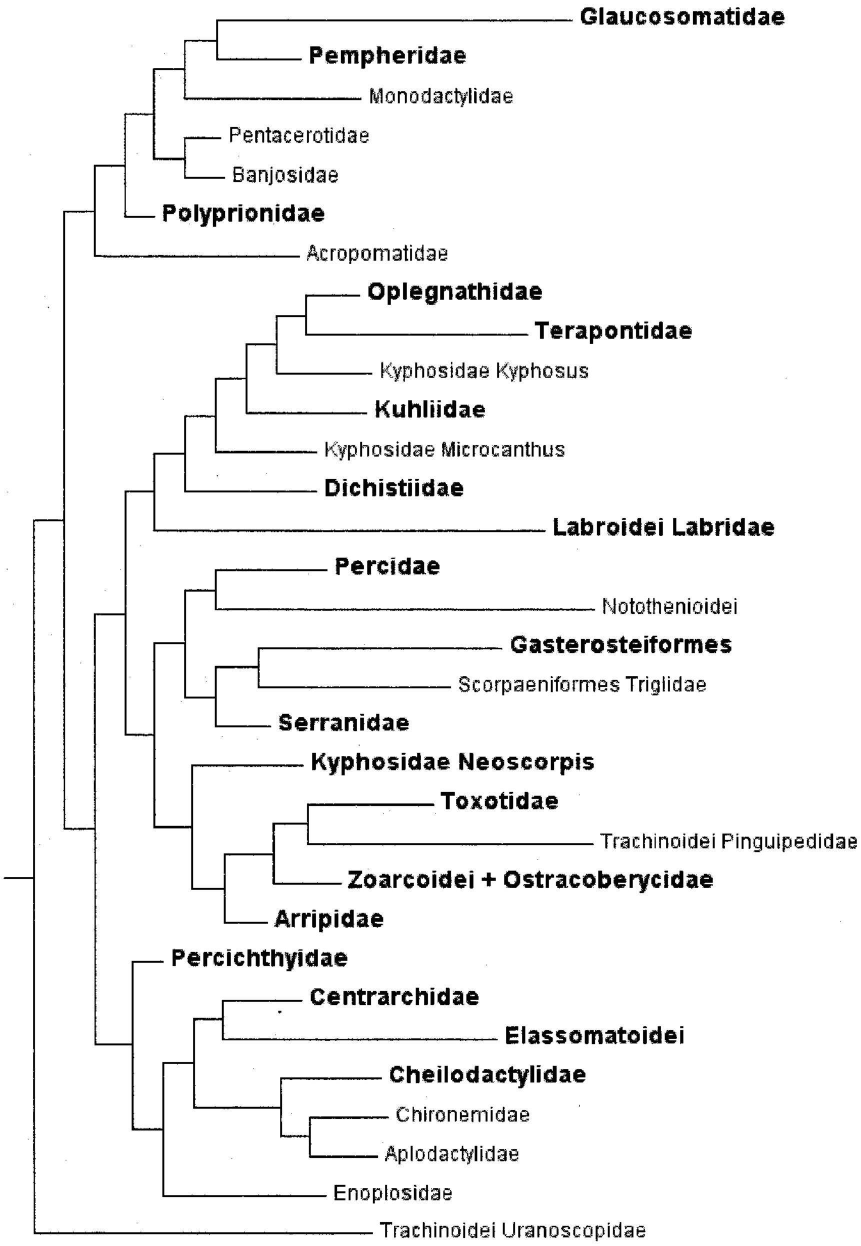


Fig 13. Group L1. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

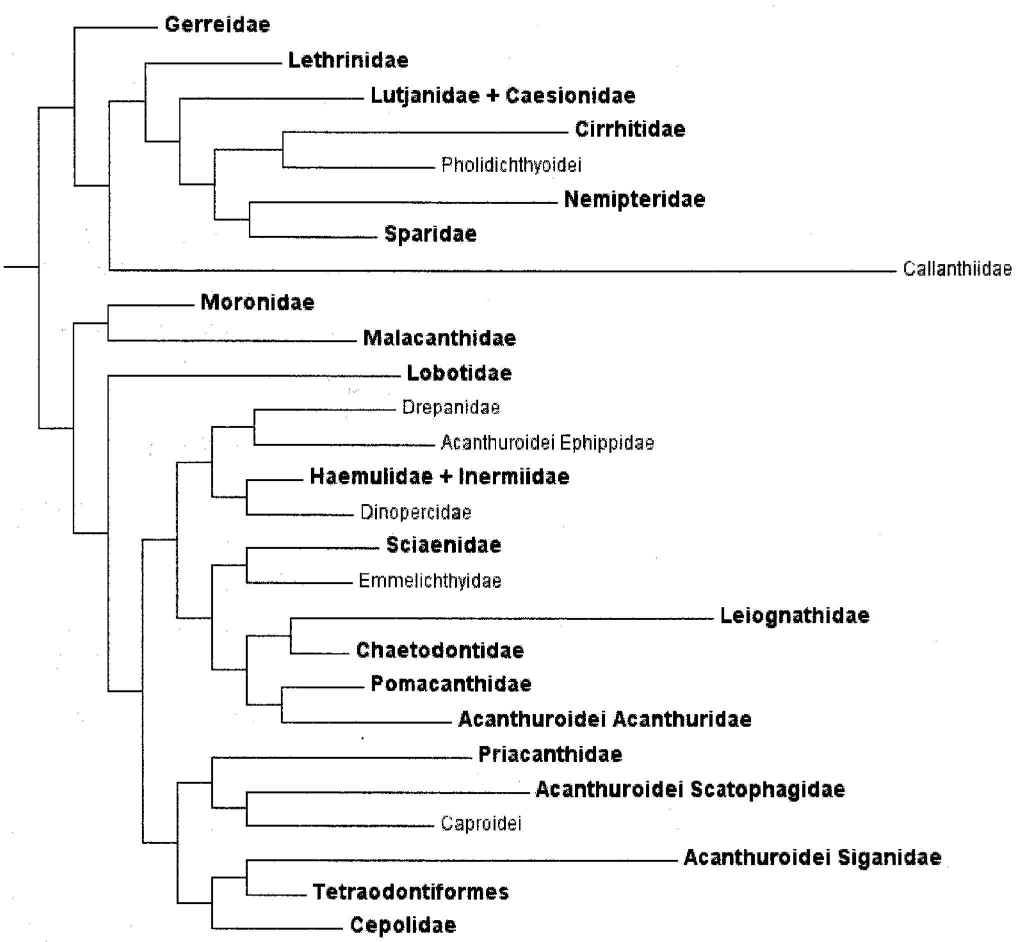


Fig 14. Group L2. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

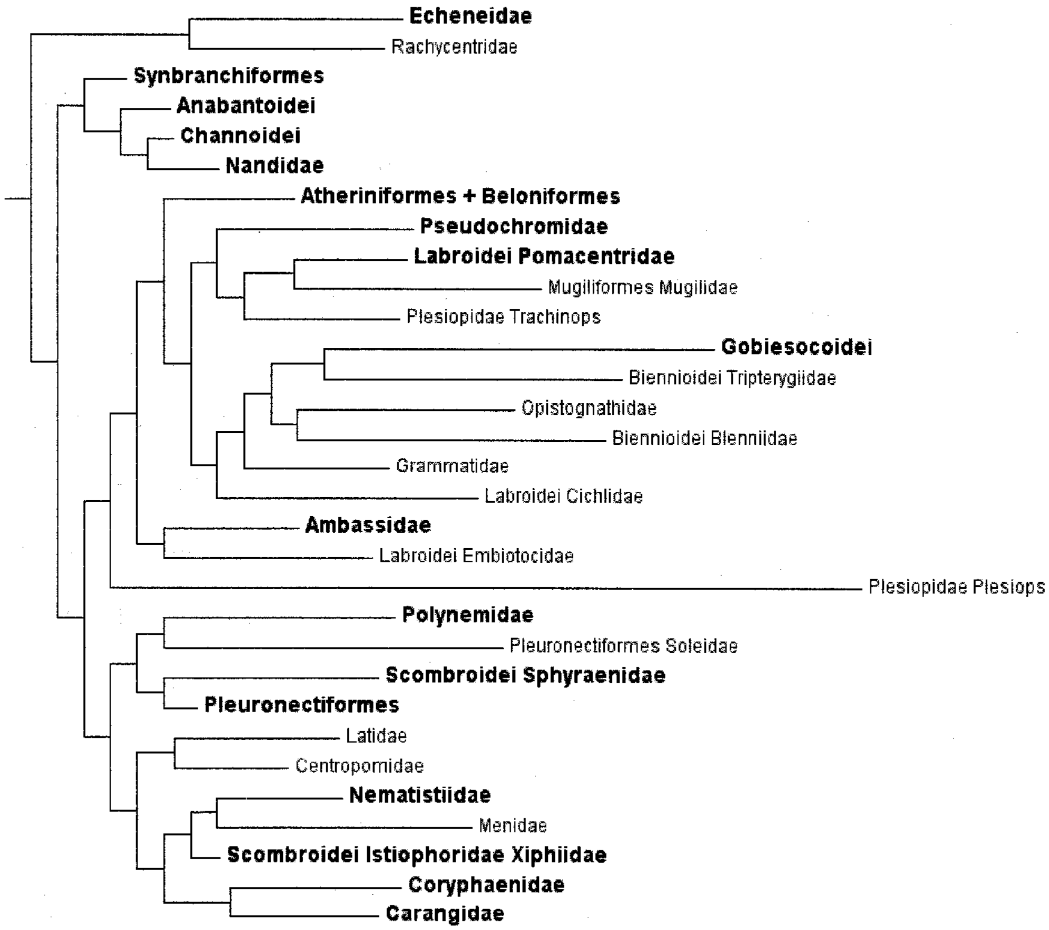


Fig. 15. Group L3. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

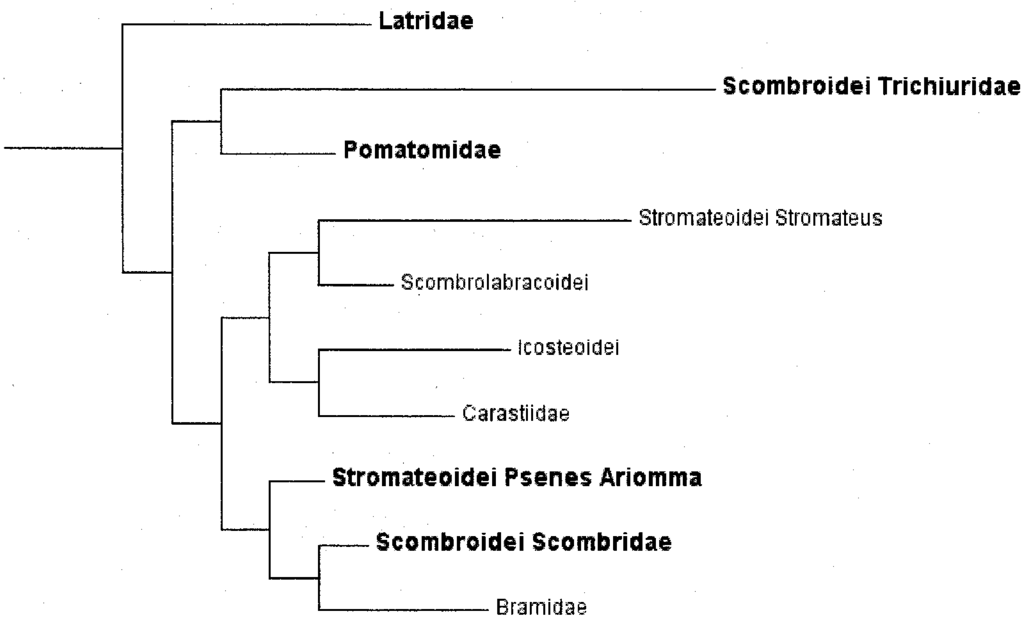


Fig. 16. Group L4. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

nodal support, respectively (Figure 8, Figure 9d). Parsimony places the Synbranchiformes sister to a group containing a percoid Plesiopidae and the labroid Embiotocidae (bootstrap and jackknife nodal support less than 50%; Figure 9d). The likelihood analysis places Synbranchiformes sister to anabantomorph taxa (Figure 15). The Gasterosteiformes are sister to the scorpaeniform family Triglidae in both analyses (Figure 8, Figure 13). Nodal supports for this clade are weak (bootstrap 56%, jackknife 58%; Figure 8). These relationships, along with previously published studies (e.g. Wiley et al., 2000; Miya et al., 2003; Chen et al., 2003; Springer and Orrell, 2004; Smith and Craig, 2007) cast doubt on the validity of the Smegmamorpha.

This study does not find a monophyletic Perciformes (sensu Nelson, 2006). Support is shown for the hypothesis of Johnson and Patterson (1993) and Nelson (2006) that the Pleuronectiformes, Scorpaeniformes, and Tetraodontiformes may be derivitives of the Perciformes. Composition and relationships within the series Percomorpha and order Perciformes hypothesized by previous authors are questioned by this dataset. Others have recently examined the limits and relationships of acanthomorph lineages and have begun to restructure these groups (Smith and Craig, 2007). They restrict the suborder Percoidei to the serranid *Acanthistius occelatus*, and the families Bathydraconidae, Bembropidae, Harpagiferidae, Niphonidae, and Percidae (Smith and Craig, 2007). Their work proposes a new group, the suborder Moronoidei, which includes the remaining families, previously placed within the suborder Percoidei. This study does not find a monophyletic Percoidei, nor does it obtain a monophyletic Moronoidei as described by Smith and Craig (2007).

Although this work fails to resolve a monophyletic Perciformes, it does present some novel and interesting relationships in terms of perciform suborder and family level groupings. Many of these will be described in the following paragraphs.

The Carangoidei (sensu Johnson, 1993), noted to contain the Nematistiidae, Carangidae, Coryphyaenidae, Rachycentridae, and Echeneidae, was not found as a monophyletic group in the parsimony or likelihood analyses. Maximum parsimony produced a group containing the phyletic sequence Coryphaenidae + (Carangidae + (Rachycentridae + Echeneidae)) (Figure 9e). However, this clade has weak nodal support with bootstrap values below 50% and a jackknife support of 54%. The Nematistiidae, along with other Percomorph taxa are in this larger clade, which has less than 50% nodal support (Figure 9e). The likelihood analysis places the Carangoidei of Johnson (1993) in a single clade, but this clade also includes other taxa such as the Latidae, Centropomidae, Menidae, and the scombroid billfishes (Istiophoridae and Xiphiidae) (Figure 15). The relationships of these families, i.e. those classified by Nelson (2006) as members of the suborder Percoidei, will be discussed in the next chapter of this dissertation.

The suborder Elassomatoidei (bootstrap 100%, jackknife 100%), a member of Johnson and Patterson's (1993) Smegmamorpha, are found sister to the percoid family Centrarchidae in both parsimony and likelihood analyses and are not seen as sister to other putative smegmamorph taxa (Figure 9b, Figure 13). Parsimony analyses show less than 50% bootstrap and jackknife supports for this clade. These results, although weakly supported, contradict previous studies, (e.g. the total evidence study of Wiley et al., 2000) that have refuted an *Elassoma*-centrarchid relationship.

The perciform suborder Labroidei is found to be polyphyletic in both the parsimony and likelihood analyses of this study. Parsimony finds the Labridae external to most percomorph taxa with 100% bootstrap and jackknife support, whereas likelihood finds the labridae sister to an group containing the families Terapontidae, Oplegnathidae, Kyphosidae, Dichistiidae, and Kuhliidae (Figure 12, Figure 13). The Cichlidae are seen in a clade containing the Gobiesocoidei, Blennioidei, Opistognathidae, and the Grammatidae in both parsimony and likelihood with below 50% nodal support seen in the parsimony analysis (Figure 9d, Figure 15). The Pomacentridae are found sister to the Mugiliformes in both the parsimony (boostrap 57%, jackknife 58%) and likelihood analyses (Figure 9d, Figure 15). The Embiotocidae are sister to the pseudochromids in the parsimony analysis with bootstrap and jackknife nodal supports less than 50%, whereas in the likelihood analysis, it is found as sister to the Ambassidae (Figure 9d, Figure 15). The monophyly of the labroids, supported "beyond any reasonable doubt" by Stiassny and Jensen (1987) is rejected by this investigation. The data presented here and in other studies, question the monophyly of the suborder (Streelman and Karl, 1997; Smith and Wheeler, 2006; Smith and Craig, 2007).

The Zoarcoidei are paraphyletic in both the parsimony and likelihood analyses without the inclusion of the percoid family Ostracoberycidae (Figure 8, Figure 13). This clade is well supported in the parsimony analysis (bootstrap 100%, jackknife 99%). Previous work has found the Zoarcoidei to be polyphyletic (Springer and Orrell, 2004). This work does not agree with Smith and Craig (2007) who found no relationship between the Ostracoberycidae and the Zoarcoidei. Future studies investigating the monophyly of this group with greater taxon sampling are warranted.

The placement of the Notothenioidei differs in the parsimony and likelihood analyses. Parsimony finds the suborder sister to the suborder Gobioidei and these two as sister to the Percidae, although these clades show less than 50% nodal support (Figure 8). In the likelihood analysis, the Gobioidei are not found in this clade and the Notothenioidei is grouped sister to the percoid family Percidae (Figure 13). To some degree, this study supports a notothenioid-percid relationship. This relationship has been previously suggested by Chen et al. (2003). However, a greater taxon sampling of the Notothenioidei is necessary in future investigations to test the monophyly of the suborder, which was questioned by Lecointre et al. (1997).

The members of the Trachinoidei included in this study do not form a monophyletic group in either the parsimony or likelihood analysis, which has been previously questioned (e.g. Johnson, 1993; Mooi and Johnson, 1997; Chen et al., 2003; Smith and Wheeler, 2006; Smith and Craig, 2007). The Pinguipedidae is sister to the percoid apogonid-epigonid clade in the parsimony analysis with nodal support less than 50% and as sister to the percoid family Toxotidae in the likelihood analysis (Figure 8, Figure 13). The Uranoscopidae are sister to the Acropomatidae, Cirrhitidae, and Pholidichthyoidei in the parsimony analysis (bootstrap and jackknife less than 50%) and sister to a large group of percomorph taxa in the likelihood investigation (Figure 7, Figure 13). This study does not support the monophyly of the Trachinoidei, which has previously been questioned.

The suborder Pholidichthyoidei is found sister to the percoid Cirrhitidae with moderate nodal support (bootstrap 69%, jackknife 66%) in the parsimony analysis (Figure 7). The parsimony analysis places the Pholidichthyoidei-Cirrhitidae clade sister to the Acropomatidae with nodal support less than 50%. In the likelihood analysis, this group is within a clade that includes members of the percoid families Sparidae, Nemipteridae, Lutjanidae, Caesionidae, and Lethrinidae (Figure 14). This study does not support previous hypotheses involving relationships of the Pholidichthyoidei with the Labroidei, Blennioidei, or Trachinoidei (Springer and Johnson, 2004; Springer and Orrell, 2004; Nelson, 1994).

Although with different internal topologies, both parsimony and likelihood place the Blennioidei in a clade containing the labroid Cichlidae, the suborder Gobiesocoidei, and the percoid families Opistognathidae and Grammatidae (Figure 9d, Figure 15). This larger clade has less than 50% nodal support in the parsimony analysis. The blennioid-gobiesocoid relationship supports the morphological findings of Springer and Orrell (2004). The relationship of the Blennioidei to the percoid families Opistognathidae and Grammatidae is similar to the findings of Smith and Wheeler (2006) and Smith and Craig (2007) who find the Grammatidae, Opistognathidae, and percoid Pseudochromidae sister to the blennioid fishes.

The Icosteoidei is sister to the percoid family Caristiidae in both parsimony and likelihood investigations (Figure 9c, Figure 16). Nodal support for this clade in the parsimony analysis is moderate (bootstrap 67%, jackknife 68%). The Icosteoidei and Caristiidae are found in a clade that includes the Scombrolabracoidei, Stromateoidei, Scombridae, and Trichiuridae. The affinity of the Icosteoidei to stromateoids is supported by Smith and Wheeler (2006) and Smith and Craig (2007). Also supported is the Icosteoidei-Scombroidei relationship postulated by Smith and Wheeler (2006).

The two callionymoid species included in this investigation are not found as a monophyletic group. One (*Callionymus*) is seen in a well supported clade (parsimony: bootstrap and jackknife values of 100%) as sister to the clade containing scorpaeniform taxa and the Kurtoidei (Figure 9d, Figure 5), and the second (*Synchiropus*) as sister to the Mullidae and has less than 50% nodal support in the parsimony analysis (Figure 10, Figure 5). Previous studies show different relationships for this suborder (see introduction), and Smith and Wheeler (2006) also failed to produce a monophyletic Callionymoidei.

The Gobioidei are found as a monophyletic group in this study (bootstrap 100%, jackknife 100%), but sister groups of the suborder differ between the parsimony and likelihood analyses. Maximum parsimony finds the Gobioidei sister to the Notothenioidei and these as sister to the percoid family Percidae (nodal support less than 50%; Figure 8). Likelihood analyses find the Gobioidei sister to a clade containing scorpaeniform, kurtoid, and callionymoid taxa (Figure 5). Previous studies suggesting affinities of the Gobioidei to callionymoids are supported in the likelihood analyses of this study (see Nelson, 2006). However, groupings of the gobioids and the trachinoids, scorpaeniform hoplichthyids, or the percoid family Apogonidae are not supported as previously suggested (Winterbottom, 1993; Smith and Wheeler, 2006).

The nurseryfish (Kurtoidei) are in a clade with the scorpaeniform Platycephalidae, and these sister to the family Scorpaenidae in both the parsimony and likelihood trees (Figure 9d, Figure 5). Bootstrap and jackknife support for this clade is 100% in the parsimony analysis. The proposed relationships of the Kurtoidei to the Beryciformes, percoid Pempheridae, and Apogonidae (Tominaga, 1968; Johnson, 1993;

Smith and Wheeler, 2006; Smith and Craig, 2007) are not supported in this study. Also, the relationship between the Kurtoidei and Gobioidei presented by Smith and Wheeler (2006) is not supported with the RAG1 dataset.

In agreement with previous molecular work (Holcroft, 2004; Smith and Wheeler, 2006), the suborder Acanthuroidei are polyphyletic in these analyses (Figure 5, Figure 10, Figure 14). Maximum parsimony finds the Siganidae sister to the percoid family Leiognathidae (bootstrap and jackknife less than 50%), the Ephippidae sister to the percoid Drepaneidae (bootstrap 75%, jackknife 75%), and the Scatophagidae in a clade containing the Priacanthidae, Cepolidae, and the Caproidei (bootstrap and jackknife less than 50%). In the likelihood analysis, the Acanthuridae are sister to the Pomacanthidae, which is sister to a group containing the Leiognathidae and the Chaetodontidae. The leiognathid-acanthuroid relationship is also seen in the morphological study of Springer and Orrell (2004). The Ephippidae + Drepaneidae are found sister to the percoid families (Haemulidae + Inermiidae) + Dinopercidae in the likelihood analysis (Figure 14). The Scatophagidae, Siganidae, the percoid families Priacanthidae and Cepolidae, the suborder Caproidei, and the Order Tetraodontiformes form a clade in the likelihood analysis (Figure 14). The relationship between acanthuroid taxa and tetraodontiform taxa is similar to previous studies that describe the interrelationships of these groups (Lauder and Liem, 1983; Holcroft, 2004).

The Scombroidei, as defined by Nelson (2006) is polyphyletic in both the parsimony and likelihood analyses. Parsimony produces a well-supported group that includes the Trichiuridae, Scombridae, Stromateoidei, Icosteoidei, Caristiidae, Bramidae, Scombrolabracoidei, Pomatomidae, and Latridae (Figure 9c; 90% bootstrap, 87% jackknife support). The other clade of scombroid taxa that includes the billfishes and the Sphyraenidae are included with other taxa such as the Carangidae, Nematistiidae, Echeneidae, Rachycentridae, Coryphaenidae, Menidae, Latidae, Centropomidae, and many pleuronectiform taxa (Figure 9e). This clade has less than 50% bootstrap/jackknife support. Likelihood analyses also present a polyphyletic Scombroidei (Figure 15, Figure 16). Recently, nuclear and mitochondrial DNA (Tmo-4C4 and cytochrome B) were used to show that the billfishes and tunas and mackerels were not a monophyletic group (Orrell et al, 2006). Collette et al. (2006) also support the separation of the billfishes from the Scombridae. Sperm morphology has also been used to describe differences between the billfishes and other scombroids (van der Straten et al., 2006). These investigations, along with the current results provide strong evidence for the separation of the billfishes and Sphyraenidae from the remaining scombroid fishes.

The Stromateoidei are not monophyletic in this study and are found in a group containing scombroid, scombrolabracoid, icosteoid, and other percoid taxa (Figure 9c, Figure 16). Nodal support in the parsimony analysis is shown for the stromateoid families Nomeidae + Ariommatidae (bootstrap 81%, jackknife 83%). Smith and Wheeler (2006) do not present a monophyletic Stromateoidei in their investigation. They found the stromateoids among many of the same taxonomic groups, including scombroid, icosteoid, and scombrolabracoid taxa.

The suborder Anabantoidei is not monophyletic in the maximum parsimony analysis (Figure 9d, Figure 9e). Two groups of labrynth fishes are seen: the Helostomatidae are sister to the Channoidei + Nandidae (bootstrap 63%, jackknife 71%)

and the Osphronemidae are in the clade containing scombroids and many of the Pleuronectiform taxa with less than 50% bootstrap and jackknife nodal support. However, the Anabantoidei are monophyletic in the likelihood and all are sister to the clade containing the Channoidei and the Nandidae (Figure 15). The Channoidei-Anabantoidei relationship is also noted in previous morphological and molecular investigations (Springer and Orrell, 2004; Smith and Wheeler, 2006). The placement of the channoid-anabantoid group sister to the percoid badids and nandids is also supported in previous studies (Britz, 2003).

Base compositional bias in the RAG1 gene could be the cause of questionable phylogenetic results in this investigation. Seven of the ten pleuronectiform taxa in this study have a GC content at the third position base of greater than 70%. The average ENC value of those seven taxa is 44.0, fourteen percent lower than the average ENC value seen for the dataset as a whole. Unequal nucleotide frequencies at the third codon position, such as those with high GC content, can result in a low ENC value. Thus, those taxa with high GC content should display a markedly lower ENC value, as is seen in many of the Pleuronectiform taxa (Wright, 1990; Chang and Campbell, 2000). Two pleuronectiform taxa (*Arnoglossus imperialis* and *Arnoglossus blochei*) have ENC values of 37.9 and 38.6 respectively. These low values, combined with their relatively high GC content at third position codons (85.7% and 83.6%) could combine to disrupt phylogenetic signal in the Pleuronectiformes and lead to the artificial groupings seen in these analyses (Chang and Campbell, 2000). Other taxonomic groupings could be affected by these properties also, as 47 of the 279 sequences included in this study have a GC content at the third codon position of over 70.0% and 224 of the 279 sequences have over 60.0% GC at the third codon position.

Nodal supports in the parsimony analysis are strong for the higher-level phylogenetic relationships found in this investigation. This includes a well-supported monophyletic grouping of the Percomorpha (sensu Johnson and Patterson, 1993), the beryciform Holocentridae as sister to this clade, and the Zeiformes as the outgroup of the dataset. Also supported are many of the smaller, more 'family-level' clades. Taxonomic resolution using the RAG1 gene may be limited to these levels as mid-level taxonomic groupings that constitute the spine of the parsimony tree show less than 50% nodal support for the dataset. Compositional biases such as those discussed above may inhibit the efficacy of RAG1 to elucidate the relationships at the mid-levels of the phylogenetic trees in this investigation (Meyer, 1994; Brocchieri, 2001). Resolution at these levels could be strengthened with an increased taxon sampling and an increased number of appropriate genetic and/or morphological characters.

Many of the relationships derived in the maximum parsimony analysis of the RAG1 dataset have nodal supports with values less than 50%. It is expected that maximum likelihood, given appropriate computer resources and time, would also present low values for these internal clades. These low support values could be indicative of some unnatural groupings. For example, in both the maximum parsimony and likelihood analyses, the Pleuronectiformes and perciform suborder Callionymoidei are not found to be monophyletic groups. Both groups have been previously described as monophyletic (e.g. Springer and Orrell, 2004). Other studies, however, have shown the Pleuronectiformes to be polyphyletic and the Callionymoidei to be paraphyletic without the inclusion of the Batrachoidiformes (Smith and Wheeler, 2006). Also, the polyphyletic Anabantoidei in the maximum parsimony analysis is likely an example of long-branch attraction due to the inherent properties of the RAG1 gene (the high GC content at the third codon position).

The taxa sampled in this study represent one of the most inclusive molecular datasets, to date, testing the monophyly of the Perciformes and phylogenetic relationships of its suborders. The strategy adopted here was to utilize a single gene while maximizing the taxon sampling of the dataset, rather than attempting a multi-gene phylogeny with limited taxa. The phylogenetic hypotheses inferred here are an important step toward an understanding of percomorph relationships and need to be further tested. However, the RAG1 gene, as Holcroft (2004) states, should not be used as a "magic bullet" in elucidating the phylogenies of large groups of fishes. The consistent lack of node support for mid-level clades in this study reinforces this notion. It is hoped that the data generated in this study will be used as the basis for further studies. If the taxon sampling is replicated and expanded using other genes, the bush at the top of the teleostean tree may eventually be resolved.

CHAPTER III

A MOLECULAR ANALYSIS OF THE FAMILIES OF THE SUBORDER PERCOIDEI

Introduction

The suborder Percoidei (Perciformes) contains 79 families, 549 genera, and approximately 3,176 species, making this the largest and most diverse of the perciform suborders (Johnson, 1984; Nelson, 2006). Ten of the percoid families are described as monotypic and twenty-six are restricted to a single genus (Nelson, 2006). Twelve percent of the percoids (380 species) are classified as freshwater species and many other species comprise a significant component of the reef environment in tropical and subtropical marine ecosystems (Nelson, 2006; Johnson, 1984).

First described by Regan (1913), the suborder was classified as a group lacking the characteristics of the other perciform fishes. Johnson (1984) noted that there is no single characteristic that unites the Percoidei into a monophyletic group. He also stated that the suborder serves as a generalized repository for perciform families that cannot be placed in one of the other suborders. Johnson (1993) acknowledged that the Percoidei is the largest and most diverse of all perciform suborders, but characterizes it as undoubtedly polyphyletic. Nelson (2006) presented a generalized list of thirteen morphological characters that separate the Percoidei from “lower teleosts” (Table 5) but do not distinguish the Percoidei as monophyletic.

Table 5. Morphological characters that separate the suborder Percoidei from the "lower teleosts". From Nelson (2006).

Morphological Character	**Lower Teleosts**	**Percoidei**
Spines in fins	Absent	Present in dorsal, anal, and pelvic fins
Dorsal fin number	One, adipose fin may also be present	Two, never an adipose fin
Scales	Cycloid	Ctenoid
Pelvic fin position	Abdominal	Thorasic
Pelvic fin rays	Six or more soft rays	One spine and five soft rays
Pectoral fin base	Ventral and horizontal	Lateral and vertical
Upper jaw bordered by	Short premaxilla and long maxilla	Premaxilla
Swim bladder	Duct present (physostomes)	Duct absent (physoclists)
Orbitosphenoid	Present	Absent
Mesocoracoid	Present	Absent
Epipleural and epicentral bones	Present	Absent
Bone cells in bone of adult	Present	Not apparent
Principal caudal fin ray number	Often 18 or 19	Never more than 17, often fewer

Few attempts have been made to characterize the Percoidei as a monophyletic group or to challenge its monophyly (Johnson, 1993). In their description of serranid and percid fishes, Smith and Craig (2007) used 4036 base pairs of nuclear and mitochondrial DNA from 180 acanthomorph fishes to attempt to resolve phylogenetic relationships within this diverse group. The aim of their study was to investigate placement of the Serranidae and Percidae within the framework of the Percomorpha. Smith and Craig (2007) utilized 93 percomorph families from 25 suborders. Their results redefine the order Perciformes and limit the suborder Percoidei to few families, instead placing most of the former percoids in the newly erected suborder Moronoidei.

Even though few investigations have been made to test the monophyly of the suborder, morphological and molecular investigations have tested individual relationships of a number of percoid families. The following paragraphs describe a subset of these studies, demonstrating the information currently available in the literature.

In a morphological analysis of latid fishes, Otero (2004) used 29 characters to demonstrate the family Centropomidae as paraphyletic and that the subfamily Latinae should be placed in a separate family. Mooi and Gill (1995) also supported the family status of the Latidae in their morphological acanthomorph investigation. Nelson (2006) stated that the Centropomidae is the sister family of the Ambassidae and the Latidae are sister to the Serannidae. These conclusions were based on the morphological work of Otero (2004). Springer and Orrell's (2004) morphological investigation found the Latidae sister to the Centropomidae in a large clade of percomorph fishes. Smith and

Wheeler (2006) placed the Centropomidae sister to the scombroid family Xiphiidae in their molecular analyses of venomous bony fishes.

Smith and Wheeler (2006) found the family Ambassidae sister to the acanthuroid Scatophagidae. Other studies have noted a relationship between the Ambassidae and the Centropomidae (Otero, 2004; Nelson, 2006). Springer and Orrell (2004) placed the ambassids sister to the scombroid family Centrolophidae in a larger clade of perciform fishes.

The family Percichthyidae are thought to be a scombroid outgroup through comparison of dentition patterns (Johnson, 1986; Johnson, 1993). Smith and Wheeler (2006) found the Percichthyidae to be polyphyletic with the genus *Bostockia* sister to the percoid family Cirrhitidae, and *Howella* sister to the percoid family Moronidae. Smith and Wheeler (2006) presented the percoid family Polyprionidae as polyphyletic within a clade containing the Acropomatidae, Pentacerotidae, Dinolestidae, Percichthyidae, and Moronidae.

Nolf (1993) noted that the family Acropomatidae has an affinity for families of the perciform suborder Scombroidei in his study of percoid otoliths. Using gill arch muscle and skeletal characters, Springer and Orrell (2004) found the Acropomatidae in a clade that includes the Percichthyidae, Terapontidae, Leptobramidae, Coryphaenidae, Glaucosomatidae, Ammodytidae (suborder Trachinoidei), Nematistiidae, Ostracoberysicae, Caristiidae, Latidae, Centropomidae, Pempheridae, Epigonidae, Kuhliidae, Moronidae, Lutjanidae, Toxotidae, Centrolophidae (suborder Scombroidei), and Ambassidae. Smith and Wheeler (2006) placed the acropomatids sister to a group that contains the percoid families Polyprionidae, Pentacerotidae, Dinolestidae, Percichthyidae, and Moronidae.

Johnson (1984, 1993) presented the Callanthiidae and Grammatidae as separate families, helping clarify the composition of the Grammatidae described by Greenwood et al. (1966). Gill and Mooi (1993) supported the monophyly of these two families. Springer and Orrell (2004) described the grammatids as the basal group of a clade containing the Opistognathidae, Gerreidae, Pseudochromidae, Nandidae, Badidae, and other percomorphs. Smith and Wheeler (2006) found the Grammatidae sister to a clade containing the Pseudochromidae, Opistognathidae, and the perciform suborder Blennioidei. Also thought to be allied with these families, the Acanthoclininae (family Plesiopidae) were found to have a close relationship with the Notograptidae (Smith-Vaniz and Johnson, 1990; Gill and Mooi 1993).

The sister group of the family Centrarchidae is the subject of much debate in the literature. Greenwood et al. (1966) placed the pigmy sunfish (Suborder Elassomatoidei, *Elassoma*) within the family Centrarchidae. Johnson (1984) rejected the relationship of these two groups. Wiley et al. (2000) noted that the Centrarchidae were not sister to the elassomatoids, but instead were the sister group of the Moronidae. Smith and Wheeler (2006) found the centrarchids sister to a clade containing the families Cheilodactylidae and Chironemidae.

Springer and Orrell (2004) found the family Percidae in a clade containing the gobioid family Rhyacichthyidae and the Sillaginidae. Le et al. (1993) recovered the percids sister to the scorpaeniform Triglidae. The Percidae have also been described as sister to a group containing scorpaeniform and serranid taxa (Smith and Wheeler, 2006).

Smith and Craig (2007) found the Percidae to be monophyletic and their results postulate the Bembropidae and notothenioids as sister groups to the percids.

The Apogonidae of Greenwood et al. (1966) included the Epigonidae and Dinolestidae. Nelson (2006) noted a primary difference between the Apogonidae and percoid family Epigonidae is that the epigonids have 25 vertebrae, rather than 24 seen in the apogonids. The dorsal gill arch elements of the family Apogonidae are similar to that of the nurseryfish (suborder Kurtoidei) supporting a relationship between these two groups (Johnson, 1993). Johnson (1993) also stated that similar structures have been found in other perciform groups, including the Gobioidei. The apogonids possess filaments around the micropyle of their eggs to bind them together, similar to those that bind nurseryfish egg masses (Johnson, 1993). Recent molecular evidence supports a relationship between the Apogonidae and the Kurtoidei, with these two groups sister to the suborder Anabantoidei (Smith and Craig, 2007).

Nolf (1993) noted that the Pomatomidae share similar otolith characteristics with the scombroid fishes. Springer and Orrell (2004) described the Pomatomidae as sister to the Symphysanodontidae. Smith and Wheeler (2006) placed the pomatomids in a clade with the Arripidae and these two families sister to a clade of scombroid taxa.

Johnson (1993) proposed that the carangoid fishes, including the percoid families Carangidae, Rachycentridae, Echeneidae, Coryphaenidae and Nematistiidae, be placed in a separate suborder, the Carangoidei. Work using larval morphological characters of these fishes has presented a monophyletic group comprised of the Echeneidae, Rachycentridae, and Coryphaenidae (Johnson, 1984). Another morphological investigation using 138 characters resolved the superfamily Echeneoidea with the phyletic sequence Coryphaenidae, (Rachycentridae, Echeneidae) (O'Toole, 2002). The phyletic sequence Nematistiidae, Echeneidae, Carangidae has also been postulated (Smith-Vaniz, 1984).

Smith and Wheeler (2006) found the percoid family Emmelichthyidae sister to a clade containing members of the perciform suborder Acanthuroidei. They also placed the monotypic Enoplosidae sister to the acanthuroid *Zanclus cornuta*. These two taxa were found sister to a clade containing the Monodactylidae, Emmelichthyidae, and various acanthuroids (Smith and Wheeler, 2006).

In his investigation of the limits and relationships of the family Lutjanidae, Johnson (1980) used morphological information to show a close relationship between the Caesionidae and the Lutjanidae. Based on information from Johnson (1980) and Carpenter (1990) describing the relationship between the subfamily Lutjaninae and Caesionidae, Nelson (1994) noted that the family Lutjanidae is paraphyletic without inclusion of the Caesionidae. However, Nelson (2006) revised this relationship and noted that the two families should remain separate until more original research can clarify the relationship between the two families.

The family Inermiidae is likely a derivative of the Haemulidae (Nelson, 2006). Johnson (1980) also supported a relationship between these two families.

In his review of percomorph phylogenetics, Johnson (1993) stated that Gosline (1962; 1968; 1971) noted an association of the Polynemidae and the Sphyraenidae, mugilids, and atherinoids. Larval characteristics of the family Polynemidae provide evidence of an affinity to the Sciaenidae (de Sylva, 1984). Freihofer (1978) noted a similar membranous prenasal canal extension in both the Polynemidae and Sciaenidae.

Johnson (1993) proposed that there was enough morphological similarity between the polynemids and sciaenids to include the two groups in the superfamily Polynemoidea. However, Springer and Orrell (2004) showed the Polynemidae and Sphyraenidae were sister groups and the Sciaenidae sister to the Bathyclupeidae. Smith and Wheeler (2006) placed the polynemids in a clade with the Menidae and the scombroid family Sphyraenidae.

Nelson (2006) noted that the Pempheridae and Glaucosomatidae are closely related based on a complex association of the swim bladder and vertebra. Johnson (1993) also noted this similarity, and postulated that the Glaucosomatidae should be placed as a subfamily within the Pempheridae. The archerfish, family Toxotidae, have been described in a clade containing the Centrolophidae and the Ambassidae (Springer and Orrell, 2004).

Molecular investigations have shown the Arripidae sister to the percoid family Pomatomidae, and these two in a larger clade that includes the family Bramidae and representatives of the perciform suborders Scombroidei, Trachinoidei, Scombrolabracoidei, and Icosteoidei (Smith and Wheeler, 2006). Contrasting Smith and Wheeler's (2006) placement of the Bramidae, Springer and Orrell (2004) proposed the family is sister to a group that contains the Platycephalidae, Priacanthidae, Leiognathidae, and other non-percoid, percomorph taxa.

The monophyly of the Dichistiidae (Coracinidae) remains uncertain, although potential affinities include the family Arripidae (Nelson, 2006). Smith and Wheeler (2006) proposed the Dichistiidae are sister to a group containing the Opistognathidae and Kyphosidae.

Although some evidence has placed the family Drepaneidae within the perciform suborder Acanthuroidei (Tang et al., 1999), Nelson (2006) classified the family as a member of the Percoidei. Greenwood et al. (1966) included *Drepane* within the acanthuroid Ephippidae, but Johnson (1984) found no evidence to relate the Drepaneidae and the Ephippidae. Tyler et al. (1989) found the Drepaneidae sister to a group containing the Chaetodontidae and Pomacanthidae based on modification of the mesethmoid. However, Johnson (1993) notes that Blum (unpublished Ph.D. dissertation) saw a close relationship between the Drepaneidae and Ephippidae. Holcroft (2004) placed the Drepaneidae in a clade with the Ephippidae, and these two sister to a monophyletic Tetraodontiformes. Smith and Wheeler (2006) described a relationship comprised of the Drepaneidae + Ephippidae and the Sciaenidae + Gerreidae.

Molecular evidence has placed the butterflyfishes (family Chaetodontidae) sister to the acanthuroid family Scatophagidae (Chen et al, 2003). Another molecular investigation placed these fishes as sister to the Acanthuridae (*Zebrasoma*; Holcroft, 2004). In her total genetic evidence tree (12S + 16S + RAG1), Holcroft (2005) found the Chaetodontidae in a clade with the percoid family Moronidae, and these two families as sister to other acanthuroid taxa. Holcroft (2005) also found the Chaetodontidae sister to acanthuroids and tetraodontiforms.

Although sometimes recognized in a separate family (Badidae; see Ruber et al., 2004a), Nelson (2006) classified the badid fishes within the family Nandidae. Ruber et al. (2004a) described the Badidae as the sister family of the Nandidae. Springer and Orrell (2004) used morphological evidence to support a relationship between the Nandidae and Badidae.

In a recent molecular investigation, the Kuhliidae were placed in a clade containing the Terapontidae and some members of the perciform suborder Trachinoidei (Smith and Wheeler, 2006). Springer and Orrell (2004) found the Kuhliidae in a clade containing the Moronidae, Lutjanidae, Toxotidae, Ambassidae, and Centrolophidae. They also did not resolve a monophyletic Terapontidae (Springer and Orrell, 2004).

Nelson (2006) placed the families Cirrhitidae, Chironemidae, Aplodactylidae, Cheilodactylidae, and Latridae in the superfamily Cirrhitoidea. Others have disagreed with this classification, placing the Cirrhitidae sister to the Percichthyidae (Smith and Wheeler, 2006). However, this study did place the Cheilodactylidae and Chironemidae as sister families (Smith and Wheeler, 2006).

The Cepolidae are another group with ambiguous relationships in the literature. Nolf (1993) suggested a relationship between the Cepolidae and the Opistognathidae based on his study of percoid otoliths. Smith and Wheeler (2006) found the cepolids sister to the Leiognathidae, whereas Springer and Orrell (2004) placed the family as basal to a large group of percomorphs.

The descriptions of percoid family relationships presented here are by no means comprehensive. The putative relationships described above from the literature depict the variations in the relationships between and among the families of the Percoidei and are relevant to the findings of this study. Morphological characters have been useful for determining limits of individual families, but have not been successful in defining the monophyly of the Percoidei or successful in determining interfamilial relationships within the entire Percoidei (Johnson, 1993; Johnson and Patterson, 1993). Studies investigating the limits and relationships of individual families are abundant, as demonstrated by the text above, but in no way test the overall phylogenetic relationships between all of the 79 percoid families described by Nelson (2006).

Although recent studies examining percoid systematics have begun to include an increased familial taxon sampling, none have attempted to place all (or most) percoid families within the Perciformes, nor have any attempted to describe or refute the monophyly of the Percoidei. Therefore, the goals of this investigation are to test the monophyly of the suborder Percoidei and to investigate the interrelationships of the families that have been classified in the suborder. This research will be done in the context of the other perciform suborders and representative percomorph outgroups as described in detail in the first chapter of this dissertation.

To develop a phylogenetic hypothesis for the Percoidei and its families within the context of other percomorph groups, this study uses approximately 1431 bases (1425-1431 bases) of the single-copy nuclear recombination activating gene 1 (RAG1). Previous systematic studies have utilized this gene because of rarity of insertions and deletions (indels), its slow evolutionary rate, and its minimal saturation of transition changes at third position codons (Groth and Barrowclough, 1999). The conserved nature of RAG1 makes it potentially useful for testing relationships within the largest suborder of fishes and its constituents. By utilizing data from the majority of percoid families, we can begin to draw hypotheses on the evolutionary history of these fishes.

Materials and Methods

This investigation utilizes the same materials and methods as the previous chapter. Thus, the methods are abbreviated here to reduce redundancy.

Taxon sampling

Since this work included genetic data from a single gene, maximization of taxa in terms of percoid family representation was imperative. Multiple taxa from each family were included where appropriate and when available (Table 6). In total, 70 of the 79 families noted in Nelson (2006) were represented. To develop hypotheses for percoid evolution within the context of the order Perciformes, representatives of all perciform suborders are included. Also included are representatives of putative perciform outgroups including members of the Zeiformes, Beryciformes, Beloniformes, Atheriniformes, Mugiliformes, Scorpaeniformes, Gasterosteiformes, Synbranchiformes, Tetraodontiformes, and Pleuronectiformes.

DNA Extraction

Genomic DNA was extracted from approximately 0.25 cm^3 of muscle, gill, or fin tissues of taxa included in this investigation, encompassing representatives of all perciform suborders and relevant outgroups (Table 3) using a Qiagen DNEasy tissue extraction kit (Qiagen Inc., Valencia, CA). Methods described by the manufacturer were followed except that the final elution was done with a single 125 uL aliquot. Tissues that could not be extracted with the DNEasy kit were extracted with a standard phenol:chloroform extraction based on the methods of Hillis et al. (1996).

Table 6. A list of the families of the suborder Percoidei (sensu Nelson, 2006) including taxa from in the present investigation and their voucher information. "---" indicates families not included in this investigation due to availability of materials. RAG-Megadataset sequences courtesy of Dr. Guillermo Orti.

Family	**Species**	**Voucher information**
Acropomatidae	*Synagrops bellus*	SIO-01-131
Ambassidae	*Ambassis agrammus*	ODU-3177
	Denariusa bandata	ODU-3179
	Ambassis macleayi	P.J. Unmack, collector/ voucher
Aplodactylidae	*Aplodactylus arctidens*	C.P. Burrige, collector/ voucher
Apogonidae	*Glossamia aprion*	RAG-Megadataset
	Cheilodipterus macrodon	No voucher
	Apogon aureus	ODU-3084
Arripidae	*Arripis trutta*	CSIRO-H-3856-01
	Arripis truttacea	CSIRO-H-4388-03
Banjosidae	*Banjos banjos*	MUFS-23047
Bathyclupeidae	---	---
Bramidae	*Brama orcini*	FMNH-BUS03-299
Caesonidae	*Gymnocaesio gymnoptera*	ODU-3046
	Caesio lunaris	ODU-3084
Callanthiidae	*Callanthias australis*	AMS I.43550003
Carangidae	*Alectis alexandrinus*	ODU-3168
	Caranx hippos	ODU-3169
	Decapterus macrosoma	Photo voucher, KEC
Caristiidae	*Caristius sp.*	NMV A 22138
Centracanthidae	*Spicara alta*	ODU-2811
	Centracanthus cirrus	ODU-3133
	Spicara maena	ODU-3134
	Spicara flexuosa	ODU-3148
Centrarchidae	*Lepomis macrochirus*	ODU-3180
	Micropterus salmoides	ODU-3181
	Lepomis cyanellus	RAG-Megadataset
Centrogeniidae	---	---
Centropomidae	*Centropomus viridus*	SIO-01-37
Cepolidae	*Acanthocepola krustensternii*	ODU-3088

Table 6 *(continued)*

Family	Species	Voucher information
	Cepola macrophthalma	Mahon photo voucher
Chaetodontidae	*Chaetodon striatus*	AY308775
	Hemitaurichtys polylepis	FMNH-BUS03-282
Cheilodactylidae	*Nemadactulus monodactylus*	ODU-3200
	Chirodactylus grandis	ODU-3199
Chironemidae	*Chironemus marmoratus*	AMS I.41268.001
Cirrhitidae	*Paracirrhites arcatus*	ODU-3189
	Cirrhitus pinnulatus	FMNH-BUS03-192
Coryphaenidae	*Coryphaena hippurus*	D. Reed, collector/ voucher
	Coryphaena sp.	RAG-Megadataset
Dichistiidae	*Dichistius capensis*	Alan Connell, collector/voucher
Dinolestidae	*Dinolestes lewini*	I.41084034
Dinopercidae	*Dinoperca petersi*	RAG-Megadataset
Drepaneidae	*Drepane punctata*	AY308772
Echeneidae	*Echeneis naucrates*	ODU-3184
	Remora australis	No voucher
Emmelichthyidae	*Erythrocles monodi*	ODU-3023
Enoplosidae	*Enoplosus armatus*	NMV A 25195-001
Epigonidae	*Epigonus telescopus*	NMV A 25142-009
Gerreidae	*Gerres argyreus*	ODU-3120
	Diapterus auratus	RAG-Megadataset
	Eucinostomus gula	RAG-Megadataset
	Diapterus peruvianus	T9647 (Degraville, nansen)
Glaucosomatidae	*Glaucosoma herbriacum*	AMNH, not processed yet
	Glaucosoma buergeri	ODU-3192
Grammatidae	*Gramma loreto*	USNM, not yet processed
Haemulidae	*Anisotremus virginicus*	ODU-2893
	Brachydeuterus auritus	ODU-3198
	Haemulon aurolineatum	RAG-Megadataset
	Haemulon plumierii	RAG-Megadataset

Table 6 (*continued*)

Family	**Species**	**Voucher information**
	Plectorhinchus macrolepis	Mahon photo voucher
Inermiidae	*Inermia vittata*	KU T-329
Kuhliidae	*Kuhlia mugil*	USNM 336646
	Kuhlia rupestris	P.J. Unmack, collector/ voucher
Kyphosidae	*Kyphosis incisor*	KU T81
	Microcanthus strigatus	AMS I.41265.002
	Neoscorpis lithophilus	Alan Connell, collector/ voucher
	Neoscorpis lithophilus	Alan Connell, collector/voucher
Lactariidae	---	---
Latidae	*Lates calcarifer*	ODU-3197
Latridae	*Latridopsis forsteri*	CSIRO-H-3774-01
	Latris lineata	CSIRO-H-4944-01
Leiognathidae	*Gazza minuta*	ODU-3094
	Leiognathus stercorarius	ODU-3103
	Leiognathus stercorarius	ODU-3103
	Leiognathus sp.	FMNH-BUS03-215
Leptobramidae	---	---
Lethrinidae	*Lethrinus harak*	ODU-3042
	Lethrinus obsoletus	ODU-3043
	Lethrinus lentjan	ODU-3060
	Lethrinus olivaceus	ODU-3190
	Gymnocranius elongatus	ODU-3202
	Lethrinus xanthochilus	USNM 349306
	Gnathodentex aureolineatus	FMNH-BUS03-040
	Gnathodentex aureolineatus	FMNH-BUS03-056
	Lethrinus atkinsoni	FMNH-BUS03-170
	Lethrinus atlanticus	ODU-3204
	Lethrinus haematopterus	USNM 006364
	Monotaxis grandoculis	MIN0017-8
Lobotidae	*Datnioides microlepis*	RAG-Megadataset
	Datnioides quadrifasciatus	RAG-Megadataset
Lutjanidae	*Pinjalo pinjalo*	ODU-3072

Table 6 (*continued*)

Family	**Species**	**Voucher information**
	Lutjanus analis	RAG-Megadataset
	Lutjanus dentatus	Mahon photo voucher
	Symphorus nematophorus	No voucher
Malacanthidae	*Lophilatilus chamaeleonticeps*	19-FFM-4-10-31-03
	Caulolatilus microps	24-ISLA-1-8-19-03
	Branchiostegus semifasciatus	Mahon, photo voucher
Menidae	*Mene maculata*	ODU-3069
Monodactylidae	*Schuettea scalaripinnis*	I.41266027
Moronidae	*Morone chrysops*	AY308767
	Dicentrarchus labrax	P. J. Unmack, collector/ voucher
	Dicentrarchus punctatus	ODU-3201
Mullidae	*Upeneus sulphureus*	ODU-3125
	Upeneus mollucensis	ODU-3126
	Mullus surmuletus	RAG-Megadataset
Nandidae	*Badis assamensis*	AY330966
	Badis corycaeus	AY330969
	Badis kanabos	AY330970
	Badis siamensis	AY330975
	Dario dario	AY330977
	Dario hysginon	AY330978
	Nandus nandus	AY330979
Nematistiidae	*Nematistius pectoralis*	ODU-3004
	Nematistius pectoralis	ODU-3004
Nemipteridae	*Scolopsis affinis*	ODU-3030
	Pentapodus bifasciatus	ODU-3031
	Scolopsis ciliata	ODU-3049
	Scolopsis taenioptera	ODU-3091
	Nemipterus marginatus	ODU-3104
	Nemipterus japonicus	ODU-3163
	Scolopsis vosmeri	ODU-2827
	Scolopsis ciliata	FMNH-BUS03-230
	Pentapodus setosus	FMNH-BUS03-256
Notograptidae	---	---
Opistognathidae	*Opistognathus aurifrons*	USNM-SABA

Table 6 (*continued*)

Family	Species	Voucher information
	Parascolopsis eriomma	FMNH-BUS03-307
Oplegnathidae	*Oplegnathus punctatus*	mvfs 21469
	Oplegnathus punctatus	mvfs 21469
Ostracoberycidae	*Ostracoberyx dorygenys*	NMV A 251030-007
Pempheridae	*Pempheris oualensis*	FMNH-BUS03-193
	Parapriacanthus ransonneti	min0022-4 22-5
Pentacerotidae	*Pseudopentaceros richardsoni*	I.41420-001
Percichthyidae	*Bostockia porosa*	P. J. Unmack, collector/ voucher
	Gadopsis marmoratus	P. J. Unmack, collector/ voucher
Percidae	*Perca flavescens*	AY308768
	Etheostoma caeruleum	AY430226
Percliidae	---	---
Plesiopidae	*Trachinops taeniatus*	I.41084015
	Plesiops cephalotaenia	FMNH-BUS03-031
Polynemidae	*Polydactylus macrochir*	Berra 1-18-01
	Pentanemus quinquarius	Mahon, photo voucher
Polyprionidae	*Polyprion americanus*	P. J. Unmack, collector/ voucher
	Stereolepis gigas	RAG-Megadataset
Pomacanthidae	*Pygoplites diacanthus*	FMNH-BUS3-013
	Genicanthus melanospilos	FMNH-BUS03-279
	Pomacanthus maculosus	No voucher
Pomatomidae	*Pomatomus saltatrix*	No voucher
	Pomatomus saltatrix	RAG-Megadataset
Priacanthidae	*Priacanthus tayenus*	ODU-3129
	Priacanthus hamrur	MIN0017-7
Pseudochromidae	*Pseudochromis sp.*	FMNH-BUS03-026
	Pseudochromis bitaenatus	FMNH-BUS03-117
Rachycentridae	*Rachycentron canadum*	ODU-3193
Sciaenidae	*Leiostomus xanthurus*	ODU-3176
	Micropogonias undulatus	ODU-3182
Scombropidae	---	---
Serranidae	*Rypticus subbifrenatus*	USNM 327568
	Cromileptes altivelis	FMNH-BUS03-233

Table 6 (*continued*)

Family	**Species**	**Voucher information**
	Epinephelus tauvina	P. J. Unmack, collector, voucher
Sillaginidae	*Sillago sihama*	ODU-3124
	Sillago aeolus	ODU-3191
Sparidae	*Boopsoidea inornata*	ODU-2791
	Argyrops spinifer	ODU-2814
	Diplodus bermudensis	ODU-2815
	Pagellus erythrinus	ODU-2841
	Boops boops	ODU-2912
	Cheimerius nufar	ODU-2933
	Pagrus caerulostictus	ODU-3027
	Lagodon rhomboides	ODU-3175
	Pagrus pagrus	ODU-3188
	Sarpa salpa	ODU-3203
	Pagrus auriga	ODU-2786
	Lithognathus mormyrus	ODU-2784
	Calamus calamus	BCA-0032
	Sparus aurata	RAG-Megadataset
	Viridentex acromegalus	17-02-04 (016)
	Rhabdosargus holubi	No voucher
	Pagrus pagrus	ODU-3188
	Oblada melanura	No voucher
	Stenotomus chrysops	VIMS VA1-00057
	Chrysoblephus anglicus	No voucher
	Pachymetopon grande	ODU-2909
Symphysanodontidae	---	---
Terapontidae	*Mesopristes argenteus*	P. J. Unmack, collector/ voucher
	Terapon theraps	ODU-3038
Toxotidae	*Toxotes lorentzi*	ODU-3178
	Toxotes chatareus	ODU-3196

Polymerase Chain Reaction (PCR)

PCR was used to isolate a 1545 base pair segment of the RAG1 gene from the genomic DNA extracts. This reaction used Takara ExTaq polymerase (Takara Mirus Bio, Madison, WI) and two external primers (Table 7). As the taxon sampling of this investigation is extremely diverse, concentrations and volumes of PCR reactions were optimized accordingly to ensure success of reactions. Amplification consisted of the following thermal program: 95°C for 1 minute; 15 cycles of 95°C for one minute, 53°C for 45 seconds, 72°C for 1 minute 30 seconds; 15 additional cycles of 95°C for 45 seconds, 51°C for 45 seconds, and 72°C for 1 minute 30 seconds; 72°C for seven minutes; 4°C incubation.

PCR reactions were run on a 1% agarose gel, visualized, and purified with the Qiagen Qiaquick gel extraction kit (Qiagen Inc., Valencia, CA). Manufacturer's recommendations were followed with the exception of the final elution which was done with 32 üL of double distilled water. This elution was done to maximize DNA concentration for the following sequencing reactions.

Cloning

Those samples that could not be sequenced directly were cloned using the Promega pGEM-T Easy vector system (Promega Co., Madison, WI). Successful colonies were screened with both PCR and restriction enzyme digests prior to culture. Overnight cultures on positive reactions were run and were then isolated with the Wizard Miniprep DNA purification system (Promega Co., Madison, WI) prior to their use in sequencing reactions.

Table 7
Oligonucleotide primer list for sequencing reactions of the RAG1 gene for this investigation. * indicate primers obtained with permission from the lab of Dr. G. Orti at the University of Nebraska-Lincoln.

Primer Name	DNA Primer Sequence
RAG1 2533F*	5' CTG AGC TGC AGT CAG TAC CAT AAG ATG T 3'
RAG1 2800F	5' CGG CGS TTT CGC TAT GAT GT 3'
RAG1 3032F*	5' AAA CTC AGA ACT GTC CTG 3'
RAG1 3500F	5' AGA GTC AAA GGN GST CNG C 3'
RAG1 4078R*	5' TGA GCC TCC ATG AAC TTC TGA AGR TAY TT 3'

Sequencing

Products from both purified PCR and cloning reactions were sequenced on either an ABI-310 or ABI-3100 capillary sequencer (Applied Biosystems, Foster City, CA). External PCR primers were used to sequence 1431 bases of the RAG1 gene and internal primers were used as necessary to aid in completion of each sequence (Table 7). Reactions were performed and purified using the manufacturer's recommendations. After purification, samples were denatured by adding 16 uL of ABI Hi-Di Formamide or TSR (Applied Biosystems, Foster City, CA) and incubated for 2 minutes at 95°C. The samples were placed onto ice until they could be run on the sequencing instrument. When necessary, internal primers were used to obtain a complete sequence for the RAG1 fragment (Table7).

Data Analysis

A complete description of sequence compilation and screening was presented in the first chapter of this dissertation and will not be repeated here. Tests for mutational site saturation, base compositional stationarity, synonymous codon bias, and GC content on the current dataset were also presented in Chapter I.

Phylogenetic analyses included a modified maximum parsimony analysis on the dataset. Due to the large size of the dataset (279 sequences), it was necessary to employ the Parsimony Ratchet method using the PAUPRat program (Nixon, 1999; Sikes and Lewis, 2001). PAUPRat was run ten times, each run consisting of 200 iterations. The shortest, most parsimonious trees from each run were combined and a consensus tree was calculated. Evaluation of each internode was done by calculation of both bootstrap and jackknife supports in PAUP*4.0b10 (Swofford, 2003). Again, because of the large size of the dataset, both jackknife and bootstrap evaluations were limited in their number of rearrangements (per addition sequence replicate) to 25,000,000.

To determine the appropriate model of substitution for likelihood analyses, MrModeltest (v2.2; Nylander, 2004) was used. The coding block for this calculation was downloaded from http://www.csit.fsu.edu/~nylander/MrModelblock and was placed at the end of the nexus datafile. The dataset was then executed in PAUP*4.0b10 (Swofford, 2003). The resulting 'mrmodel.scores' file was then run in the MrModeltest2 program (Nylander, 2004). The output file from this contained the most appropriate model of substitution for the dataset (Ronquist and Huelsenbeck 2003).

Maximum likelihood analyses were run using the GARLI program (Zwickl, 2006; version 0.94). This program uses the General Time Reversable (GTR) model of nucleotide substitution with gamma distributed rate heterogeneity and an estimated proportion of invariable sites (GTR+I+G). In order to ensure the best log likelihood (lnL) values were obtained, 10 independent runs of the likelihood analysis were performed per the author's recommendations (Zwickl, pers. comm.). A starting topology was used because of the large size of the dataset to maximize success of finding the best log likelihood (lnL) value (Zwickl, 2006).

Results

This investigation includes 279 sequences of the RAG1 gene. This included 180 percoid sequences from 173 different species. Seventy of the 79 families of the

Percoidei described by Nelson (2006) were included. The resulting dataset includes 1431 characters of the RAG1 gene, of which 1085 were parsimony informative.

Insertions and deletions, although not common, were found in the dataset. A three base insertion was found approximately 400 bases into the sequenced region of the RAG1 gene in both species of the family Lobotidae (*Datnioides microlepis* and *Datnioides quadrifasciatus*). One codon (3 base) deletions were found in the same region in *Plesiops cephalotaenia*, *Diodon hystrix*, *Takifugu rubripes*, *Sphoeroides dorsalis*, *Parosphromenus deissneri*, *Makaira nigricans*, *Uranoscopus albesca*, and in all included taxa from the families Apogonidae, Holocentridae, Carangidae, Nandidae, Leiognathidae, Nematistiidae, and Mullidae. Two codon (6 base) deletions were seen in all three species of the anabantoid genus *Trichogaster* (Osphronemidae).

The maximum parsimony analysis using the parsimony ratchet method in PAUPRat (Nixon, 1999; Sikes and Lewis, 2001) resulted in 167 most parsimonious trees, each with a total length of 16,443 steps (CI=0.170; HI=0.830; RI=0.532; RC=0.091). Both bootstrap and jackknife supports have been plotted on the 50% majority rule consensus tree created from the most parsimonious tree set (Figures 17-22). Bootstrap and jackknife supports below 50% were omitted. Those branches with labels in bold text include multiple taxa collapsed into a single branch.

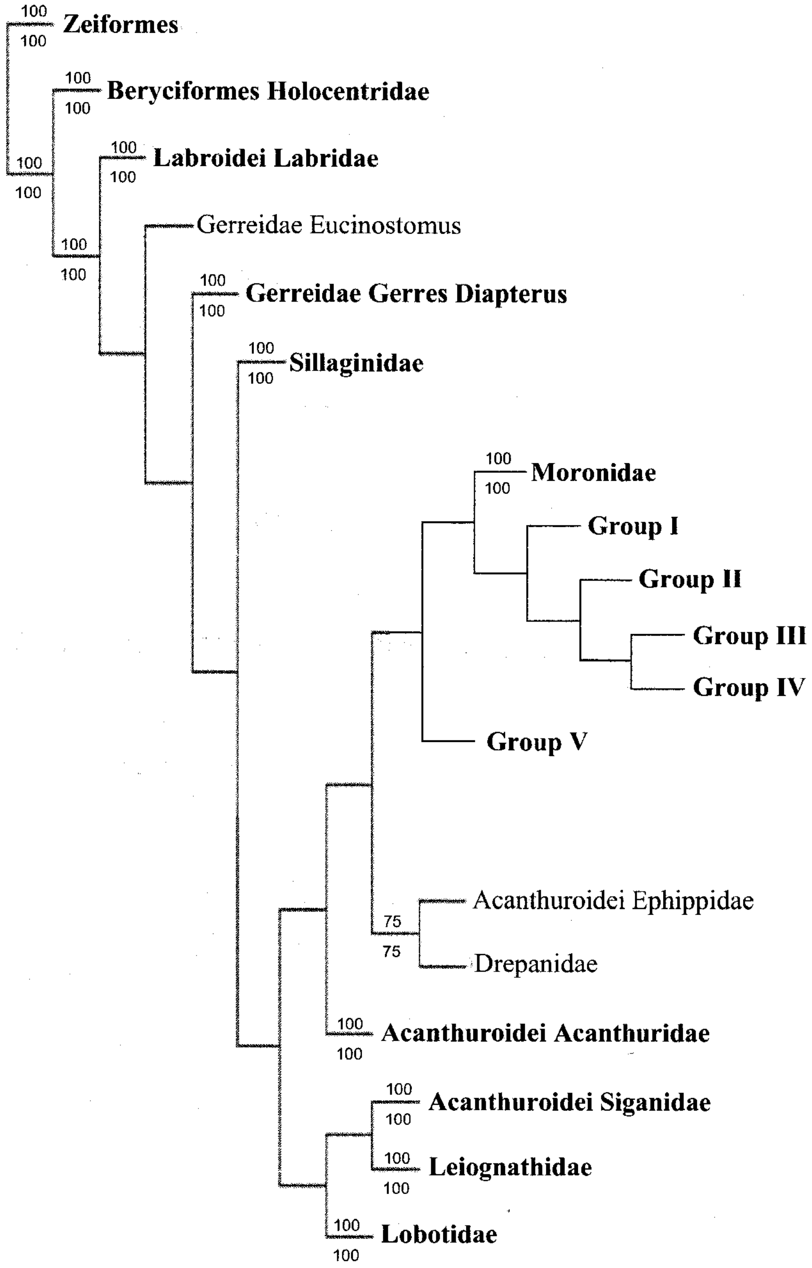


Fig 17. Maximum parsimony consensus tree of 167 most parsimonious trees. Tree statistics include: total length = 16,443 steps, CI=0.170, HI=0.830, RI=0.532, and RC=0.091. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed. Groups I-V described in the following figures.

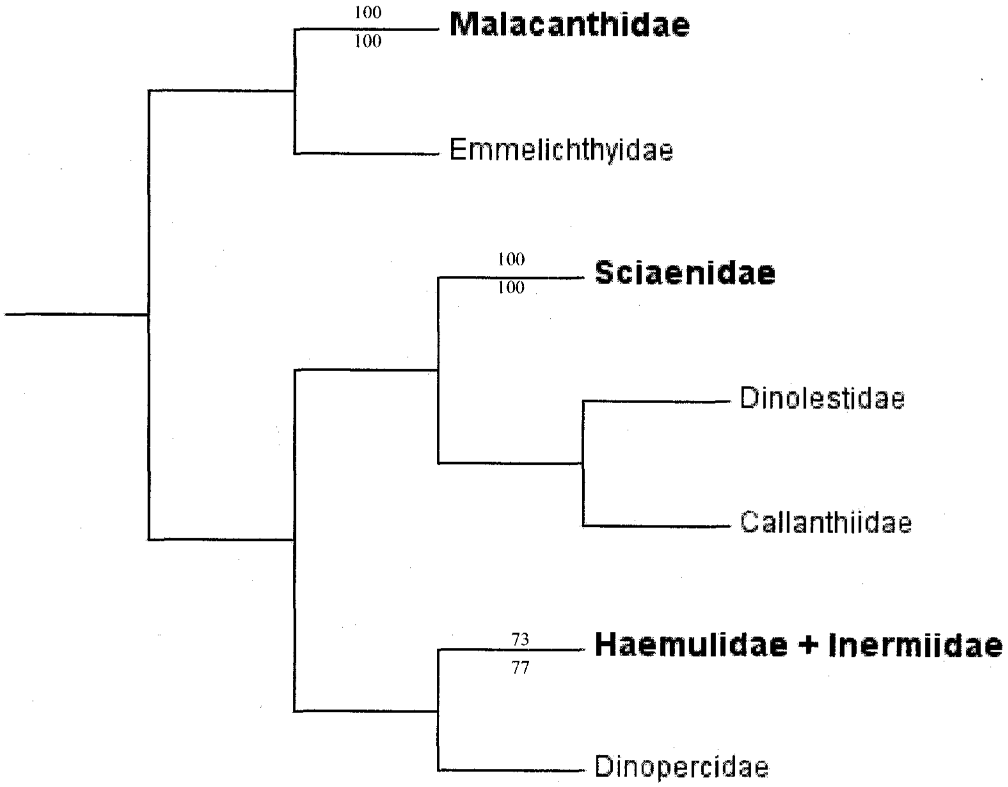


Fig 18. Group I. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

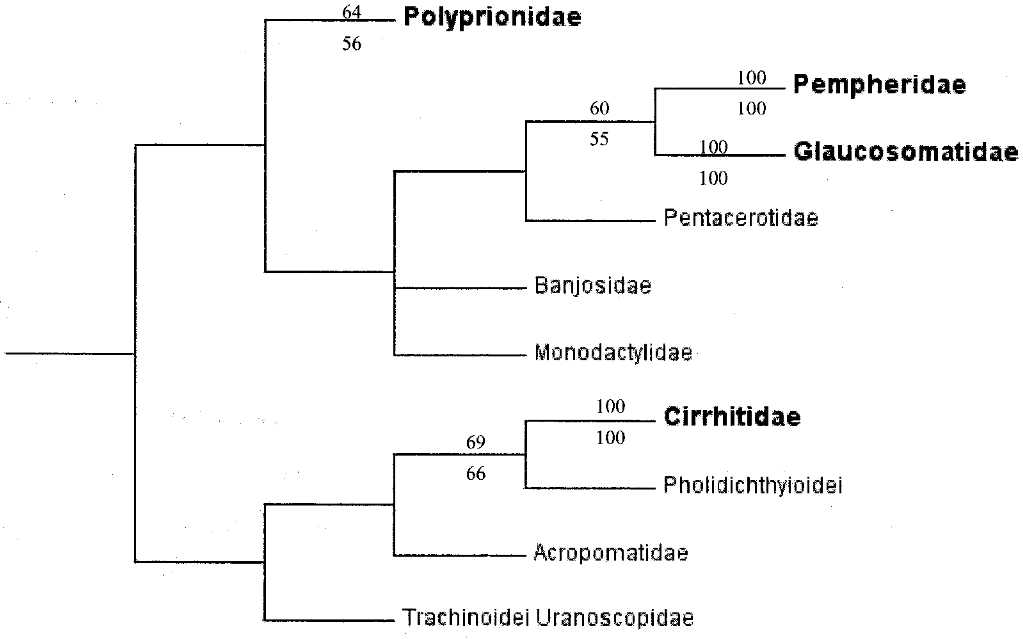


Fig 19. Group II. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

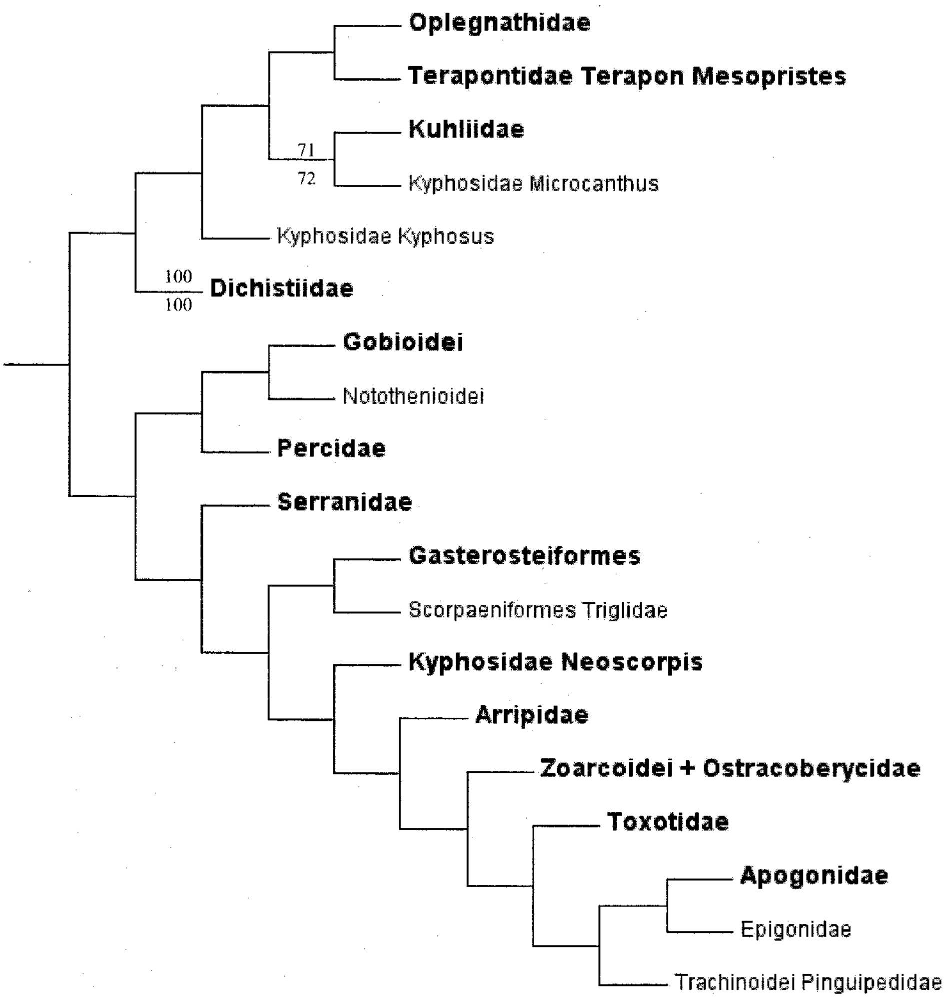


Fig. 20. Group III. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

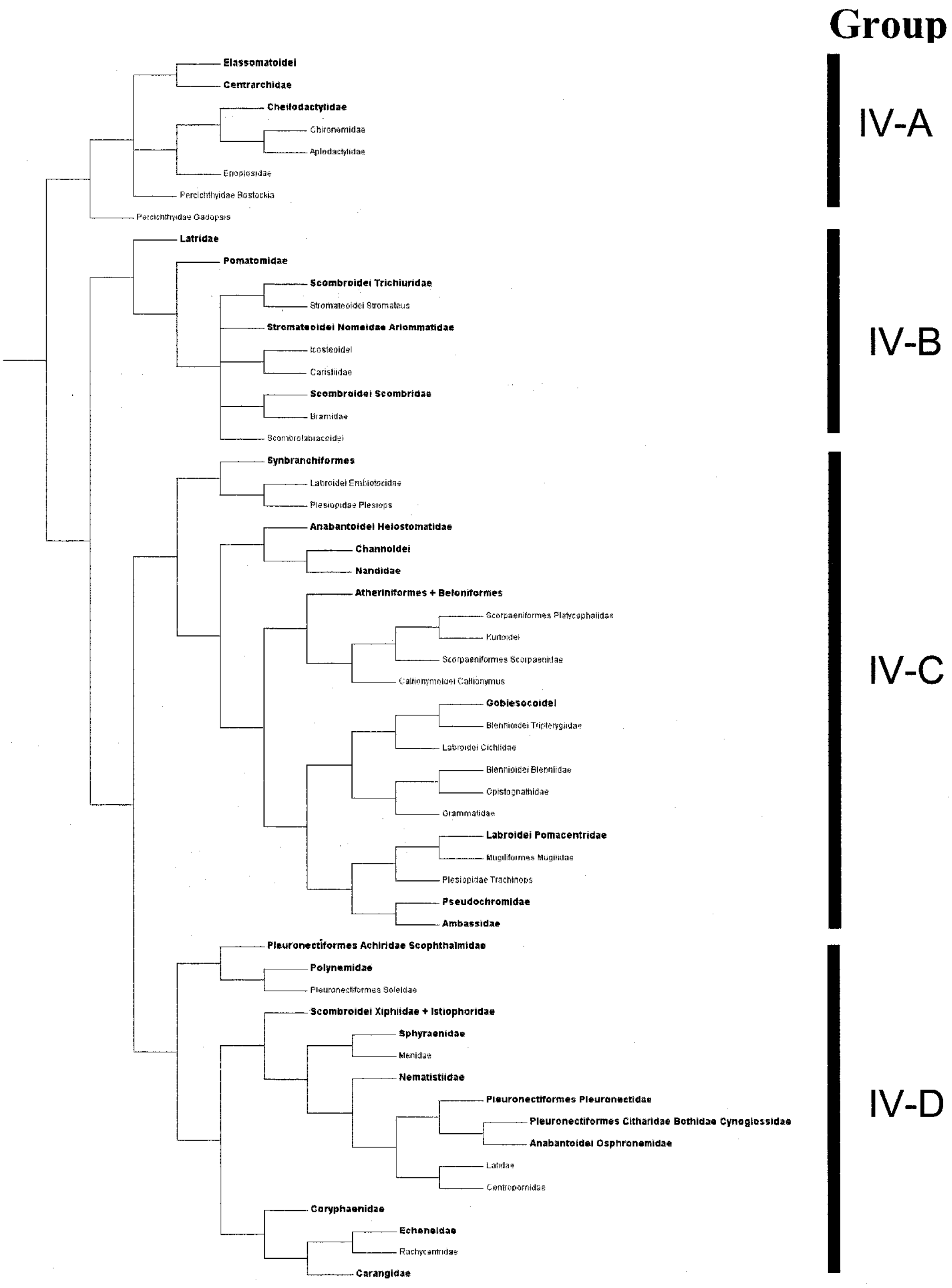


Fig. 21a. Group IV. Bold labels indicate multiple taxa are included in that group and have been collapsed. Figures 21b-e include nodal supports for clades. Unreadable taxa can be seen in the following figures (21b-e).

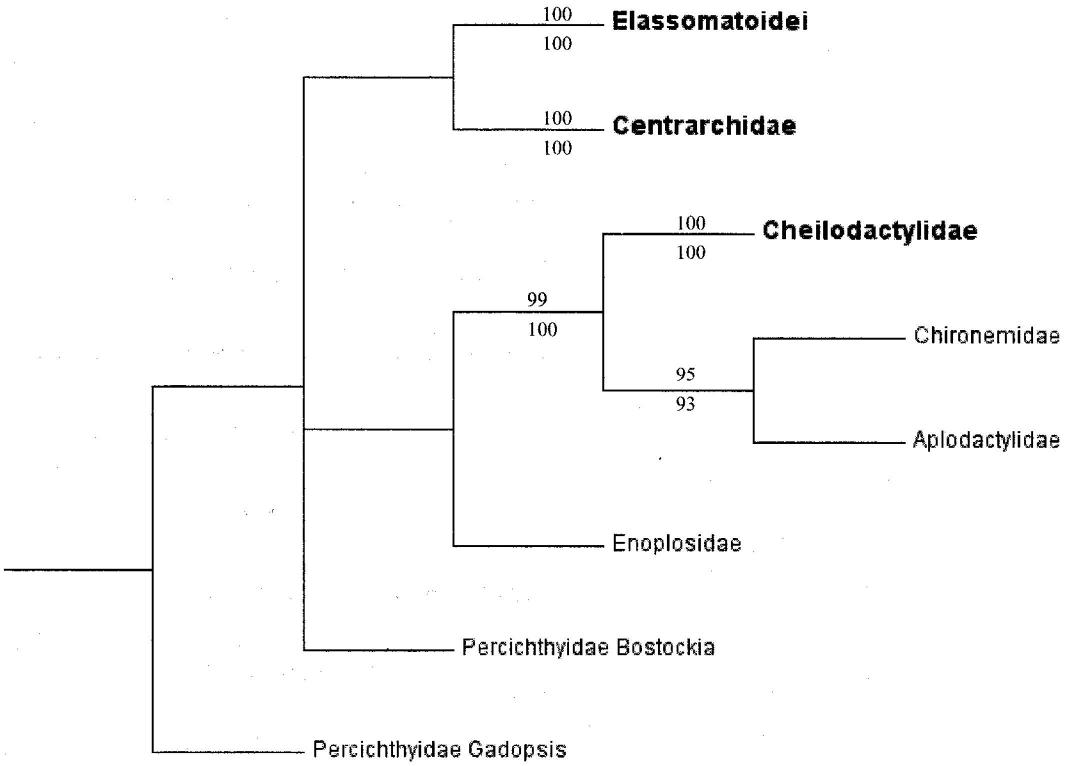


Fig. 21b. Group IV-A. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

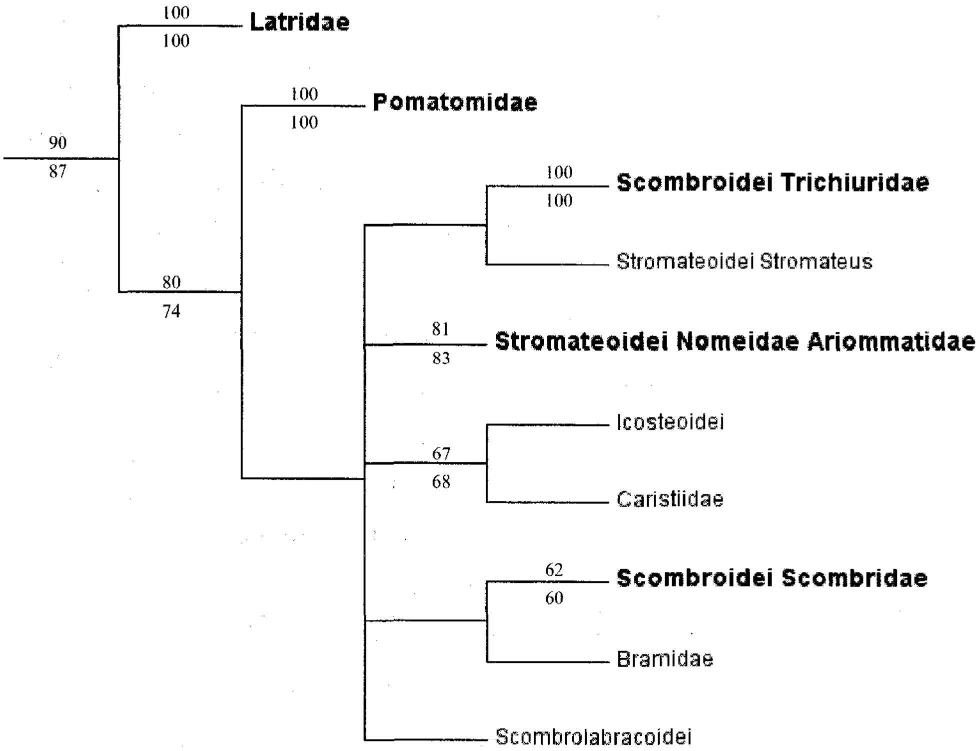


Fig. 21c. Group IV-B. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

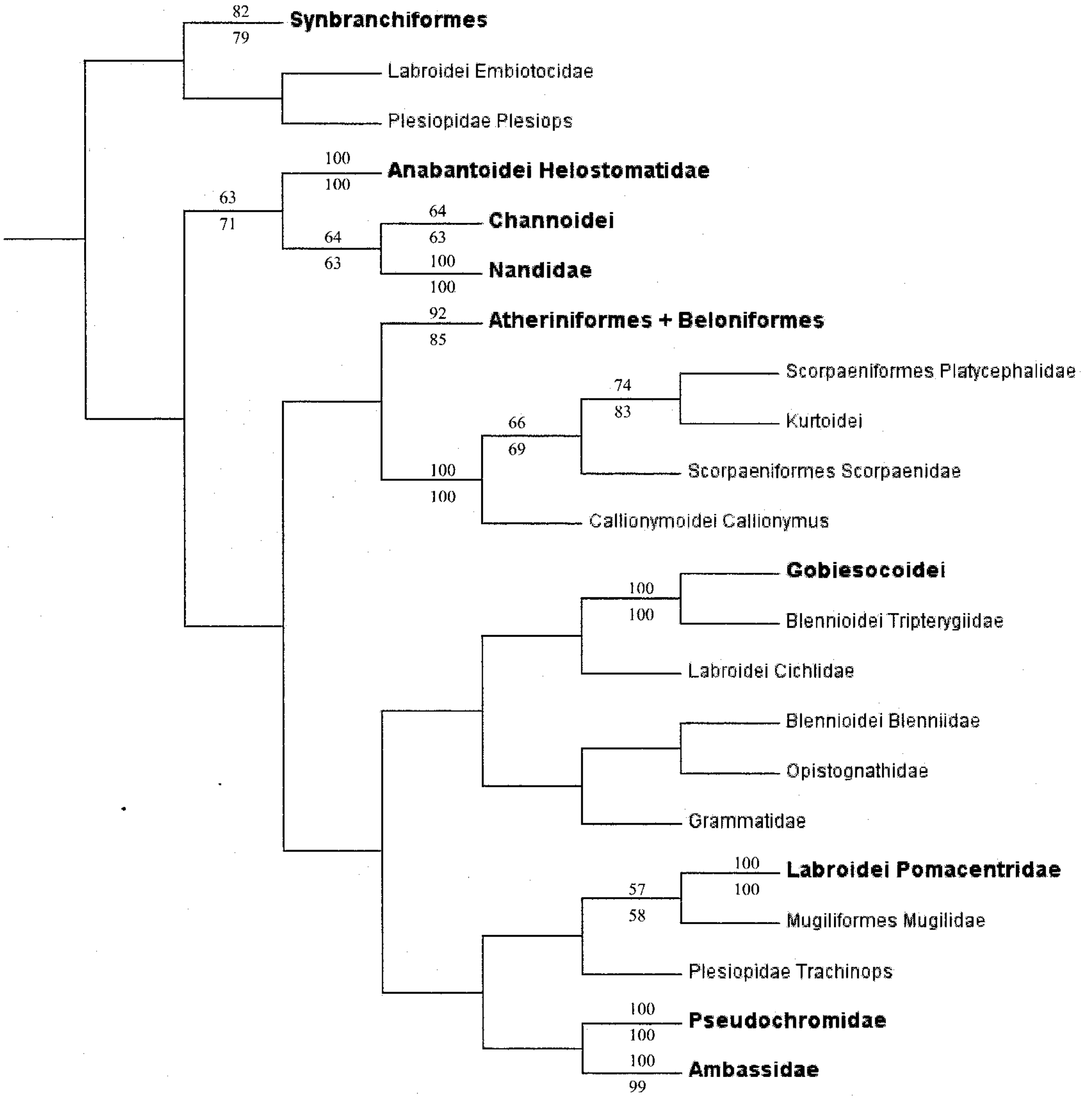


Fig. 21d. Group IV-C. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

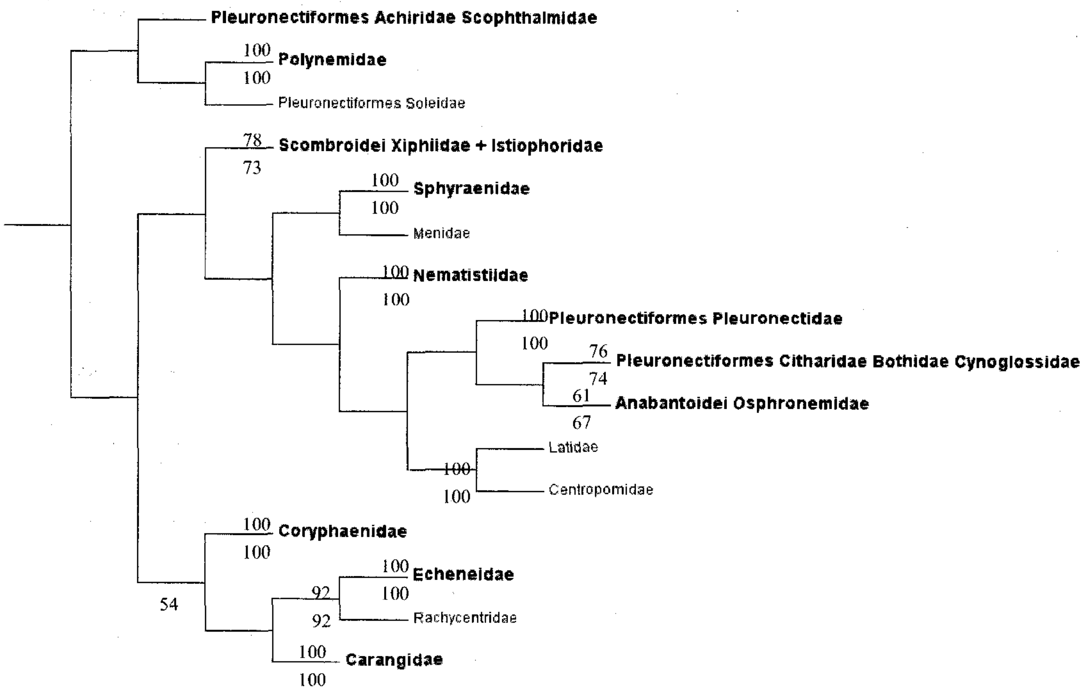


Fig. 21e. Group IV-D. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

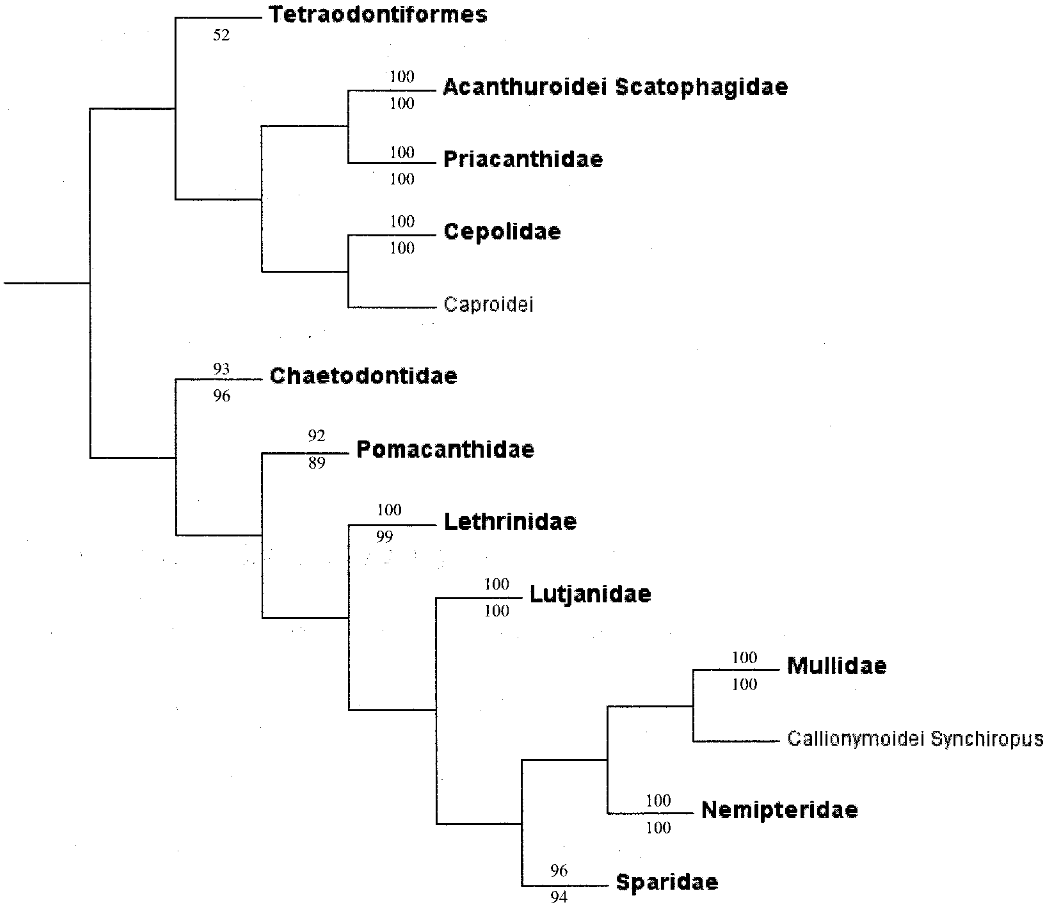


Fig. 22. Group V. Nodal supports include both bootstrap (top value) and jackknife (bottom value) inferences. Nodes lacking numbers indicate values with less than 50% bootstrap/jackknife support. Bold labels indicate multiple taxa are included in that group and have been collapsed.

The general time reversible plus proportion invariant with gamma distribution (GTR+I+G) model of evolution was found to be the best substitution model for the dataset using MrModeltest v2.2 (Nylander, 2004). This made modifications to the GARLI likelihood algorhithm setup files unnecessary, as the default model of substitution of the program is the same. The maximum likelihood analyses resulted in a best log likelihood value of -81469.25958 after 10 runs (Figures 23-27).

Discussion

In the maximum parsimony and maximum likelihood analyses, the suborder Percoidei is non-monophyletic, although the monophyly of the ingroup taxa included in this study (the Percomorpha, composition sensu Johnson and Patterson, 1993) is supported in both analyses (Figures 17-27). Bootstrap and jackknife nodal support for the ingroup percomorph clade is 100% (Figure 17). Johnson's (1993) statement that the Percoidei, the largest and most diverse suborder of fishes, is undoubtedly polyphyletic is supported with these data. This investigation does not resolve a monophyletic Moronoidei and Percoidei (sensu Smith and Craig, 2007).

Maximum parsimony and maximum likelihood analyses showed some similarities for this investigation. However, tree topology differs for many interfamiliar relationships. Monophyly of individual families and many of their interrelationships show a strong similarity between the parsimony and likelihood analyses. Although a significant number of novel relationships resolve in these analyses, many family level relationships show some homology to previous reports in the literature. The levels of

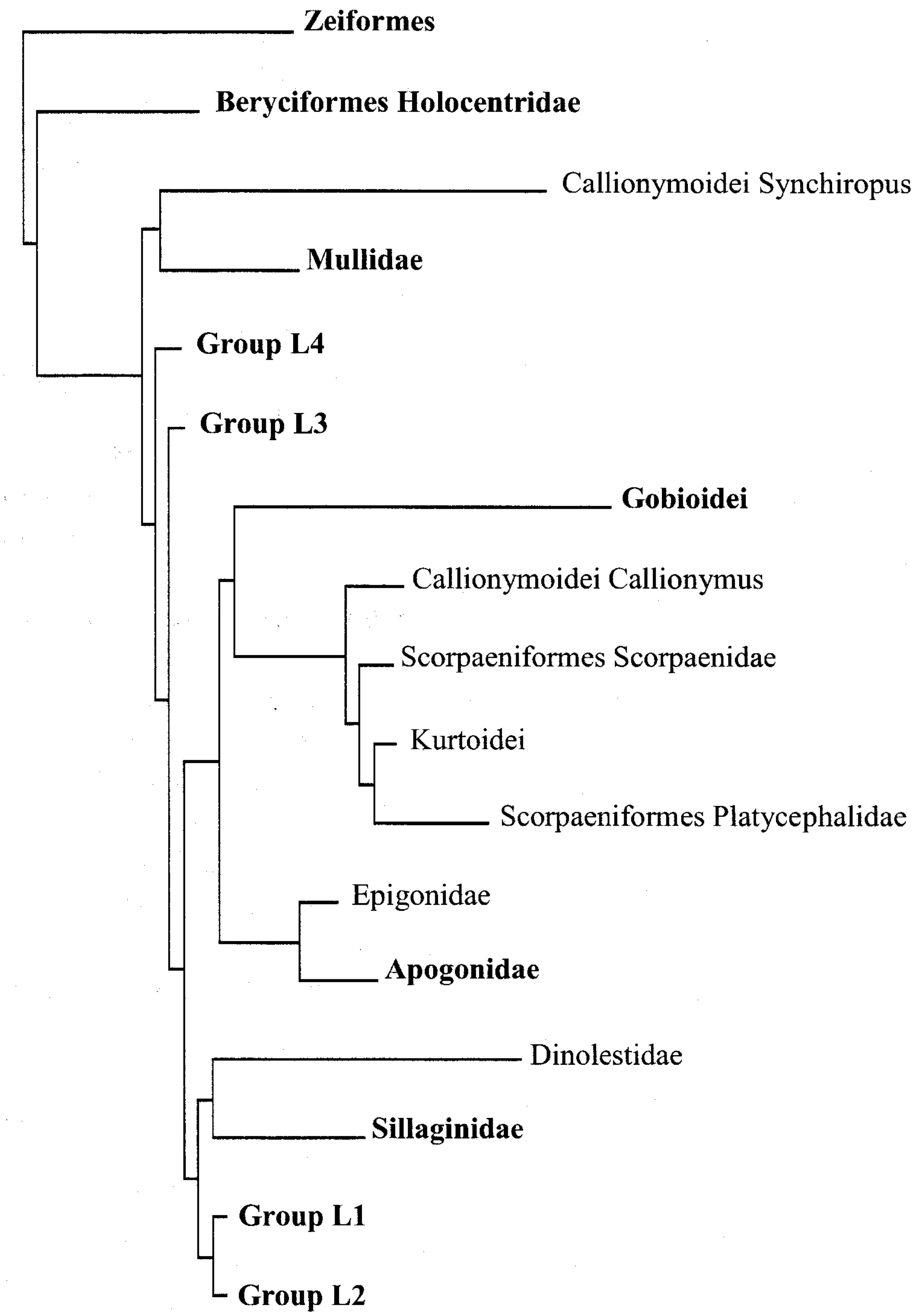


Fig. 23. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

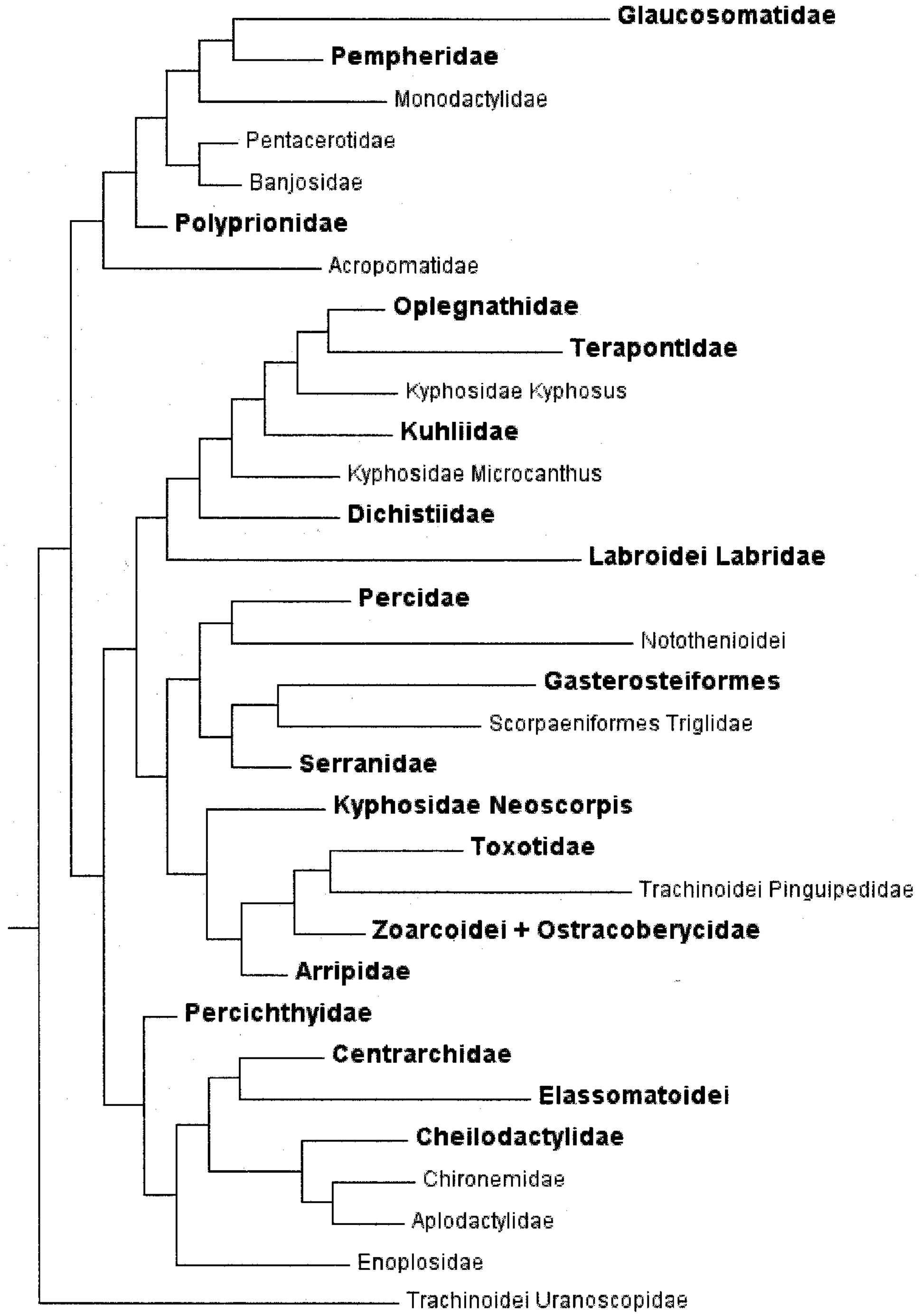


Fig. 24. Group L1. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

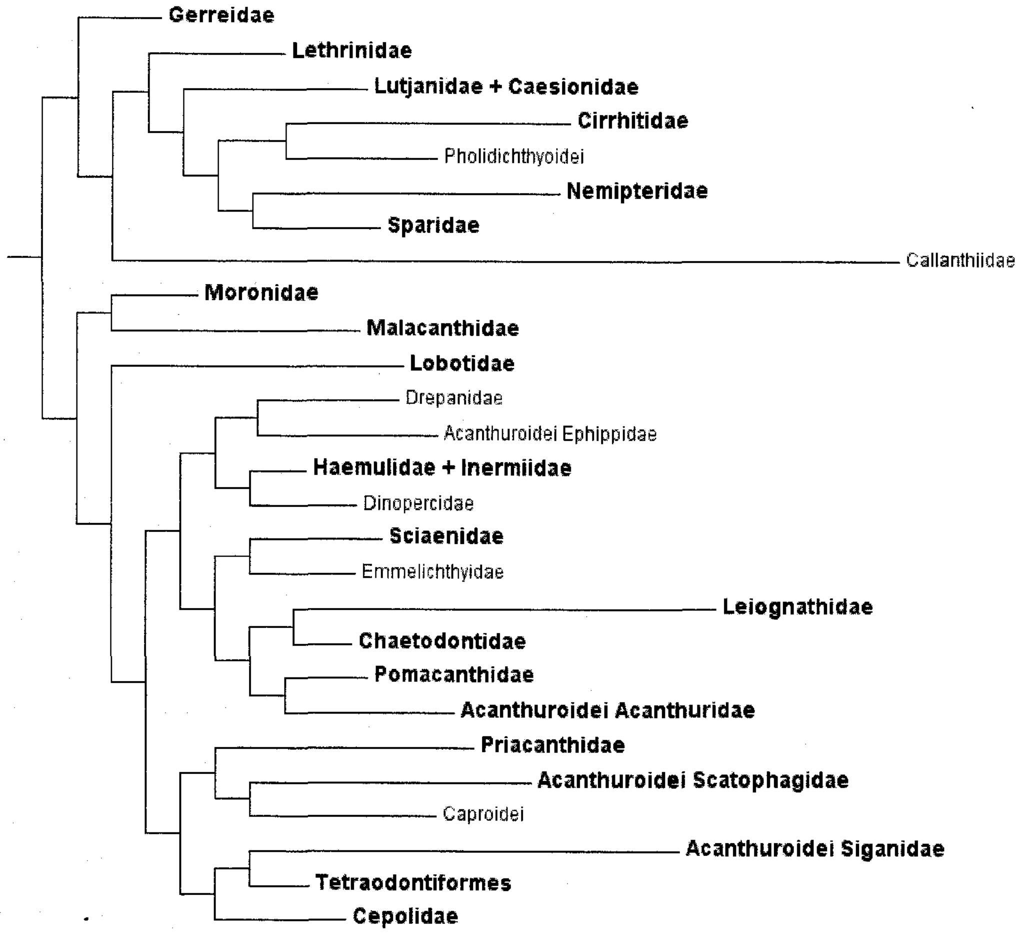


Fig. 25. Group L2. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

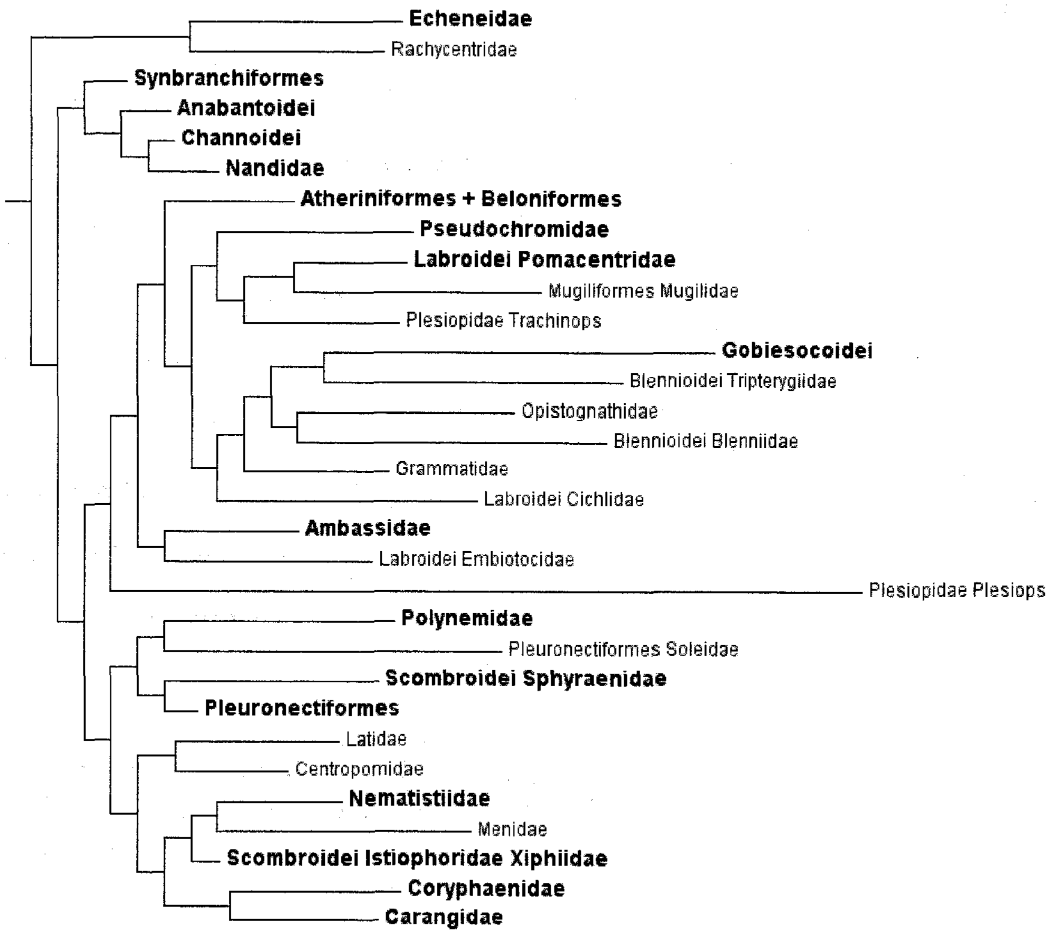


Fig. 26. Group L3. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

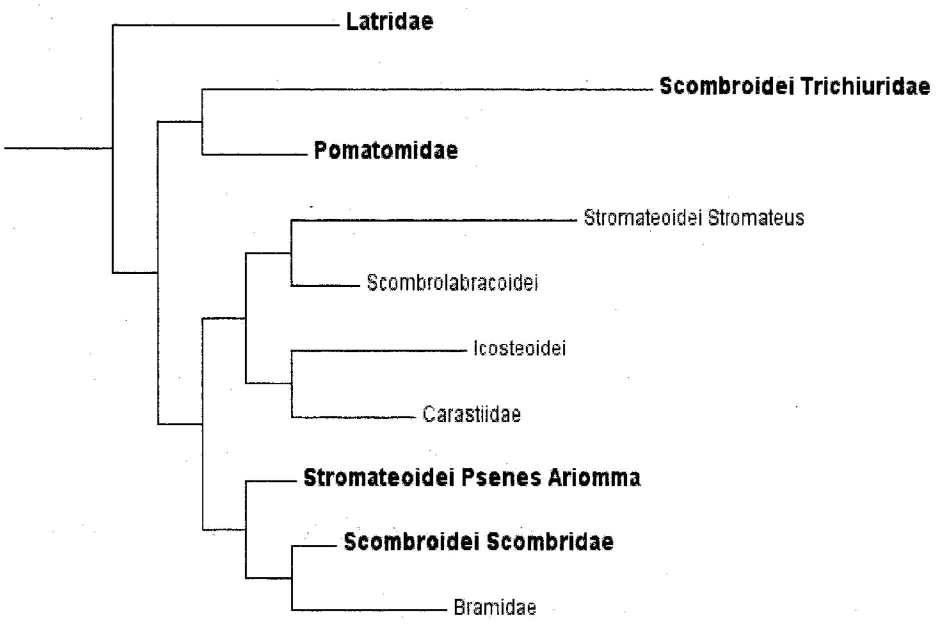


Fig. 27. Group L4. Tree resulting from the maximum likelihood analysis using the GARLI program and the GTR+ I + G model of evolution. Groups in bold include multiple taxa and have been collapsed.

nodal support are low for most of the larger clades in the maximum parsimony analysis, excluding the immediate family-level groups. Reasons for this are discussed in Chapter I of this dissertation and will be noted again at the end of this discussion.

The following discussion presents individual family relationships for the Percoidei and compares the relevant relationships to prior published records on the families and their relationships. For clarity, they are not presented in phylogenetic order. In general, they instead follow the order they are shown in the maximum parsimony analysis (Figures 17-22) in a "top to bottom" fashion. Nodal supports reported are for the clades reported in the parsimony analyses only. Support values for percoid families with multiple taxa/sequences included in this study are listed in Table 8.

The Lobotidae are found sister to a group containing the Leiognathidae and the acanthuroid family Siganidae in the maximum parsimony analysis, but without any nodal support (Figure 17). The maximum likelihood analysis places the Lobotidae as sister to a large group of percomorphs (Figure 25). These results do not agree with Smith and Craig (2007) who found the Lobotidae sister to the Moronidae. The Leiognathidae are found sister to the Chaetodontidae in the maximum likelihood analysis (Figure 25). Previous work placed the leiognathids in a clade containing the Platycephalidae, Bramidae, Priacanthidae, and other percomorph taxa (Springer and Orrell, 2004).

The Drepaneidae are sister to the acanthuroid family Ephippidae in both analyses (Figure 17; Figure 25). Parsimony analyses show this relationship with 75% bootstrap and 75% jackknife nodal support. Previous work has found the Drepaneidae sister to the ephippids, although some have placed the Drepaneidae in a clade with the

Pomacanthidae and Chaetodontidae (Greenwood et al., 1966; Holcroft, 2004; Smith and Wheeler, 2006; Tyler et al., 1989). Others have postulated that the Drepaneidae should be placed within the suborder Acanthuroidei (Tang et al., 1999). Although this study finds the Drepaneidae sister to the Ephippidae, it does not support its placement within the Acanthuroidei, as the suborder resolves as polyphyletic in all analyses (see Chapter I of this dissertation).

The Moronidae are sister to a large group of percomorph taxa in the maximum parsimony analysis (Figure 17). Likelihood results find the Moronidae sister to the Malacanthidae (Figure 25). Previous studies have shown the moronids in a clade containing the Kuhliidae, Lutjanidae, Toxotidae, Ambassidae, and Centrolophidae (Springer and Orrell, 2004). Others have described a relationship between the percichthyid *Howella* and the Moronidae (Smith and Wheeler, 2006).

The Sillaginidae and Gerreidae are basal percomorphs in the maximum parsimony analysis, and the gerreid taxa are paraphyletic (Figure 17). In the maximum likelihood analysis, the Gerreidae are sister to the clade containing the sparoid fishes and the Callanthiidae (Figure 25). The Sillaginidae are sister to the Dinolestidae in the likelihood analyses (Figure 23). In the parsimony trees, the Sciaenidae are found sister to a clade containing the Dinolestidae and the Callanthiidae (Figure 18). In contrast to this study, previous investigations have shown the Sillaginidae in a clade containing the Percidae and the gobioid family Rhyacichthyidae (Springer and Orrell, 2004). Smith and Craig (2007) found the Sillaginidae in a clade with the Callanthiidae, Mullidae, and the scorpaeniform Dactylopteridae.

Table 8
Percoid families with multiple taxa/sequences included in this study and their respective nodal supports in the maximum parsimony analysis.

Percoid Family	**Number of taxa included**	**Nodal Support (% bootstrap / % jackknife)**
Sparidae (incl. Centracanthidae	25	96/94
Lethrinidae	11	100/99
Nemipteridae	10	100/100
Nandidae (incl. Badidae)	8	100/100
Haemulidae (incl. Inermiidae)	6	73/77
Lutjanidae (incl. Caseionidae)	6	100/100
Gerreidae	4	not monophyletic
Leiognathidae	4	100/100
Ambassidae	3	100/99
Apogonidae	3	100/100
Carangidae	3	100/100
Centrarchidae	3	100/100
Kyphosidae	3	not monophyletic
Malacanthidae	3	100/100
Moronidae	3	100/100
Mullidae	3	<50%/<50%
Pomacanthidae	3	92/89
Serranidae	3	87/84
Arripidae	2	99/96
Cepolidae	2	100/100
Chaetodontidae	2	93/96
Cheilodactylidae	2	100/100
Cirrhitidae	2	100/100
Coryphaenidae	2	100/100
Echeneidae	2	100/100
Glaucosomatidae	2	100/100
Kuhliidae	2	100/100
Latridae	2	100/100
Lobotidae	2	100/100
Pempheridae	2	100/100
Percichthyidae	2	not monophyletic
Percidae	2	100/100
Plesiopidae	2	not monophyletic
Polynemidae	2	100/100
Polyprionidae	2	64/56

Table 8 (*continued*)

Percoid Family	**Number of taxa included**	**Nodal Support (% bootstrap / % jackknife)**
Priacanthidae	2	100/100
Pseudochromidae	2	100/100
Sciaenidae	2	100/100
Sillaginidae	2	100/100
Terapontidae	2	not monophyletic
Toxotidae	2	100/100
Nematistiidae	1 (2 seqs. incl.)	100/100
Oplegnathidae	1 (2 seqs. incl.)	100/100

Greenwood et al. (1966) included the Dinolestidae, along with the Epigonidae, in the Apogonidae. Smith and Wheeler (2006) found the Gerreidae sister to the Sciaenidae in their molecular investigation, unlike the results seen here. Chen et al. (2007) find a well-supported, monophyletic Gerreidae at an intermediate percomorph position and find an affinity of the gerreids to the Labridae and Scaridae. This is somewhat congruent with this investigation, which finds the Labridae sister to a paraphyletic Gerreidae in the maximum parsimony analysis (Figure 17). Likelihood places the Gerreidae as an intermediate percomorph, but do not find it near the placement of the Labridae (Figure 24). In contrast to this work, Smith and Wheeler (2006) describe the Dinolestidae in a group containing the Polyprionidae, Percichthyidae, Pentacerotidae, and Moronidae.

The Malacanthidae is found sister to the Emmelichthyidae in the parsimony analysis in a clade with less than 50% nodal support (Figure 18). Smith and Wheeler (2006) found the Malacanthidae sister to the Lutjanidae and this group sister to the Moronidae in their investigation. The Emmelichthyidae are sister to the Sciaenidae in the likelihood analysis (Figure 25). The Sciaenidae are also reported as sister to the Centrogeniidae (Smith and Craig, 2007).

The Dinopercidae are found sister to a clade containing the Haemulidae plus the Inermiidae (73% bootstrap, 77% jackknife) in both the maximum parsimony and maximum likelihood analyses (Figure 18, Figure 25). The haemulid-inermiid relationship is supported by Nelson (2006) who noted a close relationship between these two groups. The dinopercid-haemulid-inermiid relationship has less than 50% nodal support in the parsimony analysis.

The Pempheridae are sister to the Glaucosomatidae in both analyses with moderate to weak nodal support seen in the parsimony analysis (60% bootstrap, 55% jackknife; Figure 19, Figure 24). This clade is found within a group that has below 50% nodal support and contains the Monodactylidae, Pentacerotidae, Banjosidae, and Polyprionidae. Parsimony places the Acropomatidae within the sister clade to this grouping (including other percomorph taxa) and likelihood places it as the immediate sister to the clade containing the Polyprionidae, Banjosidae, Pentacerotidae, Monodactylidae, Pempheridae, and Glaucosomatidae. Smith and Wheeler (2006) also found the acropomatids in a group containing the Polyprionidae and Pentacerotidae, but also included the Dinolestidae, Percichthyidae, and Moronidae.

Both maximum parsimony and maximum likelihood analyses place the Cirrhitidae as sister to the perciform suborder Pholidichthyoidei (Figure 19, Figure 25). Nodal support for this relationship is moderate (69% bootstrap, 66% jackknife). The Cirrhitidae are sister to the percichthyid genus *Bostockia* in a molecular investigation of toxin producing fishes (Smith and Wheeler, 2006).

The parsimony and likelihood analyses find a clade containing the Dichistiidae, Kyphosidae (minus the genus *Neoscorpis*), Kuhliidae, Oplegnathidae, and Terapontidae (Figure 20, Figure 24). Nodal supports for this larger grouping in the parsimony analysis are below 50%, however, the internal groupings show some weak to moderate support (see Figure 4). The Kyphosidae, in both analyses, are polyphyletic with the inclusion of *Neoscorpis*. *Neoscorpis* is found sister to a clade containing the Toxotidae, Arripidae, Zoarcoidei + Ostracoberycidae, Apogonidae, Epigonidae, and the trachinoid Pinguipedidae in the maximum parsimony analysis (bootstrap and jackknife support below 50%; Figure 20). Likelihood results do not include the Apogonidae and Epigonidae in this clade, but place them in a group sister to other percomorphs, including the suborder Kurtoidei (Figure 23). The apogonid-epigonid relationship shows strong nodal support (99% bootstrap, 99% jackknife). The relationship between the Dichistiidae and the Arripidae noted by Nelson (2006) is not supported by this investigation. However, the connection between the Dichistiidae and the Kyphosidae was also seen by Smith and Wheeler (2006). The placement of the Apogonidae and the Kurtoidei in closely related clades within the likelihood analysis of this study is supported by Johnson (1993) who noted two major shared characteristics of the groups: the dorsal gill arch elements and the filaments around the micropyle of their eggs.

The Percidae are sister to a clade containing the Notothenioidei and the Gobioidei in the parsimony analysis and as sister to the Notothenioidei in the likelihood analysis (Figure 20, Figure 24). This grouping has below 50% nodal support in the parsimony analysis. The Serranidae are found sister to a group containing the kyphosid *Neoscorpis* clade and to the Gasterosteiformes + Triglidae (Scorpaeniformes) in the maximum parsimony analysis. Nodal supports in the parsimony analysis for the Serranidae are 87% bootstrap and 85% jackknife. Likelihood shows the Serranidae as sister to the Gasterosteiformes plus the scorpaeniform Triglidae (Figure 24). Previous studies have discussed the relationship between the Percidae and Serranidae and scorpaeniform taxa (Smith and Wheeler, 2004; Smith and Wheeler, 2006; Smith and Craig, 2007). Smith and Wheeler (2004) did not find the Serranidae as monophyletic in their investigation of the Scorpaeniformes, with the family resolving in two clades, both as paraphyletic to large groups of percomorphs. The results of Smith and Craig (2007) suggest a monophyletic Percidae and recommend taxonomic revision of the Serranidae. The lack of 100% nodal support at the family level for the Serranidae seen in this investigation suggests that inclusion of only three serranid taxa in this investigation does not provide an adequate sampling to test the monophyly of the family.

Both parsimony and likelihood analyses find the Centrarchidae sister to the Elassomatoidei (Figure 21b, Figure 24). Nodal supports in the parsimony analysis are below 50% for this clade. The Centrarchidae + Elassomatoidei clade is sister to a clade containing the Cheilodactylidae, Chironemidae, Aplodactylidae, Enoplosidae, and the Percichthyidae in both analyses. The phyletic sequence (Cheilodactylidae, (Chironemidae + Aplodactylidae)) is supported with 99% bootstrap and 100% jackknife support. Also, the relationship between the Chironemidae and the Aplodactylidae shows strong nodal support (95% bootstrap, 93% jackknife). The family Percichthyidae resolves as paraphyletic in the parsimony analysis and monophyletic in the likelihood analysis. The disputed relationship of the Centrarchidae and the Elassomatoidei is shown in both parsimony and likelihood analyses. This investigation, although lacking nodal support in the parsimony analysis, supports the work of Greenwood et al. (1966) but contradicts the studies of Johnson (1984; 1993) and the total evidence investigation of Wiley et al. (2000) who refuted a relationship between the Centrarchidae and the Elassomatoidei.

The Latridae, Caristiidae, Pomatomidae, and Bramidae are found in well supported clade among scombroid, stromateoid, icosteoid, and scombrolabracoid taxa in the maximum parsimony analysis (90% bootstrap, 87% jackknife support; Figure 21c). The Latridae are the basal group of this clade, followed by the Pomatomidae. The

Caristiidae are sister to the Icosteoidei (67% bootstrap, 68% jackknife) and the Bramidae as sister to the scombroid family Scombridae (less than 50% nodal support). Likelihood analyses find a similar clade, although the Pomatomidae are seen as sister to the scombroid Trichiuridae (Figure 27). The relationship between the Pomatomidae and scombroid taxa is also seen in a molecular investigation of scombroid and xiphoid clades (Orrell et al., 2006). This study finds Pomatomidae to be the basal group of the Scombroidei.

The Plesiopidae are polyphyletic in the parsimony and likelihood analyses. *Plesiops* is sister to the labroid Embiotocidae and *Trachinops* as sister to the Mugiliformes and the labroid Pomacentridae in the maximum parsimony tree, both relationships having less than 50% nodal support (Figure 21d). Likelihood places *Trachinops* in a similar clade, but presents *Plesiops* as sister to a large group of percomorph taxa (Figure 26). The polyphyly of the plesiopids is not seen in previous work (e.g. Smith-Vaniz and Johnson, 1990) and warrants further investigation in future studies.

The Nandidae, including the subfamilies Badinae and Nandinae, are found sister to suborder Channoidei in both parsimony and likelihood analyses (Figure 21d, Figure 26). Nodal supports for this relationship in the parsimony analysis are weak (64% bootstrap and 63% jackknife). These two groups are sister to anabantoid taxa in both trees, although the parsimony results do not show the anabantoids as monophyletic (see Chapter I for possible explanations). Maximum parsimony shows weak to moderate nodal support for this clade also (63% bootstrap, 71% jackknife). Previous work has described the Badinae and Nandinae in separate families (i.e. the Badidae and Nandidae, e.g. Ruber et al., 2004a). This work supports the close relationship between the two groups (100% nodal support in the parsimony analysis) and supports the morphological findings of Springer and Orrell (2004) who find a close relationship between the subfamilies (sensu Nelson, 2006).

The Grammatidae are found sister to a clade containing the Opistognathidae and the blennioid family Blenniidae in the parsimony analysis (less than 50% nodal support) and as sister to the Opistognathidae, and suborders Gobiesocoidei and Blennioidei in the likelihood analysis (Figures 21d, Figure 26). Although in different larger groupings, the relationship between the Grammatidae and the Opistognathidae is also found bySpringer and Orrell (2004) and in molecular investigations (Smith and Wheeler, 2006; Smith and Craig, 2007).

Maximum parsimony presents the Pseudochromidae as sister to the Ambassidae (Figure 21d). This relationship has less than 50% nodal support. The likelihood finds the Ambassidae sister to the labroid Embiotocidae and the Pseudochromidae sister to the labroid Pomacentridae, Mugiliformes, and the plesiopid *Trachinops* (Figure 26). Others have reported the Pseudochromidae in a clade with the Chaenopsidae and Blenniidae (Smith and Craig, 2007).

The threadfins, family Polynemidae, are found in a clade containing pleuronectiform taxa in the maximum parsimony analysis (Figure 21e). This grouping has nodal supports of less than 50%. Likelihood places the polynemids in a clade that contains not only pleuronectiform taxa, but the scombroid family Sphyraenidae as well (Figure 26). The relationship between the Polynemidae and the Sphyraenidae supports the work of Gosline (1962; 1968; 1971) who noted an association between these two families. The relationship between the polynemids and the Sciaenidae postulated by Freihofer (1978), de Sylva (1984) and Johnson (1993) is not supported in this investigation.

Unlike the likelihood analysis, which finds the carangoid (sensu Johnson, 1993) fishes in two separate groups (Figure 26), the maximum parsimony analysis contains a clade with the phyletic sequence Coryphaenidae + (Carangidae + (Rachycentridae + Echeneidae)) (Figure 21e). This clade shows weak jackknife support (54%) and less than 50% bootstrap support. The suggestion of Johnson (1993) to place the Carangidae, Rachycentridae, Echeneidae, Nematistiidae, and Coryphaenidae in a separate suborder (the Carangoidei) is not clearly supported in this investigation. The Nematistiidae are not found with the other putative carangoid families in the parsimony analysis and instead are found sister to other percomorph taxa including the percoid families Latidae and Centropomidae and pleuronectiform and anabantoid taxa (Figure 21e). Strong support is seen for the grouping of the Echeneidae and the Rachycentridae (92% bootstrap and 92% jackknife) although nodal supports of the clade including these fishes, the Carangidae and Coryphaenidae are less than 50%. Further testing that includes a greater taxon sampling of the carangoid fishes should be performed to test the monophyly of this putative suborder and its potential placement with respect to scombroid taxa.

The percoid family Menidae is found sister to the scombroid Sphyraenidae in the maximum parsimony analysis, and these families are in a clade that includes the billfishes (Xiphiidae, Istiophoridae, suborder Scombroidei), the anabantoid family Osphronemidae, other pleuronectiform taxa, and the percoid families Nematistiidae and the Latidae plus the Centropomidae (Figure 5e). Nodal supports for these groupings are less than 50%. Likelihood analyses find a similar clade but place the Latidae, Centropomidae, Menidae, Nematistiidae, Coryphaenidae, Carangidae, and the scombroid Istiophoridae and Xiphiidae sister to the group containing the Polynemidae, Sphyraenidae, and pleuronectiform taxa (Figure 26). See Chapter I of this dissertation for possible explanations for the polyphyly of the pleuronectiform and anabantoid taxa included in this dataset.

Parsimony analysis finds the Priacanthidae sister to the acanthuroid family Scatophagidae and the Cepolidae sister to the suborder Caproidei. These two clades are sister to the Tetraodontiformes, but this relationship has less than 50% nodal support (Figure 22). The Cepolidae are sister to the Tetraodontiformes and the acanthuroid Siganidae and the Priacanthidae as sister to the acanthuroid Scatophagidae plus the suborder Caproidei in the likelihood analysis (Figure 25). Contrasting this study, Springer and Orrell (2004) found the Priacanthidae in a clade containing the Platycephalidae, Leiognathidae and other non-percoid taxa.

The Chaetodontidae are in a clade containing the Pomacanthidae, Lethrinidae, Lutjanidae, Sparidae, Nemipteridae, Mullidae, and the callionymoid *Synchiropus* in the maximum parsimony analysis (Figure 22). This larger clade shows less than 50% nodal support. Likelihood analysis places the Chaetodontidae as sister to the Leiognathidae and these taxa as sister to the Pomacanthidae and the Acanthuridae (Figure 25). The likelihood analysis shows some similarities to prior work, as others have described the Chaetodontidae closely related to acanthuroid taxa (e.g. Chen et al., 2003; Holcroft, 2004; Holcroft, 2005). Agreeing somewhat with the pomacanthid-chaetodontid relationship seen here, Tyler et al., (1989) used morphological characters and inferred the Chaetodontidae in a clade containing the Pomacanthidae and the Drepaneidae.

The sparoid fishes (Sparidae, Centracanthidae, Lethrinidae, and Nempiteridae) are in a clade containing the Chaetodontidae, Pomacanthidae, Lutjanidae, Mullidae, and the callionymoid *Synchiropus* in the maximum parsimony analysis (Figure 22). Again, these groupings show less than 50% nodal support. The Sparidae (including the Centracanthidae) are sister to the Nemipteridae, and these taxa sister to the Pholidichthyoidei plus the Cirrhitidae in the likelihood analysis. These fishes are then in a larger clade with the Lutjanidae + Caesionidae and the Lethrinidae (Figure 25). Relationships of the sparoid families are discussed in further detail in the next chapter of this dissertation.

Both maximum parsimony and maximum likelihood anlayses inferred similar topologies in many cases in this study. However, differences are seen in many of the interfamilial relationships between the two analyses. Mid-level nodal support for the parsimony tree, i.e. the "spine" of the tree, is low (below 50%) for most parsimony relationships. Support indices in the maximum parsimony analysis were strongest at the series level (Percomorpha) and for individual families included in the study. Many of the families of the Percoidei were found with 100% nodal support (Table 8). Thirty-three percoid families with multiple taxa included in this investigation were found with greater than 90% nodal support. Four percoid families with multiple taxa/sequences were found with less than 90% nodal support and five families were found to be polyphyletic, (Table 8). Therefore, there is potential for the use of RAG1 at the intrafamilial level.

These differences in the parsimony and likelihood analyses and low nodal support indices in the parsimony analysis could be due to a variety of factors. First, this could be an issue of inadequate taxon sampling. This work utilizes 279 sequences of percomorph taxa, including 180 sequences from the Percoidei representing nearly 90% of the families in the suborder. This represents the largest sampling of percoid families in any molecular anlysis to date. Adding more taxa so that all families are represented with at least two species, and adding species so that 100% coverage of putative families may resolve some inconsistencies between maximum likelihood and parsimony analyses. However, it is established that the limits of most individual families with the Percoidei are fairly well defined (Johnson, 1993) and adding these taxa may not substantially resolve this using the RAG1 gene alone. The second possible reason for inconsistencies between analyses is that the RAG1 gene could be insufficient for resolving relationships at this phylogenetic level. The level of GC content at third codon positions and the codon bias seen in some taxa in terms of their ENC value (see chapter I of this dissertation) could distort phylogenetic signal. This distortion could be one of the reasons, for example, that the pleuronectiform taxa do not resolve as a monophyletic group. Issues with the genetic data could provide erroneous groupings and clades that could be resolved with the addition of more molecular markers.

However, increasing the number of genetic markers may never resolve all relationships among percoid families. Previous work investigating the relationships of coelacanths, lungfish, and tetrapods have utilized over 40 genes and still failed to elucidate the relationship of these groups (Rokas and Carroll, 2006). Other studies involving vertebrates have used 20 nuclear genes and have failed to resolve the relationships between the three orders of mammals (Rokas and Carroll, 2006).

Obviously not all relationships presented here are supported or conform to the conventional wisdom of the evolutionary history these fishes. This study was not designed to conclude studies of investigating interfamilial relationships of the Percoidei. Recent work redefining the Percoidei by Smith and Craig (2007) limit the suborder to few families and create the suborder Moronoidei, which includes many families previously included in the Percoidei. Studies such as this work and the Smith and Craig (2007) investigation clearly show the need for future large scale work investigating the higher level systematics of the Perciformes, the Percoidei (and the Moronoidei), and all taxa contained within these groups using multiple genes and morphological characters. Although this work does not infer a monophyletic Moronoidei or Percoidei as defined by Smith and Craig (2007), they state that taxonomic changes such as theirs are "the first steps toward the resolution of the percomorph problem". It is hoped that this dissertation will also be a step toward the resolution of what Nelson (1989) described as the bush at the top of the teleostean tree. With the data presented here as a basis, and the addition of more molecular markers and the inclusion of a greater, more thorough taxonomic sampling of percomorph taxa, especially a greater representation of the Percoidei, a better understanding of the evolution of this group of fishes may eventually be realized.

CHAPTER IV

INTERRELATIONSHIPS OF THE SUPERFAMILY SPAROIDEA USING NUCLEAR AND MITOCHONDRIAL DATA

Introduction

The putative percoid superfamily Sparoidea contains the families Nemipteridae, Lethrinidae, Centracanthidae, and Sparidae (e.g. Carpenter and Johnson, 2002). The sparoids include approximately 230 species of perciform fishes found primarily in marine and estuarine waters (Nelson, 2006). The "sparoid" fishes were first recognized by Akazaki (1962), who included the nemipterids, lethrinids, and sparids in the "spariform" fishes. Nelson (2006) stated that further research that includes a more complete sampling of the suborder Percoidei is necessary prior to formal recognition of a monophyletic Sparoidea.

The family Nemipteridae includes five genera (*Nemipterus*, *Parascolopsis*, *Pentapodus*, *Scaevius*, *Scolopsis*) and 64 species (Nelson, 2006). The nemipterids are restricted to Indo-west Pacific tropical and subtropical marine systems (Nelson, 2006).

The sparoid family Lethrinidae includes tropical coastal fishes that primarily occur in the Indo-west Pacific, with only *Lethrinus atlanticus* inhabiting the Atlantic Ocean along the western coast of Africa (Nelson, 2006). The Lethrinidae is categorized into two subfamilies: the Lethrininae and Monotaxinae (Carpenter and Allen, 1989). The family consists of five genera: *Gnathodentex* (1 species), *Gymnocranius* (8 species), *Lethrinus* (28 species), *Monotaxis* (1 species), and *Wattsia* (1 species) with 39 total species (Nelson, 2006; Carpenter and Randall, 2003). Previous work using cytochrome *b* (cytB) data did not recover a monophyletic Lethrinidae (Lo Galbo et al., 2002).

The Centracanthidae are exclusively marine fishes that inhabit the eastern Atlantic Ocean, including the Mediterranean, and the waters of South Africa (Nelson, 2006). These fishes are planktivorous and have a highly protrusible upper jaw (Nelson, 2006). The centracanthids are placed into two genera, the monotypic *Centracanthus* and *Spicara*, with a total of eight species (Nelson, 2006). Jordan and Fessler (1893) considered the Centracanthidae members of the Sparidae. Regan (1913), Smith (1938), and Johnson (1980) also noted a close relationship between the Centracanthidae and Sparidae. Others have also noted affinities of the Centracanthidae and the Sparidae (Carpenter and Johnson, 2002; Orrell et al., 2002).

The Sparidae are marine and brackish water fishes found in the Atlantic, Indian and Pacific Oceans, and are rarely found in freshwaters (Nelson, 2006). The family contains 33 genera placed in six subfamilies (the Boopsinae, Denticinae, Diplosinae, Pagellinae, Pagrinae, and Sparinae) and includes approximately 115 species (Orrell et al., 2002; Nelson, 2006). The monophyly of the subfamilies of the Sparidae is not supported in all analyses using the mitochondrial cytB gene (Orrell et al., 2002). Both morphological and molecular evidence has shown that the Sparidae is monophyletic only with the inclusion of the Centracanthidae (Carpenter and Johnson, 2002; Orrell et al., 2002).

Johnson (1980) described the sparoid fishes as a group of percoids that are circumglobal in distribution occurring in nearshore waters of both tropical and subtropical regions. He included the Lethrinidae, Nemipteridae, Sparidae, and

Centracanthidae in this group. Johnson (1980) characterized this group as possessing ctenoid or cycloid scales, and they typically have a scaly opercle and cheek (the exception occurs in *Lethrinus*). The fishes Johnson (1980) characterized as sparoids also have scales extending onto the caudal fin, lateral-line scales with a simple tube, and a lateral line that is complete and not extending far onto the caudal fin. Other morphological characteristics of the group include a moderate to small terminal mouth, 24 vertebrae (10+14), 7-15 epipleurals, and variably protrusible premaxillaries (Johnson, 1980). Johnson (1980) also noted that these fishes lack a procurrent spur, have 3-5 hypurals, 6 infraorbitals, lack a supramaxillary, and the maxillary and premaxillary are morphologically variable between the four families. Among other members of the Percoidei, Johnson (1980) hypothesized a relationship between the Lutjanoidea, Sparoidea, and Haemuloidea, although he found no support for this grouping as compared to other percoids.

Early work investigating the sparoid fishes proposed the Nemipteridae are the basal family of the group, and the Sparidae plus Lethrinidae are more derived (Akazaki, 1962). Johnson (1980) placed the lethrinids as sister to the nemipterids, and both groups sister to the Sparidae + Centracanthidae. Carpenter and Johnson (2002) used 54 morphological characters to investigate the interfamilial relationships of the Sparidae, Nemipteridae, Lethrinidae, and Centracanthidae. Their investigation supported the monophyly of the Sparoidea, and infers the Nemipteridae sister to a group containing the Lethrinidae and the Sparidae + Centracanthidae. This relationship is in agreement with Akazaki's (1962) interpretation of the group (Carpenter and Johnson, 2002).

Orrell et al. (2002) used 1140 bases of the cytB gene from 40 members of the Sparidae, 10 "closely related" species, 10 basal percoids, and two non-perciform outgroup species to test the monophyly of the Sparoidea. They found the Lethrinidae sister to the Sparidae in all analyses. Weighted parsimony produced the Nemipteridae sister to the group containing the Lethrinidae and Sparidae. Orrell et al. (2002) did not support a relationship between the Nemipteridae and Lethrinidae previously proposed by Johnson (1980). The cytB data showed marked saturation in third position substitutions and this study only produces a monophyletic Sparoidea in a weighted nucleotide phylogeny (Orrell et al., 2002).

Other investigations have also shown a lack of support for the monophyly of the Sparoidea. Orrell and Carpenter (2004) used 16S rRNA and cytB nucleotide sequences that resulted in a polyphyletic Sparoidea. Springer and Orrell (2004) found a clade with the phyletic sequence Nemipteridae + ((Centracanthidae + Sparidae) + (Callanthiidae + Lethrinidae)), making the Sparoidea monophyletic only with the inclusion of the Callanthiidae. Smith and Wheeler (2006) did not place sparoid taxa in a monophyletic group, although they have a very limited taxon sampling. They found the Sparidae (*Dentex*) sister to Caproidei. The Lethrinidae were found sister to the Nemipteridae, although this group was not near the Sparidae-Caproidei group in this multi-gene phylogeny (Smith and Wheeler, 2006).

The putative families of the superfamily Sparoidea have traditionally been placed within the perciform suborder Percoidei, but their monophyly and placement among the 78 families of this group is uncertain (Nelson, 1994; Nelson, 2006). Also, no thorough attempts have been made to diagnose a monophyletic Percoidei (Johnson, 1993). With conflicting and inconclusive investigations clouding the evolutionary history of this group of fishes, the goal of this study is to test the monophyly of the superfamily Sparoidea and the relationships between the individual families within the group. This work presents a molecular investigation of the Sparoidea including data from both nuclear recombination activating gene 1 (RAG1) and the mitochondrial cytB gene. A combined analysis of the two genes is also presented.

Materials and Methods

A total of 104 perciform species are represented in this investigation. This includes 56 members of the putative sparoid superfamily (four Centracanthidae, eleven Lethrinidae, twenty Nemipteridae, and twenty one Sparidae; Table 9). Outgroups to the putative sparoids for this study include members of the Perciformes and Pleuronectiformes. Perciform groups include the Percoidei, Anabantoidei, Caproidei, and Scombroidei. These were chosen based on availability of cytB sequences in relation to the RAG1 dataset.

Methods for generation of the RAG1 sequences have been described in the two previous chapters of this dissertation and they will not be repeated here. Cytochrome *b* sequences were obtained from the Molecular Systematics Laboratory at Old Dominion University (Logalbo and Carpenter, 2002; Sliter, 2004; Semcheski, unpublished thesis data) or from Genbank (e.g. Reed et al., 2001; Orrell et. al., 2002; Orrell and Carpenter, 2004).

Cytochrome *b* and RAG1 datasets were analyzed individually for mutational site saturation, base compositional stationarity, and GC nucleotide content. Mutational site

Table 9

Taxon sampling for the Sparoidea investigation. Included is either voucher information or Genbank accession information for each species.

Family	**Species**	**Cytochrome *b***	**RAG1**	**Combined**
Arripidae	*Arripis trutta*	AB205474	CSIRO-H-3856-01	xx
Caproidae	*Antigonia capros*	AP002943	AY308785	xx
Carangidae	*Alectis alexandrinus*	AF363738	ODU-3168	xx
	Caranx hippos	AY050720	ODU-3169	xx
Centrarchidae	*Lepomis cyanellus*	AY115974	RAG-Megadataset	xx
	Lepomis macrochirus	AB167815	ODU-3180	xx
	Micropterus salmoides	DQ451323	ODU-3181	xx
Channidae	*Channa marulia*	AY763771	AY763787	xx
	Parachanna obscura	AY763772	AY763788	xx
Citharidae	*Citharus linguatula*	AY164466	RAG-Megadataset	xx
Coryphaenidae	*Coryphaena hippurus*	AY895015	D. Reed, collector/ voucher	xx
Echeneidae	*Echeneis naucrates*	AY050763	ODU-3184	xx
Haemulidae	*Haemulon sciurus*	AF240747		
	Plectorhinchus macrolepis		Mahon Photo Voucher	
Inermiidae	*Inermia vittata*		KU T-329	
Kuhliidae	*Kuhlia mugil*	AY116003	USNM 336646	xx
Latidae	*Lates calcarifer*	DQ090955	ODU-3197	xx
Lutjanidae	*Lutjanus analis*		RAG-Megadataset	
	Lutjanus decussatus	AF240750		
	Lutjanus dentatus		Mahon Photo Voucher	
	Pinjalo pinjalo		ODU-3072	
	Symphorus nematophorus	Semcheski, unpubl.	No voucher	xx
Moronidae	*Dicentrarchus labrax*	X81566	P. J. Unmack, collector/ voucher	xx
	Morone americanus	AF240744		
	Morone chrysops	AF240745	AY308767	xx
Mullidae	*Mullus surmuletus*		RAG-Megadataset	
	Upeneus moluccensis		ODU-3126	
	Upeneus sulphureus		ODU-3125	

Table 9 (*continued*)

Family	**Species**	**Cytochrome *b***	**RAG1**	**Combined**
Nandidae	*Badis assamensis*	AY330937	AY330966	xx
	Badis corycaeus	AY330945	AY330969	xx
	Badis kanabos	AY330946	AY330970	xx
	Badis siamensis	AY330955	AY330975	xx
	Dario dario	AY330958	AY330977	xx
	Dario hysginon	AY330962	AY330978	xx
Osphronemidae	*Betta splendens*	AF519689	AF519728	xx
	Macropodus opercularis	AF519698	AF519737	xx
	Malpulutta kretseri	AF519700	AF519739	xx
	Parosphromenus deissneri	AF519701	AF519740	xx
	Pseudosphromenus cupanus	AF519699	AF519738	xx
	Trichogaster chuna	AF519696	AF519735	xx
	Trichogaster leerii	AF519695	AF519734	xx
	Trichogaster trichopterus	AY763759	ODU-3186	xx
	Trichopsis vittata	AF519697	AF519736	xx
Percidae	*Etheostoma caeruleum*	DQ465226	AY430226	xx
	Perca flavescens	DQ451358	AY308768	xx
Pomatomidae	*Pomatomus saltatrix*	AF143199	No voucher	xx
Rachycentridae	*Rachycentron canadum*	AF311947	ODU-3193	xx
Sciaenidae	*Leiostomus xanthurus*		ODU-3176	
	Micropogonias undulatus		ODU-3182	
Sphyraenidae	*Sphyraena sphyraena*		RAG-Megadataset	
Centracanthidae	*Centracanthus cirrus*		ODU-3133	
	Spicara alta	AF240738	ODU-2811	xx
	Spicara flexuosa		ODU-3148	
	Spicara maena	AF240737	ODU-3134	xx
Lethrinidae	*Gymnocranius elongatus*	AF381260	ODU-3202	xx
	Lethrinus atkinsoni	AF381255	FMNH-BUS03-040	xx
	Lethrinus atlanticus	AF381264	ODU-3204	xx
	Lethrinus haematopterus		USNM 006364	
	Lethrinus harak	AF381258	ODU-3042	xx

Table 9 (*continued*)

Family	Species	Cytochrome *b*	RAG1	Combined
	Lethrinus lentjan	AF381267	ODU-3060	xx
	Lethrinus obsoletus	AF381271	ODU-3043	xx
	Lethrinus olivaceus	AF381252	ODU-3190	xx
	Lethrinus ornatus	AF240751		
	Lethrinus xanthochilus		USNM 349306	
	Monotaxis grandoculis		MIN0017-8	
Nemipteridae	*Nemipterus japonicus*	Sliter, 2004	ODU-3163	xx
	Nemipterus marginatus	AF240754	ODU-3104	xx
	Nemipterus nematopus	Sliter, 2004		
	Nemipterus peronii	Sliter, 2004		
	Nemipterus vitiensis	Sliter, 2004		
	Parascolopsis eriomma	Sliter, 2004	FMNH-BUS03-307	xx
	Parascolopsis eriomma_2	Sliter, 2004		
	Parascolopsis tanyactis	Sliter, 2004		
	Pentapodus bifasciatus		ODU-3031	
	Pentapodus setosus	Sliter, 2004	FMNH-BUS03-256	xx
	Pentapodus trivittatus	Sliter, 2004		
	Scolopsis affinis		ODU-3030	
	Scaevuis millii	Sliter, 2004		
	Scolopsis bilineatus	Sliter, 2004		
	Scolopsis ciliata	Sliter, 2004	ODU-3049	xx
	Scolopsis ciliate_2		ODU-3049	
	Scolopsis taenioptera		ODU-3091	
	Scolopsis ciliatus	AF240753		
	Scolopsis lineatus	Sliter, 2004		
	Scolopsis margaritifer	Sliter, 2004		
	Scolopsis vosmeri	Sliter, 2004	ODU-2827	xx
Sparidae	*Argyrops spinifer*	AF240717	ODU-2814	xx
	Boops boops	X81567	ODU-2912	xx
	Boopsoidea inornata	AF240711	ODU-2791	xx
	Calamus calamus		BCA-0032	
	Cheimerius nufar	AF240707	ODU-2933	xx

Table 9 (*continued*)

Family	**Species**	**Cytochrome *b***	**RAG1**	**Combined**
	Chrysoblephus anglicus		No voucher	
	Diplodus bermudensis	AF240722	ODU-2815	xx
	Lagodon rhomboides	AF240726	ODU-3175	xx
	Lithognathus mormyrus	AF240712	ODU-2784	xx
	Oblada melanura	AF240701	No voucher	xx
	Pachymetopon grande		ODU-2909	
	Pagellus erythrinus		ODU-2841	
	Pagrus auriga	AF240728	ODU-2786	xx
	Pagrus caeruleostictus		ODU-3027	
	Pagrus pagrus	AY439119	ODU-3188	xx
	Pagrus pagrus		ODU-3188	
	Rhabdosargus holubi		No voucher	
	Sarpa salpa	AJ319812	ODU-3203	xx
	Sparus aurata	AF240735	RAG-Megadataset	xx
	Stenotomus chrysops	AF240736	VIMS VA1-00057	xx
	Virididentex acromegalus		ODU-17-02-04 (016)	

saturation was calculated using the pairwise difference command of PAUP*4.0b10 (Swofford, 2003). The transversions and transitions for each gene and for third codon positions of each gene were then plotted as functions of genetic distance vs. number of differences in Microsoft Excel. Base compositional stationarity was calculated using the x^2 statistic in PAUP*4.0b10 using the "basefreq" command (Swofford, 2003). This calculation determines whether base composition is equivalent across the taxa included in the dataset. Nucleotide composition tables were generated in Mega3.1 (Kumar et al., 1994). These calculations find GC content for each gene at each codon position and as a whole.

Maximum parsimony and maximum likelihood anlayses were performed on both the cytB and RAG1 dataset separately. A combined data analysis was also performed where two datasets were concatenated and the parsimony and likelihood analyses recalculated.

Unweighted maximum parsimony analyses were performed for the three datasets (cytB, RAG1, and the combined cytB+RAG1 dataset) in PAUP*4.0b10 (Swofford, 2003). The analyses performed a heuristic search with 1000 step-wise addition sequence replicates under the TBR (tree-bisection-reconnection) setting. Summary values from PAUP*4.0, including tree length and consistency index, were used to evaluate the trees (Swofford, 2003). Nodal supports in the form of bootstrap indices were calculated in PAUP*4.x for each of the analyses (Felsenstein, 1985; Swofford, 2003). Calculation of the bootstrap values was done using a full heuristic search and 200 replicates, with each replicate consisting of 10 step-wise additions in the TBR method.

Maximum likelihood analyses were run using the GARLI algorithm (Zwickl, D.; version 0.94). This program uses the General Time Reversable (GTR) model of nucleotide substitution with gamma distributed rate of heterogeneity and an estimated proportion of invariable sites (the GTR+I+G model of substitution). To ensure the best (i.e. lowest) log likelihood values were found for each dataset, the analyses were replicated five times.

Results

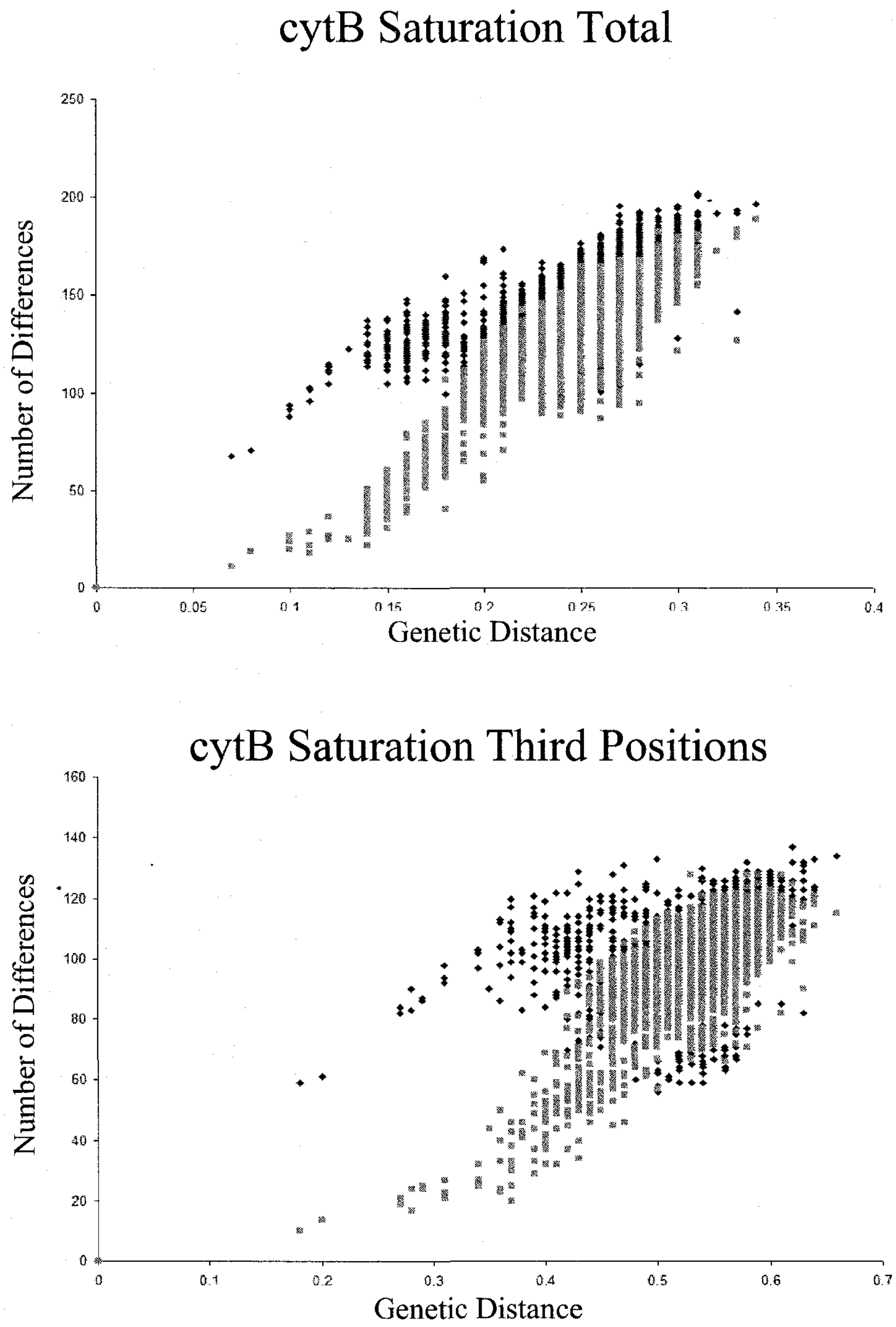
Mutational site saturation is not evident for the RAG1 and cytB genes at all positions, but some saturation (i.e. deviation from linearity) was seen in the cytB third position codons (Figures 28a, 28b). Base composition deviates from stationarity for the cytB, RAG1 and combined datasets (cytB = $\chi^2 = 320.682$, df=237, P = 0.0002; RAG1 = $\chi^2 = 318.136$, df=273, P = 0.0313; combined dataset = $\chi^2 = 241.609$, df=189, P = 0.006) showing a lack of equivalency in the data across all taxa. GC content ranges from 39.9% at the cytB second position codon to 67.7% at the RAG1 third position codon (Table 10).

Cytochrome *b* analyses resulted in a dataset comprised of 80 taxa and 1140 characters each, 628 of which are parsimony informative. Maximum parsimony analyses retained two trees each with a length of 10,576 steps (CI=0.139; RI=0.378; RC=0.053). The strict consensus tree of the cytB dataset found the individual families of the Sparidae + Centracanthidae, the Nemipteridae, and the Lethrinidae to be monophyletic.

Table 10
Average, maximimum, and minimum GC content (expressed as percent content) for each codon position of the cytB and RAG1 datasets included in this investigation.

Cytochrome *b*	**Total**	**First Position**	**Second Position**	**Third Position**
Average	45.8	52.1	39.1	46.2
Maximum	50.5	55	41.3	58.2
Minimum	37.8	45.2	35.5	31

RAG1	**Total**	**First Position**	**Second Position**	**Third Position**
Average	55	54.7	42.3	67.7
Maximum	61.8	56.6	43.9	86.9
Minimum	50.5	52.5	41.3	56.2



cytB Saturation Total

cytB Saturation Third Positions

Fig. 28a. Saturation curves for the cytB gene at all positions and third positions individually. Dark diamonds are transitions and gray squares are transversions.

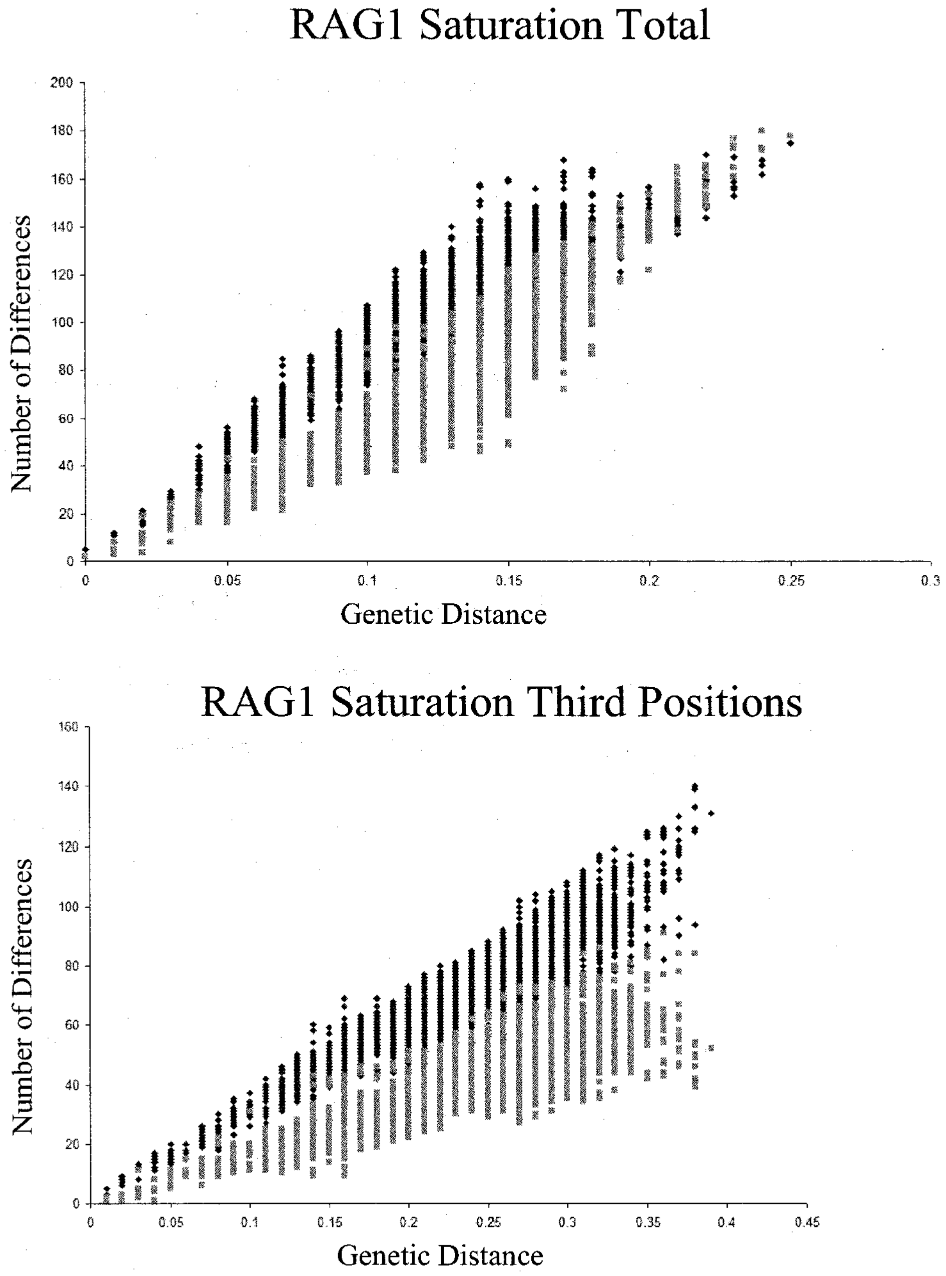


Fig. 28b. Saturation curves for the RAG1 gene at all positions and third positions individually. Dark diamonds are transitions and gray squares are transversions.

The Sparidae formed a monophyletic group only with the inclusion of the Centracanthidae and this group shows 100% bootstrap support (Figure 29). The Sparidae + Centracanthidae were found sister to a clade containing *Antigonia*, the Lutjanidae, and the Moronidae. Maximum parsimony found the Lethrinidae (less than 50% bootstrap support) sister to the Nemipteridae (73% bootstrap support). This relationship had less than 50% bootstrap support. The Lethrinidae + Nemipteridae were found sister to the Pomatomidae + Arripidae in the cytB maximum parsimony analysis. Likelihood analysis of the cytB data do result in a monophyletic Sparoidea. The Sparidae + Centracanthidae were found sister to the Nemipteridae, and these groups sister to the Lethrinidae (Figure 30). The lethrinids were paraphyletic in the likelihood analysis, with *Gymnocranius* found outside of the main lethrinid clade, sister to the Sparidae + Nemipteridae (Figure 30). The likelihood analysis finds the Sparoidea (Lethrinidae + ((Sparidae + Centracanthidae) + Nempiteridae)) sister to the Lutjanidae (Figure 30).

The RAG1 dataset included 92 sequences (91 taxa) and 1431 bases. The dataset resulted in 735 parsimony informative characters and the maximum parsimony analysis retained two trees each with a length of 4952 steps (CI=0.350; RI=0.615; RC=0.216).

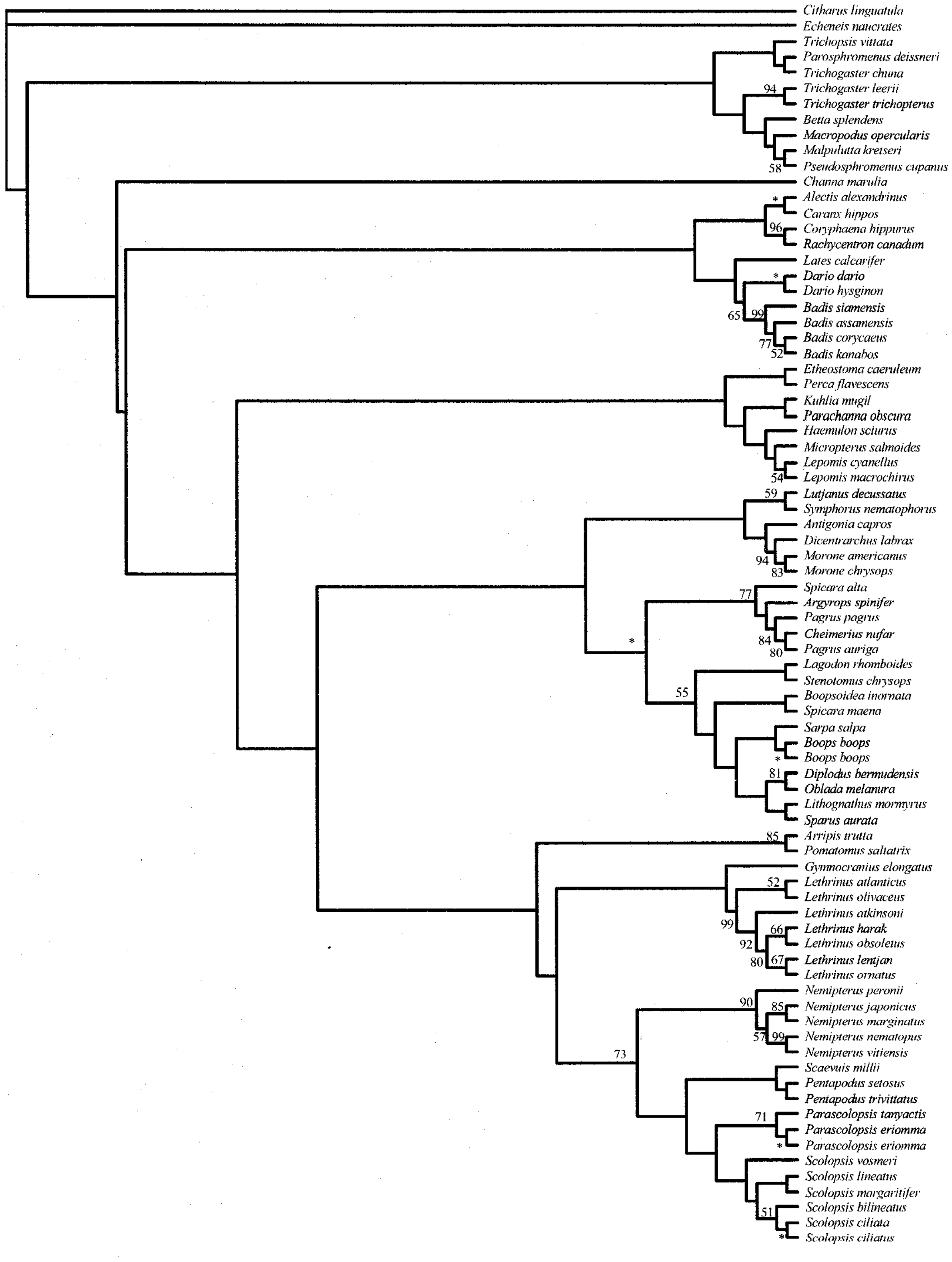


Fig. 29. Strict consensus of two most parsimonious trees from the maximum parsimony analysis of the cytB dataset. Tree length=10576 steps; CI=0.139, RI=0.378, RC=0.053. Bootstrap values for 200 replicates displayed; values below 50% are not shown. Asterisk (*) = 100% bootstrap support.

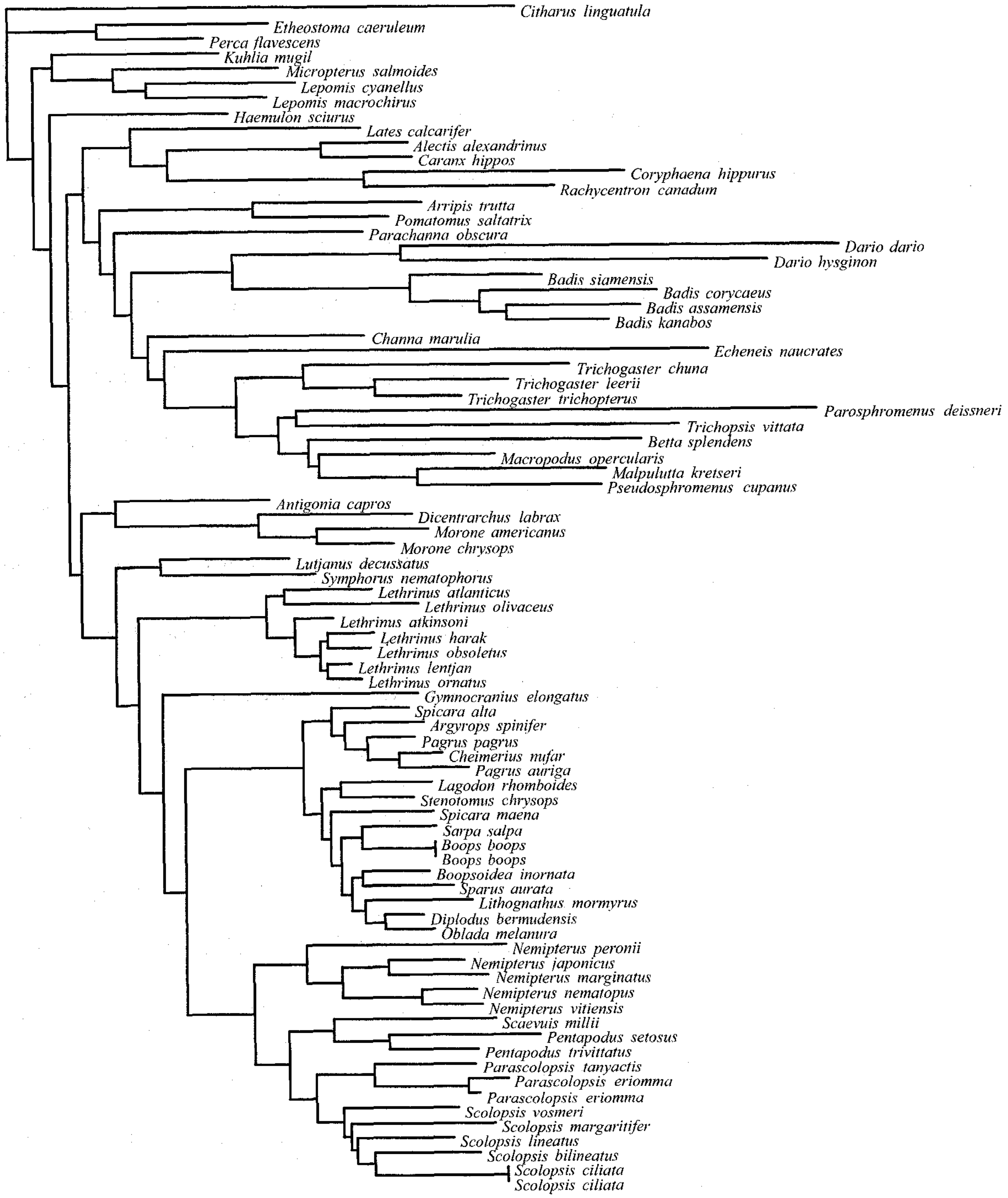


Fig 30. GARLI maximum likelihood analysis of the cytB dataset. Resulting log likelihood value is best of five replicates (lnL=-38312.933).

The strict consensus tree of the RAG1 maximum parsimony analysis shows the Nemipteridae and Lethrinidae as well supported monophyletic families, with 100% bootstrap support for each family (Figure 31). The Sparidae + Centracanthidae form a monophyletic group with 100% bootstrap support (Figure 31). The Centracanthidae is not monophyletic within the Sparidae + Centracanthidae clade (Figure 31). Maximum likelihood analyses produce a most likely tree (-log likelihood value = 27093.14) and the topology is congruent with the results of the parsimony analysis for the monophyly of the individual families (Figure 32). Topology within each family is similar for the parsimony and likelihood trees, but not identical.

The strict consensus maximum parsimony tree of the RAG1 gene finds the Sparidae + Centracanthidae sister to the Lethrinidae and this group sister to the Lutjanidae (Figure 31). The Nemipteridae are sister to the Mullidae in a clade separate from the other sparoid families (Figure 31). Likelihood analyses for the RAG1 gene find the Sparidae sister to the Nemipteridae, and these groups sister to the Lutjanidae (Figure 32). This clade is then sister to the Lethrinidae (Figure 32). The resulting phyletic sequence is (((Sparidae + Nemipteridae) + Lutjanidae) + Lethrinidae).

The combined dataset (RAG1+cytB) consisted of 64 sequences and a total of 2571 characters, of which 1255 were parsimony informative. Two most parsimonious trees were retained in the maximum parsimony analysis with the length of 12833 steps (CI=0.223; RI=0.422; RC=0.094). The Sparidae + Centracanthidae (less than 50% bootstrap support), Nemipteridae (100% bootstrap support), and the Lethrinidae (99% bootstrap support) are all found to be monophyletic in the combined data parsimony analysis (Figure 33). As with previous analyses, the Centracanthidae do not form a

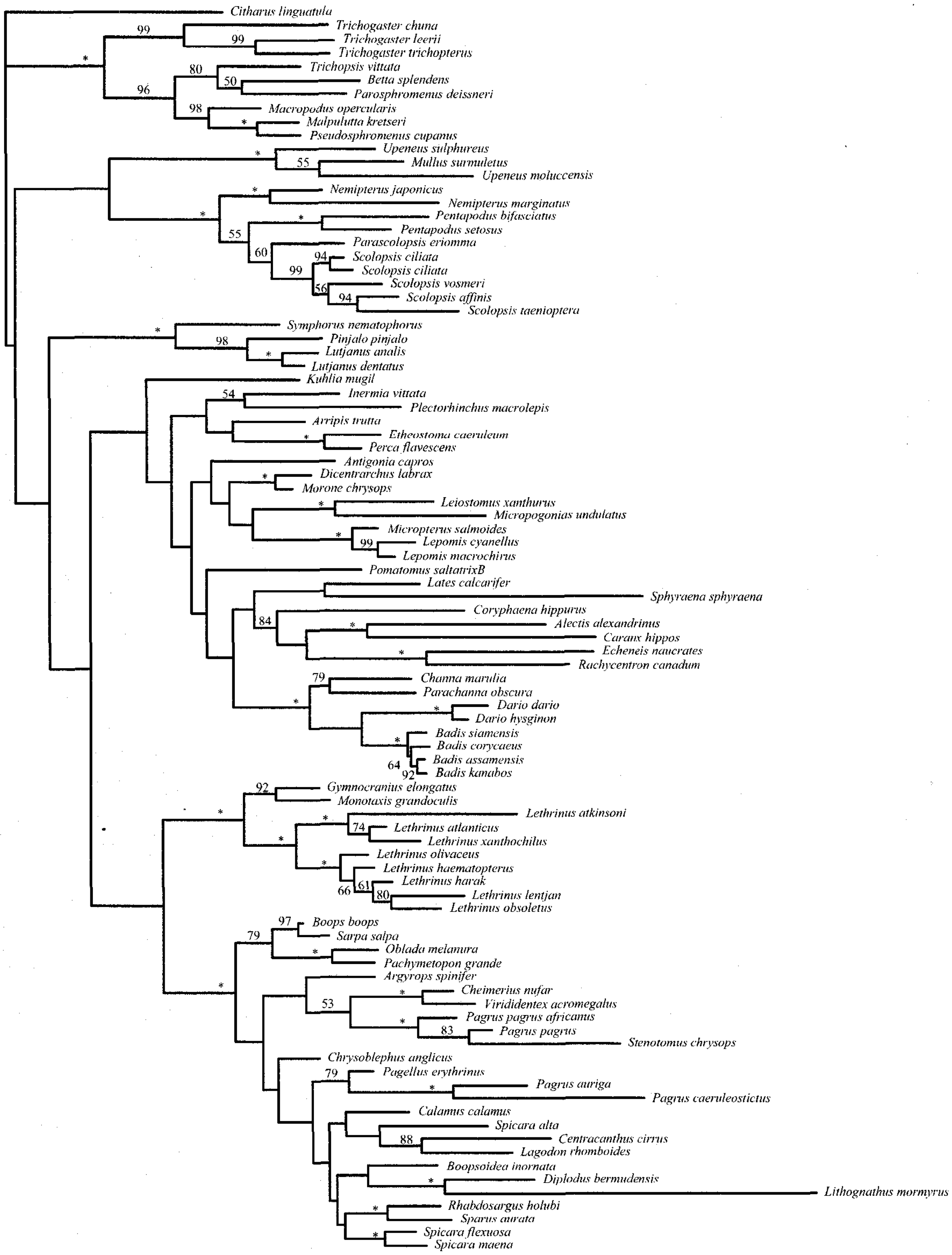


Fig. 31. Strict consensus of two most parsimonious trees from the maximum parsimony analysis of the RAG1 dataset. Tree length=4952 steps; CI=0.350, RI=0.615, RC=0.216. Bootstrap values for 200 replicates displayed; values below 50% are not shown. Asterisk (*) = 100% bootstrap support.

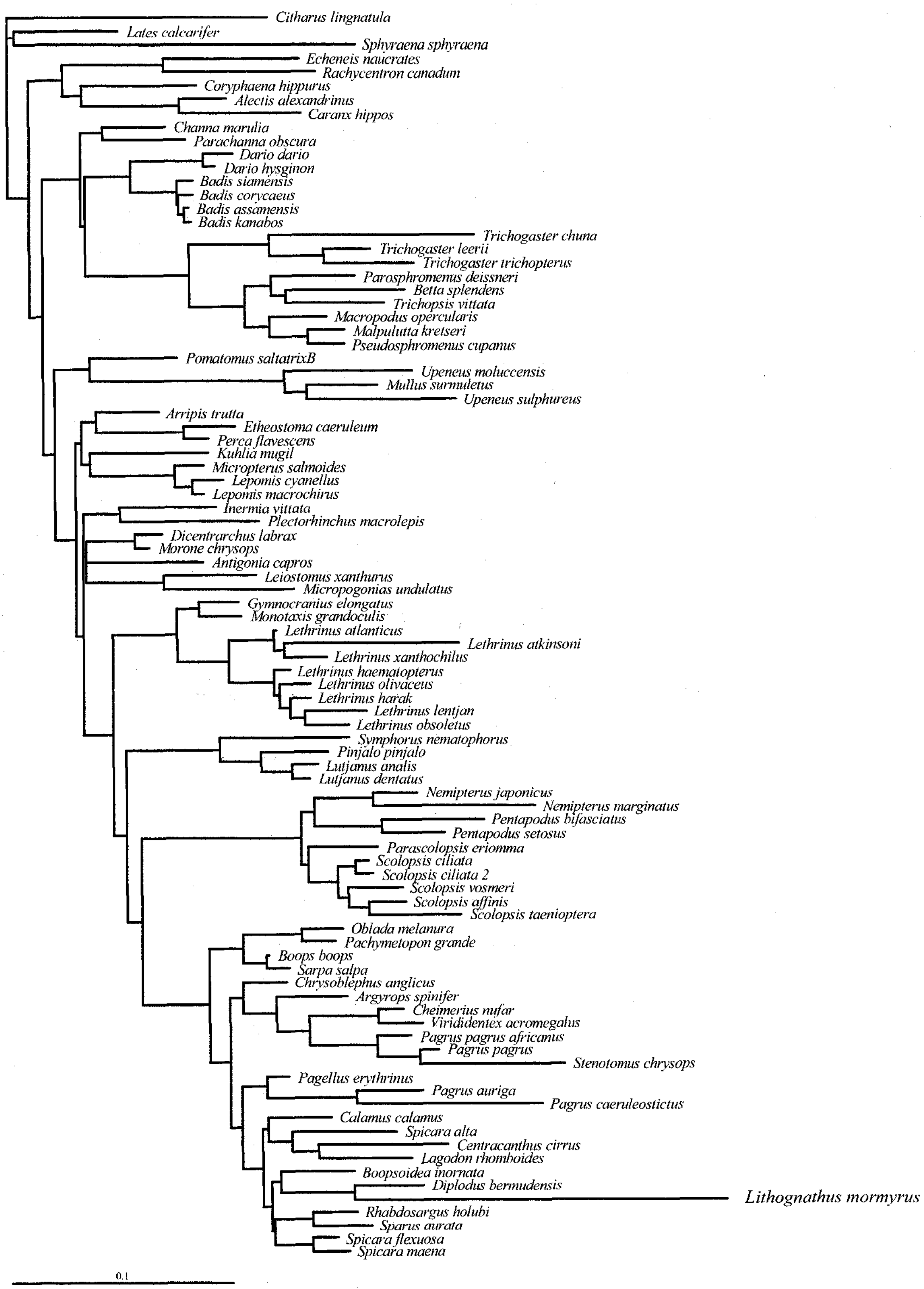


Fig. 32. GARLI maximum likelihood analysis using the GTR+I+G model of evolution of the RAG1 dataset. Resulting log likelihood value is best of five replicates (-lnL = 27093.139).

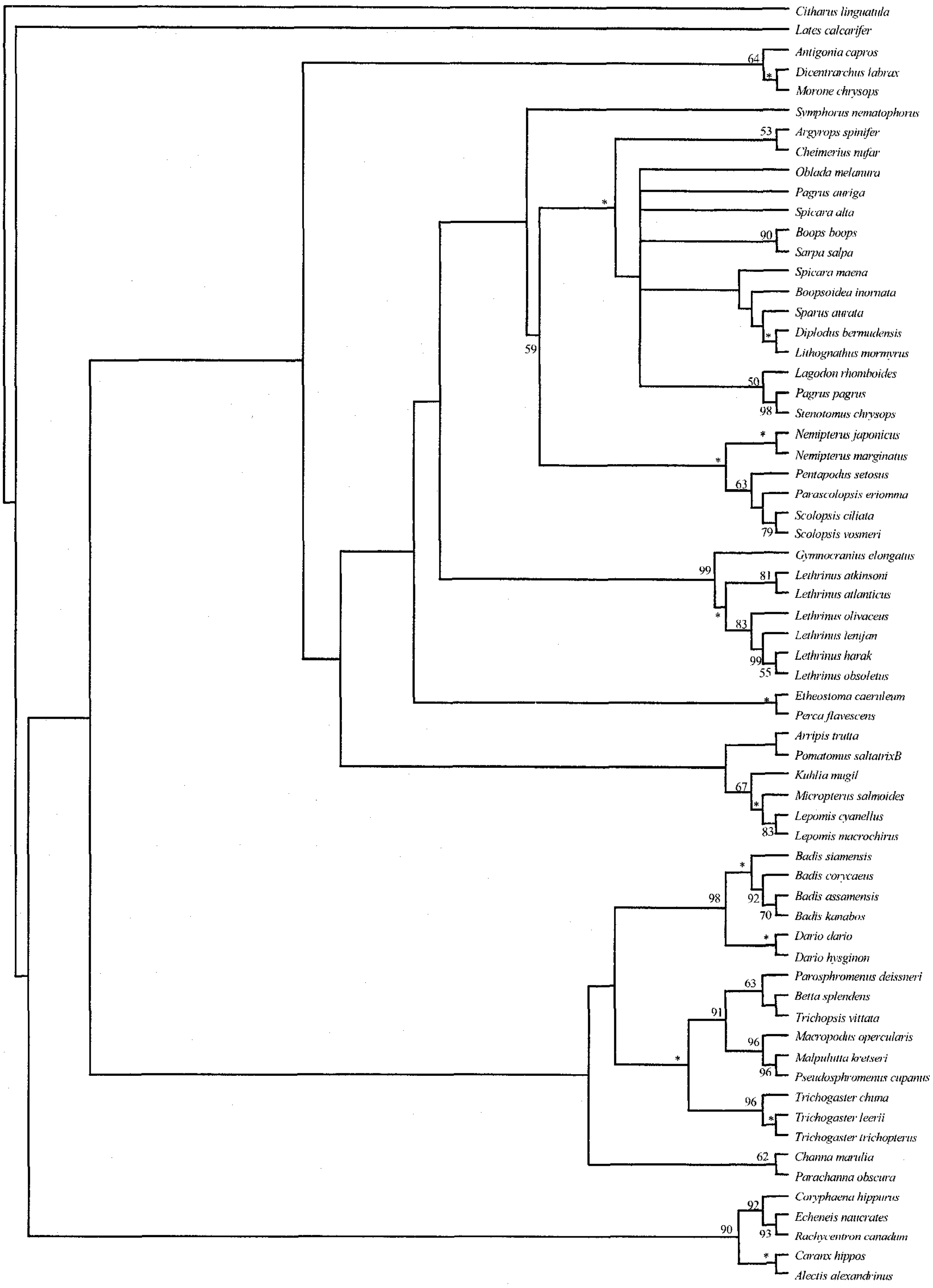


Fig. 33. Strict consensus of two most parsimonious trees from the maximum parsimony analysis of the combined RAG1+cytB datasets. Tree length= 12833 steps; CI=0.223, RI=0.422, RC=0.094. Bootstrap values for 200 replicates displayed; values below 50% are not shown. Asterisk (*) = 100% bootstrap support.

monophyletic group within the Sparidae. Although with low nodal support (59% bootstrap support), the Sparidae is found to be sister to the Nemipteridae in the parsimony analysis (Figure 33). The strict consensus of the combined dataset found a monophyletic group containing all families of the Sparoidea. However, this group was only monophyletic with the inclusion of the family Lutjanidae (Figure 33). Bootstrap support for this clade was less than 50%. Likelihood analyses of the combined dataset produced the same overall phylogeny for the families of the Sparoidea with the phyletic sequence of Lethrinidae + (Lutjanidae + (Nemipteridae + (Sparidae + Centracanthidae))) (Figure 34).

Discussion

As currently defined, the data presented in this study do not support a monophyletic superfamily Sparoidea. Analyses for both genes and the combined dataset find a monophyletic Nemipteridae, Sparidae plus Centracanthidae, and Lethrinidae. The one exception to this is the maximum likelihood phylogeny for the cytB gene (Figure 30), which places the lethrinid *Gymnocranius* sister to the Sparidae-Centracanthidae-Nemipteridae clade, and these groups sister to the remaining lethrinids.

As with previous analyses of the Sparoidea, the datasets used in this investigation do not result in a monophyletic superfamily that only includes the Sparidae, Centracanthidae, Nemipteridae, and Lethrinidae with the exception of the cytB maximum likelihood analysis (eg. Johnson, 1980; Carpenter and Johnson, 2002; Figure 30). Parsimony analyses do not find bootstrap support for nodes deeper than those at the family level. However, the combined analyses of the cytB and RAG1 gene show

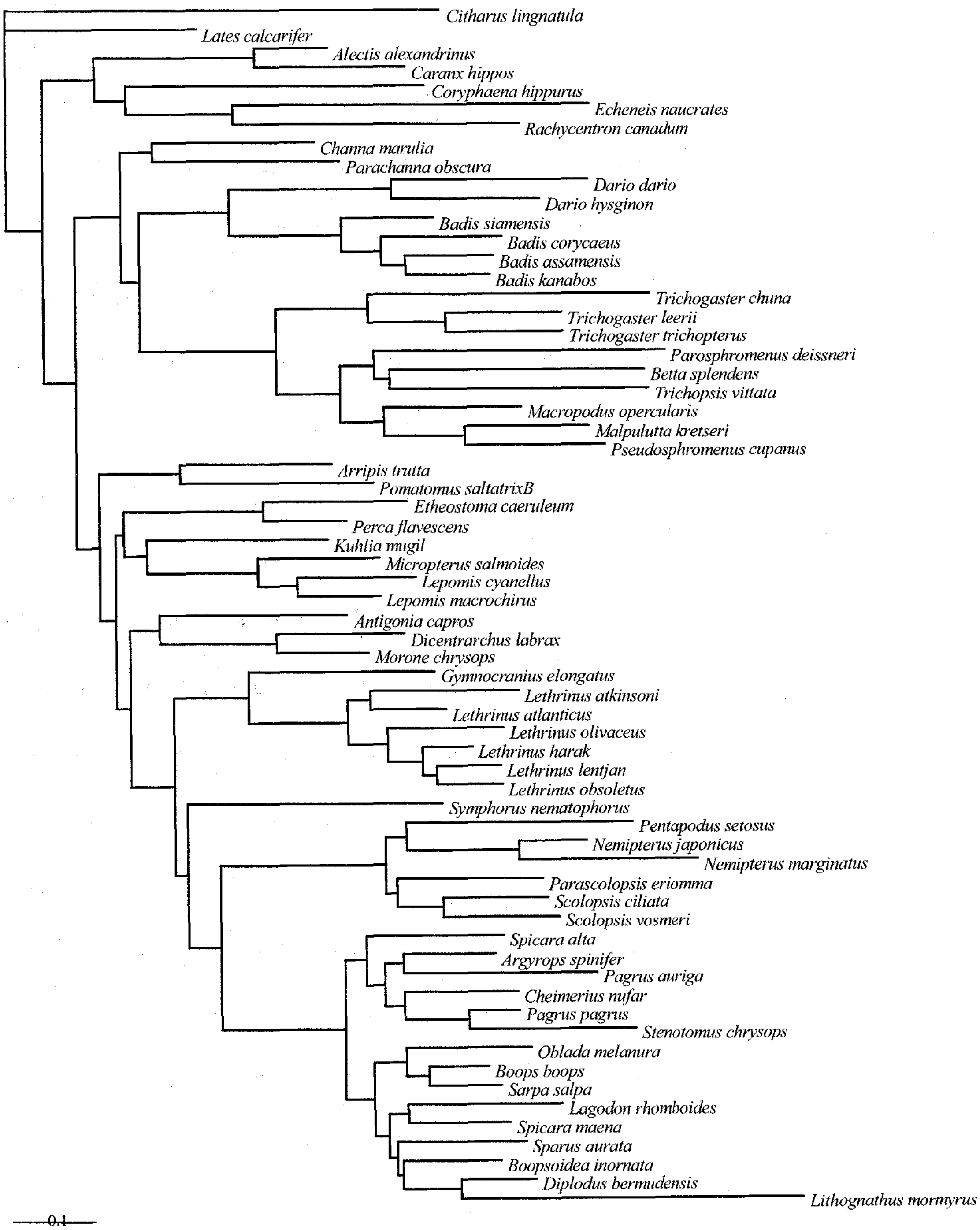


Fig 34. GARLI maximum likelihood analysis using the GTR+I+G model of evolution of the combined RAG1+cytB datasets. Resulting log likelihood value is best of five replicates (lnL= -54971.015).

interesting topology, with the sparoid fishes, along with the Lutjanidae, forming a monophyletic clade in both parsimony and likelihood analyses.

Reasons for the lack of resolution or lack of sparoid monophyly could be attributed to the taxon sampling of the included datasets. For example, the cytB dataset included only 2 lutjanid taxa, and the combined dataset only a single representative of the Lutjanidae (*Symphorus*). Taxon sampling directly impacts resolution of the accurate tree topology (Lecointre et al., 1993). Future investigations should include an increased taxon sampling of the sparoids and the Lutjanidae to ensure the relationship seen in the combined analyses is based on the true evolutionary history of the organisms and is not an artifact of insufficient taxon sampling.

The larger taxon sampling, single-gene analyses in the first two chapters of this dissertation found a monophyletic group that included the Lethrinidae, Lutjanidae + Caesionidae, Nemipteridae, Sparidae + Centracanthidae, Mullidae, and the callionymoid *Synchiropus* in the maximum parsimony analysis. Likelihood results with the greater taxon sampling also found the sparoid families and the Lutjanidae + Caesionidae in a monophyletic group, but also included the Cirrhitidae and the Pholidichthyoidei. The current work presents a more focused phylogenetic scale with two molecular markers rather than only RAG1. However, it does not present the Sparoidea in the context of all percomorph lineages and the possibility exists that some potential outgroups could have been left out of the dataset.

Other potential problems of the current work include the base compositional stationarity of the cytB and RAG1 genes for this group of taxa. Both individual datasets and the combined dataset reject stationarity (cytB = $\chi^2 = 320.682$, df=237, P = 0.0002; RAG1 = $\chi^2 = 318.136$, df=273, P = 0.0313; combined dataset = $\chi^2 = 241.609$, df=189, P = 0.006). This bias in the ratio of character states can distort phylogenetic signal and produce erroneous results (e.g. Lyons-Weiler and Hoelzer, 1999). RAG1 does not show this bias in a larger taxon sampling as seen in earlier discussions of this dissertation work, where inclusion of 279 RAG1 sequences produces a chi-squared value that does not deviate from stationarity ($\chi^2 = 855.73$; df=834; P = 0.2933). From this value, it can be implied, at least for the RAG1 dataset, that a greater taxon sampling helps negate some of the bias in base composition, which could be producing misleading topologies.

Another aspect of this work that could be producing errant topologies in the cytB and RAG1 trees is the GC content of the datasets. Although as a whole, cytB and RAG1 do not contain extreme values of GC content (45.8% and 55.0%, respectively), cytB has a lower GC content at second position codons (39.1%) and RAG1 has a high GC content at third position codons (67.7%). When different clades have a significant difference in GC content, the potential for phylogenetic error is increased (Moreira et al., 2001; Embly et al., 1992; Hasegawa and Hashimoto, 1993). Cytochrome *b* sequences in the current dataset show variation in GC content between taxa that ranges from 37.8% to 50.5% (Table 10). The minimum at the third position codon for cytB is 31%. RAG1 also shows some GC bias, especially in third position codons where the maximum value was found to be 86.9%. These extreme values could be a source of problem in topological resolution of the trees presented in this investigation, as GC content can be a very important source of uncertainty in phylogenetic resolution (Moreira et al., 1999).

The goal of this investigation was to use molecular data from the RAG1 and cytB genes to test the monophyly of the putative superfamily Sparoidea. Individual analyses using the two genes and a combined analysis of those genes do not resolve the superfamily as presented by previous studies (Akazaki, 1962; Johnson, 1980; Carpenter and Johnson, 2002). This study does support the monophyly of the sparoid families Nemipteridae, Lethrinidae (excluding the likelihood analysis of the cytB dataset), and the Sparidae + Centracanthidae. This work also supports a relationship between the sparoid families and the Lutjanidae that should be considered for future investigations. However, limited taxon sampling and genetic bias in the datasets may be present and producing erroneous tree topologies.

The interrelationships of these families among percoid and perciform taxa remain uncertain. However, future studies can use this investigation as a starting point to aid in the resolution of the putative Sparoidea. These investigations should include greater taxon sampling among sparoids, lutjanids, and other percoid taxa. Future work should also include more genetic markers to help infer the evolutionary history of the sparoid fishes.

CHAPTER V

GENERAL CONCLUSIONS

The goals of this dissertation were to test the monophyly of the order Perciformes, to investigate the interrelationships of the families putatively placed in the perciform suborder Percoidei, and to investigate the monophyly of the superfamily Sparoidea.

The first chapter of this dissertation produces a suborder level phylogeny of the order Perciformes. This includes a large taxon sampling from representatives of numerous percomorph groups, including representatives of all perciform suborders and from 70 of the 79 (sensu Nelson, 2006) percoid families. The study includes 279 RAG1 exon 3 DNA sequences of and inferred both previously hypothesized and novel interpretations of the interrelationships of these suborders and families. Genetic properties of the RAG1 have potential for phylogenetic error introduced by the high GC content in some taxa. One specific example of this can be seen in the order Pleuronectiformes, which is not inferred as monophyletic in this investigation, probably as a result of this codon bias. The GC content of this order was 57.1% for all codon positions, compared to the 53.9% for all taxa in the study. The third position codons for the pleuronectiform fishes have a GC content of 73.7% as compared to 64.8% for the total dataset.

Phylogenetic analyses in the first chapter infer the beryciform family Holocentridae sister to a monophyletic Perçomorpha. Maximum parsimony and maximum likelihood analyses infer a monophyletic series Percomorpha, but reject the monophyly of the Perciformes. Relationships for all suborders of the Perciformes are compared to previously reported hypotheses. Nodal support for the maximum parsimony analysis (bootstrap and jackknife supports) are shown to be variable across the topology of the trees. Mid-level nodal supports for most clades in the maximum parsimony analyses are low (below 50%). Support indices in the maximum parsimony analysis were strongest for the series Percomorpha and for individual families included in the study.

The second chapter of this dissertation utilizes the phylogenetic analyses produced in the first chapter and describes in detail the relationships of the percoid families included in the investigation. Previous studies had stated that the Percoidei, as traditionally defined, is most likely polyphyletic (e.g. Johnson, 1993). Therefore, it was necessary to test percoids among their putative outgroups, including members of the Perciformes and Percomorpha. This study inferred relationships for 70 of the 79 putative percoid families and included 270 species of percomorph fishes. This work presents one of the most comprehensive tests of the monophyly of Percoidei. Smith and Craig (2007) investigated percoid relationships with larger numbers of molecular markers (4036 bases). However, their work used a significantly lower number of taxa than that used in this dissertation. Percoid representation in Smith and Craig (2007), those taxa classified in their Percoidei and Moronoidei, include 71 representatives from 60 families. Only 12 of the percoid-moronoid families in Smith and Craig (2007) were represented by multiple taxa. Percoid representation in this dissertation includes 173 taxa from 70 families and only 46 of these families are represented by multiple taxa.

Phylogenetic analyses in the third chapter do not support a monophyletic Percoidei and agree with Johnson's (1993) statement that the Percoidei is undoubtedly polyphyletic. Again, family level relationships produced here show some similarity to previous work but also present some novel interpretations of the group.

Finally, the fourth chapter of this dissertation investigates a specific grouping of percoid fishes, the putative percoid superfamily Sparoidea. It tests both the monophyly of the sparoid families (Sparidae, Nemipteridae, Lethrinidae, and Centracanthidae) and the interrelationships of these families. Using RAG1 data from the previous chapters and available cytochrome b data in both individual and combined analyses, this investigation shows that the Nemipteridae and Lethrinidae are well-supported, monophyletic families. The Centracanthidae are not monophyletic and are nested within the Sparidae, forming a monophyletic group in all analyses. Analyses from the cytB, RAG1, and combined analyses of both genes do not infer a monophyletic Sparoidea as presented in previous studies (e.g. Akazaki, 1962; Johnson, 1980; Carpenter and Johnson, 2002).

Future investigations of the perciform fishes, interfamilial relationships of the Percoidei and investigations of the putative superfamily Sparoidea should include a larger sampling of genetic markers to further test the phylogenetic relationships of these groups. The relatively large segment of the RAG1 gene used here represents a substantial tes of the evolutionary relationships within this large group of fishes. However, more genetic information may help resolve mid-level nodal support for these groups. The genetic biases, including high GC content at third codon positions in RAG1, are factors that make additional genetic markers crucial for future work.

This work presents data from over 270 species of percomorph fishes. In total, this is only about 2% of the total taxa in this series. The relationships and their levels of phylogenetic support could be improved by increasing taxon sampling for all percomorph groups. This is the case not only for the perciform suborder and percoid family investigations but also the investigation of the sparoid fishes.

Although both genetic information and taxon sampling do not provide adequate levels of resolution at all levels of the phylogenies presented here, this dissertation presents one of the most inclusive investigations of perciform and percoid systematics to date. Representation of all suborders of the Perciformes and nearly 90% of the families of the Percoidei resulted in hypotheses that can be further tested. The data set produced forms a basis for future work on the systematics of this group of fishes that includes other genes and more taxa.

The results of these studies show that the current definitions of the order Perciformes, the suborder Percoidei, and the superfamily Sparoidea are inadequate. The data presented here reject the monophyly of all three groups. Further work in this area is necessary to redefine these large groups of fishes and to help elucidate their evolutionary relationships.

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APPENDIX

NOVEL RAG1 SEQUENCE DATA INCLUDED IN THIS DISSERTATION

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>Sargocentron_cornutum
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VITA

ANDREW R. MAHON

Department of Biological Sciences, Old Dominion University
Norfolk, VA 23529

Education

- Ph.D. in Ecological Sciences. Old Dominion University. 2007.
- Master of Science in Biology. University of Alabama at Birmingham. 2000..
- Master of Science in Biology. Truman State University. 1999.
- Bachelor of Science in Chemistry. Truman State University. 1997.

Instructional Experience

- **Adjunct Instructor**. Old Dominion University, Dept. of Biological Sciences. Instructor of five complete courses including Marine Biology, Principles of Ecology, Evolution, Genetics, Molecular and Immunological Techniques (graduate and undergraduate course), and Undergraduate Senior Seminar.

Publications

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Affiliations

- Society for Integrative and Comparative Biology (SICB)
- Sigma Xi, Scientific Research Society, Associate Member.
- Alpha Chi Sigma professional Chemistry fraternity, professional member.
- American Society of Ichthyologists and Herpetologists