the TIMETREE of LIFE

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Teleost fishes (Teleostei)

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Abstract

Living Teleost fishes (~26,840 sp.) are grouped into 40 orders, comprising the Infraclass Teleostei of the Class Actinopterygii. With few exceptions, morphological and molecular phylogenetic analyses have supported four subdivisions within Teleostei: Osteoglossomorpha, Elopomorpha, Otocephala (= Ostarioclupeomorpha), and Euteleostei. Despite the progress that has been made in recent years for the systematics of certain teleost groups, the large-scale pattern of teleost phylogeny remains open. The teleost timetree shows that the major groups diversified from mid-Paleozoic to early Mesozoic, 400–200 million years ago, most probably before the breakup of the supercontinents.

Teleosts are a modern group of fishes including more than 26,000 species (*1*), which are grouped into 40 orders. They are typically grouped together with the garfishes (Lepisosteiformes) and Bowfin (Amiifomes) in the Subclass Neopterygii. Teleosts are the most species-rich and diversified group of all the vertebrates. There are more teleost species than all the other vertebrates combined (*2*). They dominate in the world's rivers, lakes, and oceans. There are four subdivisions within extant teleosts: Osteoglossomorpha (e.g., mooneyes and bonytongues), Elopomorpha (e.g., eels, tarpons, and bonefishes), Otocephala (e.g., ostariophysan and clupeomorph teleosts), and Euteleostei (the remaining teleosts, e.g., Argentiniformes, Osmeriformes, Salmoniformes, and Neoteleostei) (*3*). At least 27 anatomical shared derived traits were found by de Pinna (*4*) to support the monophyly of the Teleostei. Here, we review the relationships and divergence times of the major groups of teleosts (Fig. 1).

Until recently, the classification of teleosts pioneered by Greenwood *et al.* (*5*) and expanded on by Patterson and Rosen (*6*) has followed the arrangement proposed by Nelson (*7*) and today is still reflected in fish textbooks and papers. In it, species were placed in four major groups: Osteoglossomorpha, Elopomorpha, Otocephala, and Euteleostei. This division was based on multiple morphological characters and molecular evidence.

Based on morphological characters, Osteoglossomorpha was considered as the most plesiomorphic living teleosts by several works (*6, 7*). However, the anatomical studies of Arratia (*8–10*) supported that elopomorphs, and not osteoglossomorphs, are the most plesiomorphic extant teleosts. This latter view was supported by the results of the most extensive morphologically based cladistic analysis published so far on osteichthyan higher-level phylogeny, which included 356 osteological and myological characters and 80 terminal taxa, including both extant and fossil species (*3*).

An early molecular phylogeny based on nuclear *28S rDNA* (*11*) supported a close relationship between (Osteoglossomorpha + Elopomorpha) and (Otocephala + Euteleostei). The clade (Otocephala + Euteleostei; Clupeocephala) was subsequently supported by anatomical (*3, 9*) and molecular data (*12, 13*).

Molecular studies using longer sequences—complete mitochondrial genomes and greater taxonomic coverage (*12, 13*)—indicate that the Osteoglossomorpha is the

Fig. 1 An armored catfish from South America, *Leporacanthicus triactis*. Photo credit: M. H. Sabaj.
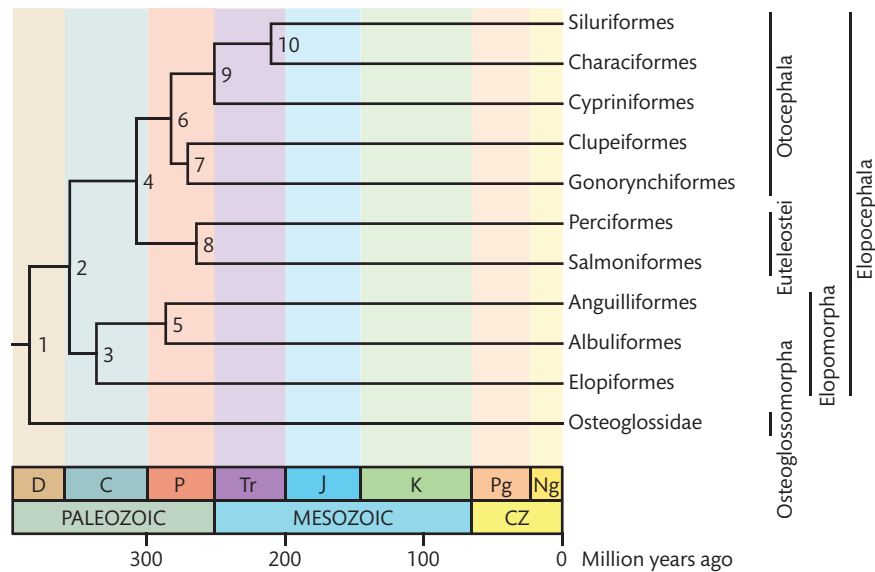
Fig. 2 A timetree of teleost fishes (Teleostei). Divergence times are shown in Table 1. The branch shown as Characiformes represents the non-monophyletic group of characiforms with species nested with other taxa from the Order Gymnotiformes as shown in ref. (*13*). *Abbreviations*: C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), Ng (Neogene), P (Permian), Pg (Paleogene), and Tr (Triassic).

most basal extant teleostean group, as first proposed by Patterson and Rosen (*6*) and subsequently supported by Lauder and Liem (*14*) and Nelson (*7*) (Fig. 2).

Only two studies have estimated the divergence times among the major lineages of Teleostei in a comprehensive manner. Both studies used the complete mitochondrial genome data and Bayesian method with different sampling and concerns (*13, 15*). Both studies used calibrations from the teleost fossil record. The relationships obtained in both studies were similar, although most of the dates estimated by Peng *et al.*'s study were older than those in Inoue *et al.*'s study (Table 1). For example, divergence between the Osteoglossomorpha and the remaining teleostean groups in Peng *et al.*'s study was estimated to be Devonian (384 million years ago, Ma), considerably older than the estimates of 285 Ma (data set 1) or 334 Ma (data set 2) and paleontological estimate of early Permian or mid-Carboniferous in Inoue *et al.*'s study.

The timetree of teleosts based on Peng *et al.* (Fig. 2) shows that most of the major splits in the tree occurred during mid-Paleozoic to early Mesozoic, 400–200 Ma. Most of those divergences took place when all the continents were joined in a single supercontinent, Pangaea. These included the divergence of osteoglossomorphs and elopocephalans, elopomorphs and clupeocephalans (Euteleostei + Otocephala), and euteleosts and otocephalans. However, the earliest fossil lineages within teleosts recorded so far were dated back to late Triassic–early Jurassic (~210–200 Ma). There is a significant difference between the time of divergence of major teleostean groups obtained from molecular clocks and those indicated by the oldest fossil record of these groups. For example, the divergence time between euteleosts and otocephalans (the origin of Otocephala) was estimated to be of ~307–230 Ma (*13, 15*). However, the oldest otocephalan fossil discovered so far is from the late Jurassic, ~150 Ma (*9*). Nevertheless, as explained by Diogo (*16, 17*), there is strong indirect evidence supporting that the origin of certain otocephalan groups such as catfishes (Siluriformes) is in fact very likely older than the direct evidence provided by the oldest fossils of those groups might indicate (e.g., evidence regarding the geographic distribution of fossil and/or extant taxa, the phylogenetic relationships between taxa from different continents, the fact that some of the oldest fossils discovered so far for a certain group occupy in fact a phylogenetically derived position within that group). For example, although the oldest catfish (siluriform) fossil discovered to date is about 75–72 Ma, a broader analysis of

Table 1. Divergence times and their confidence/credibility intervals (CI) among teleost fishes (Teleostei).

Timetree		Estimates					
Node	Time	Ref. (13)		Ref. (15)(a)		Ref. (15)(b)	
		Time	CI	Time	CI	Time	CI
1	384.0	384	447–273	285	320–253	334	372–295
2	355.0	355	420–251	265	300–234	315	352–276
3	336.0	336	401–236	–	–	–	–
4	307.0	307	371–215	230	264–200	278	314–241
5	286.0	286	352–198	228	262–199	264	301–227
6	282.0	282	343–197	201	233–172	239	275–204
7	270.0	270	332–188	–	–	–	–
8	264.0	264	327–183	191	221–164	232	267–197
9	251.0	251	311–175	–	–	–	–
10	210.0	210	265–144	–	–	–	–

Note: Node times in the timetree are based on ref. (13). Estimates from ref. (15) are from two different data sets: (a) = Data set 1 and (b) = Data set 2.

the catfish biogeographical distribution, phylogeny, and fossil record points out that by the late Cretaceous these fishes already had a worldwide distribution. This indicates that the origin of Siluriformes very likely occurred much before 75–72 Ma. The paleobiogeographic data on other teleost groups do also provide interesting indirect evidence supporting that those groups might have an older origin than that indicated by a direct and exclusive analysis of their oldest fossil (18, 19).

In summary, with respect to the divergence times obtained so far from molecular studies, they indicate that the origin of the major teleostean groups is probably much older than a direct, exclusive analysis of the oldest fossil of each of these groups might suggest. It should also be noted that there possibly still were some Pangean connections between Gondwana and Laurasia in the late Jurassic, and perhaps even in the early Cretaceous (16, 17, 20). If this is so, this would help to explain the Pangean distribution of taxa such as the cypriniforms, characiforms, and siluriforms, which are primary freshwater fishes with relatively few, and phylogenetically rather derived, marine members.

Acknowledgment

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