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Ray-finned fishes (Actinopterygii)

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Abstract

Extant Actinopterygii, or ray-finned fishes, comprise five major clades: Polypteriformes (bichirs), Acipenseriformes (sturgeons and paddlefishes), Lepisosteiformes (gars), Amiiiformes (bowfin), and Teleostei, which contains more than 26,890 species. Phylogenetic analyses of morphology and DNA sequence data have typically supported Actinopterygii as an evolutionary group, but have disagreed on the relationships among the major clades. Molecular divergence time estimates indicate that Actinopterygii diversified in the Lower Devonian (416–397 million years ago, Ma), and the major clades had diversified by the end of the Carboniferous (~300 Ma).

Actinopterygii, or ray-finned fishes, are one of the two major lineages of osteichthyan vertebrates, the other being Sarcopterygii (1). There are more than 26,890 species of actinopterygian fishes and the group has diversified into a wide range of marine and freshwater habitats (2). Typically five major clades are recognized in Actinopterygii: Polypteriformes (bichirs), Acipenseriformes (sturgeons and paddlefishes), Lepisosteiformes (gars), Amiiiformes (Bowfin), and Teleostei. In this account, we review the evidence presented for the monophyly of Actinopterygii, the phylogenetic hypotheses of relationships among the major actinopterygian clades, and the inferences of divergence times resulting from analyses of DNA sequence data sampled from whole mitochondrial genomes and nuclear genes.

The only plausible skepticism regarding the monophyly of actinopterygians was directed specifically at the phylogenetic relationships of Polypteriformes. Since the early part of the twentieth century polypteriforms have been considered actinopterygians (3) however, doubts

have been raised regarding the phylogenetic affinities of polypteriforms within Actinopterygii with an alternative hypothesis that they are more closely related to sarcopterygians (4–6). Phylogenetic analyses of morphological characters have supported the hypothesis that Polypteriformes is most closely related to all other extant actinopterygians (1, 7–15). The phylogenetic position of Polypteriformes consistently inferred from morphological data has also been supported in phylogenetic analyses of nuclear encoded 28S rRNA gene sequences (16, 17), DNA sequences from whole mitochondrial genomes (18, 19), and a combined data analysis of seven single-copy nuclear genes (20).

There is little doubt that the five major actinopterygian clades are each monophyletic (Amiiiformes contains only a single extant species, Fig. 1). However, the hypotheses of relationships among these clades have differed dramatically among analyses of both morphological and molecular data sets. These discrepancies involve the relationships of Amiiiformes and Lepisosteiformes, and whether Amiiiformes, Acipenseriformes, and Lepisosteiformes form an “ancient fish” clade.

Perhaps the most problematic aspect of actinopterygian phylogenetics involves the relationship of Lepisosteiformes and Amiiiformes. These two lineages were traditionally grouped together along with several extinct lineages in the Holostei (21, 22). Analyses of morphological characters has resulted in an alternative hypothesis that Amiiiformes is the closest relative of Teleostei and Lepisosteiformes is most closely related to this clade (23–30). However, other morphological studies (4, 31–33), and molecular phylogenetic analyses of both nuclear and mtDNA gene sequences, have resulted in a monophyletic Holostei (16, 19, 20, 29, 34).



Fig. 1 The only extant amiiform species (*Amia calva*), from Texas, USA. Credit: B. H. Bauer.

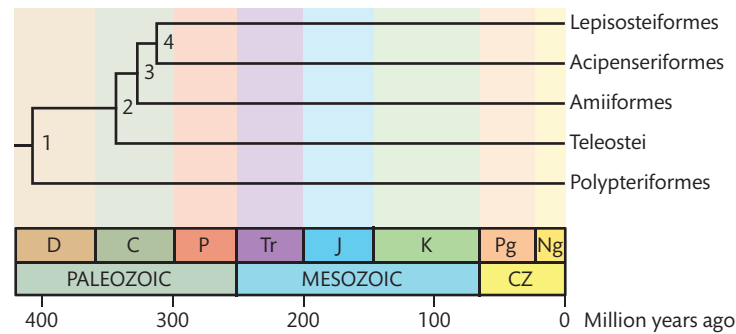


Fig. 2 A timetree of ray-finned fishes (Actinopterygii). Divergence times are shown in Table 1. *Abbreviations:* C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), Ng (Neogene), P (Permian), Pg (Paleogene), and Tr (Triassic).

One of the more recent controversies in actinopterygian phylogenetics involves the phylogenetic analysis of whole mitochondrial genome sequences that finds the Amiiiformes, Lepisosteiformes, and Acipenseriformes form a clade that is most closely related to Teleostei. This has been referred to as the “ancient fish” clade (19). Maximum likelihood Kishino-Hasegawa tree topology tests using the whole mitochondrial genome sequences were unable to reject several more traditional hypotheses of actinopterygian relationships, including Holostei as being most closely related to Teleostei, Amiiiformes most closely related to Teleostei, and a polytomy involving Lepisosteiformes, Amiiiformes, and Teleostei (19). Inoue *et al.* (19) cite support for the “ancient fish” clade in a study examining relationships among jawed vertebrates using insertions and deletions of amino acid sites in nuclear genes (35). This study did not support the monophyly of a clade containing Lepisosteiformes, Amiiiformes, and Acipenseriformes, but only provided apomorphic character states to distinguish two clades, one containing Amiiiformes, Lepisosteiformes, Acipenseriformes, and Teleostei (Actinopteri), and Teleostei as distinct from the Actinopteri (35). The inability of data sets consisting of whole mitochondrial genomes or multiple nuclear genes to reject alternative phylogenetic relationships among the major actinopterygian lineages indicates that much work remains to resolve these relationships (19, 33).

Several studies have presented molecular divergence time estimates for the Actinopterygii. Yet, these investigations differ in the type of data sampled, the calibrations used to convert estimated genetic divergence to absolute age estimates, and the methods used to account for rate heterogeneity among lineages.

The first set of studies discussed in this review address the age of the split between Actinopterygii and

Sarcopterygii, and these studies attempted to estimate divergence times among all major deuterostome or vertebrate lineages. Pairwise genetic distances of amino acid sequences sampled from 44 genes and calibrated with a single amniote fossil resulted in an age estimate for the split of Actinopterygii and Sarcopterygii at 450 ± 35.5 Ma (36). To account for heterogeneity of molecular evolutionary rates among lineages, Kumar and Hedges (36) excluded genes that exhibited rate heterogeneity. A very similar study that differed by using a combination of fossil and molecular calibrations resulted in a nearly identical age estimate for the Actinopterygii–Sarcopterygii split (37). A more recent study provided an age estimate of 476 Ma with a 95% credibility interval (CI) of (494–442) for the Actinopterygii–Sarcopterygii split using amino acid sequences from 325 nuclear genes analyzed with a Bayesian local clock method and calibrated with 13 fossils (38).

The second group of studies specifically addressed the divergence times among the major extant actinopterygian clades, and provides age estimates for the common ancestor of all living actinopterygians. Inoue *et al.* (39) presented a time-calibrated phylogeny estimated using amino acid sequences from 26 mitochondrial genomes sampled among Polypteriformes, Acipenseriformes, Lepisosteiformes, Amiiiformes, and Teleostei. The time-tree is shown in Fig. 2, and the phylogeny depicts a slight alteration of the “ancient fish” clade presented in an earlier study (19). Divergence times were estimated with a partitioned Bayesian strategy using the computer program Multidivtime, and a set of 13 fossil calibrations. Interestingly, the molecular age estimate for the common ancestor of all living Actinopterygii overlaps completely with the confidence interval estimated for the lower bound age of actinopterygians at 425.6 Ma using

Table 1. Divergence time estimates (Ma) and their confidence/credibility intervals (CI) among ray-finned fishes (Actinopterygii).

Timetree		Estimates			
Node	Time	Ref. (19)		Ref. (33)	
		Time	CI	Time	CI
1	407.0	407	376–446	–	–
2	343.0	343	310–381	372	347–391
3	327.0	327	295–366	–	–
4	312.0	312	279–351	–	–

Note: Node times in the timetree are from ref. (19).

a gap analysis of the actinopterygian fossil record (40). Additionally, the Lower Devonian molecular age estimate is consistent with phylogenetic relationships of several extinct Middle and Upper Devonian actinopterygian lineages (e.g., *Mimia*, *Moythomasia*, and *Kentuckia*) that are phylogenetically nested between Polypteriformes and Acipenseriformes. These fossil lineages were not used as calibrations by Inoue *et al.* (39), but their ages ranging between 345 and 392 Ma are very close to the molecular age estimate for the most recent common ancestor of Actinopterygii (Fig. 2; Table 1).

Hurley *et al.* (33) estimated divergence times among actinopterygian lineages using data from whole mitochondrial genomes and four nuclear genes. The phylogeny generated from a combined data analysis of the four nuclear genes was different from the tree resulting from analysis of mitochondrial genomes (Fig. 2). The phylogeny presented in Hurley *et al.* (33) did not contain the “ancient fish” clade, but this hypothesis could not be rejected in statistical comparisons of alternative phylogenies. A partitioned Bayesian strategy using the computer program Multidivtime was used to estimate divergence times. Critical information was presented to refine the fossil information used in calibrating the actinopterygian molecular phylogenies. Unfortunately, this study did not sample any polypteriform species, preventing Hurley *et al.* (33) from estimating the age of the common ancestor of all living Actinopterygii. Analysis of the nuclear genes resulted in a molecular age estimate for the common ancestor of all living actinopterygians exclusive of polypteriforms (Actinopteri) that was similar to the estimate resulting from analysis of whole mitochondrial genomes (Table 1). This was the only node shared between the actinopterygian phylogenies estimated from whole mitochondrial genomes and those inferred from nuclear genes (19, 33).

The molecular divergence times estimated for Actinopterygii support observations from the fossil record that the early diversification of this clade occurred in the Paleozoic (10–12). These age estimates also indicate that the diversification of the major extant actinopterygian clades also occurred in the Paleozoic, with subsequent diversification of major teleost clades occurring in the late Paleozoic and Mesozoic. The molecular age estimate presented for the split of Teleostei from other actinopterygians (Table 1) is more than 100 Ma older than the earliest teleost fossils (e.g., *Pholidophorus*) that date to the Middle Triassic (26, 41, 42). The earliest fossils of extant teleost lineages (e.g., Elopiformes, Osteoglossomorpha, and Ostariophysi) appear at the Upper Jurassic–Lower Cretaceous boundary (151–140 Ma) (43).

Molecular divergence times for Actinopterygii provide a broad temporal perspective to examine macroevolutionary patterns in a clade that contains more than 50% of all extant vertebrate species. We anticipate future investigations of actinopterygian divergence times to utilize the fossil record with an increased sophistication and apply new and developing tools to estimate and correct for rate heterogeneity of molecular evolutionary rates among lineages.

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