THE INTERRELATIONSHIPS OF FISHES OF THE ORDER STOMIIFORMES

BY

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Chapter One

Introduction

Introduction to Stomiiformes

The order Stomiiformes is composed of 417 species in 53 genera (Eschmeyer, 1998; Nelson, 2006), including the lightfishes, dragonfishes, viperfishes, snaggletooths, loosejaws, bristlemouths, and hatchetfishes. All members of the order are marine, and most are meso- or bathypelagic. Stomiiforms are found in all of the world's oceans. Most species are either black or silvery, and all species except one are bioluminescent. The deep-sea species usually have a reduced swim bladder, a lighter skeleton, and a high lipid content in their bodies (Herring, 2002). Stomiiforms are generally small fishes, with most species less than 10 cm long, though adults range in size from 1.5 cm to about 50 cm (Fink and Weitzman, 1982). Two six-foot-long stomiids were reportedly viewed from the window of the first manned deep-sea submersible, the bathysphere (Beebe and Crane, 1939), but no specimen was collected and it seems likely that the sighting was a case of mistaken identity or optical illusion.

Although some stomiiform species are rarely collected (e.g., *Sonoda spp., Rhadinesthes decimus, Araiophos eastropas*), other members of the order are clearly among the ocean's most numerous inhabitants. Indeed, the bristlemouth genus *Cyclothone* is often touted as being probably the most abundant vertebrate genus in the world in terms of numbers of individuals (Herring, 2002; Nelson, 2006).

Stomiiforms make up an important part of the diet of large marine vertebrates such as tunas and dolphins (Young et al., 1997; Gannon et al., 1998).

Fossil evidence of stomiiform fishes is limited. Most of the known fossil stomiiforms are from the Miocene (Grenfell, 1984; Brzobohaty and Nolf, 2002; Carnevale, 2008), or the Eocene (Patterson, 1993; Prokofiev and Bannikov, 2002). Indirect lines of evidence indicate that the stomiiform lineage arose sometime in the Mesozoic (Forey and Patterson, 2006). Gregorová (1989) describes stomiiform fossils from the Tertiary, including specimens belonging to the extant genus *Vinciguerria*. The Cretaceous genus *Idrissa* has been considered a possible stomiiform, but its placement is problematic (Arambourg, 1952; Prokofiev, 2005) and Weitzman (1967) concluded that it is not a stomiiform.

Monophyly of Stomiiformes

Even prior to the introduction of cladistic principles to ichthyology, many early workers recognized an affinity among the fishes now recognized as members of Stomiiformes, placing them together or sequentially in classifications (Gill, 1872; Günther, 1880; Brauer, 1906; Regan, 1911). Stomiiform fishes were usually classified with clupeoids (Regan, 1923; Marshall, 1960), salmonoids (Beebe and Crane, 1939; Greenwood et al., 1966), or both (Gregory and Conrad, 1936; Gosline, 1960), and early diagnoses of the stomiatoid group focus on characters that distinguish them from their putative relatives, including the presence of photophores and a mouth that continues posteroventrally past the eye. Rosen (1973) was the first to recognize the group at the ordinal level, and Fink and Weitzman (1982) provide a list of synapomorphies for the order that have remained accepted (Harold and Weitzman, 1996; Nelson, 2006).

Stomiiform Synapomorphies

1. Stomiiform photophores (light organs) have a structure that is apparently unique among teleosts. The walls of the photophores are lined by flat cells filled with guanine platelets and covered by a pigmented layer; they serve as a reflector. The interior of the photophore is filled with two different types of cells: the photocytes, light-producing cells packed with endoplasmic reticulum; and a second type of cell that has been described as "glandular" and may function as a filter (Bassot, 1966). Stomiiform photophores are not bacterial; the fish produces its own luciferin (Herring and Morin, 1978). Bassot (1966) identified three main types of photophores within the order. In type Alpha photophores, the photocytes are arranged in rows perpendicular to the long axis of the photophore. In type Beta photophores, photocytes are arranged around a central lumen that sometimes has an opening to the outside. In type Gamma photophores, the photocytes are arranged radially around the center of the organ. Both Alpha and Gamma types lack a lumen. These three photophore types have been considered in the study of stomiiform intrarelationships. Non-bacterial photophores are found in numerous species in at least six other teleost orders, but none of these photophores have a structure that is similar to that of any of the types of stomiiform photophores.

2. Stomiiforms have a unique mode of tooth attachment not found in any other teleost. The anterior border of the tooth is fused to the attachment bone or tightly bound to it by collagen, and the posterior border of the tooth is farther from the attachment bone and only bound to it loosely, if at all. The tooth is hinged, with the anterior border of the tooth serving as the axis of rotation (Fink, 1981). This type of tooth attachment is found in most adult stomiiforms on either jaw or branchial teeth (Fink and Weitzman, 1982) and is classified as Type 3 attachment by Fink (1981). Fink characterized this as one of four tooth attachment types found in actinopterygians. The other three types include Type 1 attachment, in which the tooth is fully fused to the attachment bone; Type 2 attachment, in which there is an area of unmineralized collagen at the tooth base and the tooth may be slightly depressible; and Type 4 attachment, in which the posterior edge of the tooth has a large area of collagen and the anterior edge lacks either collagen or dentine, and the tooth is hinged with a posterior axis of rotation (Fink, 1981). In addition to Type 3 attachment, Type 1 and Type 4 are found in stomiiforms (Fink, 1981; Fink and Weitzman, 1982).

3. Stomiiforms have a medial division of the adductor mandibulae muscle which is usually further divided into a ventral section inserting on the primordial ligament and a dorsal section inserting onto the maxilla (Rosen, 1973). In some stomiiform taxa, either the dorsal or ventral section is emphasized and the other is reduced or lost; in a few groups, including *Gonostoma* and *Margrethia,* there are additional sections (Fink and Weitzman, 1982). Rosen (1973) suggested that the insertion of a division of the adductor mandibulae — whether the medial division or

the dorsolateral division — on the maxilla is a neoteleostean character. Fink and Weitzman (1982) argued that the medial division and dorsolateral division are not homologous, on the grounds that their relative positions indicate distinct developmental origins. A dorsolateral division of the adductor mandibulae seems to be a synapomorphy for the Eurypterygii, whereas a medial division is found not only in stomiiforms but also in myctophids (but not the myctophid sister group, Neoscopelidae), and in some acanthomorphs (Fink and Weitzman, 1982; Winterbottom, 1974). This condition probably evolved independently in each lineage.

4. Stomiiforms have a premaxillary-rostrodermethmoid ligament that connects the dorsolateral face of the ethmoid to the contralateral premaxilla (or to both the contralateral and ipsilateral premaxillae). Most other teleosts do not have such a ligament; however, in *Galaxias* there are broad ligamentous sheaths connecting the dorsolateral surface of the ethmoid to the contralateral and ipsilateral premaxillae (Fink and Weitzman, 1982).

5. In stomiiforms, the second epibranchial has one broad proximal termination that articulates with both the second and the third pharyngobranchials. In other lower teleosts, the termination of the second epibranchial is forked, with separate processes articulating with the second and third pharyngobranchials (Rosen, 1973; Fink and Weitzman, 1982).

6. In stomiiforms the posterior branchiostegal ray is significantly and abruptly larger than those anterior to it (in a few taxa, it is the posterior two or three rays, not just one, that are larger; the abruptness of the transition is the same). In most other

teleosts, there is a gradual increase in size of branchiostegal rays from anterior to posterior (McAllister, 1968; Fink and Weitzman, 1982).

7. Most stomiiforms have branchiostegals articulating with the ventral hypohyals. Exceptions are some of the sternoptychids and the malacosteines, in which branchiostegal rays are found only on the anterior and posterior ceratohyals. No other teleost has been found to have branchiostegals on the ventral hypohyals (McAllister, 1968; Fink and Weitzman, 1982).

8. In stomiiform fishes the rete mirabile, the network of blood vessels that move gases in and out of the swim bladder, is located at the posterior end of the swim bladder. In almost all other teleosts that have a rete mirabile, it is located near the middle or toward the anterior end of the swim bladder. Some beryciform and stephanoberyciform fishes also have the rete at the posterior end of the swim bladder, but in these taxa the structure of the rete is different from that of stomiiforms (Marshall, 1960).

Molecular Systematics of Stomiiformes

Stomiiformes as a group is very morphologically divergent from other fishes. This has been useful for establishing the monophyly of the order, but makes it more difficult to determine the relationships of Stomiiformes with other fish groups. Even within the order, there is a high degree of morphological diversity but also extensive morphological homoplasy (Fink, 1984b; Harold and Weitzman, 1996). The difficulties presented by stomiiform morphology in phylogenetics suggest that molecular data may be particularly promising for resolving the relationships of this group. However, few previous studies have used molecular data to address stomiiform relationships. The only applications of molecular data to relationships within the order have been limited to the genera *Cyclothone, Gonostoma,* and *Sigmops* (Miya and Nishida, 1996; Miya and Nishida, 1997). Larger, deep-level fish phylogenies based on molecular data have included no more than five representative stomiiforms (Ishiguro et al., 2003; Miya et al., 2003; López et al., 2004). The object of my dissertation is the use of DNA sequence data to address both the inter- and intrarelationships of Stomiiformes.

Chapter Two

Interrelationships of Stomiiformes and Neoteleost Monophyly

Introduction

Interpretations of the relationships of the stomiiforms to other fishes have varied. Some early workers suggested that stomiiforms were related to the clupeoids on the basis of similarities in the caudal skeleton and the presence of two supramaxillaries in some of the taxa (Regan, 1923; Marshall, 1960). Others linked stomiiforms to the salmonoids because of the presence of a dorsal adipose fin in many taxa as well as similarity in shape of several skull bones, including the basisphenoid and pterotic (Beebe and Crane, 1939; Greenwood et al., 1966). The stomiiforms, salmonoids, and clupeoids were all united by many authors in the order Isospondyli (Gregory and Conrad, 1936; Beebe and Crane, 1939; Gosline, 1960), a group that also included elopids, albulids, osteoglossomorphs, and argentinoids. A competing hypothesis was that stomiiforms were closely related to the Iniomi, a grouping composed of fishes now considered members of Myctophiformes and Aulopiformes (Regan, 1911; Garstang, 1931). Stomiiform fishes were linked to Iniomi on the basis of characters including presence of photophores, a wide gape, and a reduced or absent swim bladder, all adaptations to life in the deep ocean. Affiliations were also suggested between the stomiiforms and the alepocephaloids (Berg, 1940) or the fossil enchodontids (Regan, 1911; Gregory and Conrad, 1936).

Weitzman (1967) argued extensively that stomiiforms are most closely related to the osmerids and galaxiids. Of the many (mostly osteological) similarities he noted between the taxa, he considered characters associated with the ethmoid region of the skull the most important. In these fishes the ethmoid itself is largely unossified but surrounded by plates of perichondral bone, whereas in most other actinopterygians, the ethmoid is mostly ossified (Gregory, 1933; Weitzman, 1967). Weitzman considered the stomiiform genera *Vinciguerria* and *Polymetme* among the most basal members of the group, stating "if no other stomiatoids existed, *Vinciguerria* could easily be considered a somewhat neotenic, sea-going osmerid with photophores" (Weitzman, 1967).

Rosen (1973) erected the clade Neoteleostei to encompass the approximately 17,000 species of higher teleosts, including stomiiforms, aulopiforms, myctophiforms, lampriforms, polymixiiforms, percopsiforms, gadiforms, and acanthopterygians. He placed Stomiiformes sister to the clade he named Eurypterygii, composed of all other neoteleosts. Rosen recognized three characters as diagnostic of Neoteleostei. The first is the presence of a large muscle originating on the seventh to ninth vertebrae and inserting on the fourth infrapharygobranchial; Rosen called this muscle the retractor arcuum branchialum, but it is now known as the retractor dorsalis (Rosen, 1973; Fink and Weitzman, 1982). The second character recognized by Rosen is the presence of dorsal projections of bone on the premaxilla: the ascending and articular premaxillary processes. The third character is the presence of a medial division of the adductor mandibulae muscle (Rosen, 1973).

Fink and Weitzman (1982) agreed with Rosen that stomiiforms are neoteleosts and sister to Eurypterygii, but they reinterpreted the diagnosis of Neoteleostei. They interpreted the adductor mandibulae condition in stomiiforms as uniquely derived in the order and list it among stomiiform synapomorphies. Similarly, they argued that the upper jaw characters listed by Rosen (1973) are not neoteleost synapomorphies. They agreed that the retractor dorsalis muscle is a neoteleost synapomorphy, although a similar muscle is found in gars, *Amia,* cyprinids, and *Lepidogalaxias* (Fink and Weitzman, 1982; Fink, 1984a). Three new synapomorphies were listed by Fink and Weitzman (1982) for Neoteleostei. The first was the presence of a single medial rostral cartilage between the premaxillae and the ethmoid region. They found the rostral cartilage present in most myctophiforms, aulopiforms, and stomiiforms. A similar structure, composed of two paired cartilages rather than one, is found in salmonids (Fink and Weitzman, 1982). The second new neoteleost synapomorphy was Type 4 tooth attachment, in which the teeth are hinged with the axis of rotation at the posterior tooth border (Fink, 1981). Although Type 3 tooth attachment is found in many stomiiforms and is a synapomorphy for the order, Type 4 attachment is found in some juvenile and small adult stomiiforms and a variety of eurypterygians. Fink (1981) also found Type 4 attachment in *Esox*. The final neoteleost character listed by Fink and Weitzman (1982) was that both the exoccipital and basioccipital, rather than just the basioccipital, articulate with the vertebral column (Weitzman, 1967; Rosen and Patterson, 1969; Fink and Weitzman, 1982). This character apparently is independently derived in *Hiodon* (Greenwood, 1973; Fink and Weitzman, 1982), and the condition in salmonids is identical to neoteleosts, to the extent that Fink and Weitzman (1982) suggest the possibility that Neoteleostei might need to be expanded to include Salmoniformes. This configuration of the occipital condyle is also found in *Lepidogalaxias* (Fink, 1984a). Finally, Fink and Weitzman (1982) concluded that *Diplophos* was the most basal member of Stomiiformes, as opposed to *Vinciguerria* or *Polymetme,* the conclusion of Weitzman (1967).

The monophyly of Neoteleostei has remained generally accepted (Lauder and Liem, 1983; Johnson, 1992; Johnson and Patterson, 1996). Johnson (1992) suggested that an important neoteleost synapomorphy is a shift in the insertion of the third internal levator muscle from the fourth pharyngobranchial to the fifth upper pharyngobranchial toothplate; he listed this synapomorphy among the four "most important" for Neoteleostei, excluding the rostral cartilage listed by Fink and Weitzman (1982) from his list.

Most authors have also agreed that Stomiiformes is sister to all other neoteleosts (Lauder and Liem, 1983; Johnson, 1992; Johnson and Patterson, 1996; Nelson, 2006). However, Olney et al. (1993) concluded that the jellynose fishes (Ateleopodidae) were not lampriforms as previously thought, and placed ateleopodids in an unresolved trichotomy with stomiiforms and eurypterygians.

There have been few molecular studies investigating the relationships of Stomiiformes with other fishes. Analyses based on whole mitochondrial genome sequences and including up to three representative stomiiform species have yielded a monophyletic Neoteleostei with Stomiiformes sister to Eurypterygii (Ishiguro et al., 2003; Miya et al., 2003; Simmons and Miya, 2004). In contrast, a study based on data from the RAG1, 12S rRNA, and 16S rRNA genes and including two representative stomiiforms recovered Stomiiformes in a clade with osmeroids and galaxioids (López et al., 2004). Whereas the mitogenomic studies agree with the currently prevailing view of stomiiform relationships, López et al. (2004) echoes the earlier hypothesis of Weitzman (1967).

The primary goal of this study is to provide a robust test of the phylogenetic position of Stomiiformes with respect to all major previous hypotheses. Simultaneously and inseparably, it is necessary to test the monophyly of Neoteleostei as currently defined. Additionally, the relationships of Ateleopodidae relative to Stomiiformes and Eurypterygii are examined.

Methods

Taxon Sampling

Taxon sampling was broad, including all of the major groups with which Stomiiformes has at some time been linked in the literature (Table 2.1). A total of 80 species were sampled, including 11 stomiiforms, two ateleopodids, 21 eurypterygians (of which four were aulopiforms), 20 "protacanthopterygians" (*sensu* Nelson 2006), 13 ostarioclupeomorphs, 10 elopomorphs, and three osteoglossomorphs. *Amia calva* was used to root the trees.

Genes

The data set is composed of sequences from three protein-coding nuclear genes (RAG1, MYH6, and ZIC1) and one protein-coding mitochondrial gene (COI). Genes were selected for analysis on the basis of several criteria: (1) relatively slowly-evolving, and thus more likely to be helpful in resolving deep phylogeny; (2) single-copy so that there was little or no doubt that the sequences I obtained represented orthologous and not paralogous genes; and (3) fragments could be successfully amplified for most or all of the targeted taxa. Several additional candidate genes were investigated and subsequently rejected for analysis because of failure to meet one or more of the criteria.

The recombination activating gene 1 (RAG1) is one of two RAG genes that both encode enzymes with important immune function in vertebrates. These enzymes are responsible for shuffling and recombining the several hundred VDJ genes into combinations that produce millions of different antibodies (Sadofsky, 2004). The RAG1 gene is well characterized and widely used for reconstruction of vertebrate phylogenies (Hrbek et al., 2006; Miya et al., 2007; Jackman et al., 2007).

The ZIC1 and MYH6 genes were both recently developed as markers for fish phylogenetics (Li et al., 2007). The alpha-myosin heavy chain (MYH6) gene is expressed in the cardiac muscle of vertebrates. It codes for one of the six chains that make up a myosin II filament, the structure that produces contractile force in a muscle cell through articulation with an actin filament (Berg et al., 2001). The zinc finger protein 1 (ZIC1) gene is expressed in the cerebellum and is involved in regulation of neural development (Aruga et al., 1998).

The cyctochrome c oxidase gene I (COI) is the only mitochondrial gene included in the dataset. Its protein product is the last enzyme in the electron transport chain of cellular respiration (Capaldi, 1990). The COI gene is widely used in eukaryote systematics (Schulte and de Quieroz, 2008; Jørgensen et al., 2008; Meixner et al., 2007). It is also the gene used for most animal taxa by the Consortium for the Barcode of Life (Kress and Erickson, 2008; Savolainen et al., 2005).

Data Collection and Alignment.

I isolated total genomic DNA from tissue samples using either the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA) or a standard desalting protocol followed by alcohol precipitation. Preserved tissue for *Ateleopus japonicus* was not available, but a sample of previously extracted DNA was generously provided by Masaki Miya (Natural History Museum, Chiba, Japan).

Target sequences were amplified using the polymerase chain reaction (Saiki et al., 1988) using standard methods. A number of templates had low DNA concentrations, which is common for meso- and bathypelagic fishes; for other taxa, DNA concentration or quality was poor because the tissues had been poorly preserved or stored. For templates in which I suspected the DNA was of poor quality (i.e., fragments were broken and short), I amplified target sequences using multiple primer pairs, each pair amplifying a shorter subregion of the total fragment (Table 2.2). For templates with low DNA concentration, I employed a "nested" PCR protocol, in which the product of a first PCR reaction was used as a template for a second round of PCR using a set of primers that are internal relative to the original set.

Successfully amplified target sequences were purified using one of three methods: the QIAquick PCR Purification Kit (QIAGEN, Valencia, CA, USA) for spin column purification, the AMPure magnetic bead purification system (Agencourt, Beverly, MA, USA), or (for the majority of sequences) enzymatic digestion with ExoSAP-It (USB/Affymetrix, Santa Clara, CA, USA). The purification process separates the amplified, double-stranded sequence from undesired molecules that could interfere with successful sequencing, including unincorporated primers and dNTPs.

Purified PCR products were cycle sequenced (Sanger et al., 1977) using dye-labeled terminators, specifically the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA). Sequences were visualized on an ABI 3100xl automated sequencer in the KU DNA Sequencing Core Facility.

I used the program Sequencher v.4.1 (1991) to view the raw sequence data, combine forward and reverse sequences (and, where applicable, multiple short fragments) into single full-length consensus sequences, correct base miscalls by the sequencer, and trim the sequences of any messy ends.

Alignment of sequences was done by eye. As I used exons of protein coding genes, alignment by amino acid sequence was straightforward and unambiguous. The program Se-Al (Rambaut, 2002) was used for manipulation of sequences and alternating between displays of amino acid and nucleotide sequences during the alignment process.

The final concatenated data matrix was composed of 858 nucleotides from the RAG1 gene, 705 from the MYH6 gene, 951 from the ZIC1 gene, and 831 from the COI gene, for a total of 3,345 data columns. Of these, 1621 were constant, 207 were uninformative, and 1517 were phylogenetically informative.

Sequence Evaluation

To examine whether base compositional bias was present in my dataset, I tested each gene fragment for each target taxon for overall GC content (i.e., percent of nucleotides that are guanine or cytosine) and GC content at third codon positions. If there is no base compositional bias, one would expect GC content to be approximately 50%. Third positions were also evaluated by themselves because the degeneracy of the genetic code means that mutations at third positions are more likely than those at other positions to be synonymous; therefore, tendency toward base compositional bias is less constrained at third positions by selection against amino acid change. Base composition was evaluated using the program Codonw (Peden, 1999). I tested the null hypothesis of base compositional stationarity among taxa using the chi-square test implemented in PAUP* 4.0 (Swofford, 2003).

I examined the extent of codon usage bias in my dataset by calculating the effective number of codons (N_C) (Wright, 1990) for each gene fragment for each taxon. Codon usage bias is possible because of the redundancy of the genetic code, with 64 possible nucleotide triplets coding for 20 amino acids. If all possible triplets coding for the same amino acid are present in equal frequency in a sequence, there is no codon bias; if some triplets are "used" more frequently than others to code for the same amino acid, bias is present. The effective number of codons is a statistic used to express the overall level of codon usage bias in a sequence (Wright, 1990). Possible values for N_C range from 20 (if only one possible triplet is used for each amino acid) to 61 (if synonymous triplets are present at nearly equal frequencies; that is, codon usage is random). I calculated N_C for sequences using the program Codonw (Peden, 1999).

Phylogenetic Analysis.

I performed a parsimony analysis on the concatenated data matrix in the program PAUP*4.0 (Swofford, 2003), using a heuristic search with 10,000 random addition sequence replicates. The Tree Bisection and Reconnection (TBR) algorithm was specified to search the treespace as widely as possible. I evaluated the support for clades in the analysis using the nonparametric bootstrap as implemented in PAUP* (Felsenstein, 1985), with 1,000 bootstrap replicates.

Maximum likelihood analysis was performed in the program GARLI v.0.95 (Zwickl, 2006) under the general time reversible model of evolution with a gamma distribution of rates among sites, allowing for a proportion of invariant sites (GTR+I+Γ). Six independent runs were performed, each beginning with a random starting tree and progressing for 10,000 generations after the last improvement in topology. I implemented the nonparametric bootstrap in GARLI with 100 replicates.

I performed Bayesian inference of phylogeny using the program MrBayes v.3.1 (Huelsenbeck and Ronquist, 2001). Four simultaneous runs were performed, each with four chains, three of which were "heated" chains. The analysis was run for four million generations, the first 25% of which were discarded as burn-in. Data partitioning was done by genome and, for the mitochondrial gene, by codon position, for a total of four partitions (nuclear genes, mitochondrial gene first positions, mitochondrial gene second positions, and mitochondrial gene third positions). This partitioning scheme was the best-performing *a priori* scheme for producing stable topology in Bayesian analysis in several vertebrate DNA datasets (McGuire et al., 2007; Oaks, 2008). It avoids excessive underparameterization, a serious problem for phylogenetic inference (Huelsenbeck, 1995; Sullivan and Swofford, 1997). A common alternate scheme of partitioning that incorporates gene identity as well as codon position, which in this data set would have yielded twelve partitions, has been shown to cause problems with overparameterization in other datasets (McGuire et al., 2007; Oaks, 2008) leading to less stable topology and branch length estimation.

For each data partition, I used MrModeltest v2.2 (Nylander, 2008) to choose, from among the 24 substitution models that are supported by MrBayes, the model that best fit the data in that partition. For the nuclear gene partition, the model chosen was GTR+I+Γ; for the mitochondrial first positions partition, the model was SYM+I+Γ;

for the mitochondrial second positions partition, the model was FB1+Γ; for the mitochondrial third positions partition, the model was GTR+Γ.

Results

Sequence Evaluation

There is some evidence of base compositional and codon bias in the sequences (Tables 2.3–2.6). Base compositional bias was highest in the RAG1 gene (mean 57.9% GC overall; mean 74% GC at third positions), moderate in the ZIC1 gene (mean 56.4% GC overall; mean 63.4% GC at third positions), and lowest in MYH6 (mean 49.1% GC overall; mean 58.1% GC at third positions) and COI (mean 46.8% GC overall; mean 44.5% at third positions). Codon bias was higher in RAG1 (mean N_C 44.28) and COI (mean N_C 46.50) and lower in ZIC1 (mean N_C 53.90) and MYH6 (mean N_C 52.21).

The null hypothesis of base compositional stationarity among taxa was rejected by the chi-square test for RAG1 (p=0.00001), MYH6 (p=0.00559), and COI (p=0.00152). The null hypothesis of stationarity was not rejected at the 0.05 level for ZIC1 (p=0.06706). When third positions were excluded, base compositional stationarity was not rejected for any of the genes (p=1.0 for each).

Phylogenetic Analysis

A single optimal tree was recovered by each method of analysis (Figures 2.1–2.3). The trees produced by all three methods of analysis are similar in topology, with resolution and branch support weakest in the parsimony tree. In all three trees, the stomiiform clade is placed with the osmeroid and galaxioid fishes. In the parsimony tree, the stomiiform *Vinciguerria* is placed sister to a clade composed of osmeroids, galaxioids, and all other stomiiforms. In the Bayesian and maximum likelihood trees, the order Stomiiformes is recovered as monophyletic and in a clade with the osmeroids and galaxioids. The clade Neoteleostei as currently defined is not recovered as a monophyletic group in any of the trees.

In all three trees, a monophyletic Eurypterygii is recovered, with Ateleopodidae placed as its sister group. Branch support for both eurypterygian monophyly and the sister group relationship between ateleopodids and eurypterygians is strong in the likelihood and Bayesian trees, but very weak in the parsimony tree.

The enigmatic *Lepidogalaxias salamandroides* is never recovered with the galaxioids, osmeroids, or esocoids, but is instead placed sister to all other euteleosts or, in the parsimony analysis, placed in an unresolved trichotomy with Clupeiformes and Euteleostei. The affiliation of the included retropinnid, *Retropinna semoni,* is solidly with the galaxiids (or at least *Galaxias*) rather than with the osmerids. The position of *Galaxiella* is not stable among the trees, and while it is not recovered as part of a monophyletic Galaxioidei in either the Bayesian or maximum likelihood trees, its placement outside the clade is not well supported by either bootstrap or posterior probability values.

The alepocephaloids are never recovered sister to the argentinoids, but rather are placed sister to Ostariophysi in all three trees. A monophyletic Ostarioclupeomorpha is never recovered in any of the trees, even if Alepocephaloidei is included. Similarly, Elopomorpha is not monophyletic in any of the three trees, but is instead recovered as two graded clades in each topology, although composition of the two clades differs in the parsimony tree versus the other two trees.

Discussion

The results of this study support the phylogenetic hypothesis proposed by Weitzman (1967) that stomiiforms are most closely related to osmeroids and galaxioids. The hypothesis originally proposed by Rosen (1973) that stomiiforms are the basal neoteleost group is not supported by these data. The conclusions of Weitzman (1967) are further corroborated by the recovery of *Vinciguerria* sister to the other included stomiiforms in this analysis, with *Diplophos* recovered as a more derived member of the group. Weitzman (1967) considered *Vinciguerria* one of the most basal stomiiforms, whereas Fink and Weitzman (1982), interpreting stomiiforms as neoteleosts, considered *Diplophos* the most basal stomiiform.

Much of the morphological evidence for the monophyly of Neoteleostei is open to alternative interpretations. For example, a retractor dorsalis muscle is also found in cyprinids, gars, *Amia,* and *Lepidogalaxias* (Fink and Weitzman, 1982; Fink, 1984a); under any existing hypothesis of fish phylogeny, this character must have evolved more than once and/or been lost in some lineages. A paired rostral cartilage is also found in salmonids and even Fink and Weitzman (1982) suggest that it could be a homologous structure to the neoteleost character that has not fused. Type 4 tooth attachment is also found in *Esox* (Fink, 1981) and is probably in need of more thorough sampling, particularly among juveniles, as the character is most prevalent among juvenile stomiiforms and lower eurypterygians. The occipital condyle composed of both basioccipital and exoccipital is also found in salmonids and *Lepidogalaxias,* and has certainly been independently derived in *Hiodon* (Fink and Weitzman, 1982; Fink, 1984a); further investigation may well prove it to be a euteleost, rather than a neoteleost, synapomorphy.

Although monophyly of Neoteleostei *sensu lato* is rejected, the monophyly of Rosen's (1973) clade Eurypterygii is supported in all analyses, in each case with ateleopodids sister to eurypterygians. This suggests a possible redefinition of the clade Neoteleostei, to include only Atelepodidae + Eurypterygii, but not Stomiiformes. The conclusions of Olney et al. (1993) that ateleopodids are not lampriforms but instead basal neoteleosts are supported.

The phylogenetic position of *Lepidogalaxias* recovered in the present study, sister to all other euteleosts, is novel. The proper placement of this unusual monotypic genus has been debated since Mees (1961) originally described it as a galaxiid. While most authors have placed *Lepidogalaxias* somewhere within Galaxiidae (Williams, 1987; Begle, 1991; Begle, 1992; Johnson and Patterson, 1996; Williams, 1996) or sister to it (Frankenberg, 1969), similarities with umbrids and esocids have frequently been noted and Rosen (1974) considered *Lepidogalaxias* and the esociforms to be sisters. Fink (1984a) noted that, like neoteleosts, *Lepidogalaxias* has a retractor dorsalis muscle as well as an occipital condyle composed of both basioccipital and exoccipital; he placed *Lepidogalaxias* in an unresolved trichotomy with the salmonids and the neoteleosts. Waters et al. (2000) used DNA sequence data from the cyctochrome b and 16S rRNA genes to test the existing phylogenetic hypotheses for *Lepidogalaxias,* and recovered the genus sister to the galaxioids; however, their analysis included only galaxioids, esociforms, and salmonids. The present placement of *Lepidogalaxias* as sister to all other euteleosts represents a new hypothesis of relationship that deserves further investigation. The genus must certainly play a critical role in ongoing investigations of euteleost phylogeny.

Even with the troublesome genus *Lepidogalaxias* excluded, galaxioid monophyly has been controversial. Rosen (1974) suggested that retropinnids are sister to osmerids, a relationship that was recovered by Waters et al. (2002) with DNA sequence data. Most other authors, however, conclude that retropinnids and galaxiids compose a monophyletic Galaxioidei (Fink, 1984a; Begle, 1991; Johnson and Patterson, 1996; Williams, 1996). The present analyses recover *Retropinna* sister to *Galaxias* or, in the parsimony tree, nested within the galaxiids. None of the analyses recovers a monophyletic Galaxiidae, and only the parsimony analysis recovers reciprocally monophyletic galaxioid and osmeroid clades. The difficulty lies with *Galaxiella*, and is suspected to be due to missing data: the DNA sample extracted for this species was of very low concentration and the RAG1 gene was never successfully sequenced for this taxon. This study was not intended to resolve relationships within the galaxioid + osmeroid clade, but it can be said that the results do not support the monophyletic retropinnid + osmerid group of Rosen (1974) and Waters et al (2002).

The placement in all three trees of Alepocephaloidei sister to Ostariophysi is in conflict with the widely accepted view (Begle, 1992; Johnson and Patterson, 1996; Nelson, 2006) that alepocephaloids are sister to the argentinoids, a relationship first proposed by Greenwood and Rosen (1971). However, some earlier authors considered alepocephaloids closely related to clupeomorphs (Berg, 1940; Gosline, 1960). More recently, a study based on whole mitochondrial genomic data recovered alepocephaloids nested within Ostarioclupeomorpha (Ishiguro et al., 2003). Furthermore, Ahlstrom et al. (1984a) found that the ontogeny of alepocephaloids did not support a close relationship with the argentinoids. It is clear that further investigation of the phylogenetic affiliations of alepocephaloids is warranted.

The fact that neither Elopomorpha nor Ostarioclupeomorpha are recovered as monophyletic groups is most directly attributable to the fact that resolution is generally lower at the deepest nodes of the trees, which may be due to saturation effects at deep levels of divergence. With this dataset, the monophyly of these groups can be neither confirmed nor confidently rejected. This simply demonstrates that problems involving the relationships of taxa whose origins and divergences are so ancient should be addressed with DNA sequences that are even more slowly evolving than those used here.

Table 2.1. Taxon sampling and tissue numbers; classification following Nelson (2006).

Neopterygii			
	Amiiformes		
		Amia calva	KU 3491
Teleostei			
Osteoglossomorpha			
	Hiodontiformes		
		Hiodon alosoides	KU 2537
	Osteoglossiformes		
		Chitala chitala	KU 2544
		Gnathonemus petersi	KU 2513
Elopomorpha			
	Elopiformes		
		Elops saurus	KU 5860
		Megalops cyprinoides	KU 5661
	Albuliformes		
		Albula vulpes	KU 3814
		Halosauropsis macrochir	KU 5945
		Notacanthus chemnitzii	KU 5937
	Anguilliformes		
		Moringua javanica	KU 4407
		Gymnothorax melatremus	KU 7238
		Derichthys serpentinus	KU 5320
		Serrivomer beanii	KU 5953
	Saccopharyngiformes		
		Eurypharynx pelecanoides	KU 5908
Ostarioclupeomorpha			
	Clupeiformes		
		Engraulis eurystole	KU 5153
		Opisthonema oglinum	KU 5846
		Dorosoma cepedianum	KU 7325
	Gonorhynchiformes		
		Chanos chanos	KU 1603
		Gonorhynchus greyi	EBU 22823
	Cypriniformes		
		Pimephales promelas	KU 5956
		Catostomus commersoni	KU 5969
	Characiformes		
		Colossoma sp.	KU 3081
	Siluriformes		
		Ictalurus punctatus	Genbank
		Noturus gyrinus	KU 1821
		Plotosus lineatus	KU 4730
		Arius felis	KU 5161
	Gymnotiformes		
		Apteronotus albifrons	KU 2528

Euteleostei			
	Argentiniformes		
		Argentina striata	KU 3283
		Dolichopteryx sp.	KU 6522
		Nansenia longicauda	KU 6511
		Bathylagus longirostris	KU 5333
		Leuroglossus stilbius	KU 3140
	Alepocephaliformes		
		Normichthys operosus	KU 5310
		Sagamichthys abei	KU 2394
		Xenodermichthys copei	KU 5276
		Rouleina attrita	KU 6515
	Osmeriformes		
		Mallotus villosus	KU 3139
		Thaleichthys pacificus	KU 3135
		Retropinna semoni	EBU 22355
		Lepidogalaxias salamandroides	EBU 21545
		Galaxias maculatus	EBU 22353
		Galaxiella nigrostriata	EBU 21542
	Salmoniformes		
		Prosopium williamsoni	UW 048051
		Oncorhynchus keta	KU 3228
	Esociformes		
		Esox lucius	KU 5414
		Umbra limi	KU 2568
Neoteleostei			
	Stomiiformes		
		Diplophos taenia	KU 3781
		Bonapartia pedaliota	KU 3789
		Margrethia obtusirostra	ORI 1406
		Gonostoma elongatum	KU 5384
		Polyipnus clarus	KU 3563
		Polymetme thaeocoryla	KU 3547
		Vinciguerria nimbaria	KU 3733
		Yarrella blackfordi	LIM A84
		Astronesthes gemmifer	KU 3106
		Borostomias elucens	ORI 1403
		Chirostomias pliopterus	KU 3113
	Ateleopodiformes		
		Ateleopus japonicus	ORI
		Ijimaia antillarum	KU 5411
Eurypterygii			
	Aulopiformes		
		Synodus foetens	KU 5069
		Chlorophthalmus agassizii	KU 1477
		Benthalbella dentata	KU 3239
		Alepisaurus ferox	KU 5393
	Myctophiformes		
		Neoscopelus macrolepidotus	KU 3297
		Diaphus dumerilii	KU 1481
		Hygophum hygomii	KU 5303
	Lampriformes		

Lampris guttatus	KU 5402
Lophotus lacepede	KU 6557
Zu cristatus	KU 5289
Regalecus glesne	KU 5286
Polymixiiformes	
Polymixia lowei	KU 5952
Percopsiformes	
Percopsis transmontana	KU 1891
Gadiformes	
Gadus morhua	Genbank
Ophidiiformes	
Brotulotaenia nigra	KU 6529
Lophiiformes	
Lophiodes reticulatus	KU 5180
Acanthopterygii	
Mugiliformes	
Mugil trichodon	KU 5833
Stephanoberyciformes	
Melamphaes suborbitalis	KU 6532
Gasterosteiformes	
Gasterosteus aculeatus	KU 5986
Scorpaeniformes	
Scorpaenopsis diabolus	KU 7052
Perciformes	
Apogon apogonoides	KU 7185

KU = University of Kansas; EBU = Evolutionary Biology Unit, Australian Museum; LIM = Leibniz Institut für Meeresbiologie, Germany; ORI = Ocean Research Institute, University of Tokyo, Japan

Table 2.2. Primers used for DNA amplification and sequencing.

Gene	**Primer**	**Primer Sequence**
RAG1	Of2[a]	5' CTGAGCTGCAGTCAGTACCATAAGATGT 3'
RAG1	Wf2i2[b]	5' ATGGGBGATRTCAGCGAGAA 3'
RAG1	Wf2i3[b]	5' GATGARAAGATGGTGCGNGAGVT 3'
RAG1	Wr2i3[b]	5' WARTTBCCRTTCATCCTCAT 3'
RAG1	Wr2i4[b]	5' CTRTARCGRCACAGCTGGTC 3'
RAG1	Wr3[b]	5' ATCTGGADGTGTAGTGCCAG 3'
RAG1	Or2[a]	5' CTGAGTCCTTGTGAGCTTCCATRAAYTT 3'
ZIC1	AF1[c]	5' GGACGCAGGACCGCARTAYC 3'
ZIC1	AF2[c]	5' GGACCGCAGTATCCCACYMT 3'
ZIC1	AF3[c]	5' TTYTCGGGGGACATGTAYGG 3'
ZIC1	AR1[c]	5' CTGTGTGTGTCCTTTTGTGRATYTT 3'
ZIC1	AR2[c]	5' GTGTGTCCTTTTGTGAATTTTYAGRT 3'
ZIC1	AR3[c]	5' GCRGCCATRTTCATGTTCA 3'
MYH6	A3F1[c]	5' CATMTTYTCCATCTCAGATAATGC 3'
MYH6	A3F2[c]	5' GGAGAATCARTCKGTGCTCATCA 3'
MYH6	A3F3[c]	5' TCCCGWGTCACYTTTCAGC 3'
MYH6	A3R1[c]	5' ATTCTCACCACCATCCAGTTGAA 3'
MYH6	A3R2[c]	5' CTCACCACCATCCAGTTGAACAT 3'
MYH6	A3R3[c]	5' GTGAAGCCRAGCACRTCAAA 3'
COI	L5698[d]	5' AGGCCTCGATCCTACAAAGKTTTAGTTAAC 3'
COI	L5956[d]	5' CACAAAGACATTGGCACCCT 3'
COI	H6864[d]	5' AGWGTWGCKAGTCAGCTAAA 3'
COI	H6855[d]	5' AGTCAGCTGAAKACTTTTAC 3'

a. Designed by G.O. Ortí, University of Nebraska - Lincoln

b. Designed by N.I. Holcroft, University of Kansas

c. Designed by C. Li, University of Nebraska - Lincoln

d. Designed by M. Miya, Natural History Museum and Institute, Chiba, Japan

Table 2.3. Base composition and codon usage in the RAG1 gene.

Species	**RAG1 GC**	**RAG1 GC3**	**RAG1 ENC**
Amia calva	0.524	0.637	50.61
Hiodon alosoides	0.590	0.760	42.99
Notopterus chitala	0.551	0.684	50.56
Gnathonemus petersi	0.553	0.697	48.60
Elops saurus	0.629	0.898	33.82
Megalops cyprinoides	0.560	0.676	44.84
Albula vulpes	0.607	0.775	41.08
Halosauropsis macrochir	0.550	0.648	47.48
Notacanthus chemnitzii	0.656	0.917	34.51
Moringua javanica	0.546	0.672	53.29
Gymnothorax melatremus	0.605	0.728	44.78
Derichthys serpentinus	0.642	0.893	36.12
Serrivomer beanii	0.613	0.779	39.86
Eurypharynx pelecanoides	0.602	0.794	41.14
Engraulis eurystole	0.607	0.784	41.33
Opisthonema oglinum	0.605	0.762	38.64
Dorosoma cepedianum	0.613	0.775	38.49
Chanos chanos	0.530	0.597	54.94
Gonorhynchus greyi	0.564	0.724	46.42
Pimephales promelas	0.531	0.615	55.18
Catostomus commersoni	0.518	0.582	50.81
Colossoma sp.	0.518	0.584	54.81
Noturus gyrinus	0.469	0.469	56.50
Ictalurus punctatus	0.479	0.490	57.49
Plotosus lineatus	0.470	0.475	56.65
Arius felis	0.472	0.477	54.90
Apteronotus albifrons	0.511	0.591	51.87
Argentina striata	0.593	0.772	41.24
Dolichopteryx sp.	0.604	0.800	41.53
Nansenia longicauda	0.622	0.857	36.53
Bathylagus longirostris	0.636	0.881	35.41
Leuroglossus stilbius	0.624	0.879	35.67
Normichthys operosus	0.660	0.963	29.20
Sagamichthys abei	0.510	0.593	60.39
Xenodermichthys copei	0.690	0.996	27.15
Rouleina attrita	0.686	0.996	27.25
Mallotus villosus	0.632	0.867	36.97
Thaleichthys pacificus	0.618	0.852	37.20
Retropinna semoni	0.568	0.711	46.08
Lepidogalaxias salamandroides	0.649	0.906	34.38

Galaxias maculatus	0.562	0.706	45.54
Galaxiella nigrostriata	—	—	—
Prosopium williamsoni	0.578	0.753	41.09
Oncorhynchus keta	0.580	0.739	43.81
Esox lucius	0.569	0.715	47.28
Umbra limi	0.545	0.636	52.23
Diplophos taenia	0.585	0.746	42.19
Bonapartia pedaliota	0.609	0.809	39.92
Margrethia obtusirostra	0.636	0.880	34.59
Gonostoma elongatum	0.614	0.825	39.01
Polyipnus clarus	0.626	0.869	36.85
Polymetme thaeocoryla	0.615	0.834	37.40
Vinciguerria nimbaria	0.561	0.689	48.85
Yarrella blackfordi	0.615	0.834	38.08
Astronesthes gemmifer	0.656	0.915	33.08
Borostomias elucens	0.673	0.955	31.55
Chirostomias pliopterus	0.670	0.957	30.93
Ateleopus japonicus	0.605	0.829	41.33
Ijimaia antillarum	0.599	0.809	42.32
Synodus foetens	0.522	0.580	50.94
Chlorophthalmus agassizii	0.582	0.716	46.81
Benthalbella dentata	0.562	0.676	47.51
Alepisaurus ferox	0.552	0.690	48.17
Neoscopelus macrolepidotus	0.635	0.878	34.87
Diaphus dumerilii	0.566	0.710	46.16
Hygophum hygomii	0.596	0.755	45.46
Lampris guttatus	0.512	0.548	51.32
Lophotus lacepede	0.548	0.667	48.40
Zu cristatus	0.578	0.777	42.97
Regalecus glesne	0.550	0.734	44.96
Polymixia lowei	0.556	0.685	49.82
Percopsis transmontana	0.594	0.803	41.42
Gadus morhua	0.552	0.669	48.39
Brotulotaenia nigra	0.517	0.603	57.00
Lophiodes reticulatus	0.515	0.589	54.83
Mugil trichodon	0.535	0.637	52.90
Melamphaes suborbitalis	0.556	0.682	47.46
Gasterosteus aculeatus	0.559	0.719	49.27
Scorpaenopsis diabolus	0.551	0.700	48.92
Apogon apogonoides	0.507	0.569	57.52
Mean	**0.579**	**0.740**	**44.28**

Table 2.4. Base composition and codon usage in the MYH6 gene.

Species	**MYH6 GC**	**MYH6 GC3**	**MYH6 ENC**
Amia calva	0.461	0.485	57.73
Hiodon alosoides	0.548	0.732	43.04
Notopterus chitala	0.488	0.560	53.91
Gnathonemus petersi	—	—	—
Elops saurus	0.486	0.557	55.94
Megalops cyprinoides	0.513	0.636	50.22
Albula vulpes	0.503	0.589	44.95
Halosauropsis macrochir	0.487	0.554	48.78
Notacanthus chemnitzii	0.483	0.574	52.32
Moringua javanica	0.501	0.597	53.80
Gymnothorax melatremus	0.577	0.848	36.51
Derichthys serpentinus	0.493	0.578	47.74
Serrivomer beanii	0.492	0.565	53.16
Eurypharynx pelecanoides	0.482	0.538	55.04
Engraulis eurystole	0.504	0.645	45.19
Opisthonema oglinum	0.483	0.580	53.33
Dorosoma cepedianum	0.490	0.598	55.14
Chanos chanos	0.456	0.454	59.87
Gonorhynchus greyi	0.446	0.466	61.00
Pimephales promelas	0.482	0.534	49.10
Catostomus commersoni	0.472	0.535	59.14
Colossoma sp.	0.492	0.595	56.29
Noturus gyrinus	0.428	0.380	52.13
Ictalurus punctatus	0.438	0.408	52.00
Plotosus lineatus	0.439	0.424	51.62
Arius felis	0.488	0.586	56.02
Apteronotus albifrons	0.442	0.437	56.81
Argentina striata	0.462	0.504	51.19
Dolichopteryx sp.	0.480	0.557	52.95
Nansenia longicauda	0.461	0.494	51.65
Bathylagus longirostris	0.473	0.511	53.21
Leuroglossus stilbius	0.476	0.562	52.92
Normichthys operosus	0.480	0.546	56.82
Sagamichthys abei	0.477	0.549	58.86
Xenodermichthys copei	0.479	0.555	57.02
Rouleina attrita	0.478	0.551	57.35
Mallotus villosus	0.477	0.559	52.37
Thaleichthys pacificus	0.474	0.533	58.05
Retropinna semoni	0.521	0.651	49.29
Lepidogalaxias salamandroides	0.437	0.416	56.06

Galaxias maculatus	0.489	0.573	55.93
Galaxiella nigrostriata	0.436	0.417	57.43
Prosopium williamsoni	0.477	0.544	54.50
Oncorhynchus keta	0.474	0.533	56.56
Esox lucius	0.474	0.520	55.60
Umbra limi	0.479	0.552	53.27
Diplophos taenia	0.478	0.543	54.32
Bonapartia pedaliota	0.478	0.561	56.81
Margrethia obtusirostra	0.487	0.567	57.66
Gonostoma elongatum	0.495	0.596	55.43
Polyipnus clarus	0.485	0.559	57.31
Polymetme thaeocoryla	0.495	0.585	56.82
Vinciguerria nimbaria	0.499	0.604	47.50
Yarrella blackfordi	0.493	0.604	56.35
Astronesthes gemmifer	0.502	0.618	53.87
Borostomias elucens	0.479	0.570	55.28
Chirostomias pliopterus	0.483	0.554	56.67
Ateleopus japonicus	—	—	—
Ijimaia antillarum	0.483	0.551	55.78
Synodus foetens	0.452	0.473	52.08
Chlorophthalmus agassizii	0.487	0.557	53.29
Benthalbella dentata	0.481	0.548	52.68
Alepisaurus ferox	0.482	0.578	52.13
Neoscopelus macrolepidotus	0.515	0.646	52.72
Diaphus dumerilii	0.584	0.864	36.90
Hygophum hygomii	0.583	0.841	38.95
Lampris guttatus	0.517	0.647	51.86
Lophotus lacepede	0.556	0.781	42.10
Zu cristatus	0.560	0.766	44.34
Regalecus glesne	0.563	0.803	40.23
Polymixia lowei	0.483	0.570	52.59
Percopsis transmontana	0.517	0.649	46.41
Gadus morhua	0.516	0.672	49.93
Brotulotaenia nigra	0.492	0.584	54.93
Lophiodes reticulatus	0.524	0.647	46.85
Mugil trichodon	0.552	0.753	43.95
Melamphaes suborbitalis	0.496	0.595	46.40
Gasterosteus aculeatus	0.544	0.730	43.32
Scorpaenopsis diabolus	0.504	0.607	52.06
Apogon apogonoides	0.477	0.536	53.19
Mean	**0.491**	**0.581**	**52.21**

Table 2.5. Base composition and codon usage in the ZIC1 gene.

Species	**ZIC1 GC**	**ZIC1 GC3**	**ZIC1 ENC**
Amia calva	0.517	0.510	61.00
Hiodon alosoides	0.508	0.454	61.00
Notopterus chitala	0.525	0.517	59.38
Gnathonemus petersi	0.565	0.631	59.94
Elops saurus	0.586	0.568	58.47
Megalops cyprinoides	0.545	0.592	54.74
Albula vulpes	0.528	0.530	59.57
Halosauropsis macrochir	0.559	0.623	54.35
Notacanthus chemnitzii	0.535	0.552	56.76
Moringua javanica	0.536	0.542	60.69
Gymnothorax melatremus	—	—	—
Derichthys serpentinus	0.592	0.706	52.25
Serrivomer beanii	0.521	0.498	59.49
Eurypharynx pelecanoides	0.519	0.509	61.00
Engraulis eurystole	0.564	0.625	53.87
Opisthonema oglinum	0.534	0.532	61.00
Dorosoma cepedianum	0.533	0.528	61.00
Chanos chanos	0.527	0.520	59.94
Gonorhynchus greyi	0.535	0.552	58.74
Pimephales promelas	0.575	0.656	53.44
Catostomus commersoni	0.584	0.665	52.50
Colossoma sp.	—	—	—
Noturus gyrinus	—	—	—
Ictalurus punctatus	0.619	0.733	48.02
Plotosus lineatus	0.617	0.746	48.14
Arius felis	—	—	—
Apteronotus albifrons	0.536	0.552	59.60
Argentina striata	0.549	0.584	55.64
Dolichopteryx sp.	0.540	0.568	56.58
Nansenia longicauda	0.552	0.601	55.46
Bathylagus longirostris	0.584	0.699	49.43
Leuroglossus stilbius	0.536	0.550	56.74
Normichthys operosus	0.575	0.668	53.62
Sagamichthys abei	0.577	0.676	51.42
Xenodermichthys copei	0.574	0.663	54.82
Rouleina attrita	0.577	0.676	52.94
Mallotus villosus	0.542	0.568	55.75
Thaleichthys pacificus	0.537	0.552	59.79
Retropinna semoni	0.523	0.514	58.44
Lepidogalaxias salamandroides	0.543	0.568	61.00
Galaxias maculatus	—	—	—

Galaxiella nigrostriata	0.503	0.456	61.00
Prosopium williamsoni	—	—	—
Oncorhynchus keta	0.578	0.701	48.01
Esox lucius	0.573	0.671	54.68
Umbra limi	0.542	0.581	59.91
Diplophos taenia	0.546	0.580	56.05
Bonapartia pedaliota	0.637	0.857	42.81
Margrethia obtusirostra	0.589	0.712	47.76
Gonostoma elongatum	0.563	0.632	54.34
Polyipnus clarus	0.566	0.638	53.74
Polymetme thaeocoryla	0.551	0.598	56.83
Vinciguerria nimbaria	0.562	0.636	57.70
Yarrella blackfordi	0.551	0.598	54.48
Astronesthes gemmifer	0.564	0.637	52.29
Borostomias elucens	0.551	0.602	54.96
Chirostomias pliopterus	0.568	0.645	53.22
Ateleopus japonicus	—	—	—
Ijimaia antillarum	0.610	0.781	46.86
Synodus foetens	0.568	0.658	52.70
Chlorophthalmus agassizii	0.555	0.614	58.39
Benthalbella dentata	0.565	0.641	54.93
Alepisaurus ferox	0.597	0.736	43.08
Neoscopelus macrolepidotus	0.571	0.676	53.17
Diaphus dumerilii	0.595	0.726	50.02
Hygophum hygomii	0.587	0.713	50.32
Lampris guttatus	0.548	0.566	56.38
Lophotus lacepede	0.596	0.733	44.87
Zu cristatus	0.641	0.866	35.63
Regalecus glesne	0.602	0.745	45.32
Polymixia lowei	0.556	0.628	57.86
Percopsis transmontana	0.577	0.672	51.46
Gadus morhua	0.580	0.699	49.90
Brotulotaenia nigra	0.609	0.790	44.40
Lophiodes reticulatus	0.584	0.700	48.77
Mugil trichodon	0.578	0.693	51.02
Melamphaes suborbitalis	0.601	0.744	47.74
Gasterosteus aculeatus	0.600	0.747	46.39
Scorpaenopsis diabolus	0.588	0.716	47.96
Apogon apogonoides	0.576	0.681	53.26
Mean	**0.564**	**0.634**	**53.90**

Table 2.6. Base composition and codon usage in the COI gene.

Species	**CO1 GC**	**CO1 GC3**	**CO1 ENC**
Amia calva	0.472	0.444	41.96
Hiodon alosoides	0.456	0.397	45.88
Notopterus chitala	0.442	0.375	44.76
Gnathonemus petersi	0.479	0.480	50.45
Elops saurus	0.496	0.513	46.09
Megalops cyprinoides	0.449	0.375	49.36
Albula vulpes	0.442	0.362	44.87
Halosauropsis macrochir	0.449	0.361	39.22
Notacanthus chemnitzii	0.421	0.325	38.58
Moringua javanica	0.442	0.364	47.03
Gymnothorax melatremus	0.481	0.471	51.40
Derichthys serpentinus	0.494	0.524	42.20
Serrivomer beanii	0.442	0.365	46.74
Eurypharynx pelecanoides	0.438	0.383	48.37
Engraulis eurystole	0.459	0.399	38.71
Opisthonema oglinum	0.473	0.442	44.44
Dorosoma cepedianum	0.485	0.473	45.68
Chanos chanos	0.484	0.466	41.87
Gonorhynchus greyi	0.509	0.560	47.73
Pimephales promelas	0.430	0.314	47.81
Catostomus commersoni	0.422	0.314	45.70
Colossoma sp.	0.458	0.422	50.36
Noturus gyrinus	0.478	0.466	47.15
Ictalurus punctatus	0.480	0.430	47.71
Plotosus lineatus	0.448	0.407	40.37
Arius felis	0.422	0.302	39.41
Apteronotus albifrons	0.450	0.415	44.55
Argentina striata	0.475	0.484	53.27
Dolichopteryx sp.	0.473	0.477	48.55
Nansenia longicauda	0.497	0.534	49.12
Bathylagus longirostris	0.510	0.572	44.57
Leuroglossus stilbius	0.469	0.453	48.63
Normichthys operosus	0.503	0.549	46.39
Sagamichthys abei	0.513	0.563	44.05
Xenodermichthys copei	0.496	0.509	46.69
Rouleina attrita	0.418	0.310	43.32
Mallotus villosus	0.468	0.447	48.40
Thaleichthys pacificus	0.476	0.471	51.48
Retropinna semoni	0.505	0.535	47.19
Lepidogalaxias salamandroides	0.419	0.360	45.42
Galaxias maculatus	0.443	0.390	57.20

Galaxiella nigrostriata	0.416	0.332	49.17
Prosopium williamsoni	0.477	0.469	50.18
Oncorhynchus keta	0.462	0.440	55.28
Esox lucius	0.437	0.372	46.38
Umbra limi	0.467	0.455	45.79
Diplophos taenia	0.522	0.585	46.05
Bonapartia pedaliota	0.487	0.487	47.10
Margrethia obtusirostra	0.486	0.491	43.16
Gonostoma elongatum	0.477	0.464	53.00
Polyipnus clarus	0.480	0.487	54.39
Polymetme thaeocoryla	0.465	0.447	41.68
Vinciguerria nimbaria	0.492	0.509	54.34
Yarrella blackfordi	0.467	0.444	44.60
Astronesthes gemmifer	0.516	0.542	38.75
Borostomias elucens	0.514	0.574	44.32
Chirostomias pliopterus	0.510	0.563	43.24
Ateleopus japonicus	0.430	0.357	41.53
Ijimaia antillarum	0.431	0.357	44.09
Synodus foetens	0.444	0.397	47.78
Chlorophthalmus agassizii	0.475	0.466	52.44
Benthalbella dentata	0.473	0.462	50.62
Alepisaurus ferox	0.499	0.536	43.90
Neoscopelus macrolepidotus	0.463	0.424	49.99
Diaphus dumerilii	0.491	0.498	45.37
Hygophum hygomii	0.493	0.523	43.80
Lampris guttatus	0.502	0.542	43.12
Lophotus lacepede	0.450	0.381	45.71
Zu cristatus	0.430	0.329	47.19
Regalecus glesne	0.457	0.404	39.64
Polymixia lowei	0.444	0.390	45.08
Percopsis transmontana	0.501	0.520	42.72
Gadus morhua	0.420	0.303	48.04
Brotulotaenia nigra	0.480	0.469	53.25
Lophiodes reticulatus	0.503	0.560	53.61
Mugil trichodon	0.484	0.478	49.04
Melamphaes suborbitalis	0.484	0.482	47.54
Gasterosteus aculeatus	0.449	0.397	43.15
Scorpaenopsis diabolus	0.471	0.461	43.31
Apogon apogonoides	0.460	0.401	48.84
Mean	**0.468**	**0.445**	**46.50**

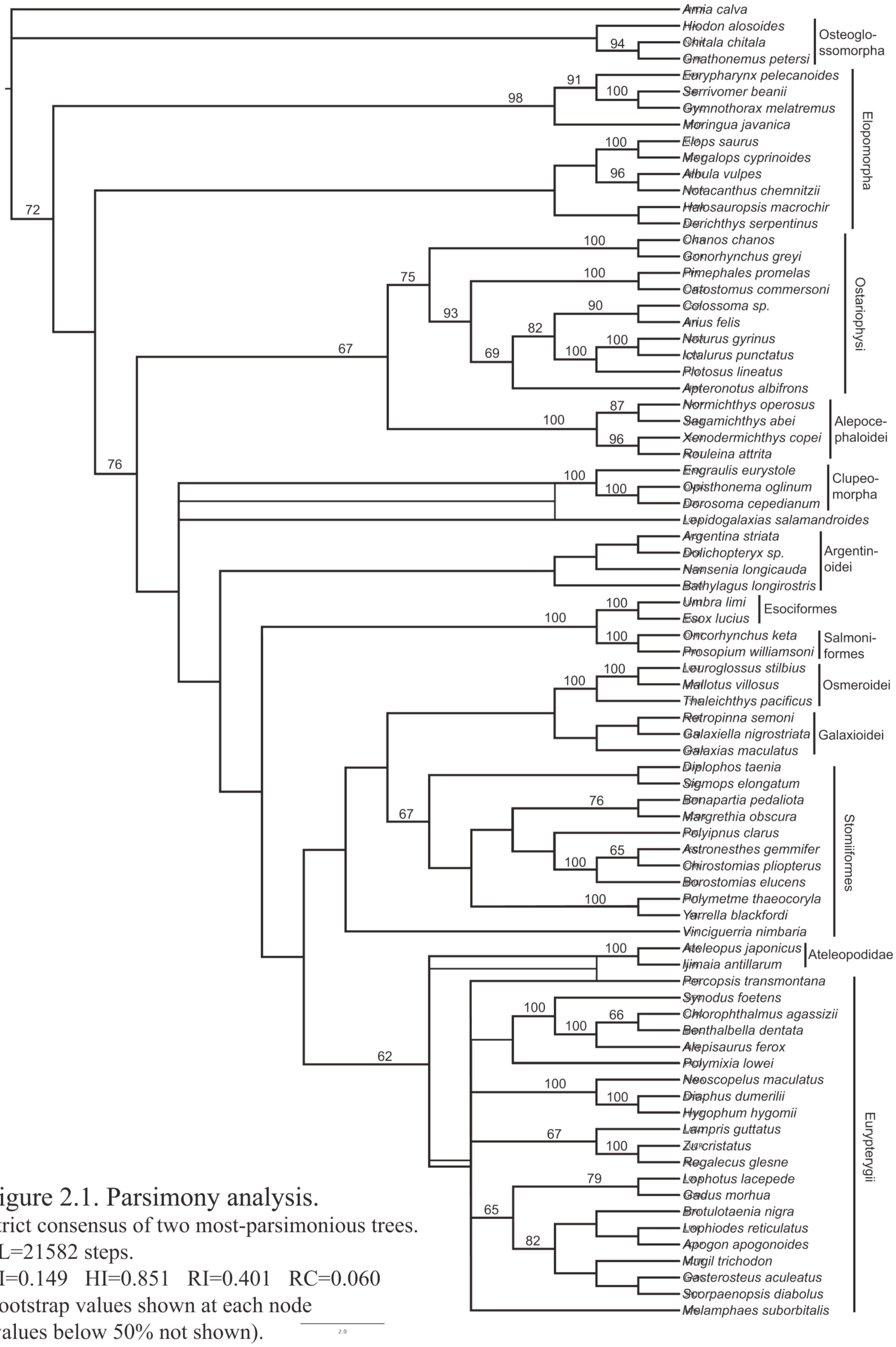

Figure 2.1. Parsimony analysis.
Strict consensus of two most-parsimonious trees.
TL=21582 steps.
CI=0.149 HI=0.851 RI=0.401 RC=0.060
Bootstrap values shown at each node
(values below 50% not shown).

Figure 2.2. Maximum likelihood analysis.
ln likelihood = -81227.0038
Bootstrap values shown at nodes
(values below 50% not shown).

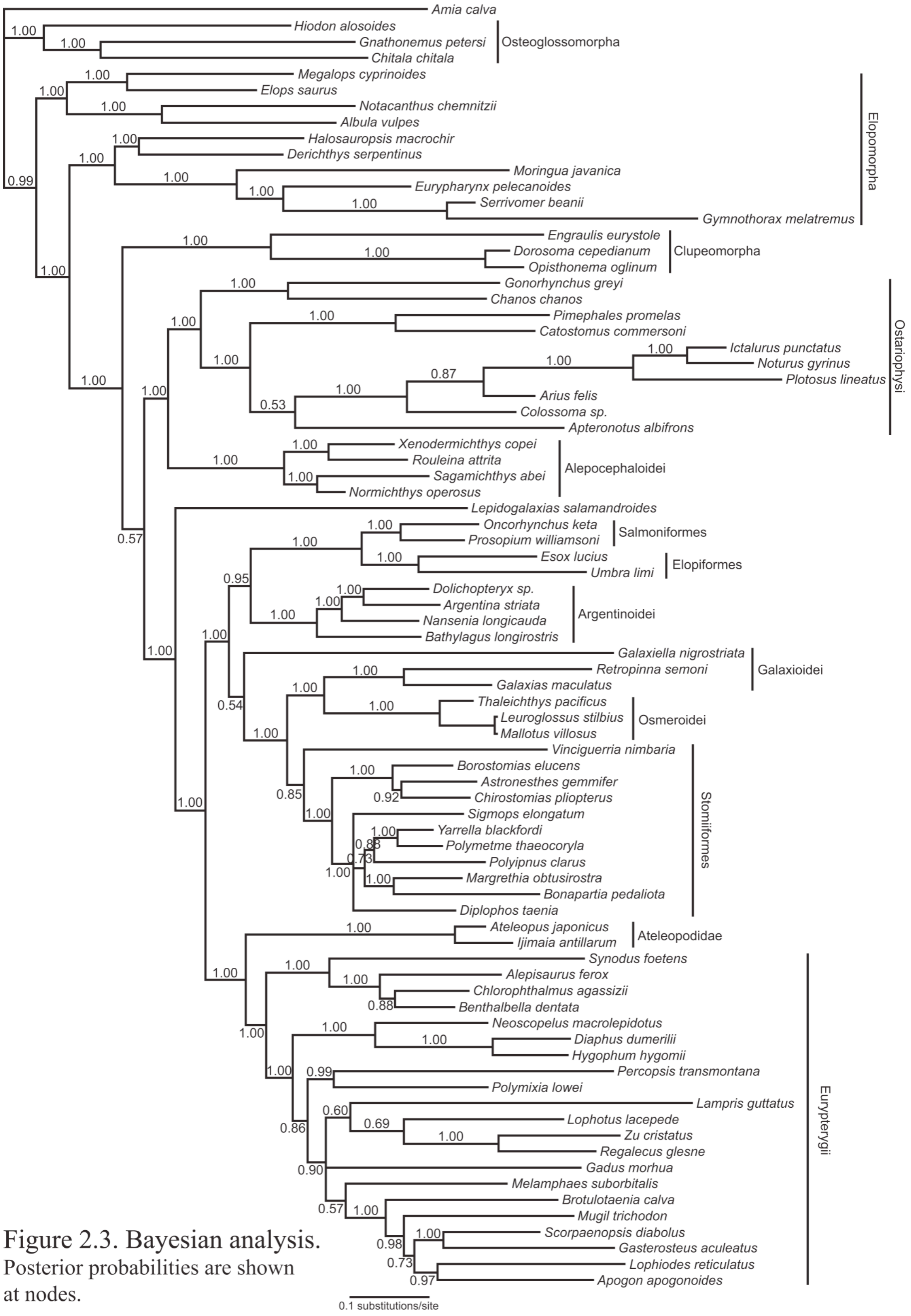

Figure 2.3. Bayesian analysis. Posterior probabilities are shown at nodes.

Chapter Three

Intrarelationships of Stomiiformes

Introduction

The 417 species of stomiiform fishes are currently classified by most authors in four families: Gonostomatidae, the bristlemouths, including the genera *Bonapartia, Cyclothone, Gonostoma, Margrethia,* and *Sigmops*; Phosichthyidae, the lightfishes, including the genera *Ichthyococcus, Phosichthys, Pollichthys, Polymetme, Vinciguerria, Woodsia,* and *Yarrella*; Sternoptychidae, the hatchetfishes and allies, including the genera *Araiophos, Argyripnus, Argyropelecus, Danaphos, Maurolicus, Polyipnus, Sonoda, Sternoptyx, Thorophos,* and *Valenciennellus*; and Stomiidae, the dragonfishes, including the genera *Aristostomias, Astronesthes, Bathophilus, Borostomias, Chauliodus, Chirostomias, Echiostoma, Eupogonesthes, Eustomias, Flagellostomias, Grammatostomias, Heterophotus, Idiacanthus, Leptostomias, Malacosteus, Melanostomias, Neonesthes, Odontostomias, Opostomias, Pachystomias, Parabathophilus, Photonectes, Photostomias, Rhadinesthes, Stomias, Tactostoma, Thysanactis,* and *Trigonolampa* (Nelson, 1994; Harold and Weitzman, 1996; Eschmeyer, 1998). A fifth family is recognized by Nelson (2006), who erected the provisional family Diplophidae to contain the *incertae sedis* genera *Diplophos, Manducus,* and *Triplophos.*

Stomiiforms have been consistently recognized as a cohesive group since Brauer (1906) arranged them together in his classification. Over the next hundred years, the classification of stomiiform subgroups has (like the classifications of many other fish groups) undergone a great deal of flux. Stomiiform classification in particular has been complicated by the wealth of new taxa discovered with increased exploration of the deep ocean and by the extensive morphological homoplasy within the group (Fink, 1984b; Harold and Weitzman, 1996).

Regan (1923) recognized two groups within the stomiiforms: the first was composed of Sternoptychidae (which at the time included only the deep-bodied forms: *Argyropelecus, Polyipnus,* and *Sternoptyx*) and Gonostomatidae *sensu lato* (which also included *Diplophos, Triplophos,* and *Manducus*; the genera now placed in Phosichthyidae; and the maurolicine genera, now considered the non-deep-bodied sternoptychids). The second group was composed entirely of genera now considered members of Stomiidae. In contrast, Parr (1927; 1930) named three major groups: the Heterophotodermi, composed of the deep-bodied sternoptychids and Gonostomatidae *sensu lato*; the Lepidophotodermi, composed of *Stomias* and, provisionally at least, *Chauliodus*; and the Gymnophotodermi, composed of all other known stomiids. Regan and Trewavas (1929; 1930) agreed with the conclusions of Regan (1923), while Beebe and Crane (1939) concurred with Parr (1927; 1930) on the three major groups of stomiiforms.

Grey (1960) considered the relationships of the family Gonostomatidae *sensu lato* and concluded that it was composed of three lineages: one composed of *Yarrella, Polymetme, Pollichthys, Vinciguerria, Ichthyococcus, Woodsia, Phosichthys,* and *Triplophos*; one composed of *Argyripnus, Maurolicus, Sonoda, Valenciennellus,* *Danaphos,* and *Thorophos*; and one composed of *Margrethia, Cyclothone, Gonostoma, Bonapartia, Manducus,* and *Diplophos*.

Weitzman (1974) concluded that there were two major clades within Stomiiformes, which he gave the rank of infraorder: Gonostomata, composed of the gonostomatids (including *Diplophos, Manducus,* and *Triplophos,* at the time placed within Gonostomatidae) and the sternoptychids; and Photichthya, composed of the stomiids and a family he proposed, Phosichthyidae. The phosichthyids had all been previously placed in the Gonostomatidae and correspond almost exactly, with the exception of *Triplophos*, to one of the three lineages shown by Grey (1960). Weitzman (1974) described Phosichthyidae as "a collection of relatively primitive Photichthya", giving no synapomorphies for the family. The two infraorders were diagnosed largely by the number of pectoral fin radials; members of Gonostomata have four and members of Photichthya have three or fewer. However, four pectoral fin radials is the plesiomorphic condition for stomiiforms and therefore cannot be a synapomorphy for the Gonostomata (Ahlstrom et al., 1984b; Harold and Weitzman, 1996). Weitzman also concluded that the maurolicine genera, formerly placed in Gonostomatidae and representing another of Grey's (1960) lineages, were closely related to the deep-bodied sternoptychids and placed the maurolicines in Sternoptychidae.

Ahlstrom (1974) recognized a single family composed of all stomiiforms that have elongate gill rakers, which includes the gonostomatids, the sternoptychids, and the phosichthyids, as well as the genus *Stomias*. The character state of elongate gill rakers, however, is plesiomorphic for stomiiforms (Ahlstrom et al., 1984b).

Weitzman (1967) and Fink and Weitzman (1982) were concerned with the relationships of Stomiiformes to other fishes, but provide important hypotheses about the sister group to other stomiiforms. Weitzman (1967) noted that *Vinciguerria* and *Polymetme* were morphologically primitive relative to other stomiiforms, and concluded that they were the most basal taxa. Fink and Weitzman (1982), on the other hand, argued that *Diplophos* (*sensu lato,* including the genus *Manducus*) is sister to all other stomiiforms.

Fink (1976; 1985) revised the superfamily Stomiatoidea, then composed of the families Astronesthidae (*Astronesthes, Borostomias, Heterophotus, Neonesthes,* and *Rhadinesthes*), Chauliodontidae (*Chauliodus*), Stomiatidae (*Stomias*), Melanostomiatidae (*Bathophilus, Chirostomias, Echiostoma, Eustomias, Flagellostomias, Grammatostomias, Leptostomias, Melanostomias, Odontostomias, Opostomias, Pachystomias, Photonectes, Tactostoma, Thysanactis,* and *Trigonolampa*), Idiacanthidae (*Idiacanthus*), and Malacosteidae (*Aristostomias, Malacosteus,* and *Photostomias*). His phylogenetic analyses showed that the five stomiatoid families compose a single monophyletic group, and his revision united them as the family Stomiidae (Fink, 1985). The previously recognized families are still retained in most classifications at the subfamily rank (Nelson, 1994; Nelson, 2006), even though Astronesthinae and Melanostomiinae seem to be grades rather than clades (Fink, 1976; Fink, 1985).

Ahlstrom et al. (1984) concluded that *Manducus* was sister to all other stomiiforms, with *Diplophos* the next genus to diverge. They supported the monophyly of the Sternoptychidae sensu Weitzman (1974) based on a similar pattern of photophore development in all sternoptychids they examined. They also concluded that *Bonapartia, Margrethia,* and *Gonostoma* composed a monophyletic group based on prolonged metamorphosis, although they conceded that it was possible that *Cyclothone* was a member of that monophyletic group and had lost the prolonged metamorphosis as part of the overall paedomorphosis seen in *Cyclothone*.

Harold and Weitzman (1996) placed *Woodsia* sister to Stomiidae, with *Ichthyococcus* sister to that clade, and *Phosichthys* sister to that one in turn. They recovered Phosichthyidae as a grade leading to Stomiidae, with *Triplophos* sister to all of Photichthya. Harold (1998) recovered Gonostomatidae *sensu stricto* sister to Sternoptychidae, with that clade sister to the *Triplophos* + Photichthya clade. He placed a clade composed of *Diplophos* and *Manducus* sister to all other stomiiforms.

Despite the numerous previous hypotheses of relationship for stomiiforms, most authors admit that we still know little about the relationships within the group (Fink, 1985; Harold and Weitzman, 1996; Harold, 1998). Several of the currently recognized taxa are assumed to be paraphyletic (Nelson, 2006). All previous hypotheses of relationship for the order as a whole have been based exclusively on morphological data, which is known to be highly homoplastic in both adults and larvae (Ahlstrom et al., 1984b; Fink, 1984b; Harold and Weitzman, 1996). The present study is the first use of DNA sequence data to address the order-wide problem of stomiiform phylogeny.

Methods

Taxon Sampling

The goal of the taxon sampling for this study was to include at least one species in every stomiiform genus; however, complete sampling of all genera was not possible because of the difficulty of obtaining tissue samples for some genera. A total of 63 stomiiform species are included, representing 43 of the 53 genera (Table 3.1). Stomiiform genera not included in this study are *Manducus, Araiophos, Argyripnus, Danaphos, Sonoda, Thorophos, Woodsia, Eupogonesthes, Opostomias,* and *Parabathophilus*. Six other lower euteleosts are included, along with an ateleopodid, an aulopiform, and a myctophiform. The trees are rooted with the clupeiform *Chirocentrus dorab*.

Genes

The data set includes sequences from three protein-coding nuclear genes (RAG1, MYH6, and ENC1) and one protein-coding mitochondrial gene (COI). Genes were selected using the same criteria outlined in Chapter Two. The zinc finger gene ZIC1, used in the analysis of stomiiform interrelationships, could not be reliably amplified in many taxa within the order, so it was excluded from this analysis. Instead, the present analysis included data from the ectodermal neural cortex gene

ENC1, a gene known to govern early neural development in mice (Hernandez et al., 1997). ENC1 was established as a marker for fish phylogenetics by Li et al. (2007). Data from the RAG1, MYH6, and COI genes were also included in this study.

Data Collection and Alignment

I used either the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA) or a standard desalting protocol with alcohol precipitation to extract total genomic DNA from tissue samples. A tissue sample for *Thysanactis dentex* was not available, but previously extracted DNA was generously provided by Masaki Miya (Natural History Museum, Chiba, Japan).

I amplified target sequences using the polymerase chain reaction (Saiki et al., 1988) with standard protocols. Many of the stomiiform tissues were of poor quality, yielding low DNA concentrations. Consequently, I frequently employed a "nested" PCR protocol for these difficult templates, using multiple rounds of amplification. The product of the first amplification would serve as the template for the next reaction using a set of primers internal to the previous pair (Table 3.2).

Successfully amplified sequences were purified using either enzymatic digestion with ExoSAP-It (USB/Affymetrix, Santa Clara, CA, USA), magnetic bead separation with the AMPure system (Agencourt, Beverly, MA, USA), or spin column purification with the QIAquick PCR Purification Kit (QIAGEN, Valencia, CA, USA). Purified products were cycle sequenced (Sanger et al., 1977) using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA).

Sequences were read on an ABI 3100xl automated sequencer in the KU DNA Sequencing Core Facility.

I viewed the sequences, cleaned up base miscalls, concatenated fragments, and trimmed sequences using the program Sequencer v. 4.1 (1991). Sequences were aligned by eye in the program Se-Al (Rambaut, 2002) using amino acid translations as a guide. As all sequences used were from protein-coding genes, alignment was unambiguous.

The final concatenated data matrix was composed of 843 nucleotides from the RAG1 gene, 732 nucleotides from the MYH6 gene, 792 from the ENC1 gene, and 831 from the COI gene, for a total of 3198 bases. Of the included characters, 1578 were invariant, 286 of variable characters were uninformative, and 1334 were phylogenetically informative.

Sequence Evaluation

I examined base compositional and codon usage biases in the sequences by calculating the overall GC content, GC content at third codon positions, and the effective number of codons, N_c (Wright, 1990) for each gene fragment for each taxon. The program Codonw (Peden, 1999) was used to calculate GC content and N_c.

Phylogenetic Analysis

Parsimony analysis of the concatenated data matrix was performed in the program PAUP*4.0 (Swofford, 2003), using heuristic search with 10,000 random addition sequence replicates and the Tree Bisection and Reconnection (TBR) algorithm. I evaluated the support for clades in the analysis using the nonparametric bootstrap implemented in PAUP* (Felsenstein, 1985), with 1,000 bootstrap replicates.

I performed maximum likelihood analysis in the program GARLI v.0.95 (Zwickl, 2006) under the general time reversible model of evolution with a gamma distribution of rates among sites, allowing for a proportion of invariant sites (GTR+I+Γ). Six independent runs were performed, each beginning with a random starting tree and progressing for 10,000 generations after the last improvement in topology. I implemented the nonparametric bootstrap in GARLI with 100 replicates.

I used the program MrBayes v.3.1 (Huelsenbeck and Ronquist, 2001) to reconstruct the phylogeny using Bayesian inference. Four simultaneous runs were performed, each with four chains: one cold chain and three "heated" chains. The analysis was run for four million generations, the first 25% of which were discarded as burn-in. Data partitioning was done by genome and, for the mitochondrial gene, by codon position, for a total of four partitions (nuclear genes, mitochondrial gene first positions, mitochondrial gene second positions, and mitochondrial gene third positions). Justification of this partitioning scheme is outlined in the Methods of Chapter Two. I used MrModeltest v2.2 (Nylander, 2008) to choose the most appropriate substitution model for each data partition. For the nuclear gene partition, the model chosen was GTR+I+Γ; for each of the three mitochondrial data partitions, the model was GTR+Γ.

Results

Sequence Evaluation

There is some evidence of base compositional and codon bias in the sequences (Tables 3.3–3.6). Base compositional bias was most pronounced in the RAG1 (mean 62.5% GC overall; mean 85.0% GC at third positions) and ENC1 (mean 60.7% GC overall; mean 84.5% GC at third positions) genes, and not pronounced in MYH6 (mean 48.4% GC overall; mean 57.7% GC at third positions) and COI (mean 48.3% GC overall; mean 48.3% at third positions). Codon bias was strong in RAG1 (mean N_C 37.25), ENC1 (mean N_C 37.07.28), moderate in COI (mean N_C 46.22) and weak in ZIC1 (mean N_C 55.37).

The null hypothesis of base compositional stationarity among taxa was rejected by the chi-square test for RAG1 (p=0.00001), ENC1 (p=0.00107), and COI (p=0.03498). The null hypothesis of stationarity was not rejected for MYH6 (p=1.0). When third positions were excluded, base compositional stationarity was not rejected for any of the genes (p=1.0 for each).

Phylogenetic Analysis

The trees produced by all three methods of analysis were similar in topology (Figures 3.1–3.3), with resolution and branch support lowest in the parsimony tree. In general, bootstrap support and posterior probability values were suboptimal, and surprisingly were lower overall than values for the trees in Chapter Two, which addressed deeper divergences. Branch lengths for early divergences within

Stomiiformes were short, which probably contributed to lower support values for clades.

All three analysis methods produced topologies with a monophyletic Stomiiformes. In all three trees, the genera *Valenciennellus, Pollichthys,* and *Vinciguerria* were recovered as the most basal taxa within the order. In the parsimony and likelihood trees, a clade composed of those three genera is sister to all other stomiiforms. In the Bayesian tree, a *Valenciennellus* + *Pollichthys* clade is sister to all other stomiiforms, with *Vinciguerria* then sister to the remaining taxa.

Of the four or five currently recognized stomiiform families, none is recovered as monophyletic with its present composition. Gonostomatidae is monophyletic in each topology only if *Bonapartia* is excluded. A clade composed of sternoptychids, phosichthyids, *Diplophos*, *Triplophos,* and *Chauliodus* is recovered in all three topologies. Stomiidae is monophyletic only if *Chauliodus* is excluded (*Stomias* must also be excluded in the parsimony tree). *Phosichthys* is sister to the stomiids in all three trees, with *Ichthyococcus* sister to the *Phosichthys* + Stomiidae clade.

Both Phosichthyidae and the sternoptychid subfamily Maurolicinae are generally suspected of being polyphyletic (Nelson, 2006), so it is not surprising that they are not monophyletic in any of the three trees. The subfamily Sternoptychinae composed of the deep-bodied hatchetfishes *Argyropelecus, Polyipnus,* and *Sternoptyx,* on the other hand, has traditionally been considered a monophyletic group. It is not recovered as a monophyletic lineage in any of the three current trees.

The relationships within the family Stomiidae recovered here are generally similar to the conclusions of Fink (1985), the most striking differences being the placement of *Stomias* sister to all other stomiids in the likelihood and Bayesian trees and outside the family altogether in the parsimony tree, and the recovery of *Chauliodus* outside the family in all three trees.

Discussion

The present analyses reject the hypothesis of Fink and Weitzman (1982) that *Diplophos* is sister to all other stomiiforms. The conclusion of Weitzman (1967) that *Vinciguerria* and *Polymetme* are among the most basal members of the order is partly supported: *Vinciguerria* is among the basal members of the stomiiform lineage in all three trees, but *Polymetme* is strongly supported as sister to *Yarrella* in a much more derived position in the tree. Furthermore, *Valenciennellus* and *Pollichthys* are also recovered at the base of the tree.

The present analyses support the strictest interpretation of Gonostomatidae except that *Bonapartia* is excluded, making the family even smaller. All three trees support the hypothesis that the abundant genus *Cyclothone* is nested within *Gonostoma* (Harold, 1998; Miya and Nishida, 2000).

Harold (1998) concluded that the monotypic genus *Triplophos* was not related to the gonostomatids, but was instead closer to the phosichthyids. The present analyses do not recover *Triplophos* with either of these groups, but recover them instead in a clade with the hatchetfishes *Sternoptyx* and *Argyropelecus sladeni*. Whether any morphological characters support this placement is unknown.

The lack of a monophyletic Sternoptychinae in any of the tree topologies is unexpected, given the strong overall similarity among the three hatchetfish genera. Monophyly of the hatchetfish clade is apparently supported by many morphological characters (Schultz, 1961; Harold and Weitzman, 1996). It is possible that the present topologies failed to recover a group that is truly monophyletic, probably because of short branch lengths at deeper levels within the stomiiform clade. If the diversification of hatchetfishes was rapid, there may be insufficient molecular signal to detect the monophyly of the lineage. On the other hand, it is also possible that Sternoptychinae is truly not monophyletic, and the deep-bodied condition evolved multiple times, or was lost in *Maurolicus* and *Triplophos*. Many of the morphological characters supporting monophyly of the subfamily are characters associated with a deep-bodied, laterally compressed body form, such as a long, slender preopercle and opercle and a vertically oriented pelvic girdle. The genus *Argyropelecus* was also not recovered as monophyletic, with *Argyropelecus sladeni* recovered separately from the other two included species, *A. gigas* and *A. aculeatus*. Although Harold (1993) concluded that *Argyropelecus* is monophyletic, Harold and Weitzman (1996) only found three characters supporting its monophyly, and each of them is homoplastic.

Neither the family Phosichthyidae nor the subfamily Maurolicinae are recovered as monophyletic groups in the present trees; instead, their members are scattered throughout the phylogeny. Both of these groups were long suspected to be paraphyletic collections of generalized stomiiform species, so this finding is neither surprising nor troubling. However, taxon sampling among Maurolicinae was particularly weak in this study. Inclusion of the missing taxa in future analyses may signficantly alter the phylogeny.

The trees produced here indicate that the viperfish genus *Chauliodus* is not a stomiid. The parsimony tree, at least, places *Stomias* outside the family as well — a placement, which, if it were accepted, would necessitate a new name for the remainder of the family. These two genera already differ from other stomiids by having scales, or a scalelike hexagonal pattern on the body. *Chauliodus* also differs from all other stomiids by having the dorsal fin far anterior relative to the pelvic fins. All other stomiids have the dorsal fin origin above or posterior to the pelvic fin origin. Parr (1927; 1930) recognized that *Stomias* and *Chauliodus* might not belong with other stomiids and placed them in their own group, his Lepidophotodermi. The close relationship between *Stomias* and *Chauliodus* proposed by many authors (Parr, 1927; Fink, 1985; Harold and Weitzman, 1996; Nelson, 2006) is not supported here.

The relationships of the loosejaws, in the stomiid subfamily Malacosteinae, have been difficult to resolve. The common name for the group comes from the extremely long jaws with the floor of the mouth completely absent in *Aristostomias, Malacosteus,* and *Photostomias*. The genus *Pachystomias,* which has a partial membrane between the mandibular rami, has also been recognized as a member of a monophyletic Malacosteinae (Goodyear, 1980; Fink, 1985). The genera *Pachystomias, Aristostomias,* and *Malacosteus* are remarkable for their ability to both produce and detect long-wavelength red light. Red wavelengths attenuate quickly in seawater, so the red part of the spectrum is filtered out of the downwelling sunlight from the surface long before light reaches the mesopelagic zone, and most midwater organisms have lost the ability to visually detect red wavelengths. The longwave-detecting loosejaws produce red light in a photophore below the eye, illuminating nearby prey items without alerting them to the fish's presence (Partridge and Douglas, 1995; Herring, 2002). The absence of a floor of the mouth and longwave light production/detection are both compelling characters that would support different phylogenetic hypotheses. Fink (1985) left the subfamily as a polytomy. The present analyses recover *Pachystomias* as sister to a clade composed of the other three genera, meaning that the loss of the floor of the mouth is a synapomorphy and longwave detection is homoplastic. This conclusion is not surprising given that the mechanism of longwave detection in *Malacosteus* is different from that in *Aristostomias* and *Pachystomias*. While *Aristostomias* and *Pachystomias* each have three visual pigments they produce themselves, *Malacosteus* detects red light using a visual pigment derived from chlorophyll, which it must obtain from its diet by eating zooplankton that have in turn eaten chlorophyllous phytoplankton (Partridge and Douglas, 1995; Herring, 2002). A sister group relationship between *Malacosteus* and *Photostomias* is further supported by the loss of the mental barbel present in other stomiids (Fink, 1985).

In the likelihood and Bayesian trees, where branch lengths are shown, it is clear that branch lengths are very short for the earliest divergences within the stomiiform clade. This suggests a rapid early evolutionary radiation within Stomiiformes. Known stomiiform fossils, dating to the Miocene, Eocene, and even the Tertiary, are morphologically similar to extant taxa and in many cases can be placed in, or sister to, moderately derived extant genera (Gregorová, 1989; Prokofiev, 2001; Carnevale, 2002; Prokofiev and Bannikov, 2002; Carnevale, 2008). The paleontological evidence supports the hypothesis that much of the morphological diversification of stomiiform fishes happened early in the history of the lineage.

Reasons for a rapid early stomiiform radiation could be related to the invasion of a new habitat, the deep open ocean. The phylogenetic hypothesis from the previous chapter suggests that the stomiiform sister group is a clade composed of galaxioids and osmeroids, all of which are freshwater, brackish, anadromous, or marine in littoral or epipelagic zones. Indeed, the uniqueness of stomiiform adaptations to the deep sea, such as the photophore structure not seen in any other fishes (Fink and Weitzman, 1982) indicate that stomiiforms are the product of an independent invasion of the deep ocean. Considering that the deep open ocean is by far the largest habitat on the planet, making up an estimated 95% or more of the volume where life is known to occur (Herring, 2002), it might seem that entering this habitat would provide boundless opportunity for diversification; however, the deep open ocean also seems relatively homogenous, with few barriers to dispersal. Although there is evidence that sister species in the genus *Cyclothone* exhibit allopatric distributions, suggesting vicariant speciation (Miya and Nishida, 1996; Miya and Nishida, 1997), little is known about the patterns and processes of speciation in the ocean's midwaters.

In summary, this study confirms that most of the classification currently in use for stomiiform fishes does not reflect monophyletic groups. Clearly, much work remains to be done to resolve the relationships of the fishes in this order. The apparently rapid diversification of stomiiforms detected with this data set will require a much larger molecular dataset to successfully resolve. In addition, taxa that were missing from this analysis must be added to future analyses as tissue samples become available for molecular work.

Table 3.1. Taxon sampling and tissue numbers; classification following Nelson (2006).

Neopterygii	
Teleostei	
Ostarioclupeomorpha	
Clupeiformes	
Chirocentrus dorab	Genbank
Euteleostei	
Argentiniformes	
Argentina striata	KU 3283
Nansenia longicauda	KU 6511
Bathylagus longirostris	KU 5333
Osmeriformes	
Mallotus villosus	KU 3139
Thaleichthys pacificus	KU 3135
Galaxias maculatus	EBU 22353
Salmoniformes	
Oncorhynchus keta	KU 3228
Neoteleostei	
Stomiiformes	
"Diplophidae" (*incertae sedis* taxa)	
Diplophos taenia	KU 3781
Triplophos hemingi	COC
Gonostomatidae	
Bonapartia pedaliota	KU 3789
Cyclothone acclinidens	KU 2247
Cyclothone microdon	KU 3736
Cyclothone parapallida	SIO 02-47
Cyclothone pseudopallida	SIO 02-47
Gonostoma elongatum	KU 5384
Margrethia obtusirostra	ORI 1406
Sigmops bathyphilus	KU 3654
Sigmops longipinnis	SIO 02-47
Sternoptychidae	
Maurolicinae	
Maurolicus australis	NMV 25100-004
Maurolicus weitzmani	KU 3553
Valenciennellus tripunctulatus	KU 3732
Sternoptychinae	
Argyropelecus aculeatus	KU 3805
Argyropelecus gigas	KU 5299
Argyropelecus sladeni	KU 2259
Polyipnus clarus	KU 3563
Polyipnus kiwiensis	NMV 25167-012
Sternoptyx obscura	ORI 1407
Sternoptyx pseudobscura	KU 5299
Phosichthyidae	
Ichthyococcus ovatus	KU 38789*
Phosichthys argenteus	NMV 23566
Pollichthys mauli	KU 7273

Polymetme thaeocoryla	KU 3547
Vinciguerria nimbaria	KU 3733
Vinciguerria poweriae	KU 1257
Yarrella blackfordi	LIM A84
Stomiidae	
Astronesthinae	
Astronesthes gemmifer	KU 3106
Borostomias elucens	ORI 1403
Heterophotus ophistoma	KU 5277
Neonesthes capensis	KU 7482
Rhadinesthes decimus	KU 6506
Stomiinae	
Chauliodus danae	KU 5382
Chauliodus sloani	KU 3751
Stomias affinis	ORI 1405
Stomias atriventer	SIO 01-74
Melanostomiinae	
Bathophilus pawneei	KU 3646
Bathophilus vaillanti	KU 3102
Chirostomias pliopterus	KU 3113
Echiostoma barbatum	KU 5281
Eustomias filifer	KU 8136
Eustomias furcifer	KU 7464
Eustomias jimcraddocki	KU 5895
Eustomias polyaster	KU 5900
Flagellostomias boureei	KU 3121
Grammatostomias flagellibarba	KU 6509
Leptostomias gladiator	KU 8148
Leptostomias longibarba	KU 3695
Melanostomias bartonbeani	KU 6514
Odontostomias micropogon	COC
Photonectes braueri	NMV 25111-036
Photonectes margarita	KU 7443
Tactostoma macropus	KU 3237
Thysanactis dentex	ORI
Trigonolampa miriceps	KU 3258
Idiacanthiinae	
Idiacanthus fasciola	KU 3101
Malacosteinae	
Aristostomias polydactylus	ORI 1408
Aristostomias scintillans	KU 2292
Aristostomias tittmanni	KU 3707
Malacosteus niger	KU 3804
Pachystomias microdon	NMV 25122-011
Photostomias guernei	KU 3811
Ateleopodiformes	
Ijimaia antillarum	KU 5411
Eurypterygii	
Aulopiformes	
Synodus foetens	KU 5069
Myctophiformes	
Neoscopelus macrolepidotus	KU 3297

*Number indicates voucher number; tissue harvested from whole fish preserved in ethanol.
KU = University of Kansas; COC = Centro Oceanografico de Canarias; EBU = Evolutionary Biology Unit, Australian Museum; LIM = Leibniz Institut für Meeresbiologie, Germany; NMV = Museum Victoria, Australia; ORI = Ocean Research Institute, University of Tokyo, Japan; SIO = Scripps Institute of Oceanography

Table 3.2. Primers used for DNA amplification and sequencing.

Gene	**Primer**	**Primer Sequence**
RAG1	Of2[a]	5' CTGAGCTGCAGTCAGTACCATAAGATGT 3'
RAG1	Wf2i2[b]	5' ATGGGBGATRTCAGCGAGAA 3'
RAG1	Wf2i3[b]	5' GATGARAAGATGGTGCGNGAGVT 3'
RAG1	Wr2i3[b]	5' WARTTBCCRTTCATCCTCAT 3'
RAG1	Wr2i4[b]	5' CTRTARCGRCACAGCTGGTC 3'
RAG1	Wr3[b]	5' ATCTGGADGTGTAGTGCCAG 3'
RAG1	Or2[a]	5' CTGAGTCCTTGTGAGCTTCCATRAAYTT 3'
ENC1	LF1[c]	5' GACATGCTGGAGTTTCAGGA 3'
ENC1	LF2[c]	5' ATGCTGGAGTTTCAGGACAT 3'
ENC1	LF3[c]	5' AAGAGCAAGGARCTGGTRGA 3'
ENC1	LR1[c]	5' ACTTGTTRGCMACTGGGTCAAA 3'
ENC1	LR2[c]	5' AGCMACTGGGTCAAACTGCTC 3'
ENC1	LR3[c]	5' ATCTCTTTGGCYTTCTGGTC 3'
MYH6	A3F1[c]	5' CATMTTYTCCATCTCAGATAATGC 3'
MYH6	A3F2[c]	5' GGAGAATCARTCKGTGCTCATCA 3'
MYH6	A3F3[c]	5' TCCCGWGTCACYTTTCAGC 3'
MYH6	A3R1[c]	5' ATTCTCACCACCATCCAGTTGAA 3'
MYH6	A3R2[c]	5' CTCACCACCATCCAGTTGAACAT 3'
MYH6	A3R3[c]	5' GTGAAGCCRAGCACRTCAAA 3'
COI	L5698[d]	5' AGGCCTCGATCCTACAAAGKTTTAGTTAAC 3'
COI	L5956[d]	5' CACAAAGACATTGGCACCCT 3'
COI	H6864[d]	5' AGWGTWGCKAGTCAGCTAAA 3'
COI	H6855[d]	5' AGTCAGCTGAAKACTTTTAC 3'

a. Designed by G.O. Ortí, University of Nebraska - Lincoln
b. Designed by N.I. Holcroft, University of Kansas
c. Designed by C. Li, University of Nebraska - Lincoln
d. Designed by M. Miya, Natural History Museum and Institute, Chiba, Japan

Table 3.3. Base composition and codon usage in the RAG1 gene.

Species	**RAG1 GC**	**RAG1 GC3**	**RAG1 N_C**
Chirocentrus dorab	0.638	0.889	32.91
Oncorhynchus keta	0.580	0.739	43.810
Argentina striata	0.593	0.772	41.240
Nansenia longicauda	0.622	0.857	36.530
Bathylagus longirostris	0.636	0.881	35.410
Mallotus villosus	0.632	0.867	36.970
Galaxias maculatus	0.562	0.706	45.540
Thaleichthys pacificus	0.618	0.852	37.200
Ijimaia antillarum	0.599	0.809	42.320
Synodus foetens	0.522	0.580	50.940
Neoscopelus macrolepidotus	0.635	0.878	34.870
Diplophos taenia	0.585	0.746	42.190
Triplophos hemingi	0.587	0.752	44.150
Bonapartia pedaliota	0.609	0.809	39.920
Cyclothone acclinidens	0.592	0.792	43.190
Cyclothone microdon	0.589	0.783	44.560
Cyclothone parapallida	0.585	0.782	44.200
Cyclothone pseudopallida	0.591	0.771	41.080
Gonostoma elongatum	0.614	0.825	39.010
Sigmops bathyphilus	0.661	0.943	31.200
Sigmops longipinnis	0.624	0.859	37.890
Margrethia obtusirostra	0.636	0.880	34.590
Maurolicus australis	—	—	—
Maurolicus weitzmani	0.581	0.717	44.350
Valenciennellus tripunctulatus	0.578	0.718	47.190
Argyropelecus aculeatus	0.578	0.719	44.760
Argyropelecus gigas	0.579	0.734	42.040
Argyropelecus sladeni	0.576	0.721	43.600
Polyipnus clarus	0.626	0.869	36.850
Polyipnus kiwiensis	0.613	0.827	39.490
Sternoptyx obscura	0.586	0.755	43.570
Sternoptyx pseudobscura	0.584	0.752	43.770
Ichthyococcus ovatus	0.654	0.939	31.790
Phosichthys argenteus	0.672	0.976	29.520
Pollichthys mauli	0.533	0.636	52.730
Polymetme thaeocoryla	0.615	0.834	37.400
Vinciguerria nimbaria	0.561	0.689	48.850
Vinciguerria poweriae	0.590	0.733	41.710
Yarrella blackfordi	0.615	0.834	38.080
Astronesthes gemmifer	0.656	0.915	33.080
Borostomias elucens	0.673	0.955	31.550

Heterophotus operosus	0.662	0.947	30.240
Neonesthes capensis	0.673	0.969	30.250
Rhadinesthes decimus	0.674	0.959	30.170
Stomias affinis	0.618	0.846	34.520
Stomias atriventer	0.560	0.677	46.510
Chauliodus danae	0.607	0.814	39.350
Chauliodus sloani	0.601	0.798	40.660
Bathophilus pawneei	0.659	0.939	32.870
Bathophilus vaillanti	0.669	0.938	32.180
Chirostomias pliopterus	0.670	0.957	30.930
Echiostoma barbatum	0.661	0.933	32.060
Eustomias filifer	0.635	0.877	34.510
Eustomias furcifer	0.638	0.893	34.860
Eustomias jimcraddocki	0.641	0.891	34.840
Eustomias polyaster	0.598	0.772	40.690
Flagellostomias boureei	0.669	0.955	31.050
Grammatostomias flagellibarba	0.665	0.934	32.030
Leptostomias gladiator	0.673	0.973	29.740
Leptostomias longibarba	0.681	0.987	28.990
Melanostomias bartonbeani	0.519	0.588	54.790
Odontostomias micropogon	0.678	0.974	29.610
Pachystomias microdon	0.670	0.945	31.330
Photonectes braueri	0.667	0.967	30.360
Photonectes margarita	0.659	0.947	30.360
Tactostoma macropus	0.675	0.958	30.440
Thysanactis dentex	0.692	0.996	28.520
Trigonolampa miriceps	0.671	0.961	30.460
Idiacanthus fasciola	0.664	0.930	31.630
Aristostomias polydactylus	0.656	0.916	32.810
Aristostomias scintillans	0.644	0.882	36.050
Aristostomias tittmanni	0.654	0.918	33.500
Malacosteus niger	0.666	0.952	30.200
Photostomias guernei	0.663	0.926	32.740
Mean	**0.625**	**0.850**	**37.251**

Table 3.4. Base composition and codon usage in the MYH6 gene.

Species	**MYH6 GC**	**MYH6 GC3**	**MYH6 N_C**
Chirocentrus dorab	0.485	0.580	52.61
Oncorhynchus keta	0.472	0.543	56.87
Argentina striata	0.460	0.517	51.07
Nansenia longicauda	0.457	0.502	51.83
Bathylagus longirostris	0.471	0.524	52.67
Mallotus villosus	—	—	—
Galaxias maculatus	—	—	—
Thaleichthys pacificus	0.469	0.538	58.84
Ijimaia antillarum	0.483	0.551	55.78
Synodus foetens	0.446	0.472	51.99
Neoscopelus macrolepidotus	0.512	0.658	51.67
Diplophos taenia	0.472	0.540	53.83
Triplophos hemingi	—	—	—
Bonapartia pedaliota	—	—	—
Cyclothone acclinidens	0.498	0.620	59.08
Cyclothone microdon	0.543	0.735	45.30
Cyclothone parapallida	—	—	—
Cyclothone pseudopallida	0.553	0.742	44.35
Gonostoma elongatum	0.495	0.595	55.43
Sigmops bathyphilus	—	—	—
Sigmops longipinnis	0.483	0.566	54.61
Margrethia obtusirostra	0.481	0.567	57.65
Maurolicus australis	0.494	0.596	56.88
Maurolicus weitzmani	0.478	0.575	52.36
Valenciennellus tripunctulatus	0.498	0.623	56.63
Argyropelecus aculeatus	0.491	0.594	52.74
Argyropelecus gigas	0.483	0.578	54.96
Argyropelecus sladeni	0.481	0.574	56.62
Polyipnus clarus	0.479	0.558	56.92
Polyipnus kiwiensis	—	—	—
Sternoptyx obscura	—	—	—
Sternoptyx pseudobscura	—	—	—
Ichthyococcus ovatus	0.486	0.555	55.83
Phosichthys argenteus	0.481	0.565	55.49
Pollichthys mauli	0.474	0.536	56.77
Polymetme thaeocoryla	0.488	0.581	56.67
Vinciguerria nimbaria	0.499	0.604	47.50
Vinciguerria poweriae	—	—	—
Yarrella blackfordi	0.486	0.601	56.28
Astronesthes gemmifer	0.496	0.617	54.79
Borostomias elucens	0.473	0.569	55.87

Heterophotus operosus	0.478	0.570	57.11
Neonesthes capensis	0.482	0.579	58.18
Rhadinesthes decimus	0.478	0.570	57.77
Stomias affinis	0.481	0.564	53.54
Stomias atriventer	0.481	0.560	53.60
Chauliodus danae	0.488	0.588	54.98
Chauliodus sloani	0.485	0.581	53.07
Bathophilus pawneei	0.482	0.583	57.04
Bathophilus vaillanti	0.486	0.591	57.63
Chirostomias pliopterus	0.477	0.553	57.69
Echiostoma barbatum	0.478	0.574	58.14
Eustomias filifer	0.483	0.568	57.92
Eustomias furcifer	0.482	0.568	56.91
Eustomias jimcraddocki	0.488	0.581	57.00
Eustomias polyaster	0.483	0.574	56.73
Flagellostomias boureei	0.478	0.573	55.86
Grammatostomias flagellibarba	0.477	0.568	55.13
Leptostomias gladiator	0.481	0.566	55.80
Leptostomias longibarba	0.483	0.581	55.29
Melanostomias bartonbeani	0.482	0.574	57.64
Odontostomias micropogon	0.478	0.566	56.44
Pachystomias microdon	0.482	0.578	56.57
Photonectes braueri	0.476	0.568	56.07
Photonectes margarita	0.477	0.579	56.85
Tactostoma macropus	0.476	0.566	58.33
Thysanactis dentex	—	—	—
Trigonolampa miriceps	0.482	0.572	57.36
Idiacanthus fasciola	0.476	0.566	53.55
Aristostomias polydactylus	0.486	0.594	55.92
Aristostomias scintillans	0.494	0.591	58.22
Aristostomias tittmanni	0.487	0.582	55.13
Malacosteus niger	0.474	0.562	58.34
Photostomias guernei	0.484	0.590	58.69
Mean	**0.484**	**0.577**	**55.37**

Table 3.5. Base composition and codon usage in the ENC1 gene.

Species	**ENC1 GC**	**ENC1 GC3**	**ENC1 N_C**
Chirocentrus dorab	0.668	0.984	25.83
Oncorhynchus keta	0.595	0.828	37.46
Argentina striata	0.605	0.858	36.68
Nansenia longicauda	0.603	0.827	36.76
Bathylagus longirostris	0.646	0.960	29.47
Mallotus villosus	—	—	—
Galaxias maculatus	—	—	—
Thaleichthys pacificus	0.645	0.940	31.33
Ijimaia antillarum	—	—	—
Synodus foetens	0.519	0.583	51.04
Neoscopelus macrolepidotus	0.524	0.618	49.53
Diplophos taenia	0.603	0.838	37.80
Triplophos hemingi	0.606	0.827	37.79
Bonapartia pedaliota	—	—	—
Cyclothone acclinidens	—	—	—
Cyclothone microdon	0.630	0.902	33.47
Cyclothone parapallida	0.625	0.886	33.55
Cyclothone pseudopallida	0.634	0.901	32.71
Gonostoma elongatum	0.655	0.976	28.41
Sigmops bathyphilum	0.667	0.980	28.92
Sigmops longipinnis	0.668	0.988	28.99
Margrethia obtusirostra	0.651	0.964	29.31
Maurolicus australis	0.566	0.745	44.22
Maurolicus weitzmani	0.575	0.747	46.11
Valenciennellus tripunctulatus	0.607	0.845	34.19
Argyropelecus aculeatus	0.584	0.781	40.81
Argyropelecus gigas	0.596	0.821	39.41
Argyropelecus sladeni	0.593	0.820	38.83
Polyipnus clarus	0.584	0.773	42.41
Polyipnus kiwiensis	0.588	0.788	41.61
Sternoptyx obscura	0.617	0.870	35.26
Sternoptyx pseudobscura	0.616	0.865	35.85
Ichthyococcus ovatus	—	—	—
Phosichthys argenteus	0.618	0.930	29.72
Pollichthys mauli	0.651	0.924	32.70
Polymetme thaeocoryla	0.635	0.917	32.56
Vinciguerria nimbaria	0.613	0.833	38.57
Vinciguerria poweriae	—	—	—
Yarrella blackfordi	0.630	0.905	32.46
Astronesthes gemmifer	0.595	0.816	38.57
Borostomias elucens	0.652	0.951	30.74

Heterophotus operosus	0.585	0.793	40.15
Neonesthes capensis	0.594	0.825	38.78
Rhadinesthes decimus	0.651	0.959	29.69
Stomias affinis	0.636	0.905	33.54
Stomias atriventer	0.622	0.870	35.05
Chauliodus danae	0.634	0.914	30.58
Chauliodus sloani	0.627	0.896	32.12
Bathophilus pawneei	0.584	0.788	40.13
Bathophilus vaillanti	0.583	0.785	40.42
Chirostomias pliopterus	0.603	0.839	37.82
Echiostoma barbatum	0.592	0.813	39.17
Eustomias filifer	0.587	0.798	41.04
Eustomias furcifer	0.590	0.809	40.10
Eustomias jimcraddocki	0.587	0.802	40.09
Eustomias polyaster	0.584	0.793	41.59
Flagellostomias boureei	0.593	0.818	40.76
Grammatostomias flagellibarba	0.592	0.810	40.21
Leptostomias gladiator	0.596	0.831	39.47
Leptostomias longibarba	0.599	0.827	39.51
Melanostomias bartonbeani	0.591	0.807	39.15
Odontostomias micropogon	0.596	0.826	39.44
Pachystomias microdon	0.600	0.835	37.70
Photonectes braueri	0.595	0.829	38.87
Photonectes margarita	0.597	0.827	38.50
Tactostoma macropus	0.595	0.817	39.52
Thysanactis dentex	—	—	—
Trigonolampa miriceps	0.594	0.825	37.48
Idiacanthus fasciola	0.596	0.803	37.77
Aristostomias polydactylus	0.583	0.798	41.07
Aristostomias scintillans	0.585	0.798	40.74
Aristostomias tittmanni	0.585	0.801	40.64
Malacosteus niger	0.600	0.836	38.10
Photostomias guernei	0.618	0.880	34.47
Mean	**0.607**	**0.845**	**37.07**

Table 3.6. Base composition and codon usage in the COI gene.

Species	**COI GC**	**COI GC3**	**COI N_C**
Chirocentrus dorab	0.539	0.638	49.83
Oncorhynchus keta	0.462	0.440	55.28
Argentina striata	0.475	0.484	53.27
Nansenia longicauda	0.497	0.534	49.12
Bathylagus longirostris	0.510	0.572	44.57
Mallotus villosus	0.468	0.447	48.40
Galaxias maculatus	0.443	0.390	57.20
Thaleichthys pacificus	0.476	0.471	51.48
Ijimaia antillarum	0.431	0.357	44.09
Synodus foetens	0.444	0.397	47.78
Neoscopelus macrolepidotus	0.463	0.424	49.99
Diplophos taenia	0.522	0.585	46.05
Triplophos hemingi	0.487	0.513	50.54
Bonapartia pedaliota	0.487	0.487	47.10
Cyclothone acclinidens	0.460	0.429	42.67
Cyclothone microdon	0.469	0.462	43.56
Cyclothone parapallida	0.467	0.430	43.32
Cyclothone pseudopallida	0.467	0.430	43.32
Gonostoma elongatum	0.477	0.464	53.00
Sigmops bathyphilum	0.466	0.412	43.93
Sigmops longipinnis	0.455	0.397	43.02
Margrethia obtusirostra	0.486	0.491	43.16
Maurolicus australis	0.490	0.505	48.50
Maurolicus weitzmani	0.497	0.527	40.52
Valenciennellus tripunctulatus	0.468	0.426	44.29
Argyropelecus aculeatus	0.439	0.375	46.58
Argyropelecus gigas	0.448	0.397	45.48
Argyropelecus sladeni	0.481	0.491	46.03
Polyipnus clarus	0.480	0.487	54.39
Polyipnus kiwiensis	0.481	0.477	42.34
Sternoptyx obscura	0.487	0.486	43.95
Sternoptyx pseudobscura	0.449	0.387	49.09
Ichthyococcus ovatus	0.485	0.480	51.31
Phosichthys argenteus	0.511	0.559	43.48
Pollichthys mauli	—	—	—
Polymetme thaeocoryla	0.465	0.447	41.68
Vinciguerria nimbaria	0.492	0.509	54.34
Vinciguerria poweriae	—	—	—
Yarrella blackfordi	0.467	0.444	44.60
Astronesthes gemmifer	0.516	0.542	38.75
Borostomias elucens	0.514	0.574	44.32

Heterophotus operosus	0.469	0.453	48.59
Neonesthes capensis	0.489	0.490	40.68
Rhadinesthes decimus	0.501	0.534	47.83
Stomias affinis	0.515	0.570	41.30
Stomias atriventer	0.512	0.554	47.27
Chauliodus danae	0.490	0.502	48.90
Chauliodus sloani	0.509	0.571	49.72
Bathophilus pawneei	0.503	0.538	54.24
Bathophilus vaillanti	0.527	0.619	44.80
Chirostomias pliopterus	0.510	0.563	43.24
Echiostoma barbatum	0.492	0.524	51.32
Eustomias filifer	0.483	0.473	44.42
Eustomias furcifer	0.471	0.432	43.00
Eustomias jimcraddocki	0.486	0.488	40.33
Eustomias polyaster	0.482	0.468	43.24
Flagellostomias boureei	0.527	0.587	33.35
Grammatostomias flagellibarba	0.463	0.424	45.96
Leptostomias gladiator	0.490	0.491	44.10
Leptostomias longibarba	0.444	0.382	42.58
Melanostomias bartonbeani	0.446	0.350	38.80
Odontostomias micropogon	0.495	0.509	43.09
Pachystomias microdon	0.490	0.505	47.99
Photonectes braueri	0.501	0.535	47.13
Photonectes margarita	0.499	0.542	46.91
Tactostoma macropus	0.517	0.562	43.22
Thysanactis dentex	—	—	—
Trigonolampa miriceps	0.495	0.485	44.56
Idiacanthus fasciola	0.485	0.495	45.63
Aristostomias polydactylus	0.486	0.484	50.30
Aristostomias scintillans	0.458	0.435	40.73
Aristostomias tittmanni	0.472	0.458	52.03
Malacosteus niger	0.489	0.516	47.91
Photostomias guernei	0.458	0.408	48.37
Mean	**0.483**	**0.483**	**46.22**

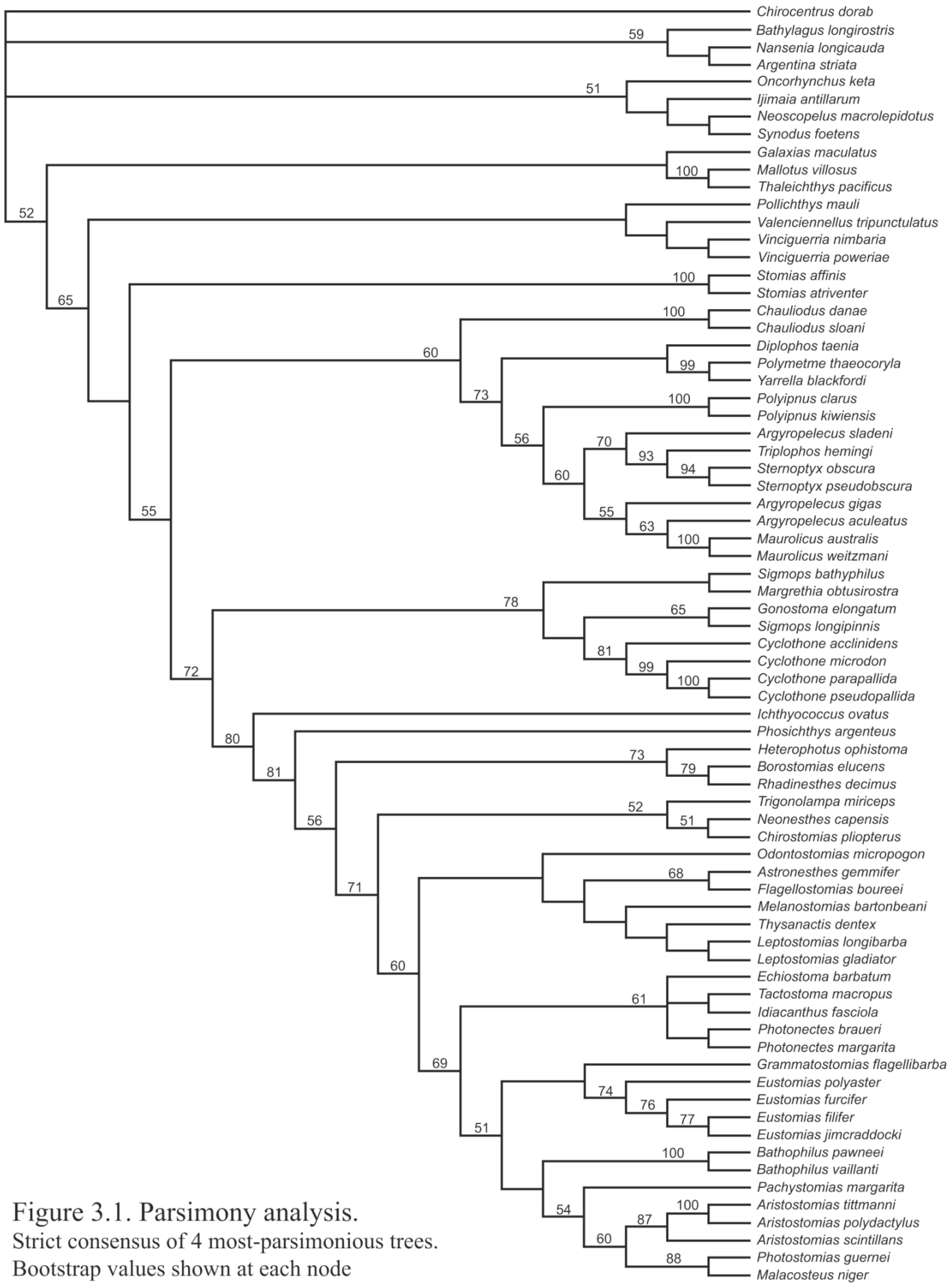

Figure 3.1. Parsimony analysis.
Strict consensus of 4 most-parsimonious trees.
Bootstrap values shown at each node
(values below 50% not shown).

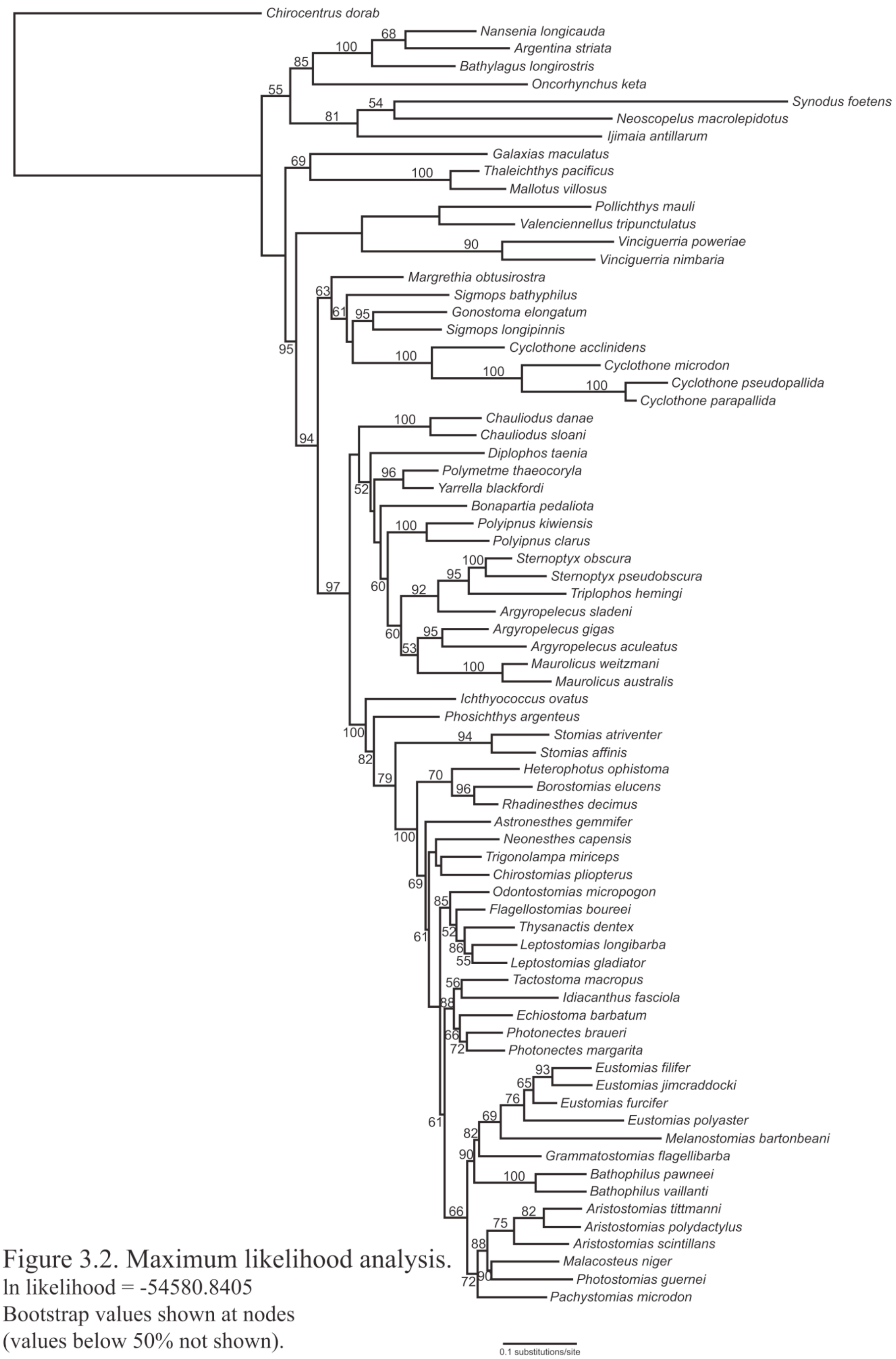

Figure 3.2. Maximum likelihood analysis.
ln likelihood = -54580.8405
Bootstrap values shown at nodes
(values below 50% not shown).

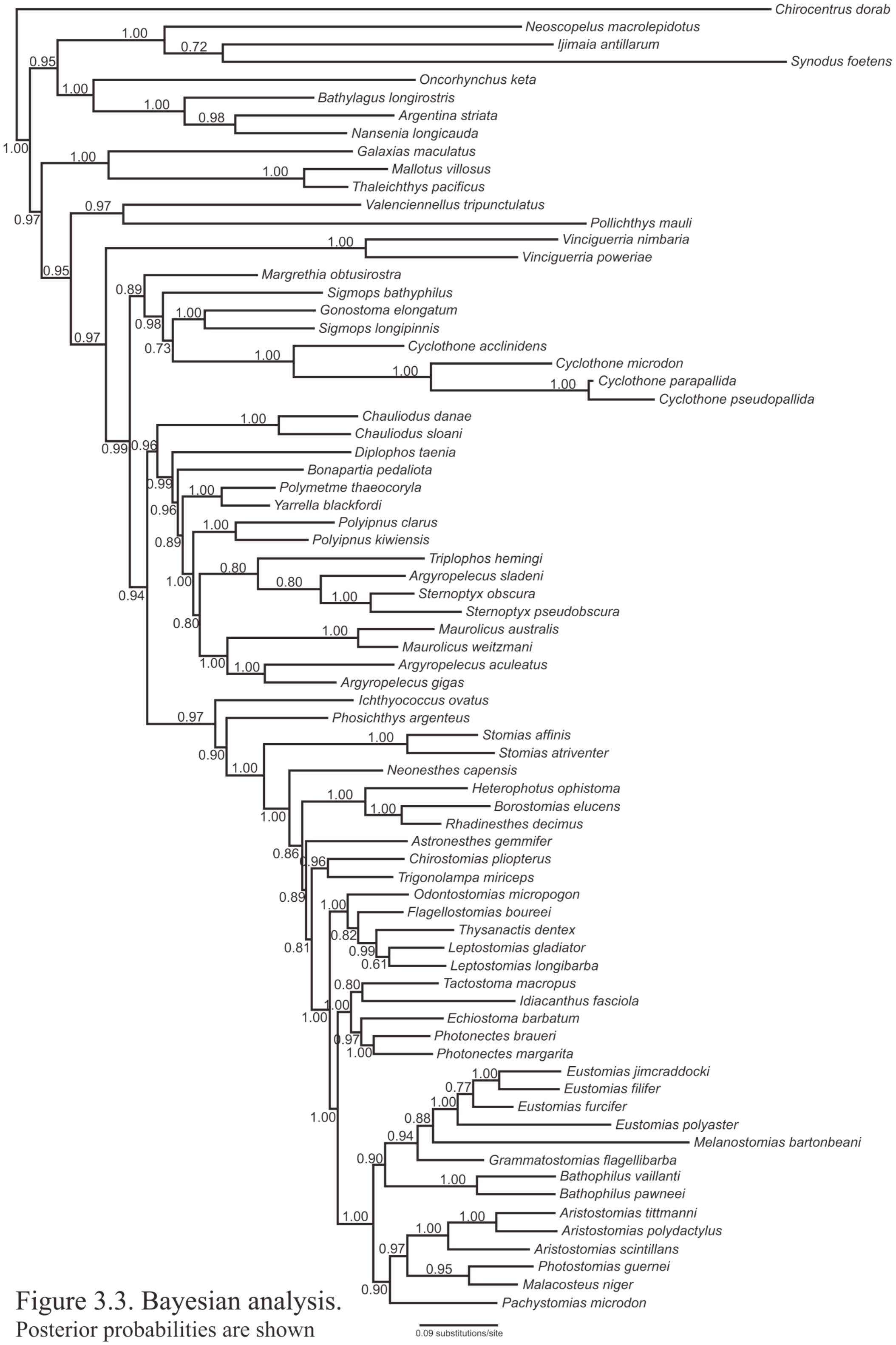

Figure 3.3. Bayesian analysis.
Posterior probabilities are shown at nodes.

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Appendix 1: Sequence Data for Chapter Two

Amia calva

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Hiodon alosoides

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Chitala chitala

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Gnathonemus petersi

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Elops saurus

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Megalops cyprinoides

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Albula vulpes

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Halosaurposis macrochir

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Notacanthus chemnitzii

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Moringua javanica

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Gymnothorax melatremus

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Derichthys serpentinus

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Serrivomer beanii

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Eurypharynx pelecanoides

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Engraulis eurystole

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Opisthonema oglinum

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Dorosoma cepedianum

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Chanos chanos

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Gonorhynchus greyi

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Pimephales promelas

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Apteronotus albifrons

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Argentina striata

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Nansenia longicauda

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Bathylagus longirostris

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Leuroglossus stilbius

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Normichthys operosus

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Sagamichthys abei

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Xenodermichthys copei

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Rouleina attrita

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Mallotus villosus

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Thaleichthys pacificus

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Retropinna semoni

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Lepidogalaxias salamandroides

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Galaxias maculatus

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Galaxiella nigrostriata

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Prosopium williamsoni

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Oncorhynchus keta

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Esox lucius

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Umbra limi

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Diplophos taenia

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Bonapartia pedaliota

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Margrethia obtusirostra

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Gonostoma elongatum

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Polyipnus clarus

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Polymetme thaeocoryla

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Vinciguerria nimbaria

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Yarrella blackfordi

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Astronesthes gemmifer

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Borostomias elucens

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Chirostomias pliopterus

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Ateleopus japonicus

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Ijimaia antillarum

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Synodus foetens

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Chlorophthalmus agassizii

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Benthalbella dentata

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Alepisaurus ferox

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Neoscopelus macrolepidotus

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Diaphus dumerilii

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Hygophum hygomii

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Lampris guttatus

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Lophotus lacepede

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Zu cristatus

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Regalecus glesne

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Polymixia lowei

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Percopsis transmontana

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Gadus morhua

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Brotulotaenia nigra

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Lophiodes reticulatus

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Mugil trichodon

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Melamphaes suborbitalis

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Gasterosteus aculeatus

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Scorpaenopsis diabolus

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Apogon apogonoides

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Appendix 2: Sequence Data for Chapter Three

Chirocentrus dorab

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NN

Oncorhynchus keta

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Argentina striata

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Nansenia longicauda

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Bathylagus longirostris

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Mallotus villosus

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Galaxias maculatus

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Thaleichthys pacificus

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Ijimaia antillarum

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Synodus foetens

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Neoscopelus macrolepidotus

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Diplophos taenia

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Triplophos hemingi

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Bonapartia pedaliota

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Cyclothone acclinidens

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Cyclothone microdon

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Cyclothone parapallida

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Cyclothone pseudopallida

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Gonostoma elongatum

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Sigmops bathyphilus

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Sigmops longipinnis

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Margrethia obtusirostra

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Maurolicus australis

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Maurolicus weitzmani

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Polyipnus kiwiensis

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Sternoptyx obscura

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Sternoptyx pseudobscura

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Ichthyococcus ovatus

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Phosichthys argenteus

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Pollichthys mauli

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Polymetme thaeocoryla

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Vinciguerria nimbaria

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Vinciguerria poweriae

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Yarrella blackfordi

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Astronesthes gemmifer

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Borostomias elucens

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Heterophotus ophistoma

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Neonesthes capensis

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Rhadinesthes decimus

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Stomias affinis

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Stomias atriventer

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Chauliodus danae

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Chauliodus sloani

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Bathophilus pawneei

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Bathophilus vaillanti

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Chirostomias pliopterus

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Echiostoma barbatum

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Eustomias filifer

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Eustomias furcifer

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Eustomias jimcraddocki

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Eustomias polyaster

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Tactostoma macropus

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Thysanactis dentex

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Trigonolampa miriceps

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Idiacanthus fasciola

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Aristostomias polydactylus

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Aristostomias scintillans

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Aristostomias tittmanni

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Malacosteus niger

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