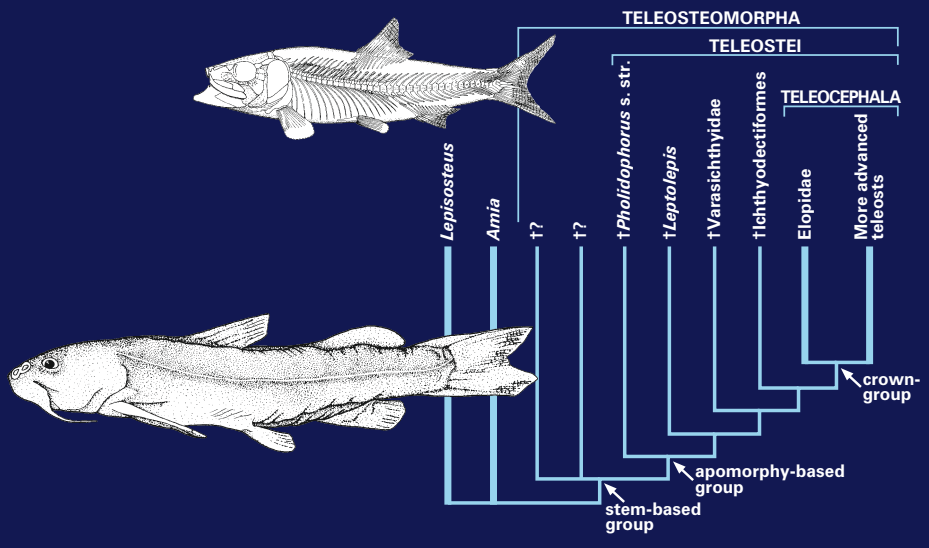
Origin and Phylogenetic Interrelationships of Teleosts

Honoring Gloria Arratia

Joseph S. Nelson, Hans-Peter Schultze &
Mark V. H. Wilson (editors)



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Phylogeny of teleosts based on mitochondrial genome sequences

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Abstract

Mitochondrial DNA sequences have long been used for molecular phylogenetic analyses; however, their ability to resolve deep diverging lineages has been mixed. Recently, mitochondrial genome sequences have been applied to many questions in fish phylogeny and systematics. Using data sets with large numbers of characters may be useful for resolving higher taxa such as families and orders. Relationships among many actinopterygian orders or other higher groups remain elusive based on morphological and limited molecular data. I used a set of all 13 mitochondrial protein coding genes from 230 mitochondrial genomes in a large-scale phylogenetic analysis of teleost fishes. The analysis included all available taxa from many basal teleost families representing all basal orders. Maximum likelihood and Bayesian analyses revealed a general structure of teleost relationships with many current hypotheses supported. However, some clades that are important for understanding teleost diversification were not recovered with strong support. Analyses revealed that searches for optimal phylogenetic trees were sensitive to nucleotide composition, taxon sampling, and outgroup selection. The resulting best phylogenetic hypothesis is discussed in the context of other recent molecular phylogenetic studies of fishes and with respect to conventionally understood teleost interrelationships.

Introduction

Since DNA sequences first became available in numbers sufficient for comparative analysis, mitochondrial DNA sequences have figured prominently in molecular phylogenetic studies of vertebrates and other animal taxa (Moritz et al. 1987, Avise et al. 1987). The effectively haploid, maternal inheritance of mitochondrial DNA (mtDNA) results in extremely low variation within individuals and recombination appears to be insignificant, if it occurs at all (Birky 2001, Ballard & Rand 2005). Mitochondrial lineages are thus strictly bifurcating even within species, providing for straightforward phylogenetic analyses. Mitochondrial genes also tend to evolve rapidly relative to nuclear genes. While it is paradoxical that genes involved in a fundamental process of aerobic metabolism (oxidative phosphorylation) should be poorly conserved, this attribute makes mtDNA particularly useful for resolving relationships among closely related taxa. However, the rapid accumulation of substitutions in mtDNA may lead to undesirable levels of homoplasy when divergent lineages are analyzed (Zardoya & Meyer 1996). Consequently, investigations using portions of mitochondrial genomes to resolve relationships among higher order groups (e.g., taxonomic orders and classes) often yielded unconvincing results. Many such studies employed differential character-state weighting or complete exclusion of specific character types, often with limited success. Thus, while the lack of mitochondrial recombination and heteroplasmy simplify phylogenetic patterns, greater substitution rates can obscure relationships at higher taxonomic levels.

It is apparent that given enough time all but the most slowly evolving genes will accumulate so many nucleotide substitutions, including multiple substitutions at the same site, that little or no phylogenetic signal will remain in DNA sequences. The stochastic nature of substitutions, however, means that the boundary between historical signal and noise is fuzzy and will vary by gene and for particular taxa. Given equal nucleotide frequencies, the point at which noise effectively overwhelms historical signal seems to occur at around 50-60 % overall divergence. Adjacent to this effective noise boundary is a window of

roughly 35-50 % divergence (the so-called twilight zone) within which limited historical signal is retained and with appropriate methodological approaches might be extracted from the noise. Deep divergences within taxonomic orders or classes often fall within this twilight zone for mtDNA. It is generally accepted that increasing the number of characters and/or taxa should provide an increase in phylogenetic power. This view is based on the logic that historical signal is concordant while homoplasy is randomly distributed among taxa. Hence, increasing the amount of data per taxon should increase the number of characters that are congruent with the historically correct tree, but there should be a much lower increase in support for any particular incorrect tree(s). Adding taxa can decrease the number of character-state changes to be inferred between nodes thereby increasing the accuracy of ancestral state reconstructions and reducing the misleading effects of homoplasy, particularly on long phyletic branches.

Genomics as a discipline essentially began in the 1980s with the sequencing of a few complete mitochondrial genomes. Early sequences included human, mouse, cow, chicken, clawed frog, trout, and carp. Relationships among these few taxa inferred with large portions of the genome (such as all protein genes) generally reflected established evolutionary patterns (e.g., Cummings et al. 1995). Additional studies confirmed the established view that some classes of characters or character state changes (3rd codon positions, transition substitutions) exhibit substantial homoplasy while also contributing a substantial fraction of the phylogenetically informative variation (Kumar 1996, Kocher & Carleton 1997). It was also apparent that using one or a few "exemplar" taxa to represent major groups may lead to long-branch attraction problems where a large number of substitutions per branch can lead to random convergence of states among unrelated taxa (Curole & Kocher 1999). In addition, a lack of appropriate outgroups can hinder estimation of ancestral states and polarization of unordered character states. In some cases, the only available outgroups were distant or were themselves on such long phyletic branches as to make them ineffective (e.g., Arnason et al. 2002). Thus the availability of larger character sets has been beneficial but it only partially solved problems presented by shorter sequences. It appeared that the historical information content of mitochondrial genomic sequences could be more fully realized with the use of increasingly complex but realistic molecular evolutionary models and thorough taxonomic sampling with appropriate outgroups (e.g., Miya & Nishida 2000, Miya et al. 2003). As a result, the mitogenomics era was born.

There are now more sequenced mitochondrial genomes available for actinopterygian fishes than any other class of organisms, with 387 ray-fin sequences listed in the NCBI organelle database as of Jan. 1, 2008. This is due in large part to the work of Masaki Miya, Mutsumi Nishida, and their colleagues. This group has published phylogenetic analyses for many ray-finned fish groups, providing important new perspectives and in some cases reassessment of current hypotheses of relationships. The large number of mitogenomes available now provides the opportunity for a global analysis of actinopterygian phylogeny. Recent improvements in maximum likelihood search algorithms, such as those implemented by Garli (Zwickl 2006) and RAxML (Stamatakis 2006), make the use of complex evolutionary models with large sets of taxa feasible in reasonable time frames. Here I present an analysis of all mitochondrial protein-coding genes from 230 ray-finned fish taxa. The taxonomic focus is on basal actinopterygian and basal teleost groups. Most of the sequences are publicly available and have been used for analyses within specific groups. The primary objective was to assess the utility of mt genomes to resolve basal teleost relationships in large-scale analyses. I employed several different character subsets and data partition schemes to explore some of the factors affecting nucleotide character evolution in mt genomes and to assess their influence on phylogenetic tree construction. The results presented are discussed in the context of a survey of recent molecular-based hypotheses for teleost groups.

Materials and Methods

The original data matrix was assembled from all actinopterygian mitogenome sequences available in May 2007 on the NCBI organelle database as well as a few new sequences that had not yet been posted. The protein-coding genes from these 330 sequences were extracted and assembled separately. Sequences for each gene were translated into amino acid sequences aligned with ClustalW (Thompson et al. 1994) as implemented in MEGA4 (Tamura et al. 2007) with gap opening penalty = 30 and gap extension penalty = 5. Insertions occurring in single sequences were removed as were all nucleotides in stop or partial stop codons. Cases of reading frame overlap between the ATP8-ATP6 and ND4L-ND4 genes were trimmed from the

3' end of the upstream gene so that all characters appeared in the matrix only once. Once each gene was aligned, all were concatenated into a single matrix of 11,397 nucleotide characters. For the purposes of this contribution and to increase computational speed the matrix was reduced to 230 taxa by excluding many acanthopterygian species. The final matrix included all available species up to Acanthopterygii (except for several highly similar *Anguilla* and *Oncorhynchus* sequences) and 25 acanthopterygian taxa for phylogenetic perspective. All included species are listed in the Appendix.

Phylogenetic analyses were performed using RAxML 7.0.4 (Stamatakis 2006), Garli 0.96 (Zwickl 2006) and MrBayes 3.1 (Ronquist & Huelsenbeck 2003). Among available models of nucleotide substitution the general time reversible (GTR) model with gamma estimation of among site rate variation (G) and some proportion of invariant sites (I) was shown to be the best model according to ModelTest ver. 3.7 (Posada & Crandall 1998) and MrAIC (Nylander 2004). Analyses were performed on desktop computers and high performance computing clusters at the Oklahoma Supercomputing Center (http://oscer.ou.edu/). Analyses with RAxML started from randomized parsimony trees with standard search parameters under the GTRMIX model which performs tree searches under 25 discrete rate classes and estimates final likelihoods under the full gamma model. A thorough search for the maximum likelihood tree and bootstrapping (250 pseudoreplicates) were performed. Garli used a stepwise procedure to generate starting trees and ten independent searches were performed. The search termination threshold was set to 20,000, meaning that searches were terminated if no likelihood improvement of > 0.01 was achieved for 20,000 generations. Bootstrapping with Garli employed a termination threshold of 2,000 for each of 250 pseudoreplicates. MrBayes was run with default parameters (including flat priors) for 2.3 million generations under the GTR+I+G model with four gamma rate categories. This analysis took long to stabilize with the standard deviation of split frequencies never dropping below 0.03 and likelihood values increasing slowly but consistently until after 1million generations. The final 1 million generations (burn in = 1.3 million) were used for analyses.

All three phylogenetic programs were used on unpartitioned data where a single set of model parameters is estimated based on all included characters and on several partitioned data sets where model parameters are estimated independently for each partition. Unpartitioned data sets included 1) the entire set of characters, 2) conversion of 3rd codon position nucleotides to purines or pyrimidines (R/Y coding), 3) exclusion of all 3rd codon position nucleotides, and 4) exclusion of both 3rd codon positions and the entire ND6 gene. Partitioned analyses were performed with RAxML and MrBayes and included: 1) two partitions corresponding to genes that evolve "fast" and "slow", 2) three partitions corresponding to the three codon positions, 3) six partitions for the three codon positions in the "fast" and "slow" genes, and 4) 21 partitions for the three codons in seven gene-rate classes. Gene-specific substitution rates were determined by constructing neighbor joining trees from Tamura-Nei distances for each gene. Then the distribution of gene tree lengths was used to manually identify discrete rate classes.

Frequencies of each nucleotide were determined for each species for entire sequence and for each codon position in order to assess the level of compositional heterogeneity among taxa. While sweeping exclusion of characters is generally not preferred, here it was used for comparative purposes to assess character quality. This was motivated by the general observations that 3rd codon positions evolve much more rapidly than 1st and 2nd positions and are subject to nucleotide compositional heterogeneity among taxa. The ND6 gene is encoded on the DNA strand opposite to all the other protein genes and typically has a substantially different nucleotide composition. Such compositional heterogeneity may contribute to convergent similarity among unrelated taxa.

Results and Discussion

Phylogenetic analyses

All analyses conducted on all characters, including RY coding of 3rd positions, yielded similar trees, and the various partition schemes had no effect on resulting tree topologies. Two notable features of these analyses were poor resolution of basal actinopterygians and curious relationships wherein many clupeiform and gonorynchiform taxa were found as sister to, or embedded within, euteleost taxa. The basal actinopterygian taxa appeared in several arrangements but never with strong bootstrap or posterior probability values. The most frequent result was as shown in Figure 1A, where the sister group to teleosts was Acipenseriformes + Lepisosteiformes. Because this phylogenetic hypothesis has not been

Table 1.
Nucleotide frequencies for various codon positions of the 10 % of taxa with the highest frequency of nucleotide G at 3rd codon positions and the 10 % of taxa with the lowest frequencies of nucleotide G at 3rd positions. The ND6 gene was excluded from calculations. Taxa in boldface are clupeiforms, gonorynchiforms, osmeroids, galaxioids, or stomiiforms that are grouped together under some circumstances (see text for discussion).

Species	G all pos	C all pos	T all pos	A all pos	G pos1&2	G pos3
Albula glossodonta	0.24	0.22	0.35	0.20	0.21	0.29
Galaxias maculatus	0.21	0.28	0.31	0.20	0.21	0.20
Chirocentrus dorab	0.20	0.33	0.26	0.21	0.20	0.19
Retropinna retropinna	0.20	0.32	0.29	0.19	0.21	0.19
Sardinops melanostictus	0.20	0.30	0.28	0.23	0.20	0.18
Gonorynchus greyi	0.20	0.33	0.26	0.21	0.21	0.18
Diplophos taenia	0.19	0.33	0.27	0.20	0.20	0.18
Opsariichthys bidens	0.19	0.28	0.29	0.24	0.20	0.16
Salangichthys microdon	0.19	0.33	0.27	0.21	0.20	0.16
Plecoglossus altivelis	0.19	0.33	0.28	0.20	0.20	0.16
Synodus variegatus	0.18	0.29	0.29	0.24	0.19	0.16
Jenkinsia lamprotaenia	0.19	0.32	0.27	0.21	0.21	0.15
Opsariichthys uncirostris	0.18	0.29	0.29	0.25	0.20	0.15
Notropis stramineus	0.18	0.28	0.29	0.25	0.20	0.15
Cyprinella spiloptera	0.18	0.28	0.29	0.25	0.20	0.15
Hemibarbus longirostris	0.18	0.28	0.28	0.26	0.20	0.14
Bathygadus antrodes	0.18	0.20	0.38	0.24	0.20	0.14
Campostoma anomalum	0.18	0.29	0.29	0.25	0.20	0.14
Engraulis japonicus	0.18	0.28	0.29	0.25	0.20	0.13
Etheostoma radiosum	0.17	0.29	0.30	0.23	0.20	0.13
Alburnus alburnus	0.17	0.29	0.28	0.26	0.20	0.13
Cromeria nilotica	0.17	0.28	0.28	0.27	0.19	0.13
Pseudaspius leptocephalus	0.17	0.29	0.27	0.26	0.20	0.13
Schistura balteata	0.14	0.29	0.27	0.30	0.19	0.05
Puntius ticto	0.14	0.26	0.28	0.32	0.19	0.05
Puntius tetrazona	0.14	0.26	0.29	0.32	0.19	0.05
Trachyrincus murrayi	0.14	0.26	0.32	0.27	0.19	0.05
Polymixia lowei	0.14	0.29	0.28	0.29	0.19	0.05
Anguilla megastoma	0.14	0.27	0.26	0.33	0.19	0.05
Polypterus senegalus	0.13	0.27	0.31	0.30	0.18	0.05
Tinca tinca	0.14	0.27	0.29	0.31	0.19	0.04
Phractolaemus ansorgii	0.14	0.30	0.26	0.30	0.18	0.04
Anguilla marmorata	0.14	0.27	0.26	0.33	0.19	0.04
Anguilla australis	0.14	0.27	0.26	0.32	0.19	0.04
Leptobotia mantschurica	0.14	0.29	0.27	0.30	0.19	0.04
Osteoglossum bicirrhosum	0.13	0.30	0.27	0.30	0.18	0.04
Cololabis saira	0.13	0.27	0.31	0.28	0.18	0.04
Corydoras rabauti	0.14	0.29	0.27	0.31	0.18	0.04
Squalogadus modificatus	0.14	0.27	0.31	0.27	0.19	0.04
Botia macracantha	0.14	0.27	0.28	0.31	0.19	0.04
Apteronotus albifrons	0.13	0.30	0.27	0.29	0.18	0.04
Polypterus ornatipinnis	0.13	0.27	0.29	0.31	0.17	0.04
Denticeps clupeoides	0.13	0.26	0.30	0.31	0.18	0.03
Arius seemani	0.13	0.29	0.28	0.29	0.18	0.03
Labeo senegalensis	0.14	0.29	0.26	0.31	0.19	0.03

supported by either morphological or molecular data, alternative analyses were pursued. Exclusion of 3rd codon positions and/or the ND6 gene failed to recover any consistent topological pattern or provide improved support for any phylogenetic arrangement of these basal taxa. The unusually long branch separating the Polypteriformes from the remaining actinopterygians suggested that Polypteriformes were too distant to serve as a useful outgroup. When the three polypteriform species were excluded and a single acipenseriform *(Acipenser transmontanus)* was designated as the outgroup, phylogenetic relationships varied with the data set used. This outgroup choice was based on the fact that virtually all hypotheses for basal actinopterygian relationships place Acipenseriformes as basal to, or in a basal monophyletic group with, Lepisosteiformes and Amiiformes. Acipenseriformes were always recovered as a monophyletic group with 100 % bootstrap support regardless of data set used. However, relationships among the other basal actinopterygians varied with the analysis performed: 1) a monophyletic Holostei (Amiiformes + Lepisosteiformes) were recovered (bootstrap 70 %) when all characters were included; 2) Lepisosteiformes was sister to teleosts (bootstrap 22 %) when 3rd positions were coded as R/Y; and 3) *Amia* was sister to teleosts (as in Fig. 2) when 3rd codon positions were excluded. Use of the acipenseriform outgroup caused no differences in relationships among teleosts but did markedly increase bootstrap support for many teleost nodes.

The second unexpected result from analyses of all characters involved the polyphyletic arrangement of several members of Clupeiformes and Gonorynchiformes (Fig. 1B). Again, this topology was recovered regardless of data partitions or whether 3rd codon positions were coded as four-state or two-state (R/Y). Nucleotide frequency analyses revealed an extreme range in frequencies of the nucleotide G, particularly at 3rd codon positions (Table 1). Frequencies of G at 3rd positions ranged from about 3 % to almost 30 %. Although it appears that much of the variation in G frequency is compensated by complementary changes in the frequency of nucleotide A, RY coding of 3rd positions was not sufficient to alter the placement of clupeiform and gonorynchiform species. Many of the problematic clupeiform and gonorynchiform species share high G frequencies with several osmeroids, galaxioids, and stomiiforms. Species from these five groups with particularly high G frequencies at 3rd positions appear in bold in Table 1 and are indicated on the tree in Figure 1B. Results from analyses with 3rd codon positions excluded placed these taxa in more traditionally assumed phylogenetic positions. This suggests that nucleotide compositional bias is heterogeneously distributed on the tree and that 3rd codon positions are disproportionately affected based on their higher substitution rate. Similar extreme nucleotide frequencies may lead to convergence of nucleotide states among unrelated taxa and consequently they may be grouped together. The similarity of hypotheses based on morphological data with trees recovered when only 1st and 2nd codon positions included is quite unlikely to be due to chance coincidence, as was also noted by Miya & Nishida (2000). Most other relationships did not differ substantially with the inclusion or exclusion of 3rd codon positions. However, because 3rd codon positions were deemed positively misleading for some taxa, the focus hereafter is on analyses conducted with 3rd positions excluded. Inclusion or exclusion of the ND6 gene altered likelihood bootstrap and Bayesian posterior probability values but the differences were not always in the same direction and the magnitude of difference was typically less than 10 %. As a result ND6 was retained for all analyses discussed below.

Phylogenetic results with 3rd positions excluded and employing *Acipenser* as the outgroup are illustrated in Figure 2. The tree shown was the best found by RAxML with bootstrap values placed on the nodes. Garli found this same topology as the best tree and bootstrap support was similar. The Bayesian consensus tree was identical to that shown except for two nodes indicated in the figure. The overall branching pattern for ray-fin orders is largely consistent with recent views of actinopterygian relationships. However, there are a few departures and cases where support for relationships is weak. It has been well noted that Bayesian posterior probability values are frequently higher than corresponding likelihood bootstrap values, a condition that appears to be due, at least in part, to greater sensitivity to model misspecification by the Bayesian method (Huelsenbeck & Rannala 2004). We might consider support for particular nodes to be considered weak where Bayesian posteriors are lower that about 0.80 or bootstrap proportions are lower than about 60. When both bootstrap and posterior probability values are low, we clearly should have limited confidence in the reality of such nodes. However, in several cases only one support value is low while the other appears to be strong. In these cases, a conservative approach is to acknowledge the uncertainty suggested by the lower value and treat such nodes as questionable even if they represent the best hypothesis currently available.

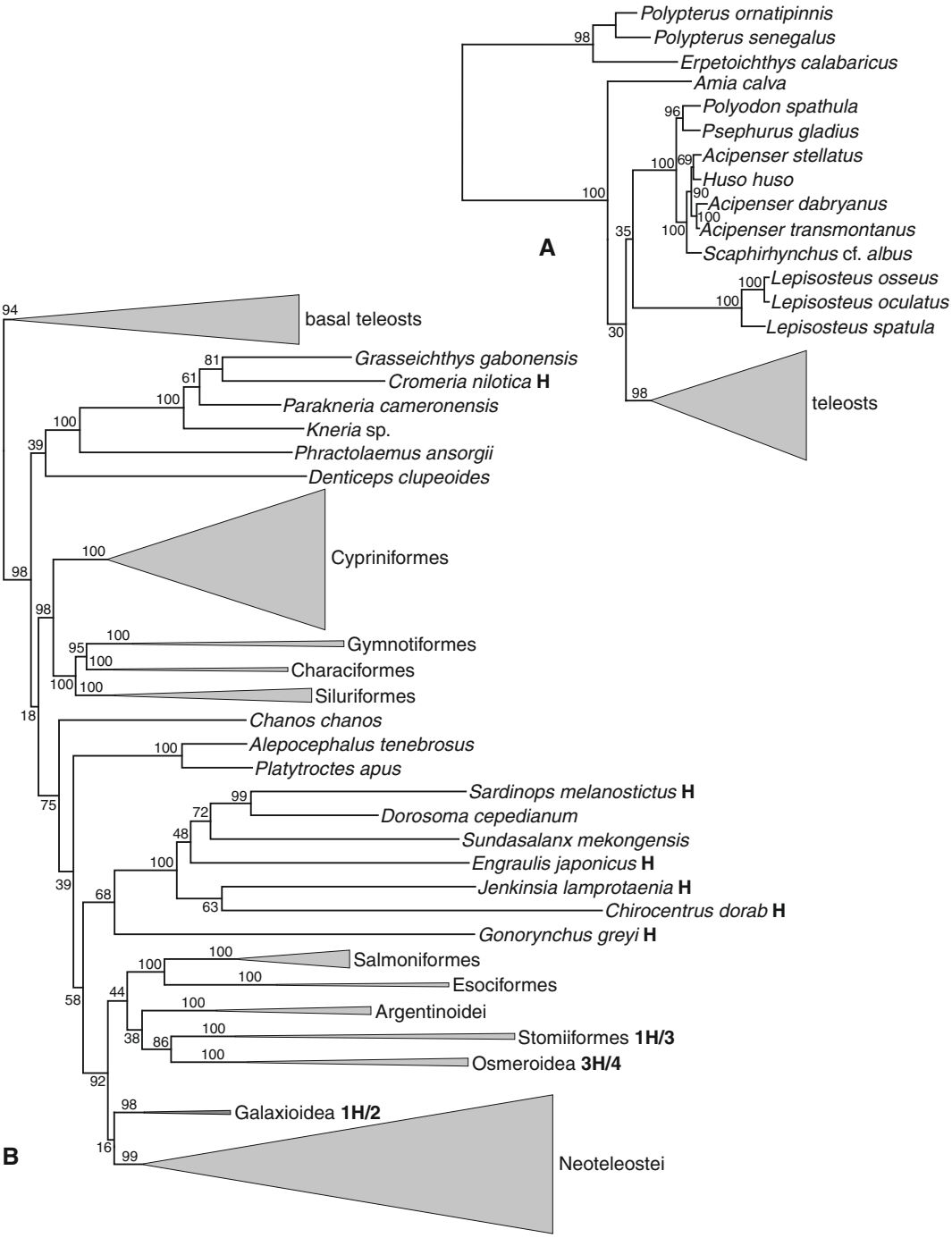

Fig. 1.
Phylogenetic results yielded by analyses of all characters. **A,** relationships among basal actinopterygians with Polypteriformes used as outgroup; **B,** relationships of clupeiform and gonorynchiform taxa with 3rd codon positions included. Species names followed by a **H** indicate a high frequency of G as listed in Table 1; for higher taxon names the number of **H** species is given over the total number in the clade.

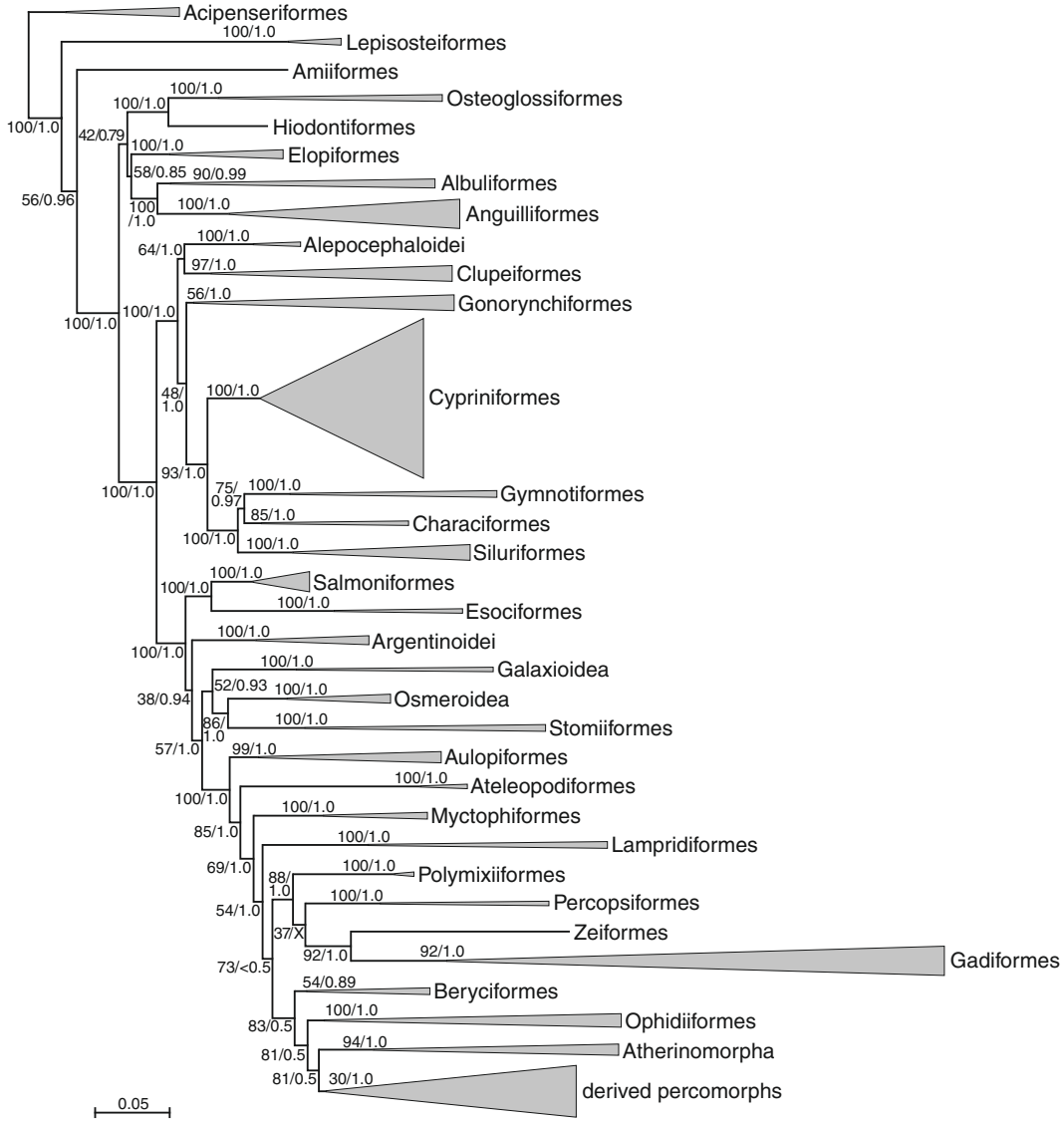

Fig. 2.
Phylogenetic results recovered by maximum likelihood and Bayesian analyses on the data set with 3rd codon positions excluded. The phylogeny is shown for taxonomic orders where they are monophyletic, and for suborder or superfamily otherwise (nomenclature follows Nelson 2006). The tree shown is the maximum likelihood tree with support values on nodes (not a consensus tree). Support values are non-parametric bootstrap values from 250 pseudoreplicates with RAxML (listed as percent in left or upper value) and Bayesian posterior probabilities from 1 million post-burnin generations (as decimals in right or lower values). Scale bar indicates probability of nucleotide change per site.

The sister group of teleosts

Relationships among the basal actinopterygians have been a persistent question. This situation is particularly problematic because these lineages are old yet have few extant representatives, mostly of relatively recent origin. That the Polypteriformes are basal to all other ray-finned fishes seems well established

(Stiassny et al. 2004, Venkatesh et al. 2001, Inoue et al. 2003). However, monophyly of the Neopterygii and/or Holostei, or some other arrangement, has not been conclusively demonstrated. Much of the recent thinking about basal relationships has tentatively recognized a halecostome hypothesis sensu Patterson (1973) including a monophyletic Neopterygii [Lepisosteiformes + Amiiformes + Teleostei] with *Amia* as the sister to teleosts. Yet, based on morphological characters of both extant and fossil material, Arratia (2001) could not conclusively support this pattern or one with a monophyletic Holostei [Lepisosteiformes + Amiiformes] as sister to teleosts because her resultant topologies varied with the outgroup used. Moreover, Grande (2005) proposed resurrection of the Holostei, and Hurley et al. (2007) recovered this pattern when fossil data were included in their analysis. Azuma et al. (2008) also presented a tree with the holostean arrangement but bootstrap support was weak and the topology varied with taxa and genes used. Hurley et al. (2007) also analyzed approximately 2,500 bp from four nuclear genes, recovering the halecostome arrangement but with weak support. Results of an analysis of nearly 3,000 amino acid sites from portions of nine nuclear genes supported the Holostei arrangement (Kikugawa et al. 2004). A third hypothesis, the "ancient fish" clade [Acipenseriformes + Lepisosteiformes + Amiiformes], was supported by Venkatesh et al. (2001) in analysis of insertion/deletion data from four nuclear genes, and was also recovered by Inoue et al. (2003) using 1st and 2nd codon positions of 12 mitochondrial protein genes (ND6 excluded) and stem regions of tRNA genes.

The present results add little to resolve the situation. The instability of topology depending on method of analysis and data set along with low support values suggest that the historical signal in the data is weak relative to relationships among these taxa. Moreover, exclusion of Polypteriformes makes root placement uncertain. If Acipenseriformes are in fact the appropriate outgroup, then Figure 2 supports the Neopterygii hypothesis. However, if the true root is between *Amia* and teleosts, then the ancient fish hypothesis would be supported. It is interesting that Inoue et al. (2003) obtained strong support for an ancient fish clade (1.0 Bayesian posterior probability) using a similar data set. Differences between that study and this one include a smaller number of taxa used, the inclusion of tRNA regions, and inclusion of elasmobranch outgroups by Inoue et al. (2003).

Basal teleosts

The Teleostei was found to be monophyletic with strong support, a hypothesis that has not been in serious doubt. The most frequently invoked hypothesis of basal teleost relationships is: (Osteoglossomorpha (Elopomorpha ((Clupeomorpha, Ostariophysi) (Protacanthopterygii, Neoteleostei))). Yet there has been some question as to whether osteoglossomorphs or the elopomorphs are the basal teleost group, or whether the two form a basal teleost clade (see Arratia 1997, 1999). Lê et al. (1993) recovered osteoglossomorphs and elopomorphs as a monophyletic group using nuclear 28S ribosomal RNA sequences as did Hoegg et al. (2004) based on nuclear protein gene sequences. Several studies based on mitochondrial genomes found the osteoglossomorphs to be the basal teleost group (Inoue et al. 2001, 2003, 2004). As with the Inoue et al. (2003) study mentioned above, all of these mitogenomic analyses employed 1st and 2nd codon positions from 12 protein genes along with stem regions from tRNA genes. Results obtained here with a larger sampling of taxa, find the osteoglossomorphs and elopomorphs as monophyletic, although support for this group was not particularly strong. The sister group relationship between Osteoglossiformes and Hiodontiformes was well supported. The Elopomorpha was monophyletic but the node grouping Elopiformes with the Albuliformes + Anguilliformes clade was fairly weak. A clade containing the Albuliformes, Anguilliformes, and Saccopharyngiformes was well supported with Albuliformes basal. However, as was also found by Inoue et al. (2004), Anguilliformes was paraphyletic with respect to Saccopharyngiformes due to strong support for a clade containing Anguillidae as sister to the two saccopharyngiform taxa (not shown, bootstrap 100, posterior probability 1.0).

The position of Clupeomorpha has been a long-standing question, however there now appears to be compelling evidence from both morphological and molecular studies that it is the sister-group to Ostariophysi, with the two forming the monophyletic Ostarioclupeomorpha or Otocephala (e.g., Arratia 1997, de Pinna & Grande 2003, Lê et al. 1993, Lecointre 1995, Lecointre & Nelson 1996, Lavoué et al. 2005). As a result, the Ostariophysi is now considered to be among the basal teleosts with Protacanthopterygii recognized as the basal member of the Euteleostei (Johnson & Patterson 1996). Support for this relationship appears strong with the present data. Within the Clupeiformes, well-supported relationships are consistent with those found by Lavoué et al. (2006) with *Denticeps* at the basal position and *Sundasalanx* embedded within this clade rather than with osmeriforms (Ishiguro et al. 2005).

A curious result is the placement of the two alepocephaloid taxa as sister to the Clupeiformes. While support for the aleopocephaloid + clupeiform clade is not strong, the clade grouping the alepocephaloids within the Ostarioclupeomorpha is well supported. In analyses that included all codon positions, the two alepocephaloids were grouped with the problematic clupeiforms and gonorynchifoms in a more derived position (Fig. 1B) although support was low. It does not appear, however, that the affinity of alepocephaloids with clupeiforms and gonorynchiforms is driven by similar nucleotide composition as the latter group exhibits some of the highest frequencies of nucleotide G in the dataset, while the alepocephaloids exhibit low G frequencies. Affinity of these alepocephaloids to the ostarioclupeiforms, rather than with argentinoids, was also reported by Ishiguro et al. (2003), Lavoué et al. (2005), and Lavoué et al. (2006) using mitogenomic data. A more recent mitogenomic study by Lavoué et al. (2008) included 11 alepocephaloid taxa and again found strong support for placing them in the Otocephala (= Ostarioclupeomorpha) (bootstrap and posterior probability 100 %). That report placed alepocephaloids as sister to Ostariophysi under maximum likelihood (bootstrap <50) or sister to Clupeiformes in Bayesian analysis (posterior probability 0.55). The evidence in support of a Clupeiformes + Alepocephaliformes + Ostariophysi clade appears compelling.

Within the Ostariophysi we find the relationships (Gonorynchiformes (Cypriniformes (Gymnotiformes (Siluriformes, Characiformes)))). Among the gonorynchiforms, *Gonorynchus* is basal with *Chanos* diverging next. Relationships among the remaining taxa are consistent with Lavoué et al. (2005). Saitoh et al. (2006) recently published an extensive analysis of 53 cypriniform mitogenomes and while the present analysis includes more cypriniform taxa, we find no substantive differences from their phylogenetic conclusions. While there has been general agreement that Gonorynchiformes are the basal ostariophysans and Cypriniformes are the basal otophysan order, several hypotheses exist for relationships among the Gymnotiformes, Siluriformes, and Characiformes. Molecular studies have supported a characiform + gymnotiform clade: Ortí & Meyer (1996), based on 1st and 2nd codon positions from the nuclear ependymin gene; Dimmick & Larson (1996), based on nuclear and mitochondrial ribosomal RNA genes; and Peng et al. (2006), based on mitogenomes. Using mitochondrial rRNA genes Ortí & Meyer (1997) found a most parsimonious tree that suggested affinity between gymnotiforms and siluriforms but support was weak and they considered relationships among the three orders unresolved. Lavoué et al. (2005) recovered a characiform + siluriform clade based on mitogenomic sequences. Current results provide modest support for resolving the trifurcation with a charciform + apteronotiform clade. Mitogenomic data are available for only two characiforms and three gymnotiforms (two of which are from the same genus) so greater resolution of this problem is likely with more diverse sampling of these taxa.

Euteleosts

The monophyly of Euteleostei appears strong. Taxa typically included in Protacanthopterygii are clearly the basal euteleosts however the included taxa and relationships within this group have been the subject of much recent activity. The current results do not recover Protacanthopterygii as monophyletic yet support for node making these groups serially paraphyletic is weak. Two notable clades with strong support include the sister-group relationship of Salmoniformes + Esociformes and the Stomiiformes + osmeroids. Based on morphological data, Johnson & Patterson (1996) recognized two protacanthopterygian orders: the Salmoniformes, including Salmonoidei and Osmeroidei and the Argentiniformes, including Argentinoidei and Alepocephaloidea. The Esociformes were excluded and placed as sister to the neoteleosts. Nelson (2006) recognized four orders within Protacanthopterygii: Salmoniformes, Esociformes, Argentiniformes (including Argentinoidei and Alepocephaloidei), and Osmeriformes (including Osmeroidea and Galaxioidea). Recently, López et al. (2004) analyzed portions of the nuclear RAG1 gene and mitochondrial 12S and 16S ribosomal RNA sequences from a diverse sample of protacanthopterygian taxa putatively related to Esociformes. In addition to an unambiguous sister-group relationship of Esociformes + Salmoniformes, they noted that the retropinnids (galaxioids in most treatments) were sister to the osmeroids, and stomiiforms formed a close relationship to this retropinnid + osmeroid clade. These results were obtained from analysis of RAG1 alone and with the nuclear and mitochondrial data combined. The present results based on mitochondrial protein genes from a different sample of taxa are congruent with those of López et al. (2004), including a clade containing *Retropinna* with the osmeroids (bootstrap 100, posterior probability 1.0). These results are also consistent with those of Ishiguro et al. (2003) using mitogenome data, with the exception that these authors found the stomiiforms to be the basal neoteleost lineage. Finally, there is strong support for the monophyly and sequential relationships of the Aulopiformes, Ateleopodiformes, and Myctophiformes leading up to the Acanthomorpha.

Lampridiformes appears to be the basal acanthomorph group; however, this was not true of the Bayesian analysis where the Lampridiformes, Paracanthopterygii, and remaining acanthomorphs formed a three-way polytomy. Current analyses agree with Miya et al. (2005) by including Polymixiiformes, Percopsiformes, Zeiformes, and Gadiformes in Paracanthopterygii. Figure 2 depicts Percopsiformes as sister to Zeiformes + Gadiformes but in the Bayesian analysis and maximum likelihood with Garli, Percopsiformes and Polymixiiformes formed a clade (posterior probability 0.65, bootstrap 47). Support is strong for the sister group relationship of Zeiformes + Gadiformes similar to that previously found by Wiley et al. (2000) and Miya et al. (2003, 2005). Phylogenetic position of the single batrachoidiform, *Porichthys myriaster*, was quite unstable, appearing as sister to the Lampridiformes in Bayesian analysis or within the derived percomorphs in likelihood (with low support in either case) and is not included in Figure 2. The phylogenetic position of this group is discussed in depth by Miya et al. (2005) with the conclusion that the toadfishes are more derived than previously thought and belong within the Percomorpha. The basal Acanthopterygii branch contained a paraphyletic Beryciformes with Stephanoberyciformes contained within it, consistent with Berycomorpha as discussed by Miya et al. (2005). Percomorpha contains a basal ophidiiform branch and a sister-group relationship between atherinomorphs and the remaining percomorphs. The intent here was not to rigorously analyze acanthopterygians as taxon sampling remains sparse relative to the extensive diversity of this group. These taxa were included primarily to provide perspective on character state polarities with respect to basal teleosts. As such, comment on phylogenetic relationships of included acanthopterygians is unwarranted.

Many aspects of the teleost evolutionary tree now seem well established; however, important remaining questions include identification of the sister group to teleosts, the basal teleost lineage, and relationships of derived otophysans. In addition, the basal euteleost lineages, including many taxa traditionally included in Protacanthopteryii and the Stomiiformes, will clearly require additional data for satisfactory resolution. The major differences between the present analysis and the several mitogenomic studies cited herein, are that here analyses were performed on all taxa simultaneously rather than analyzing groups individually, there are more representative taxa for many groups, and tRNA data were not included (I also note that all mitogenomic studies from the Miya/Nishida group from 2005 to present also included ribosomal RNA gene sequences). Where topological results differed, there were generally low bootstrap values or posterior probabilities for the alternative branching patterns presented here. Moreover, there were several cases where topologies were the same as previous studies but support values were lower in the present study. This suggests that there may be some phylogenetic signal in the tRNA (and/or rRNA) sequences that elevates branch support. The large number of taxa also increases opportunity for similarity of nucleotide composition to mislead phylogenetic analysis (Foster 2004, Jermiin et al. 2004). Inclusion of a large number of unrelated taxa with similar nucleotide composition may allow these taxa to be grouped together due simply to the homoplasy induced by their common compositional bias. When such unrelated taxa are not analyzed simultaneously, or if only a few exemplar species are included from such groups, the misleading signal arising from compositional bias appears to be much reduced. Only taxa with multiple species exhibiting extreme cases of bias were subject to spurious phylogenetic inference. It is fortuitous that only 3rd codon positions appeared to be subject to the extreme bias that may influence phylogenetic results. Thus, although vertebrate mitochondrial genomes are subject to a range of nucleotide biases, due at least in part to their asymmetric mode of replication, appropriate character selection may help ameliorate phylogenetic complications.

While it is generally accepted that the inclusion of more taxa contributes to phylogenetic structure by breaking up long branches (Poe 1998, Zwickl & Hillis 2002), more taxa may also increase homoplasy (Kim 1998). It is intuitive that the more sequences in a data matrix, the more likely it is that convergent and reversed changes will be observed at particular nucleotide sites. Thus in some cases increasing taxon sampling may actually lead to reduced support for group monophyly even when a group is actually monophyletic. It appears that this may be applicable to the present analyses as we observe several cases (note above) where support values are lower than in previous studies that either included fewer taxa per group or focused on individual groups rather than analysis of all taxa simultaneously. This effect is not necessarily independent from problems introduced by nucleotide bias and the two may compound one another.

The present results are in agreement with previous mitogenomic studies in the conclusion that, at least for the deepest branches, 3rd codon positions are of dubious phylogenetic value. While many teleost relationships are well resolved and highly supported by molecular data, several of the areas of greatest

uncertainty emerging from morphological analyses remain unclear with molecular (mostly mitochondrial) data as well. This would be expected if these lineages emerged over short evolutionary time-spans resulting in relatively few informative morphological or molecular characters available for resolution of these branches. Increasing the number of taxa with mitochondrial genomes for poorly sampled groups may help clarify these issues but more characters, necessarily from nuclear genes, may well be needed. Despite a number of shortcomings, mitochondrial genome data have provided substantial improvement in our understanding of fish phylogeny and have taken us much closer to a robust phylogenetic hypothesis for all teleost fishes.

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Appendix

Species from which mitochondrial genome sequences were included in this study. Taxonomy follows Nelson (2006).

Polypteriformes	
Polypteridae	*Polypterus ornatipinnis*
	Polypterus senegalus senegalus
	Erpetoichthys calabaricus
Acipenseriformes	
Acipenseridae	*Acipenser dabryanus*
	Acipenser stellatus
	Acipenser transmontanus
	Huso huso
	Scaphirhynchus cf. *albus*
Polyodontidae	*Polyodon spathula*
	Psephurus gladius
Lepisosteiformes	
Lepisosteidae	*Lepisosteus oculatus*
	Lepisosteus osseus
	Lepisosteus spatula
Amiiformes	
Amiidae	*Amia calva*
Hiodontiformes	
Hiodontidae	*Hiodon alosoides*
Osteoglossiformes	
Osteoglossidae	*Osteoglossum bicirrhosum*
	Scleropages formosus
Pantodontidae	*Pantodon buchholzi*
Elopiformes	
Elopidae	*Elops hawaiensis*
	Elops saurus
Megalopidae	*Megalops atlanticus*
	Megalops cyprinoides
Albuliformes	
Albulidae	*Albula glossodonta*
	Pterothrissus gissu
Halosauridae	*Aldrovandia affinis*
Notacanthidae	*Notacanthus chemnitzi*
Anguilliformes	
Synaphobranchidae	*Synaphobranchus kaupii*
Muraenidae	*Gymnothorax kidako*
Congridae	*Conger myriaster*
Ophichthidae	*Ophisurus macrorhynchos*
Anguillidae	*Anguilla anguilla*
	Anguilla australis australis
	Anguilla bicolor bicolor
	Anguilla japonica
	Anguilla marmorata
	Anguilla megastoma
	Anguilla mossambica
Eurypharyngidae	*Eurypharynx pelecanoides*
Saccopharyngidae	*Saccopharynx lavenbergi*
Clupeiformes	
Denticeptidae	*Denticeps clupeoides*
Chirocentridae	*Chirocentrus dorab*
Engraulidae	*Engraulis japonicus*
Clupeidae	*Jenkinsia lamprotaenia*
	Sardinops melanostictus
	Dorosoma cepedianum
Sundasalangidae	*Sundasalanx mekongensis*
Gonorynchiformes	
Gonorynchidae	*Gonorynchus greyi*
Chanidae	*Chanos chanos*
Phractolaemidae	*Phractolaemus ansorgii*
Kneridae	*Kneria* sp.
	Parakneria cameronensis
	Cromeria nilotica
	Grasseichthys gabonensis
Cypriniformes	
Catostomidae	*Myxocyprinus asiaticus*
	Carpiodes carpio
	Cycleptus elongatus
	Moxostoma poecilurum
	Hypentelium nigricans
	Minytrema melanops
	Catostomus commersonii
	Xyrauchen texanus
Gyrinocheilidae	*Gyrinocheilus aymonieri*
Balitoridae	*Vaillantella maassi*
	Crossostoma lacustre
	Homaloptera leonardi
	Lefua echigonia
	Schistura balteata
	Barbatula toni
Cobitidae	*Cobitis sinensis*
	Cobitis striata
	Misgurnus nikolskyi
	Acantopsis choirorhynchos
	Pangio anguillaris
	Botia macracantha
	Leptobotia mantschurica
Cyprinidae	*Acheilognathus typus*
	Ischikauia steenackeri
	Barbus barbus
	Barbus trimaculatus
	Pseudorasbora pumila
	Pungtungia herzi
	Pelecus cultratus
	Gobio gobio
	Biwia zezera
	Gymnocypris przewalskii
	Esomus metallicus
	Alburnus alburnus
	Puntius tetrazona
	Puntius ticto
	Labeo senegalensis
	Labeo batesii

	Barbodes gonionotus
	Zacco sieboldii
	Aphyocypris chinensis
	Gnathopogon elongatus
	Tinca tinca
	Notemigonus crysoleucas
	Rhodeus ocellatus
	Tribolodon nakamurai
	Campostoma anomalum
	Carassius auratus
	Carassius carassius
	Chanodichthys mongolicus
	Chondrostoma lemmingii
	Coreoleuciscus splendidus
	Cyprinella lutrensis
	Cyprinella spiloptera
	Cyprinus carpio
	Danio rerio
	Opsariichthys bidens
	Opsariichthys uncirostris
	Gila robusta
	*Pogonichthys macrolepidot*us
	Hemibarbus barbus
	Hemibarbus labeo
	Hemibarbus longirostris
	Hemibarbus mylodon
	Notropis stramineus
	Phenacobius mirabilis
	Phoxinus perenurus
	Pseudaspius leptocephalus
	Rhodeus uyekii
	*Sarcocheilichthys variegatu*s
	Xenocypris argentea
Gymnotiformes	
Apteronotidae	*Apteronotus albifrons*
	Apteronotus leptorynchus
Sternopygidae	*Eigenmannia* sp.
Characiformes	
Alestiidae	*Phenacogrammus interrupt*us
Characidae	*Chalceus macrolepidotus*
Siluriformes	
Ariidae	*Arius seemani*
Amblycipididae	*Liobagrus obesus*
Bagridae	*Pseudobagrus tokiensis*
Callichthyidae	*Corydoras rabauti*
Cranoglanidae	*Cranoglanis bouderius*
Ictaluridae	*Ictalurus punctatus*
Pangasiidae	*Pangasianodon gigas*
Esociformes	
Esocidae	*Esox lucius*
Umbridae	*Dallia pectoralis*
Salmoniformes	
Salmonidae	*Coregonus lavaretus*
	Salvelinus alpinus
	Salvelinus fontinalis
	Salmo salar
	Oncorhynchus mykiss
	Oncorhynchus clarkii
	Oncorhynchus tshawytscha
	Oncorhynchus keta
	*Oncorhynchus masou maso*u
Argentiniformes	
Alepocephalidae	*Alepocephalus tenebrosus*
Platytroctidae	*Platytroctes apus*
Argentinidae	*Glossanodon semifasciatus*
Opisthoproctidae	*Opisthoproctus soleatus*
Microstomatidae	*Bathylagus ochotensis*
	Nansenia ardesiaca
Osmeriformes	
Galaxiidae	*Galaxias maculatus*
	Galaxiella nigrostriata
Retropinnidae	*Retropinna retropinna*
Osmeridae	*Plecoglossus altivelis*
	Salangichthys microdon
	Salanx ariakensis
Stomiiformes	
Chauliodontidae	*Chauliodus sloani*
Gonostomatidae	*Diplophos taenia*
	Gonostoma gracile
Aulopiformes	
Aulopidae	*Aulopus japonicus*
Chlorophthalmidae	*Chlorophthalmus agassizi*
Harpadontidae	*Harpadon microchir*
	Saurida undosquamis
Synodontidae	*Synodus variegatus*
Myctophiformes	
Myctophidae	*Diaphus splendidus*
	Myctophum affine
Neoscopelidae	*Neoscopelus microchir*
Ateleopodiformes	
Ateleopodidae	*Ateleopus japonicus*
	Ijimaia dofleini
Lampridiformes	
Lampididae	*Lampris guttatus*
Trachipteridae	*Trachipterus trachypterus*
	Zu cristatus
Polymixiiformes	
Polymixiidae	*Polymixia japonica*
	Polymixia lowei
Batrachoidiformes	
Batrachoididae	*Porichthys myriaster*
Gadiformes	
Bregmacerotidae	*Bregmaceros nectabanus*
Gadidae	*Gadus morhua*
	*Melanogrammus aeglefinu*s
	Merlangius merlangus
	Theragra chalcogramma
	Theragra finnmarchica
Lotidae	*Lota lota*

Macrouridae	*Bathygadus antrodes*
	Caelorinchus kishinouyei
	Ventrifossa garmani
	Squalogadus modificatus
	Trachyrincus murrayi
Melanonidae	*Melanonus zugmayeri*
Moridae	*Physiculus japonicus*
Lophiiformes	
Lophiidae	*Lophius americanus*
	Lophius litulon
Caulophrynidae	*Caulophryne pelagica*
Melanocetidae	*Melanocetus murrayi*
Chaunacidae	*Chaunax abei*
	Chaunax tosaensis
Ophidiiformes	
Ophiidae	*Bassozetus zenkevitchi*
	Sirembo imberbis
Bythitidae	*Cataetyx rubrirostris*
	Diplacanthopoma brachysoma
Carapidae	*Carapus bermudensis*
Percopsiformes	
Percopsidae	*Percopsis transmontana*
Aphredoderidae	*Aphredoderus sayanus*
Beryciformes	
Berycidae	*Beryx splendens*
Holocentridae	*Ostichthys japonicus*
Stephanoberyciformes	
Melamphaidae	*Scopelogadus mizolepis*
Zeiformes	
Zeidae	*Zeus faber*
Atheriniformes	
Melanotaeniidae	*Melanotaenia lacustris*
Beloniformes	
Adrianichthyidae	*Oryzias latipes*
Exocoetidae	*Exocoetus volitans*
Cyprinodontiformes	
Poeciliidae	*Gambusia affinis*
Cyprinodontidae	*Cyprinodon rubrofluviatilis*
Scorpaeniformes	
Cottidae	*Cottus reinii*
Sebastidae	*Sebastes schlegeli*
Perciformes	
Carangidae	*Caranx melampygus*
	Trachurus trachurus
Centrarchidae	*Micropterus salmoides*
Moronidae	*Morone saxatilis*
Percidae	*Etheostoma radiosum*
Scombridae	*Auxis thazard*
	Scomberomorus cavalla
	Thunnus thynnus thynnus
Pleuronectiformes	
Pleuronectidae	*Platichthys bicoloratus*
	Solea senegalensis
Paralichthyidae	*Paralichthys olivaceus*
Tetraodontiformes	
Tetraodontidae	*Takifugu rubripes*
Balistidae	*Sufflamen fraenatus*
Molidae	*Mola mola*

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The origin and the phylogenetic interrelationships of teleosts have been controversial subjects ever since Greenwood, P. H., Rosen, D. E., Weitzman, S. H. and Myers, G. S. in 1966 presented a revision of teleost phylogeny. Different taxa (*Amia*, *Lepisosteus*, *Amia* + *Lepisosteus*, †Pycnodontiformes, †*Dapedium*, †Pachycormiformes, and others) have been proposed as the sister group of teleosts. Tremendous advances have occurred in our knowledge of Neopterygii, basal to teleosts, and in their major component the teleosts over the past 40 years. Many new key fossils have been studied, and many extant teleost clades have been traced back to the Jurassic in detailed studies by Gloria Arratia in 1987, 1996, and 2000. In addition to new fossils, a large number of new morphological and molecular characters have been incorporated in recent phylogenetic analyses, adding to our arsenal of approaches. This book gives a modern view of these approaches. It includes a compilation of synapomorphies of numerous teleostean taxa with a new proposal of their classification, a proposal that pycnodonts are the fossil sister group of teleosts, a phylogeny based on mitochondrial genome sequences, separate analyses of basal teleostean taxa (Osteoglossomorpha, Clupeiformes, Gonorynchiformes, Cypriniformes, Characiformes, Siluriformes, Salmoniformes, Esociformes) and the euteleostean Aulopiformes, karyological studies of Cyprinodontidae, and morphological analyses of the posterior part of the neurocranium. A biography of Gloria Arratia is also presented.

The book represents contributions to the symposium "Origin and phylogenetic interrelationships of teleosts" sponsored by the American Society of Ichthyologists and Herpetologists (ASIH) and organized by the three editors of this volume and held at the Society's annual meeting in St. Louis, Missouri, on 14 July 2007. At the same meeting, Gloria Arratia was honored with the Robert H. Gibbs, Jr. Memorial Award, 2007, for her outstanding contributions to systematic ichthyology. The volume presents the current state of phylogenetic knowledge of the origin of teleosts and the interrelationships of teleost groups, both key issues in fish systematics, based on both morphological (of extant and fossil taxa) and molecular evidence. The many contributors to the volume present and evaluate progress in studying both characters and taxa and in establishing databases (morphological and molecular) that will be of use in future.

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