Genome structures resolve the early diversification of teleost fishes

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Abstract: Accurate species phylogenies are a prerequisite for evolutionary research. Teleosts are by far the largest and the most diversified group of extant vertebrates, but relationships among the three oldest lineages of extant teleosts remain unresolved. Based on seven high-quality new genome assemblies in Elopomorpha (tarpons, eels), we revisited the topology of the deepest branches of the teleost phylogeny using independent gene sequence and chromosomal rearrangement phylogenomic approaches. These analyses converged to a single scenario that unambiguously places the Elopomorpha and Osteoglossomorpha (bony-tongues) in a monophyletic group sister to all other teleosts, i.e., the Clupeocephala lineage. This finding resolves over 50 years of controversy on the evolutionary relationships of these lineages and highlights the power of combining different levels of genome-wide information to solve complex phylogenies.

One-Sentence Summary: Whole-genome analyses place Elopomorpha (tarpons, eels) and Osteoglossomorpha (bony-tongues) as sister groups at the deepest branching of crown teleosts.

Main Text

Species phylogenies retrace sister-group relationships resulting from evolutionary histories and pathways from common ancestors to descendant species (*1*). Accurate species phylogenies are important for our understanding and representation of the evolution of life on earth, but they are also a fundamental prerequisite for evolutionary analyses at the developmental, anatomical, genetic, and species levels.

With more than 30,000 species, teleost fishes are by far the largest and the most diversified clade of extant vertebrates (*2*). Understanding their phylogeny has been and is still subject to many disputes at different taxonomic levels (*2*, *3*). Among these debates, a long-standing and unresolved question concerns the topology of the earliest-branching clades of crown teleosts, i.e., the Elopomorpha (named after "*Elops*-like" and including tarpon, bonefish and eels) and the Osteoglossomorpha (named after "bony-tongues" and including goldeye, arapaima, and elephantnose fish) relative to all the other extant teleosts in the Clupeocephala lineage (including for instance zebrafish, a major biomedical species) (*3*, *4*).

Based on anatomical and morphological characters, Elopiformes (tarpons and ladyfishes) were first suggested to be the most "primitive living teleosts" nearly 100 years ago ((*5*) cited in (*4*)). Since then, Elopomorpha and Osteoglossomorpha have been alternatively placed as the earliest branching clade of teleosts. A first scenario, proposed in 1977 (*6*), placed the Osteoglossomorpha as the earliest teleost crown group and outgroup to the Elopocephala consisting of Elopomorpha and Clupeocephala. (Fig. 1A). This scenario was later challenged in 1997 (*7*, *8*) by the placement of Elopomorpha as the earliest branching clade of teleosts, with Osteoglossomorpha and Clupeocephala composing the Osteoglossocephala clade (Fig. 1B). These early controversies were based on morphological evidence and remained largely unsolved, but the most recent authoritative view still considers the Elopomorpha as the earliest branching clade of crown teleosts (*2*).

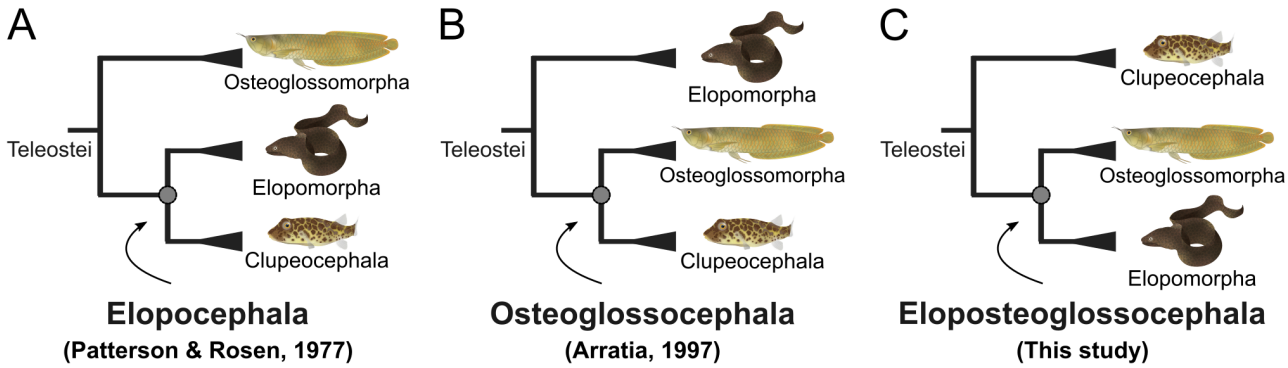


Figure 1: Alternative phylogenetic hypotheses for the earliest-branching teleost clades. The Elopocephala (*6*) **(A)**, Osteoglossocephala (*7*) **(B)** and Eloposteoglossocephala **(C)** hypotheses respectively, propose Clupeocephala and Elopomorpha, Clupeocephala and Osteoglossomorpha or Osteoglossomorpha and Elopomorpha as sister groups (see text for details).

With the emergence of molecular phylogenetic approaches in the nineties, this question was extensively revisited using gene sequence phylogeny reconstructions (reviewed in (*3*, *9*)). Despite extensive efforts, including several large-scale multi-locus approaches (*10–12*), no consensus has, however, been reached in favor of neither the Elopocephala nor the Osteoglossocephala hypothesis. In addition, a third topology placing Elopomorpha and Osteoglossomorpha as sister groups (Fig. 1C) was even suggested in the early nineties (*13*) and since then supported by a few more recent studies (*11*, *14–18*). This clade, which we tentatively named the Eloposteoglossocephala (Fig. 1C), was never formally retained, probably because this topology was not supported by any morphological evidence (*3*). The prevailing hypothesis, confirmed by a recent meta-analysis of gene sequence phylogeny studies (*9*), thus remains the Osteoglossocephala hypothesis that places Elopomorpha as the earliest branching clade of extant teleosts (*12*)). However, the precise phylogenetic relationships of these major teleost lineages are still debated and have even been recently reviewed by Dornburg and Near (*3*) as one of the major unresolved questions of the twenty-first century regarding the evolution of actinopterygian fishes. To promote a reexamination of this problem, they provocatively proposed to retain “the unconventional and intriguing possibility of an osteoglossomorph and elopomorph sister group relationship” (*3*).

To resolve the phylogenetic relationships of these early-branching teleost clades, we first sequenced, assembled, and annotated high-quality reference genome sequences of seven species that represent

major Elopomorpha orders or families (Fig. 2 and table S1) for which chromosome-level whole-genome resources were lacking. We combined genome information from these seven Elopomorpha species with 18 additional publicly available genome assemblies including four Osteoglossomorpha, 10 Clupeocephala and four vertebrate outgroups, including the spotted gar and bowfin non-teleost fishes, to perform phylogenomic analyses.

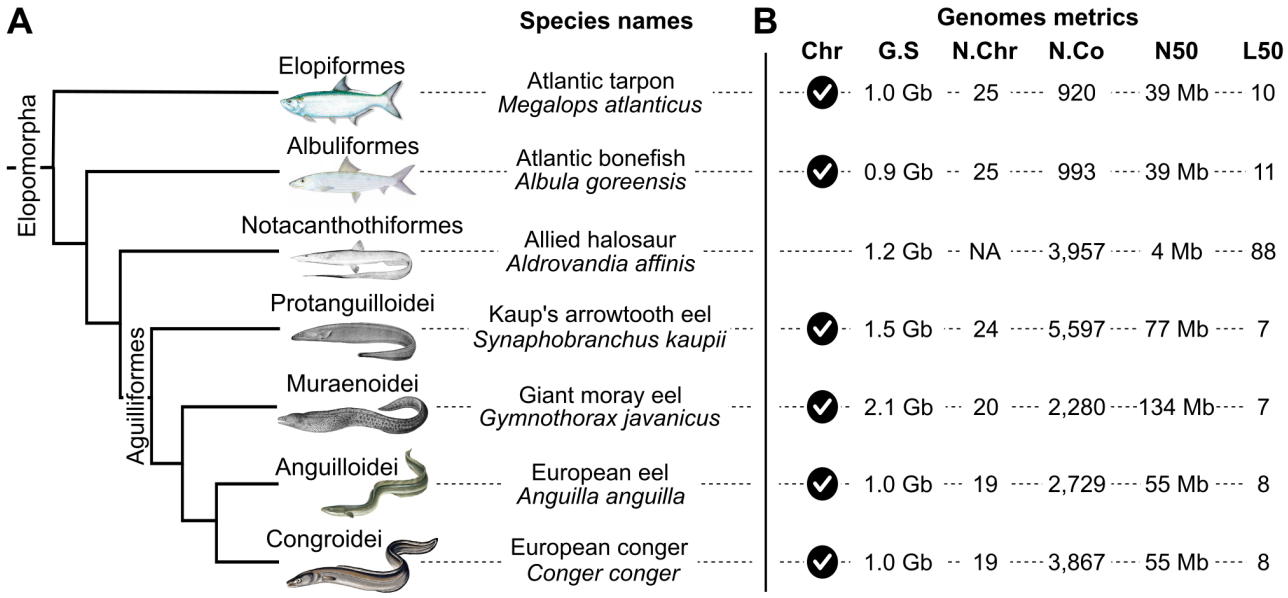
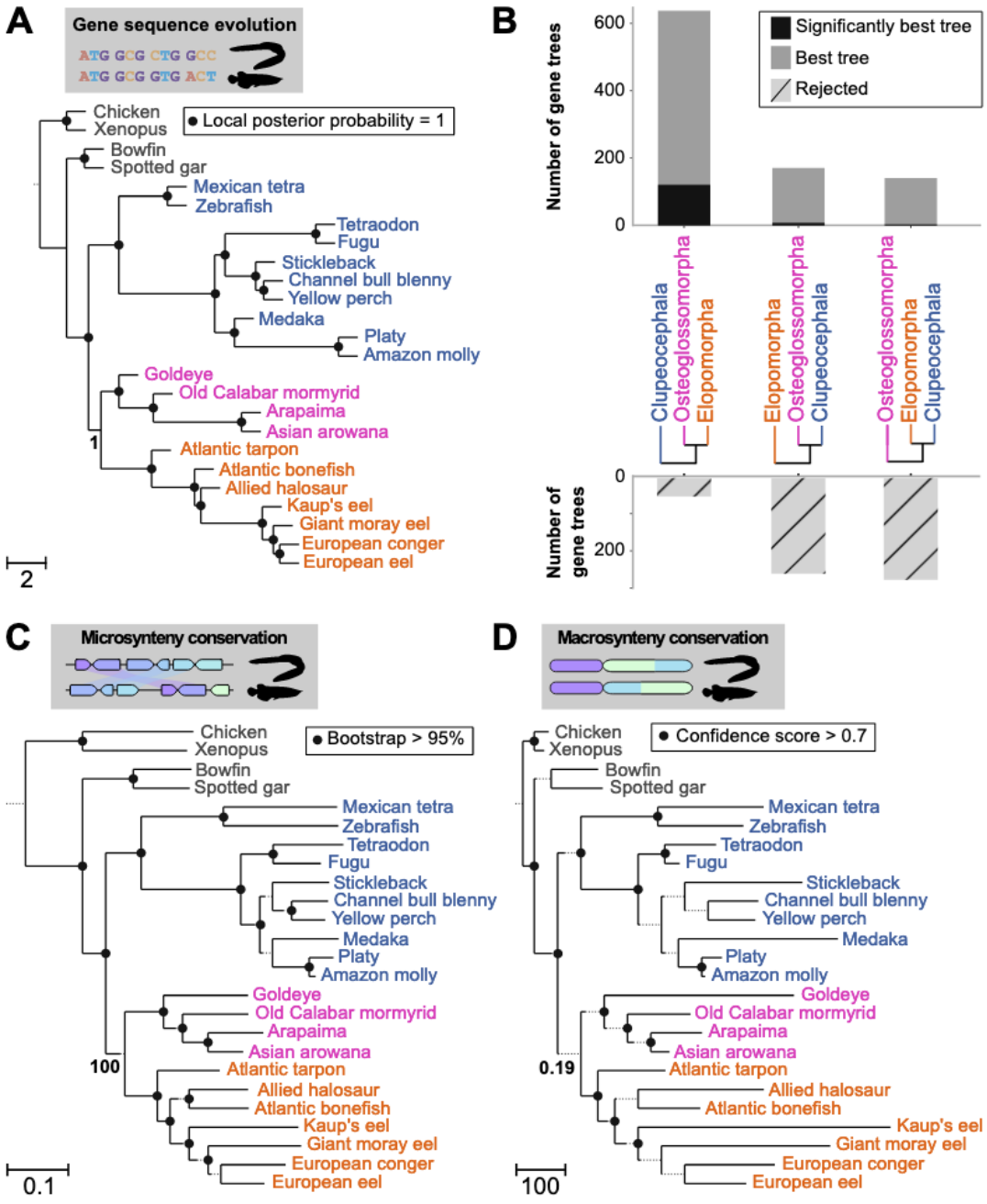


Figure 2: Phylogeny of representative Elopomorpha species. (A) This tree topology is based on ref. (*19*) and includes each species for which we provide novel whole-genome assemblies. **(B)** Six of these seven genomes were assembled at chromosome scale (Chr) with high-quality genome assembly metrics. G.S = genome size, N.Chr = haploid chromosome number, N.Co = number of contigs, N50 = sequence length at which half of the genome assembly is covered by longer sequences, L50 = smallest number of scaffolds needed to sum to half of the predicted genome size.

A major challenge for achieving accurate phylogenetic analysis of teleost genomes is their high number of duplicate (paralogous) gene copies. Many of these paralogs are inherited from a whole genome duplication (WGD) in their last common ancestor (*20*), and are known to mislead phylogenetic reconstructions (*11*). To mitigate the effect of paralog inclusion, we applied a WGD-tailored pipeline leveraging gene sequences and synteny conservation (supplementary materials,

Methods section) to select 955 high-confidence 1-to-1 orthologous genes across all the 25 genomes we analyzed. This list represents by far the largest molecular dataset considered for teleost phylogeny reconstruction, both in terms of included Elopomorpha genomes and of total alignment size (see fig. S1). We then performed phylogenetic reconstructions of these 955 individual gene trees using summary analyses with ASTRAL (Fig. 3A, and fig. S2 for protein trees), as well as Maximum Likelihood analyses of their concatenated sequences both at the nucleotide and amino-acid levels (fig. S3 and S4). These analyses all provided highly significant support for the Eloposteoglossocephala hypothesis that places Osteoglossomorpha and Elopomorpha as sister groups. Additionally, this Eloposteoglossocephala clade was further supported by gene-genealogy interrogation, which directly compares the likelihood of each of the three evolutionary scenarios based on individual gene sequence alignment (Fig. 3B).

However, because previous sequence-based studies have yielded opposing results to resolve the three early diverging teleost branches (*9*, *11*), we also used two novel genome-wide methods to infer species trees based on conservation of genome structures. First, we analyzed the conservation of gene adjacencies between 3,041 orthologous marker genes covering 57-98% of each teleost genome, and inferred a Neighbor-Joining species tree from local microsyntenic conservation (*21*). Second, we analyzed macrosyntenic evolution by measuring the fraction of shared chromosomal breakpoints between species with PhyChro (*22*). These two complementary approaches (Figs. 3C-3D, fig. S5) also provided convergent and robust support for the Eloposteoglossocephala scenario, confirming the results from gene sequence phylogenies.



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142 **Figure 3: Different phylogenomic reconstruction methods converge to support Osteoglossomorpha and**
143 **Elopomorpha as sister groups.** (**A**) Species tree inferred under the multispecies coalescent model (*23*) from 955
144 single-copy gene trees. This method measures internal branch lengths in coalescent units, while lengths at terminal
145 branches are represented as equal and arbitrary. Node support is calculated as a local posterior probability. (**B**)
146 Molecular gene genealogy interrogation: number of gene trees supporting each hypothesis (top, gray bars),
147 significantly supporting each hypothesis (top, black bars), and number of significantly rejected gene trees (bottom,
148 dashed bar). (**C**) Neighbor-Joining species tree estimated from gene adjacencies between 3,041 marker genes.
149 Branch lengths represent the proportion of broken adjacencies and nodes are supported by bootstrap values. (**D**)
150 Best-supported species tree based on shared synteny breakpoints. Branch lengths are an estimate of the number of
151 breakpoints. Node supports correspond to the fraction of informative breakpoints that support the clade (*22*). (**A-D**)
152 Broken lines have been added to very short branches, for visualization purposes.

Finally, by looking at all potential chromosomal macro-rearrangements we identified a single chromosomal fusion exclusively shared between karyotypes of Osteoglossomorpha and Elopomorpha species (Fig. 4, fig. S6). Together with the absence of other rearrangements that would be consistent with alternative groupings, this identical chromosomal macro-rearrangement further supports that the two groups descend from a common ancestor, strengthening the phylogenomics evidence for the Eloposteoglossocephala clade.

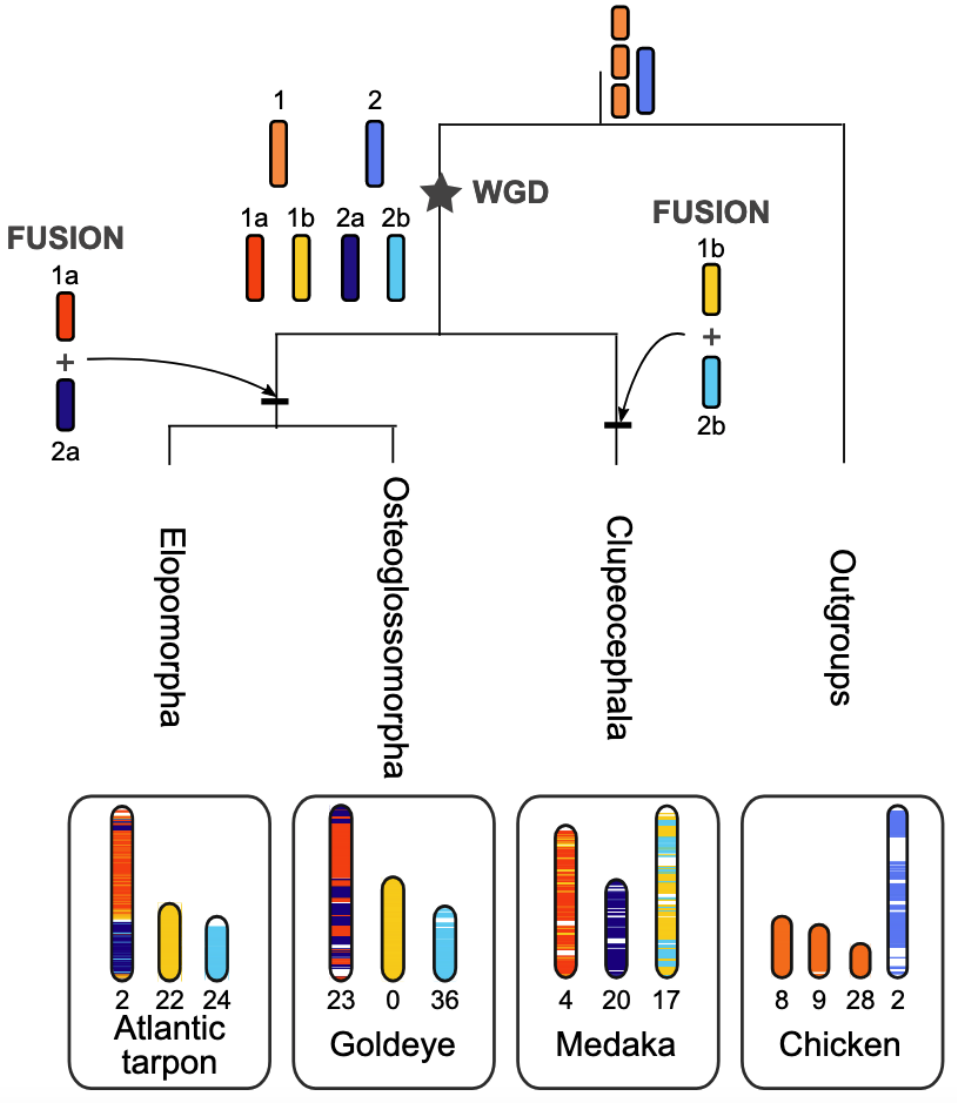

Figure 4: Chromosomal rearrangement shared within the Eloposteoglossocephala clade. Inferred rearrangement scenario for two pairs of duplicated chromosomes (1a-1b and 2a-2b) in teleosts. Osteglossomorpha and Elopomorpha share the 1a-2a chromosomal fusion, while Clupeocephala experienced an independent fusion between 1b and 2b.

Using a combination of new whole-genome resources for Elopomorpha and an array of complementary phylogenomic reconstruction methods, we unambiguously resolved the long-standing question of the topology of the deepest branches in the phylogeny of extant teleost fishes. This achievement highlights the power of genome-wide methods to resolve complex and ancient phylogenies, especially when these methods consider a variety of informative evolutionary characters in complement to sequence information. Chromosome rearrangements, in particular, are fixed at a low rate and thus are less prone to mutational saturation and character reversal, which can occur in sequence-based phylogenies (*24*).

Our results resolve over 50 years of controversy and demonstrate that Elopomorpha and Osteoglossomorpha constitute a clade for which we propose the name Eloposteoglossocephala (supplementary materials, section 1). This conclusion raises questions about the paucity of anatomical evidence in favor of this hypothesis, despite more than 70 years of extensive research (*3*, *4*). We carefully reexamined the available literature on these anatomical characters in light of our results and we were not able to find a morphological character exclusively and unambiguously shared by Elopomorpha and Osteoglossomorpha (supplementary materials, section 2). However, the fusion of the retroarticular with the angular and/or the articular, a derived character previously considered a synapomorphy of the Elopomorpha (*25*, *26*), has been shown to be shared with at least mormyrids among bony-tongues (*26*, *27*). Even if this character is described as either present (*27*) or ambiguous in goldeye *Hiodon alosoides*, and absent in two other Osteoglossomorpha (*26*), we propose this derived state as a morphological synapomorphy of the Eloposteoglossocephala, which was secondarily lost in some Osteoglossomorpha. We anticipate that based on our results, more character mapping and new targeted anatomical and morphological searches will soon provide novel and non-ambiguous synapomorphies shared by the Eloposteoglossocephala.

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Data and materials availability: The Whole Genome Shotgun projects for the seven Elopomorpha species are available in the Sequence Read Archive (SRA), under the following BioProject references PRJNA702045 (*Conger conger*), PRJNA692825 (*Albula goreensis*), PRJNA743502 (*Aldrovandia affinis*), PRJNA690086 (*Megalops atlanticus*), PRJNA693699 (*Anguilla anguilla*), PRJNA743503 (*Synaphobranchus kaupii*), PRJNA702255 (*Gymnothorax javanicus*). All genome assemblies plus their annotations are also available in the omics Dataverse (Open source research data repository) server (https://doi.org/10.15454/GWL0GP). All input data (sets of orthologous marker genes, CDS codons alignments, gene coordinates files) and the generated reconstructed species phylogenies have been deposited in Zenodo (doi: 10.5281/zenodo.6414307), along with all scripts and environments to reproduce the analyses.