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# The Emerging Phylogenetic Perspective on the Evolution of Actinopterygian Fishes

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phylogenomics, Actinopterygii, Percomorpha, *Lepidogalaxias*, vertebrates

## Abstract

The emergence of a new phylogeny of ray-finned fishes at the turn of the twenty-first century marked a paradigm shift in understanding the evolutionary history of half of living vertebrates. We review how the new ray-finned fish phylogeny radically departs from classical expectations based on morphology. We focus on evolutionary relationships that span the backbone of ray-finned fish phylogeny, from the earliest divergences among teleosts and nonteleosts to the resolution of major lineages of Percomorpha. Throughout, we feature advances gained by the new phylogeny toward a broader understanding of ray-finned fish evolutionary history and the implications for topics that span from the genetics of human health to reconsidering the concept of living fossils. Additionally, we discuss conceptual challenges that involve reconciling taxonomic classification with phylogenetic relationships and propose an alternate higher-level classification for Percomorpha. Our review highlights remaining areas of phylogenetic uncertainty and opportunities for comparative investigations empowered by this new phylogenetic perspective on ray-finned fishes.

# 1. INTRODUCTION

## 1.1. The Twenty-First Century Vertebrate Tree of Life and Its Challenges to Twentieth Century Paradigms

Phylogenetic trees are an integral component of comparative analyses that span topics ranging from human cancer biology (Somarelli et al. 2020) to the factors that have shaped patterns of uneven species richness across the planet (Rabosky et al. 2018). Understanding the phylogeny of major groups of organisms has attracted the attention of evolutionary biologists since Charles Darwin drafted his famous "I think" diagram in 1837 (Barrett et al. 1987). However, it took more than 100 years for Darwin's abstract concept of the tree of life to develop into an explicit, data-driven approach to phylogeny reconstruction.

For ichthyology, the early twenty-first century represents a phylogenetic renaissance. Over the past 20 years, hundreds of researchers have contributed resolved molecular phylogenies at varying time scales across the diversity of fishes (e.g., Irisarri et al. 2017, Ronco et al. 2020), ushering in a paradigm shift in the systematics of ray-finned fishes, Actinopterygii. Collectively, these phylogenetic studies have fundamentally altered our understanding of the architecture of the actinopterygian tree of life. This dramatic restructuring of evolutionary hypotheses has provided unprecedented insights into some of the most vexing problems in vertebrate systematics and has called into question many long-held morphological hypotheses of evolutionary relationships (e.g., Gill & Mooi 2002, Lauder & Liem 1983, Nelson 1989, Stiassny et al. 2004). In this review, we explore this newly emerged phylogenetic perspective on ray-finned fishes and examine how it changes our understanding of evolutionary patterns and processes.

Ray-finned fishes contain more than 34,190 species, which comprise nearly 53% of all living vertebrates and include important model organisms such as zebrafish and sticklebacks, spectacular adaptive radiations such as African rift lake cichlids (Ronco et al. 2020) and Antarctic notothenioids (Daane et al. 2019), and species fundamental to food-web dynamics or multibillion-dollar fishing (Ward & Myers 2005) and tourism (Bessa et al. 2017) industries. While the ability to speciate rapidly in virtually any aquatic habitat is a hallmark of ray-finned fish diversification (Daane et al. 2019, Rabosky et al. 2018, Ronco et al. 2020), the resulting difficulty in disentangling homology from homoplasy in the face of such diversification contributed to a long history of conflicting ideas on their phylogenetic relationships. By the mid-twentieth century, the prevailing hypotheses of ray-finned fish relationships were shaped by a history of research that spanned early pre-Darwinian attempts at classification (Müller 1845), the codification of taxonomic families of ray-finned fishes and their classification (e.g., Jordan 1923), an identification of the major subgroups of teleosts (e.g., Greenwood et al. 1966), and early applications of Hennigian phylogenetic systematics (e.g., Nelson 1969). This work, spanning approximately 150 years, resulted in confidence that many of the major groups of ray-finned fishes recognized today, including sturgeons, gars, eels, salmon, pufferfishes, and flatfishes, are each monophyletic (see the sidebar titled Major Lineages of Ray-Finned Fishes). However, the affinities of these lineages to each other often hinged on arguments for or against the interpretation of a few key characters (Patterson 1973, Patterson & Rosen 1977, Rosen 1973). As such, the ability to discriminate among alternate phylogenetic hypotheses was limited, and much of the backbone of the actinopterygian tree of life remained either unresolved or was addressed with conflicting hypotheses and often-contentious interpretations (e.g., Arratia 1998, Patterson 1998).

# 2. THE TWENTY-FIRST CENTURY PHYLOGENY OF RAY-FINNED FISHES

The consensus of phylogenetic hypotheses based on morphology provided the basis for review papers and authoritative reference texts on the relationships, diversity, and classification of

## MAJOR LINEAGES OF RAY-FINNED FISHES

Actinopterygii includes all ray-finned fish lineages. All but 51 of the more than 34,000 species of Actinopterygii are classified in Teleostei (**Figure 1**).

Osteoglossomorpha (e.g., arowanas, elephant fishes, and Mooneye) is an early diverging lineage of teleosts that is found in freshwater habitats mostly in the tropics.

Elopomorpha (e.g., tarpon, bonefish, and eels) is another early diverging lineage of teleosts found mostly in marine habitats.

Otocephala is a clade of teleosts that contains Clupeiformes (herrings), Alepocephaliformes (slickheads), and Ostariophysi (see below).

Ostariophysi contains more than 11,250 species and is the dominant lineage of freshwater fishes on all continents except Australia. Ostariophysans include minnows, catfishes, piranhas, and tetras (**Figure 1**).

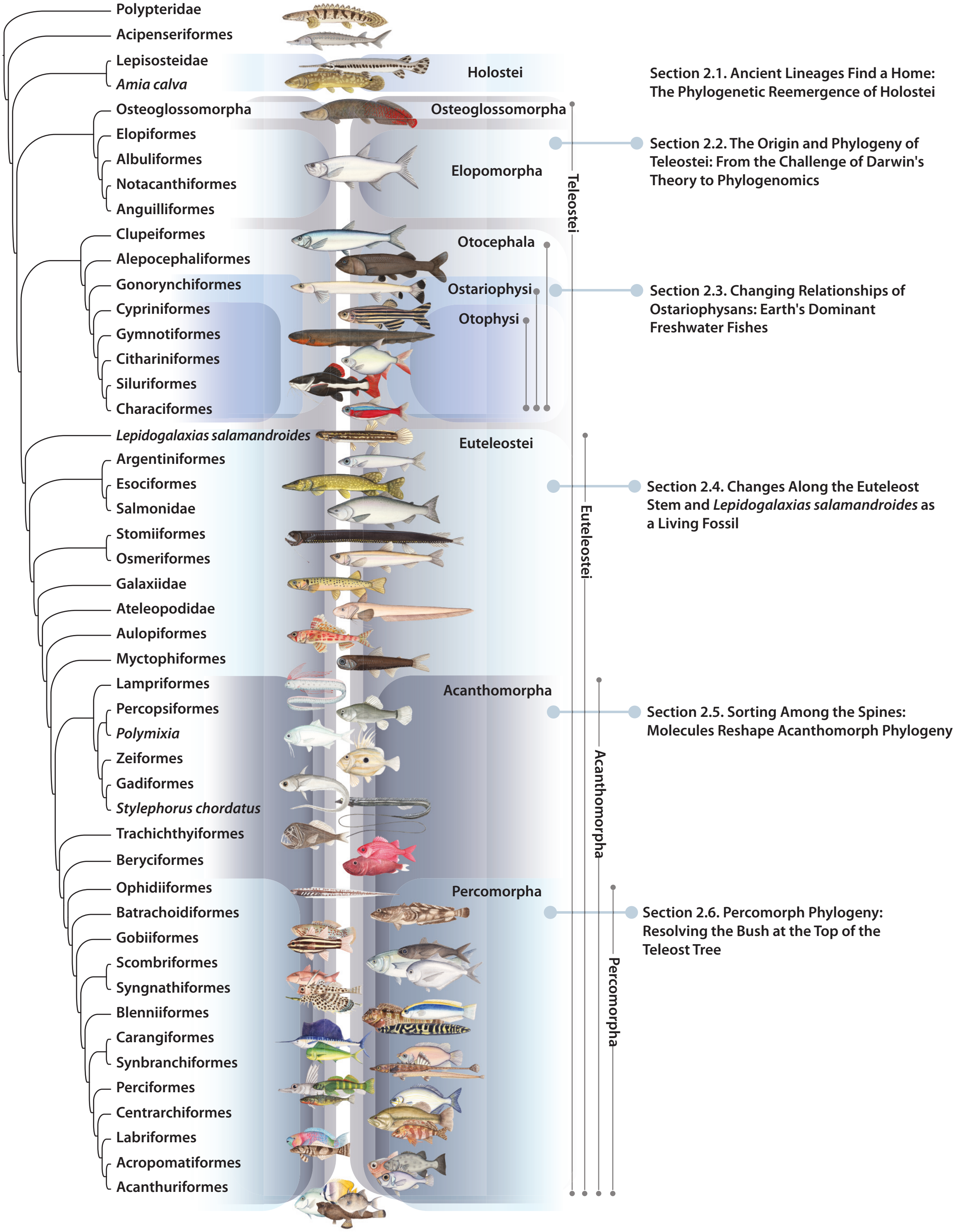
Euteleostei is the clade of all teleosts excluding osteoglossomorphs, elopomorphs, and otocephalans (**Figure 1**).

Acanthomorpha are the spiny-rayed fishes and the dominant lineage of ray-finned fishes in marine habitats. The clade includes more than 25% of all living vertebrate species. While most acanthomorphs are classified in Percomorpha (see below), other familiar acanthomorph lineages include the economically important Gadiformes (cods) and Trachichthyiformes (roughies and their relatives), as well as emergent model systems in Percopsiformes (cavefishes and their relatives) (**Figure 1**).

Percomorpha is a hyperdiverse subclade of Acanthomorpha with more than 18,450 species classified in 288 taxonomic families. Percomorphs dominate all marine habitats occupied by ray-finned fishes and include iconic lineages such as seahorses, tunas, anglerfishes, and pufferfishes, as well as iconic freshwater lineages such as cichlids, sticklebacks, and black basses (**Figure 1**).

ray-finned fishes (e.g., Gill & Mooi 2002; Lauder & Liem 1983; Nelson 1989, 2006; Stiassny et al. 2004). Some phylogenetic inferences remained robust after the inclusion of molecular characters, as exemplified by both morphological and molecular phylogenies supporting some relationships, such as bichirs (Polypteridae) as the sister lineage of all other ray-finned fishes or the monophyly of Teleostei. Nonetheless, the emerging DNA sequence–based phylogenetic hypothesis of the early twenty-first century has modified nearly all of the relationships among the major clades of ray-finned fishes (**Figure 1**). For example, molecular phylogenies consistently identify pikes and mudminnows (Esociformes) as the sister lineage to trouts and salmons (Salmonidae) and resolve deep-sea anglerfishes (Lophiiformes) in a derived clade of percomorphs. Both of these configurations contrast sharply with the twentieth century resolution based on morphology. Many of the changes to the actinopterygian phylogeny involve redefining major groups that include some of the most economically important lineages of fishes, thereby linking lineages as seemingly disparate as seahorses and tunas. A resolved and confidently supported phylogeny of ray-finned fishes has finally come into focus (**Figure 1**).

In this review, we highlight six areas of major changes in actinopterygian phylogeny (**Figure 1**). We (*a*) review the new phylogeny and its implications for a monophyletic Holostei; (*b*) discuss difficulties in resolving relationships among the three earliest diverging lineages of teleosts; (*c*) review the changes and challenges to understanding the relationships of the species-rich ostariophysans; (*d*) outline the newly resolved phylogeny among the major lineages of euteleosts; (*e*) zoom in on the relationships among the spiny finned fishes, Acanthomorpha; and (*f*) highlight the phylogenetic resolution of percomorphs, long famous as the largest polytomy in the vertebrate tree of life (Nelson 1989). Throughout our discussion of each component of the new molecular actinopterygian phylogeny, we highlight major phylogenetic changes, remaining challenges, and



**Section 2.1. Ancient Lineages Find a Home: The Phylogenetic Reemergence of Holostei**

**Section 2.2. The Origin and Phylogeny of Teleostei: From the Challenge of Darwin's Theory to Phylogenomics**

**Section 2.3. Changing Relationships of Ostariophysans: Earth's Dominant Freshwater Fishes**

**Section 2.4. Changes Along the Euteleost Stem and *Lepidogalaxias salamandroides* as a Living Fossil**

**Section 2.5. Sorting Among the Spines: Molecules Reshape Acanthomorph Phylogeny**

**Section 2.6. Percomorph Phylogeny: Resolving the Bush at the Top of the Teleost Tree**

(*Caption appears on following page*)

**Figure 1** (*Figure appears on preceding page*)

The emerging phylogeny of all major lineages of ray-finned fishes, Actinopterygii, summarized from several molecular phylogenetic studies. The group names used in Percomorpha are different from some recent classifications and are discussed in Section 2.7.

novel evolutionary insights. The emergence of a stable and well-resolved phylogeny of ray-finned fishes is within reach. We hope that this review guides and catalyzes research efforts to resolve the remaining conflicts surrounding the interrelationships of major clades while simultaneously highlighting opportunities for novel comparative studies unlocked by this scientific achievement.

## 2.1. Ancient Lineages Find a Home: The Phylogenetic Reemergence of Holostei

With more than 34,000 species, teleost fishes dominate the living biodiversity of neopterygians (Fricke et al. 2021a, 2021b). This diversity stands in stark contrast to the 51 species of nonteleost ray-finned fishes, including the eight living species of Holostei (gar and bowfin) that comprise the only nonteleost neopterygians (**Figures 1** and **2**) and were dubbed "living fossils" by Darwin (1859, p. 107). The monophyly of Holostei was supported in one of the earliest cladistic perspectives on the relationships of vertebrates (Nelson 1969). However, a phylogenetic hypothesis based on skeletal morphology that prevailed for the last three decades of the twentieth century resolved Holostei as paraphyletic, with *Amia calva* (Bowfin) as the sister lineage of teleosts (Gardiner et al. 1996, Patterson 1973) (**Figure 2**). In contrast to the seemingly strong morphological support for holostean paraphyly, essentially every molecular phylogenetic analysis from the earliest efforts based on partial-gene DNA sequences to phylogenomic analyses resolve Holostei as monophyletic (Braasch et al. 2016, Hughes et al. 2018, Inoue et al. 2003, Near et al. 2012, Normark et al. 1991). In light of this conflict, a critical examination of morphology in Bowfin, gars, and teleosts demonstrated that nearly all of the proposed characters supporting the monophyly of *Amia* plus teleosts were also present in gars and are not synapomorphies for a clade constrained to *Amia* plus teleosts (Grande 2010). Extensive analysis of morphology discovered at least 13 character states that support the monophyly of Holostei (Grande 2010). As such, Holostei exemplifies one of the first conflicts in ichthyological systematics between morphological and molecular phylogenetic analyses (Patterson 1994) that was reconciled through continued morphological and genomic phylogenetic analyses, which in this case offered overwhelming support for the monophyly of Holostei (Grande 2010, Hughes et al. 2018, Near et al. 2012, Thompson et al. 2021).

The resolution of a monophyletic Holostei creates an opportunity for understanding the evolutionary consequences of genome duplication events and refining our ability to make genomic comparisons between teleosts and other vertebrate lineages. All living teleosts experienced a genome duplication event in their early evolutionary history. However, holosteans did not. As such, holosteans provide the opportunity to understand the origins of genes and gene families that are fragmented or disjointed in the genomes of teleosts. Using holostean genomes as a bridge aids in identifying teleost gene origins and syntenic relationships. Moreover, holostean genomes illuminate the role the teleost genome duplication event played as a substrate for functional innovation. For example, sequencing of the spotted gar (*Lepisosteus oculatus*) and Bowfin genomes reveals families of innate immune receptors that were previously thought to be teleost-specific (Braasch et al. 2016, Thompson et al. 2021). Rather than representing a teleost novelty, one of these gene families likely represents the vestiges of an ancient gene family that gave rise to V(D)J recombination and adaptive immunity in vertebrates (Dornburg et al. 2021). With the rapid accumulation of publicly available teleost and nonteleost actinopterygian genomes that include holosteans and earlier diverging lineages (e.g., Höhne et al. 2021), the ability to broadly sample the deepest divergences of the ray-finned fish tree of life holds tremendous potential for teleost comparative genomics.

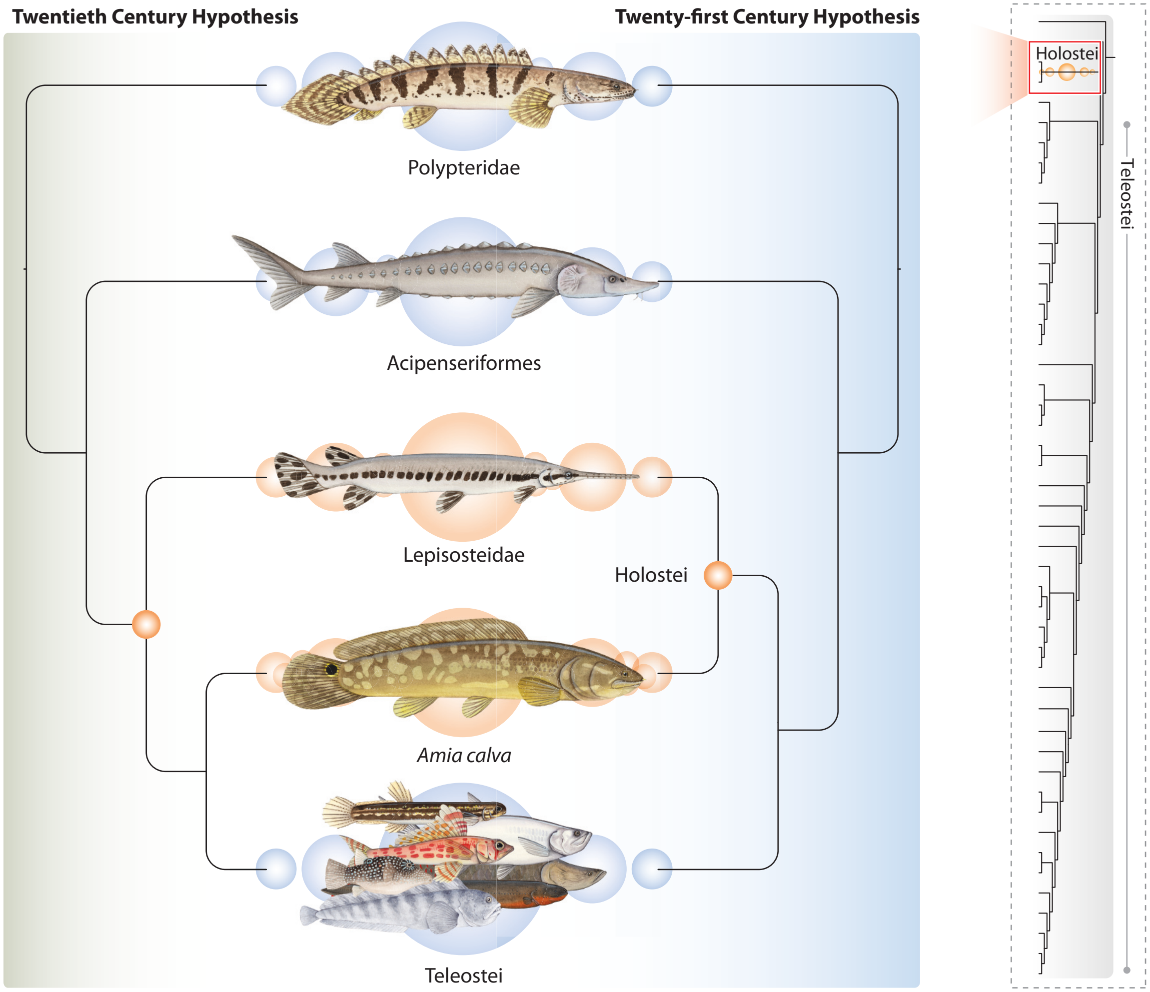


**Figure 2**

Contrasting phylogenetic hypotheses of neopterygian fishes. The prevailing twentieth century hypothesis based on morphology places *Amia calva* as the sister lineage of Teleostei (*left*). In contrast, the twenty-first century phylogenetic hypothesis resulting from analyses of both morphological and molecular analyses resolves a monophyletic Holostei (*Amia* and Lepisosteidae) as sister lineage of Teleostei (*right*). The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**). Orange shaded bubbles highlight changes in the delimitation of Holostei between the twentieth century and twenty-first century phylogenies. Blue shaded bubbles indicate congruence between the twentieth century and twenty-first century phylogenies.

In addition to teleost comparative genomics, holosteans also facilitate linking the genomes of model teleost organisms such as Zebrafish (*Danio rerio*) and Medaka (*Oryzias latipes*) to humans. The teleost genome duplication event resulted in the fragmentation of genomic loci important to human health in model teleosts, thereby challenging translational medicine. However, holosteans offer a bridge for comparative genomics between humans and teleosts (Braasch et al. 2016). For instance, the Spotted Gar genome highlights the orthology between human and fish microRNAs and conserved noncoding elements (Braasch et al. 2016). The latter are found in the genome of Zebrafish and are linked to human disease genotypes, creating a guide for functional experiments relevant to human health. Likewise, the recent sequencing of the Bowfin genome illuminates synteny between human, Zebrafish, and holostean major histocompatibility loci (Thompson et al. 2021). These examples illustrate that holostean genomes, which did not undergo the round of genome duplication that characterizes teleosts, are vital to understanding mechanisms of vertebrate genome evolution. In turn, this understanding enables a more effective harnessing of fish models in comparative genomics aimed toward applications for human health.

## 2.2. The Origin and Phylogeny of Teleostei: From the Challenge of Darwin's Theory to Phylogenomics

Teleosts as a group were named and diagnosed in the mid-nineteenth century (Müller 1845) and are the most species-rich clade of ray-finned fishes. By the middle of the twentieth century the monophyly of Teleostei was no longer in question (Greenwood et al. 1966), but the challenge of delimiting the major lineages of teleosts and inferring their phylogenetic relationships remained (Arratia 1997, Patterson & Rosen 1977, Rosen 1973). A consensus emerged that the major clades of teleosts are the Osteoglossomorpha (e.g., arowanas, elephant fishes, and Mooneye), Elopomorpha (e.g., tarpons, bonefishes, and eels), Ostariophysi (e.g., catfishes, piranhas, and minnows), Clupeiformes (e.g., shads and anchovies), and Euteleostei (all remaining teleosts). Three of these five major teleost lineages, elopomorphs, ostariophysans, and euteleosts, appear in the fossil record in a short interval of time ~150 Mya during the Late Jurassic (Arratia 1997). The sudden appearance of major teleost lineages was identified by Darwin (1859) as a problem for reconciling his perspective of gradual evolutionary change with the rapid origin of distinct phenotypes and lineages. Not surprisingly, the teleost problem that posed a challenge to Darwin (1859) is also correlated with the difficulty in using morphological characters to resolve the relationships among these earliest diverging lineages.

Patterson & Rosen (1977) proposed an arrangement that would come to dominate hypotheses of teleost phylogeny in the later twentieth century (Gill & Mooi 2002; Lauder & Liem 1983; Nelson 1989, 2006). Through mapping morphological characters onto a phylogeny, they placed Osteoglossomorpha as the sister lineage of all other teleosts (**Figure 3*a***) and identified two osteological traits to support the monophyly of elopomorphs plus all other teleosts. However, 20 years later, Arratia (1997) challenged this osteoglossomorph-first paradigm by performing parsimony analyses on a data matrix of morphological character states coded from living and fossil teleosts. These analyses resulted in a phylogeny where Elopomorpha is the sister lineage of all other teleosts (**Figure 3*b***). Patterson (1998) undermined the credibility of Arratia's (1997) analysis by casting doubt on the tree-search algorithm, the number of character state changes supporting alternative hypotheses, and even the use of data matrices in phylogenetics. It became clear that morphology was not resolving the problem of early teleost diversification. An important review of fish phylogenetics at the turn of the twenty-first century encapsulated the uncertainty by depicting the phylogeny of elopomorphs, osteoglossomorphs, and all other teleosts as unresolved (Stiassny et al. 2004, figure 24.1).

Over the past 30 years, several molecular phylogenetic studies supported traditional relationships within elopomorphs and provided new perspectives on relationships within osteoglossomorphs (JN Chen et al. 2014, Dornburg et al. 2015a, Hilton & Lavoué 2018, Inoue et al. 2004). However, molecular studies have resulted in every possible phylogenetic resolution of the interrelationships among elopomorphs, osteoglossomorphs, and all other teleosts. One of the earliest molecular systematic studies of ray-finned fishes resolved Elopomorpha and Osteoglossomorpha as a clade that is the sister lineage of all other teleosts (**Figure 3*c***), a hypothesis quickly dismissed by the authors of the study because it was never proposed by morphological systematists (Vân Lê et al. 1993). Subsequent analyses of whole mitochondrial (mt)DNA genomes, concatenated

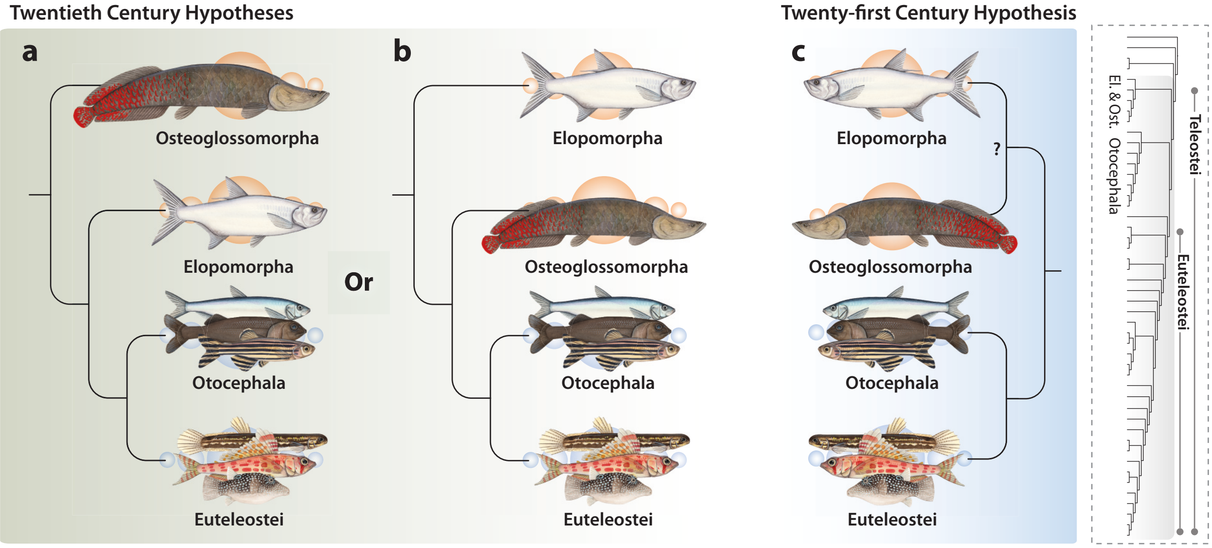


**Figure 3**

Phylogenetic relationships among the earliest diverging lineages of Teleostei. Investigations at the turn of the twentieth century presented two competing hypotheses: that either (*a*) Osteoglossomorpha (arowanas, elephant fishes, Mooneye) is the sister lineage of all other teleosts or (*b*) Elopomorpha (eels, tarpons, and bonefishes) is the sister lineage to all other teleosts. In contrast, analyses of genomic-scale data often resolve (*c*) Elopomorpha and Osteoglossomorpha as sister lineages. The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**). Orange shaded bubbles highlight conflict in the resolution of Elopomorpha and Osteoglossomorpha across the twentieth and twenty-first century phylogenies. Blue shaded bubbles indicate congruence between the twentieth century and twenty-first century phylogenies. Abbreviations: El., Elopomorpha; Ost., Osteoglossomorpha.

data sets from a few nuclear genes, combinations of mtDNA and nuclear genes, and ultraconserved elements (UCEs) have resulted in phylogenies in which either the osteoglossomorphs or elopomorphs are resolved as the sister lineage of all other teleosts, often with weak to moderate node support (Betancur-R et al. 2013, JN Chen et al. 2014, Faircloth et al. 2013, Inoue et al. 2001, Near et al. 2012). More recently, several phylogenomic-scale analyses (Chen et al. 2015; Hao et al. 2020; Hughes et al. 2018, figures S2, S3, S4, and S5; Vialle et al. 2018; Wcisel et al. 2020) of whole genomes or transcriptomes using both DNA sequences and amino acids from protein-coding genes harken to the earliest molecular studies in strongly resolving elopomorphs and osteoglossomorphs as a clade (**Figure 3*c***). In these phylogenomic studies, statistical tree topology tests soundly reject the two alternative hypotheses (Bian et al. 2016). Because none of the classic morphological studies had considered the hypothesis that elopomorphs and osteoglossomorphs form a monophyletic group, some investigators have rejected these molecular results out of hand. In doing so, they assume that the other competing phylogenetic hypotheses of early teleost diversification have substantial morphological support (**Figure 3**). They do not.

Efforts to resolve the earliest divergences among the major lineages of living teleosts epitomize a common trend in early twenty-first century phylogenetics where competing data sets and analysis pipelines offer conflicting results. Modern phylogeneticists possess an increasingly powerful set of tools to test rigorously and objectively for sources of phylogenetic incongruence. It is now possible to test whether conflict within and among data sets stems from conflicting gene histories (Zhang et al. 2018), model misspecification (Jermiin et al. 2020), character acquisition biases such as elevated GC content (Romiguier et al. 2016), loss of phylogenetic informativeness through time (Zhou et al. 2020), or undetected contaminated or misidentified DNA sequences (Simion et al. 2020). Such approaches have been brought to bear on other similarly recalcitrant nodes in the tree of life (Espeland et al. 2018) and certainly find utility in resolving the deepest parts of the teleost phylogeny. Although recent work using phylogenetic informativeness profiles suggests that homoplasy is masking the signal of elopomorphs as sister to all other teleosts (Takezaki 2021), consideration of the signal-to-noise ratios supporting this relationship as well as other sources of conflict are needed to increase confidence in this resolution. To motivate such studies, we retain the unconventional and intriguing possibility of an osteoglossomorph and elopomorph sister group relationship as a resolution requiring additional investigation and scrutiny (**Figure 3*c***), because it is one that appears frequently and is surprisingly well supported by available phylogenomic data sets (Bayesian and bootstrap values >95%) (e.g., Bian et al. 2016; Hao et al. 2020; Hughes et al. 2018, figures S2, S3, S4, and S5).

## 2.3. Changing Relationships of Ostariophysans: Earth's Dominant Freshwater Fishes

The Ostariophysi contains at least 11,280 teleost species, which comprise more than 60% of all freshwater fishes (Fricke et al. 2021b, Nelson et al. 2016). The major lineages of Ostariophysi include the relatively depauperate Gonorynchiformes (Milkfish, beaked sandfishes, and snake mudheads) and the Otophysi, which includes the vast majority of species. Otophysan species are classified among the Cypriniformes (4,694 species of carps, minnows, and loaches), Characiformes (2,170 species of tetras, piranhas, and headstanders), Citheriniformes (113 species of citharinids and distichodontids), Siluriformes (4,010 species of catfishes), and Gymnotiformes (262 species of Neotropical knifefishes and electric eels). Evidence for monophyly of ostariophysans and otophysans was established early in the phylogenetic study of teleosts (Fink & Fink 1981, Greenwood et al. 1966, Rosen & Greenwood 1970). However, molecular phylogenetic analyses have realigned the delimitation and interrelationships of major ostariophysan clades and resolved the phylogenetic placement of this important lineage within Teleostei. Phylogenetic hypotheses based on morphology delimit the Clupeocephala as the lineage containing all teleosts to the exclusion of Osteoglossomorpha and Elopomorpha. Within Clupeocephala, the Clupeiformes (shads, anchovies, and alewives) were proposed as the sister lineage to a delimitation of Euteleostei that includes the Ostariophysi (Patterson & Rosen 1977). In contrast, the earliest molecular analyses of ray-finned fish phylogeny resolved a clade containing clupeiforms and ostariophysans as the sister lineage of euteleosts (Vân Lê et al. 1993) (**Figure 1**). This clade containing Clupeiformes and Ostariophysi was subsequently supported with a number of proposed morphological synapomorphies (Arratia 1997, Johnson & Patterson 1996, Lecointre & Nelson 1996) and named Otocephala (Johnson & Patterson 1996).

The composition of Otocephala was unexpectedly expanded as a result of phylogenetic analyses of DNA sequences from whole mtDNA genomes that strongly resolve the deep-sea marine fish clade Alepocephaliformes (slickheads and tubeshoulders) in a clade with clupeiforms and ostariophysans (Ishiguro et al. 2003, Lavoué et al. 2005) **(Figure 1**). The monophyly of the expanded Otocephala that includes Alepocephaliformes is repeatedly supported in phylogenetic analyses of small nuclear gene data sets as well as a data set consisting of DNA sequences from more than 800 exons (Betancur-R et al. 2013, Near et al. 2012, Straube et al. 2018). Alepocephaliforms exhibit substantial adaptations to deep-sea habitats including the absence of a swim bladder and reduced skeletal ossification. At face value, such traits appear to greatly complicate the discovery of morphological characters that diagnose the expanded Otocephala. Careful reviews of proposed morphological synapomorphies identified the fusion of hemal spines to the centra of

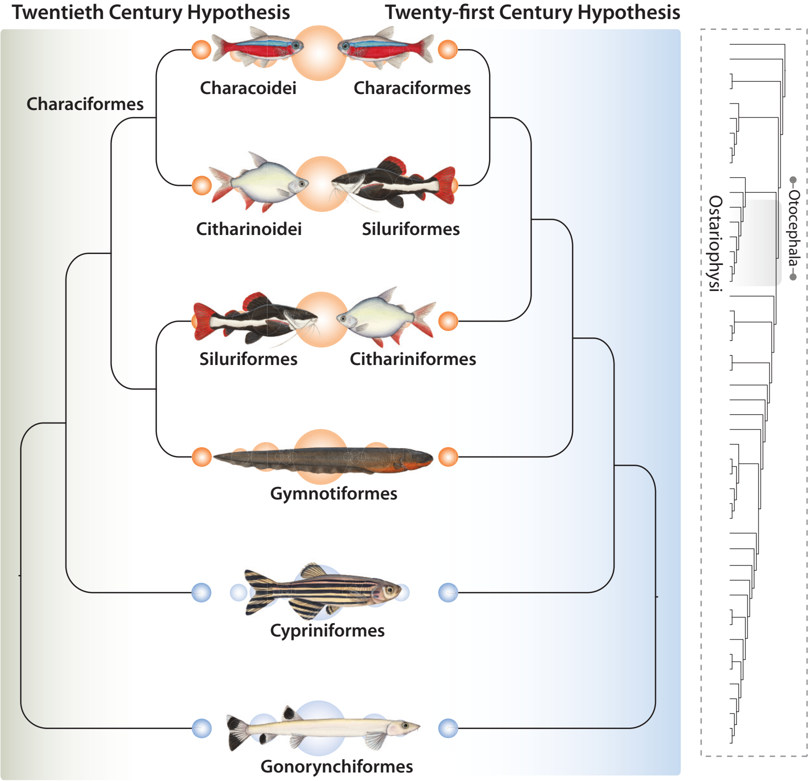


**Figure 4**

Contrasting phylogenetic hypotheses of Ostariophysi. The prevailing twentieth century hypothesis based on morphology delimits the Characiformes as containing Characoidei and Citharinoidei and resolves Siluriformes (catfishes) as the sister lineage of Gymnotiformes (Neotropical knifefishes and electric eels) (*left*). Investigations in the twenty-first century consistently resolve the classically delimited Characiformes as paraphyletic and do not support a clade containing the Siluriformes and Gymnotiformes (*right*). The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**). Orange shaded bubbles highlight major clades in the twentieth century phylogeny where delimitation has changed in the twenty-first century. Blue shaded bubbles indicate congruence between the twentieth century and twenty-first century phylogenies.

vertebrae early in development, fusion of the extrascapular and parietal bones, and silvery areas associated with the swim bladder as a strong candidates for diagnostic morphological traits for the expanded Otocephala (Arratia 2018, Straube et al. 2018).

Within Otocephala, molecular analyses are consistent in their support of the monophyly of ostariophysans and otophysans with Cypriniformes representing the sister lineage of all other otophysans (Arcila et al. 2017, Betancur-R et al. 2013, Hughes et al. 2018, Nakatani et al. 2011, Near et al. 2012). However, molecular studies dramatically depart from morphological expectations of relationships among the Characiformes, Citariniformes, Siluriformes, and Gymnotiformes in the Otophysi (**Figure 4**). Molecular phylogenetic studies consistently fail to resolve the monophyly of Siluriphysi (Chakrabarty et al. 2017; Dai et al. 2018; Hughes et al. 2018, figures S2, S4, and S5; Melo et al. 2021; Near et al. 2012), a hypothesized clade consisting of Gymnotiformes and Siluriformes based on morphological evidence from the passive electroreception system and other traits (Albert 2001, Fink & Fink 1981, Liu et al. 2016) (**Figure 4**). Likewise, most molecular analyses do not support monophyly for the traditional delimitation of Characiformes, which previously included the Cithariniformes (**Figure 4**). From the earliest single-locus molecular phylogenetic analyses in the mid-1990s to phylogenetic analyses of genomic-scale data sets in the early twenty-first century (Chakrabarty et al. 2017, Dai et al. 2018, Nakatani et al. 2011, Ortí & Meyer 1996), the classic delimitation of Characiformes is consistently resolved as paraphyletic with South American and African characoids and catfishes (Siluriformes), which are often resolved as sister lineages to the exclusion of the African citharinoids (**Figure 4**) (Chakrabarty et al. 2017; Hughes et al. 2018, figures S2, S4, and S5; Melo et al. 2021; Mirande 2017; Simion et al. 2020). This departure from morphology-based expectations of evolutionary relationships in ostariophysans remains an area of great interest in ichthyology.

The phylogenetic relationships of characiforms, citharimiforms, siluriforms, and gymnotiforms were recently addressed in phylogenomic analyses with conflicting results (Arcila et al. 2017, Chakrabarty et al. 2017, Melo et al. 2021). However, a recent study suggests the mechanisms driving incongruence between these analyses are likely problems associated with methods of tree inference and the presence of misidentified specimens or DNA sequence contamination (Simion et al. 2020). Both of these obstacles can haunt any phylogenomic analysis. The rapid pace of sequencing necessitates the rapid development of new methods and software. Unfortunately, this rapid pace of development often leaves software bugs and other issues in its wake that can affect phylogenetic inferences (Simion et al. 2020). Contamination and specimen misspecification also threaten accurate phylogenetic inference, requiring specific pipelines to identify and remove compromised sequence data (Lee et al. 2017, Simion et al. 2020). Given these findings, we feel that it is time to consider that the best-supported phylogenetic hypothesis of Otophysi does not include a clade containing Citharimiformes and Characiformes and that the morphologically delimited Siluriphysi is not monophyletic (**Figure 4**). This phylogeny implies the passive electroreception in siluriforms and gymnotiforms, which is facilitated by specialized neural anatomy, cytology, and physiology, has either more than one evolutionary origin or multiple losses in ostariophysans (Albert et al. 1998, Fink & Fink 1996). In addition, it appears that traits associated with the skull, vertebrae, caudal skeleton, and teeth thought to support shared common ancestry of Characiformes and Citharimiformes are plesiomorphic relative to Siluriformes (Chakrabarty et al. 2017; Fink & Fink 1981, 1996; Melo et al. 2021).

### 2.4. Changes Along the Euteleost Stem and *Lepidogalaxias salamandroides* as a Living Fossil

Encompassing more than 20,880 species, Euteleostei is the most species rich named clade of teleost fishes (Fricke et al. 2021a). The vast majority of euteleost species are in the subclade Neoteleostei, which includes the hyperdiverse Acanthomorpha (**Figures 1** and **5**). While the concept of Euteleostei and the discovery of morphological characters supporting the monophyly of the lineage date to the earliest phylogenetic studies of teleosts (Greenwood et al. 1966, Rosen 1973), relationships among the major euteleost lineages have eluded a confident resolution for the past 50 years (Johnson & Patterson 1996, Li et al. 2010, Straube et al. 2018). A consistent phylogeny of euteleosts has only recently emerged from molecular studies that use a small number of nuclear genes (Near et al. 2012) or phylogenomic data sets (Straube et al. 2018). In addition to resolving the relationships within acanthomorphs discussed in the next section, other important achievements in the phylogeny of euteleosts include the phylogenetic resolution of the enigmatic and biologically bizarre Salamanderfish (*Lepidogalaxias salamandroides*) and identification of the sister lineage of the hyperdiverse Neoteleostei (**Figure 5**).

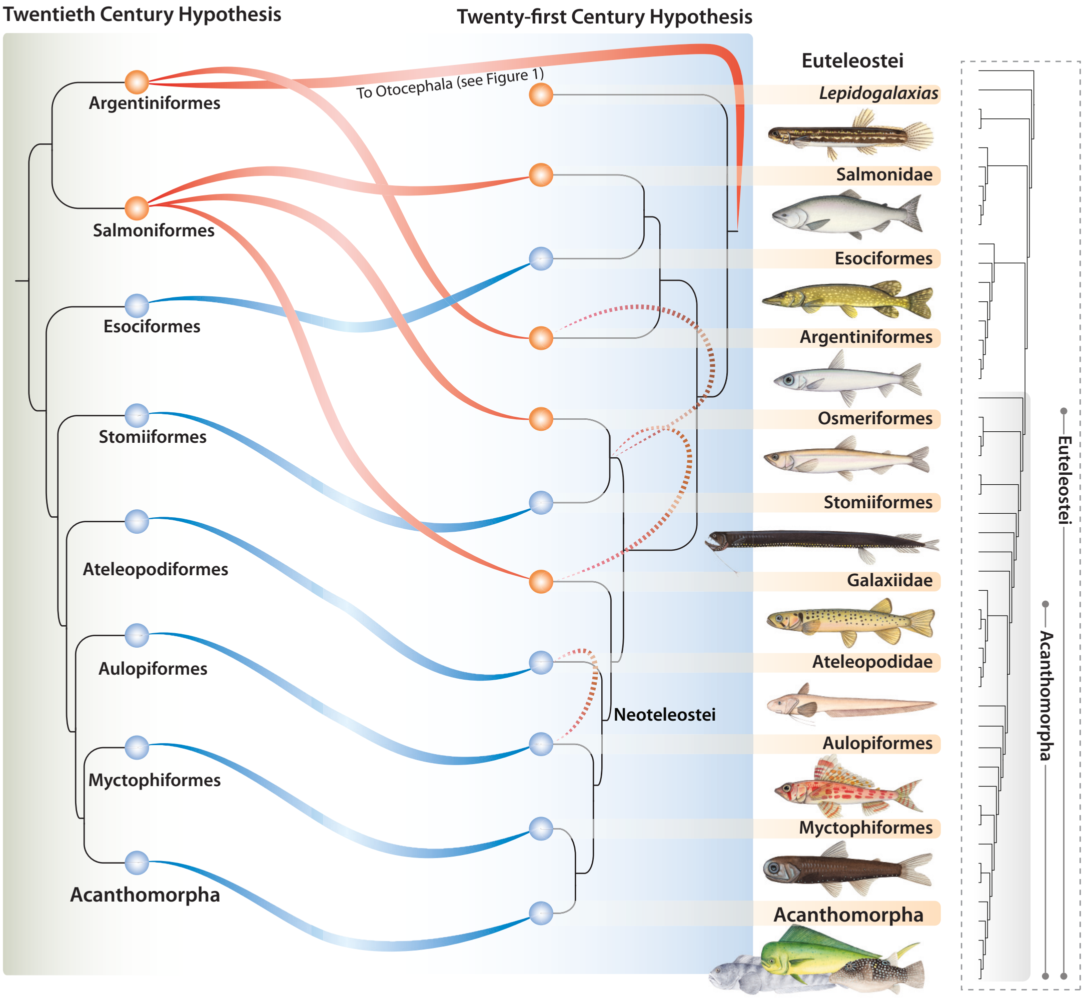


**Figure 5**

Contrasting changes in phylogenetic perspective among the early diverging Euteleostei. The consensus twentieth century phylogeny based on morphology is shown on the left. The emerging twenty-first century phylogeny resulting from molecular analyses is shown on the right. Blue ribbons connect major lineages that have the same delimitation in the two phylogenies. Red ribbons connect major clades in the twentieth century phylogeny where delimitation has changed in the twenty-first century. The red dashed ribbons highlight remaining uncertainty in the phylogenetic resolution of the indicated nodes between studies. The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**).

One of the most notable discoveries in euteleost phylogeny is the consistent and strongly supported resolution of *Lepidogalaxias salamandroides* as the sister lineage of all other Euteleostei (Betancur-R et al. 2013, Campbell et al. 2017, Hughes et al. 2018, Li et al. 2010, Near et al. 2012, Straube et al. 2018) (**Figure 5**). With a maximum standard length of 67 mm, the Salamanderfish was first discovered in 1959 and is found in a restricted geographic area of southwestern Australia. The species occupies small ephemeral freshwater streams where individuals estivate by burying in groundwater-moistened sand when streams dry in summer droughts (Berra & Allen 1989). *Lepidogalaxias* is unique among all ray-finned fishes in the ability to bend the head downward and side to side at a neck facilitated by modifications to the first vertebra (Berra & Allen 1989). The unusual anatomy of *Lepidogalaxias* hampered confident phylogenetic resolution using morphology, with earlier hypotheses including placement within the Esociformes (pikes and mudminnows) (Rosen 1974), the Galaxiidae (Williams 1997), and in a clade containing galaxiids and Osmeriformes (freshwater smelts) (Johnson & Patterson 1996, Wilson & Williams 2010). The resolution of one species, *Lepidogalaxias salamandroides*, as the sister lineage to a clade containing more than 20,880 species of euteleosts highlights one of the largest disparities in clade species richness among all vertebrates (**Figures 1** and **5**). The only other instance is the two closely related species of coelacanths that are the sister lineage of the clade containing the approximately 36,861 living species of Sarcopterygii (tetrapods, lungfishes, and coelacanths).

*Lepidogalaxias* is unique in that it is the lone survivor of a species-depauperate lineage that has persisted for more than 200 million years (Hughes et al. 2018, Near et al. 2012), exhibits a relict geographic distribution, lacks obvious morphological synapomorphies with other euteleost lineages, and appears to be a phylogenetic relict that has a significantly lower rate of lineage diversification ($1.0 \times 10^{-6}$ lineages/Ma) when compared to the background rate estimated for all ray-finned fishes ($1.8 \times 10^{-2}$ lineages/Ma) (Near et al. 2014). This insight into the evolutionary history of *Lepidogalaxias* presents an opportunity to redefine Darwin's concept of a living fossil as a term to highlight phylogenetically unique lineages across the tree of life (Turner 2019). Living fossils like *Lepidogalaxias* represent deeply divergent phylogenetic lineages with no living morphological analogs. Given the extreme environmental conditions in this region of Australia and the presence of other vertebrate species with similar adaptations that also exhibit deep phylogenetic branching (Zhang et al. 2017), it is unlikely that *Lepidogalaxias* represents an ancestral phenotype. Living fossils need not represent an ancestral phenotype, nor are they expected to, unless their rate of morphological evolution effectively stalls. Instead, living fossils may be thought of as unusual phylogenetic relics that have managed to persist to the present day and may include multiple species.

In addition to resolving *Lepidogalaxias* as the sister lineage of all euteleosts, essentially all molecular phylogenetic studies resolve the economically and recreationally important Salmonidae (trouts, salmons, and whitefishes) plus Esociformes (pikes and mudminnows) as a monophyletic group and the Stomiiformes (dragonfishes) plus Osmeriformes (freshwater smelts) as a clade (**Figure 5**) (Betancur-R et al. 2013, Campbell et al. 2017, Hughes et al. 2018, Li et al. 2010, Near et al. 2012, Straube et al. 2018). Likewise, multiple studies resolve the Southern Hemisphere freshwater and diadromous Galaxiidae as the sister lineage of the species-rich Neoteleostei (Hughes et al. 2018, figures S2, S3, S4, and S5; Near et al. 2012; Straube et al. 2018) (**Figure 5**). What remains unresolved is the phylogenetic relationship of the mainly bathypelagic Argentiniformes (marine smelts), which include the morphologically unique deep-sea barreleye fishes and the argentines or herring smelts. There are at least three different resolutions resulting from molecular analyses: as the sister lineage of the clade containing Salmonidae and Esociformes (Hughes et al. 2018, figures S3, S4, and S5; Near et al. 2012; Straube et al. 2018) (**Figures 1** and **5**); the sister lineage of a clade containing Galaxiidae, Salmonidae, and Esociformes (Betancur-R et al. 2013); or, in an analysis that did not include Galaxiidae, as the sister lineage of a clade containing Osmeriformes, Stomiiformes, and Neoteleostei (Campbell et al. 2017). As we move deeper into the phylogenomic era, the placement of Argentiniformes within euteleosts remains an unresolved issue.

## 2.5. Sorting Among the Spines: Molecules Reshape Acanthomorph Phylogeny

With more than 19,470 species, Acanthomorpha, or spiny-rayed fishes, make up nearly 30% of all living vertebrates. One of the most notable achievements of the earliest studies of teleost phylogeny was the discovery of morphological characters that supported acanthomorph

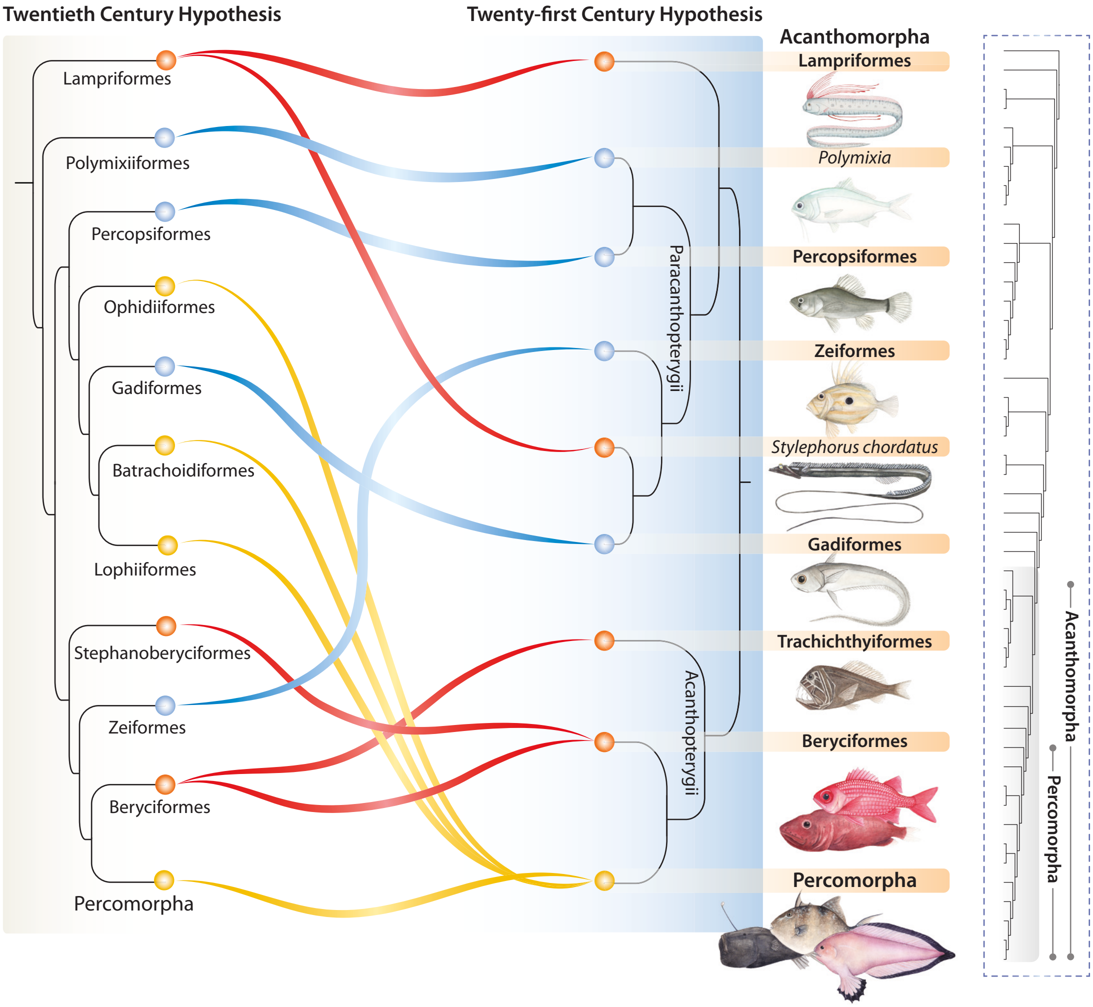


**Figure 6**

Contrasting phylogenetic hypotheses of Acanthomorpha between the consensus twentieth century phylogeny based on morphology (*left*) and the emerging twenty-first century phylogeny resulting from molecular analyses (*right*). Blue ribbons connect major lineages that have the same delimitation in the two phylogenies. Red ribbons connect major clades in the twentieth century phylogeny where delimitation has changed in the twenty-first century. Yellow ribbons connect major clades in the twentieth century phylogeny that are phylogenetically delimited as Percomorpha in the twenty-first century. The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**).

monophyly (Johnson & Patterson 1993, Rosen 1973, Stiassny 1986, Stiassny & Moore 1992). While molecular analyses consistently support the monophyly of acanthomorphs, these studies resulted in relationships that differ from those inferred from morphological studies and lead to new delimitations of the major acanthomorph lineages such as Lampriformes (oarfishes and opahs), Paracanthopterygii (cods, dories, beardfishes, etc.), and Percomorpha (e.g., tunas, seahorses, and seabasses) (Betancur-R et al. 2013; W-J Chen et al. 2014; Hughes et al. 2018; Miya et al. 2005; Near et al. 2012, 2013) (**Figure 6**). For example, in morphological phylogenies, the Lampriformes are consistently resolved as the sister lineage of all other acanthomorphs (Davesne et al. 2016, Johnson & Patterson 1993), and for nearly a century, they were delimited to include the morphologically bizarre deep-sea Tube-Eye (*Stylephorus chordatus*) (Olney et al. 1993, Regan 1924). In contrast, molecular analyses resolve lampriforms as either the sister lineage of the Acanthopterygii, which includes the Percomorpha (Grande et al. 2013, Hughes et al. 2018, Malmstrøm et al. 2017, Near et al. 2013), or as the sister lineage of the inclusive Paracanthopterygii (Alfaro et al. 2018, Betancur-R et al. 2013, W-J Chen et al. 2014), with the Tube-Eye as the sister lineage of the economically important Gadiformes (cods) (Alfaro et al. 2018, Betancur-R et al. 2013, Hughes et al. 2018, Miya et al. 2007, Near et al. 2013) (**Figure 6**). Even more strikingly, molecular analyses have completely overturned the classical concept of the Paracanthopterygii (**Figure 6**).

The acanthomorph subclade Paracanthopterygii was first proposed in the formative classification of Greenwood et al. (1966) and was modified to include a disparate set of nonpercomorph acanthomorphs (Patterson & Rosen 1989, Rosen & Patterson 1969). The morphological delimitation of Paracanthopterygii was based on four osteological synapomorphies and included the Percopsiformes (trout-perches, pirate perch, and cavefishes), Ophidiiformes (cusk-eels), Gadiformes (cods), Batrachoididae (toadfishes), and Lophiiformes (anglerfishes) (Patterson & Rosen 1989). However, molecular analyses result in phylogenies that suggest a very different composition of paracanthopterygians (**Figures 1** and **6**). First, there is the stark difference in resolution of the batrachoids, ophidiiforms, and lophiiforms. Ophidiiforms and batrachoids resolved as the first two branching lineages in Percomorpha, and Lophiiformes were relocated to a position nested well within Percomorpha as a close relative of the tetraodontoids (pufferfishes, triggerfishes, and ocean sunfishes) (Alfaro et al. 2018; Betancur-R et al. 2013; Hughes et al. 2018; Malmstrøm et al. 2017; Miya et al. 2003, 2005; Near et al. 2012, 2013). The migration of Lophiiformes into percomorphs is of particular note as this change would be akin to placing a morphologically established lineage of marsupials as the sister lineage to rodents or vipers as the sister lineage of *Anolis* lizards (**Figure 6**).

The shift in the phylogenetic resolution of Lophiiformes ranks among the most momentous in twenty-first century vertebrate phylogenetics. Moreover, resolution of batrachoids, ophidiiforms, and lophiiforms provided an emergent molecular phylogenetic delimitation of Paracanthopterygii that is strongly supported to include percopsiforms and gadiforms from the morphology-based demarcation of the group (Patterson & Rosen 1989), as well as *Stylephorus chordatus*; the Zeiformes (lookdown dories); and the phylogenetically enigmatic *Polymixia* (beardfishes), which are the sole living remnant of a Cretaceous fossil-rich clade (Alfaro et al. 2018, W-J Chen et al. 2014, Davesne et al. 2016, Grande et al. 2013, Hughes et al. 2018). Some uncertainty concerning the relationships of lineages in this clade remains (**Figure 6**), but a compelling phylogeny inferred using UCE loci resolves all acanthomorphs into two major clades (Alfaro et al. 2018): the Lampriformes–Paracanthopterygii and the Acanthopterygii (**Figure 6**).

The Acanthopterygii include the deep-sea Trachichthyiformes (roughies, flashlight fishes, and pinecone fishes), the deep sea- and reef-dwelling Beryciformes (alfonsinos, flabby whale fishes, and squirrelfishes), and the hyperdiverse Percomorpha that are the globally dominant group of vertebrates in near-shore marine habitats (Rabosky et al. 2018) (**Figure 6**). Morphological studies identified the major lineages comprising the Acanthopterygii (Johnson & Patterson 1993, Moore 1993). However, molecular studies differ on both the composition of these lineages and their phylogenetic relationships. The earliest molecular studies identified the sister lineage of percomorphs as either a monophyletic group consisting of Trachichthyiformes and Beryciformes (Near et al. 2012, 2013) or the beryciform subclade Holocentridae (squirrelfishes) (Betancur-R et al. 2013). Phylogenomic analyses resolve the Beryciformes, which includes Holocentridae, as the percomorph sister lineage (Alfaro et al. 2018; Dornburg et al. 2017; Hughes et al. 2018, figures S2–S5; Malmstrøm et al. 2017) (**Figure 6**). Resolving these relationships is critical, as the vast species richness and rapid diversification of percomorphs is put into context largely through the identification of its sister lineage within the Acanthopterygii (Alfaro et al. 2018, Friedman 2010, Near et al. 2013). A continued effort to reconcile these competing phylogenetic hypotheses, as well as the other remaining problematic nodes, is within reach. The success of molecular phylogenetics in resolving relationships within Acanthomorpha results from tremendous effort by numerous independent groups of researchers. Building on these achievements, we are now poised to achieve a full resolution of species-level acanthomorph relationships and thereby establish the comparative foundation from which to assess the general rules that govern their diversification.

### 2.6. Percomorph Phylogeny: Resolving the Bush at the Top of the Teleost Tree

Percomorpha is the most species-rich lineage of vertebrates that most people have never heard of. Ironically, it includes many of the most familiar, economically and recreationally important species of ray-finned fishes. With more than 18,480 species, percomorphs make up 25.5% of all living vertebrates and more than half of all living species of actinopterygians. From 2010 to 2020 ichthyologists described an average of more than 190 new species of percomorphs a year (Fricke et al. 2021b). Percomorphs are classified into 288 taxonomic families (Fricke et al. 2021a) and include 67% of all taxonomic families of ray-finned fishes. The number of percomorph families is on par with the number of families of living birds (252) (Gill et al. 2020) but dwarfs the number of families of mammals (167) (Burgin et al. 2018), squamate reptiles (58) (Uetz et al. 2020), amphibians (74) (**https://amphibiaweb.org**), and turtles (14) (Thomson et al. 2021). At approximately 120 Ma, the molecular age estimate for the crown node of percomorphs is older than the age estimate of living birds (72 Ma) (Prum et al. 2015) but younger than the crown lineage ages for mammals (180 MA) (Upham et al. 2019), squamate reptiles (190 Ma) (Burbrink et al. 2020), amphibians (323 Ma) (Kumar et al. 2017), and turtles (208 Ma) (Thomson et al. 2021). While the majority of percomorph taxonomic families were well established by the first half of the twentieth century (Greenwood et al. 1966, Jordan 1923), the incredible diversity within and among these taxonomic families hampered confident delimitation of major percomorph lineages and resolution of their phylogenetic relationships. Percomorphs were famously labeled as the "bush at the top" of the teleost phylogeny (Nelson 1989, p. 328), which reflected the impediments systematists faced in using morphological characters to resolve the phylogenetic relationships of the hundreds of lineages that comprise Percomorpha. This state of affairs was summarized in one of the most influential phylogenetic studies of percomorphs in the twentieth century as "any tree can be justified by special pleading, by insisting that certain characters are uniquely derived but others are more labile or plastic" while recognizing that "very few of the characters found among percomorphs and their relatives are uniquely derived" (Johnson & Patterson 1993, p. 555). Although the last century ended on a sentiment that "progress will not be made without some special pleading" (Johnson & Patterson 1993, p. 555) for the validity of morphological character–based inference, the application of molecular systematics has fundamentally altered the composition and relationships of Percomorpha without such a plea (**Figure 7**).

Prior to the application of molecular data, the vast majority of species and taxonomic families of percomorphs were classified in the catch-all taxon Perciformes, which was assumed to be a paraphyletic assemblage (Johnson & Patterson 1993, Nelson 2006). In addition to Perciformes, percomorphs included a few of the morphologically most bizarre lineages of teleosts that were also ranked as taxonomic orders such as the Pleuronectiformes (flatfishes), Tetraodontiformes (pufferfishes, triggerfishes, and ocean sunfishes), and Gasterosteiformes (sticklebacks and seahorses). Any lineage of percomorphs that was not as morphologically distinctive as flatfishes or pufferfishes was relegated to Perciformes, which at the turn of the century contained more than 10,000 species and 160 taxonomic families (Nelson 2006). From the earliest molecular studies

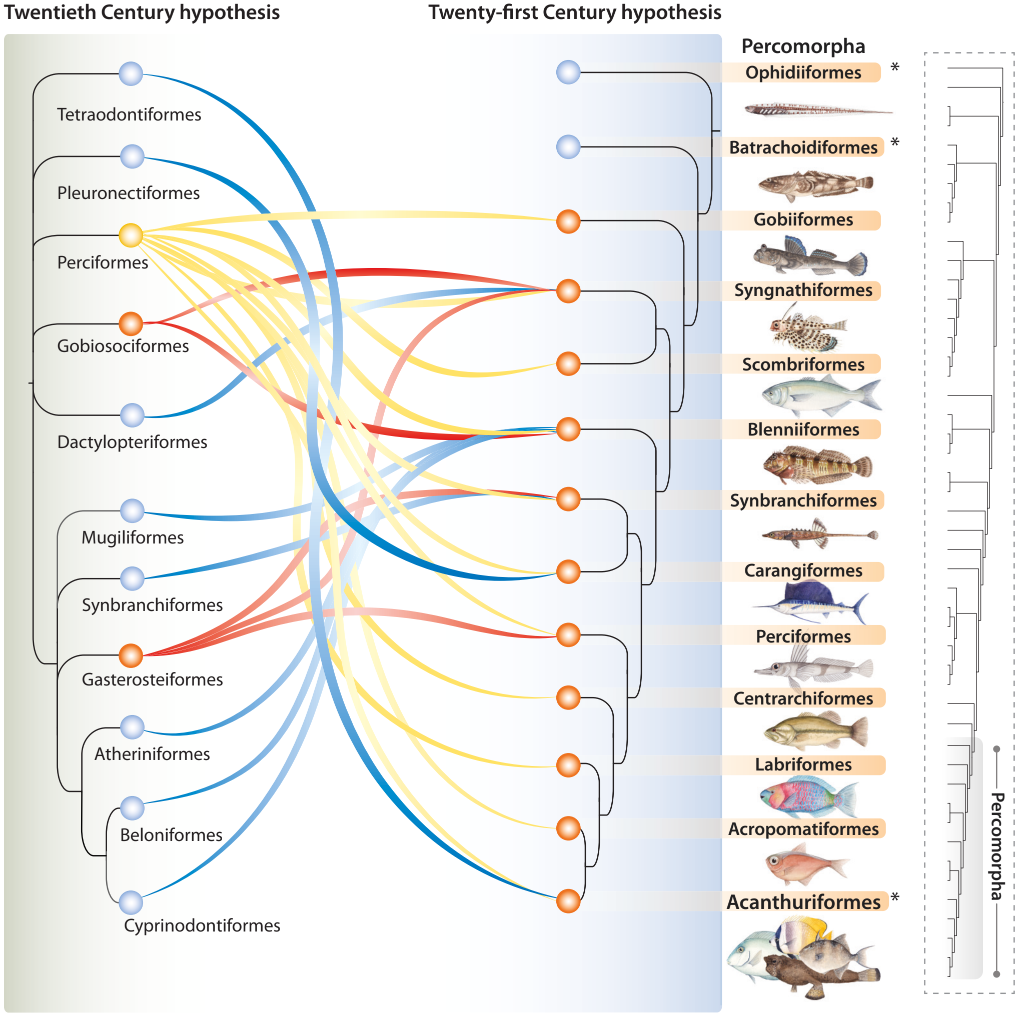


**Figure 7**

Contrasting changes in the phylogenetic resolution of major lineages of Percomorpha between the consensus twentieth century phylogeny (*left*) and the emerging twenty-first century phylogenetic perspective (*right*). Blue ribbons connect major lineages that have the same delimitation in the two phylogenies, with blue dots on the left indicating clades that have remained unchanged. Red ribbons connect major clades in the twentieth century phylogeny where delimitation has changed in the twenty-first century, with red circles indicating major clades that were not resolved prior to this century. Yellow ribbons connect the twentieth century delimitation of Perciformes to almost every major lineage of Percomorpha in the twenty-first century phylogeny. Names indicated with an asterisk indicate lineages or the inclusion of lineages hypothesized to represent early diverging acanthomorphs in the twentieth century delimitation (see **Figure 6**). The inset box indicates the scope of the focal nodes relative to the emerging ray-finned fish tree of life (**Figure 1**).

using single loci to the use of genomic-scale DNA sequence data sets, the emergent phylogeny of Percomorpha revealed that the Perciformes contained lineages spanning nearly the entire backbone of the percomorph phylogeny (Alfaro et al. 2018; Betancur-R et al. 2013; Chen et al. 2003; Hughes et al. 2018; B Li et al. 2009; CH Li et al. 2008; Miya et al. 2003, 2005; Near et al. 2012, 2013; Sanciangco et al. 2016; Smith & Craig 2007; Smith & Wheeler 2004, 2006)

(**Figure 7**). This phylogenetic perspective has enabled the disassembly of Perciformes with the migration of more than 100 taxonomic families to other major percomorph lineages (**Figure 7**).

Increased resolution of the phylogenetic relationships within and among major percomorph lineages has provided the basis for investigating their evolutionary diversification. For example, resolution of relationships within the pelagic lineage Scombriformes (tunas, barracudas, and cutlassfishes) catalyzed the reconstruction of an adaptive radiation in the wake of the Cretaceous–Paleogene mass extinction event (Friedman et al. 2019). Likewise, phylogenetic resolution within and among numerous clades of percomorphs that occupy coral reef habitats revealed the role of tectonic processes such as the closure of the Tethys seaway in shaping modern coral reef fish communities (Dornburg et al. 2015b, Leprieur et al. 2016, Renema et al. 2008, Siqueira et al. 2019). Comprehensive phylogenies of percomorph lineages have also revealed patterns of convergent evolution in transitions between benthic and pelagic habitats (Friedman et al. 2020, Ribeiro et al. 2018, Rincon-Sandoval et al. 2020). More broadly, a phylogenetic approach that placed marine percomorphs in the context of all marine teleosts suggests that rates of speciation are highest among percomorphs in polar regions, indicating an inverse latitudinal gradient in lineage diversification rates (Rabosky et al. 2018). Collectively, these studies exemplify new insights gained from a densely sampled and well-resolved percomorph phylogeny. Given the diversity of percomorph fishes, we anticipate a future rich in studies that further harness the emerging phylogenetic perspective as a comparative foundation to investigate topics that span all aspects of their ecology and evolution, thereby providing a basis for establishing more general rules of vertebrate diversification.

## 2.7. A Phylogenetically Informed Classification of Percomorpha

**Supplemental Material >**

The disassembly of Perciformes provides an opportunity to reshape the classification of percomorphs to better reflect interfamilial phylogenetic relationships. Initial efforts at building classifications based on the new phylogeny are impressive, but in an attempt to preserve the ordinal ranks of the clades, such as the Pleuronectiformes, Tetraodontiformes, Mugiliformes, and Atheriniformes, the most recently proposed classification delimits 33 taxonomic orders with 10% of all percomorph families remaining unassigned to a taxonomic order (Betancur-R et al. 2017). In **Figures 1** and **7** and **Supplemental Table S1** we offer an alternative classification of Percomorpha. The names of the orders in our percomorph classification continue a convention in ichthyological systematics to establish a link with one of the constituent taxonomic families and use the -iformes suffix (Berg 1947, Goodrich 1909, Greenwood et al. 1966, Nelson et al. 2016). For example, our delimitation of Blenniiformes includes the Blenniidae and 46 other families that consist of 5,865 species identified as a monophyletic group in molecular phylogenetic studies (Alfaro et al. 2018, Betancur-R et al. 2013, Hughes et al. 2018, Li et al. 2009, Near et al. 2013, Wainwright et al. 2012). Previously named Ovalentaria (Wainwright et al. 2012), this diverse clade of percomorphs includes blennies, cichlids, livebearers, and mullets, which are currently classified among seven orders (Betancur-R et al. 2017), one of which, Mugiliformes, includes a single family, Mugilidae. By not requiring the percomorph classification to include many historical ordinal groups such as Pleuronectiformes, the strategy we propose minimizes the inflation of group names and allows a more consistent distribution of diversity among named ordinal ranked groups. Given the emerging consensus on phylogenetic relationships from genomic data, it also avoids the trap of being tied to historical, morphology-based classifications that likely reflect lineages diversifying to different adaptive zones rather than phylogenetic history per se (Holt & Jønsson 2014). The classification proposed in **Figures 1** and **7**, and **Supplemental Table S1** places all 288 percomorph families into 13 inclusive orders, each averaging 22.1 families [standard deviation (SD) = 18.7, range 1–56 families] and 1,422.9 species (SD = 1,676.2, range 84–5,865 species). This ratio of species and families in our revised classification of percomorphs is similar to the ratios in the Betancur-R et al. (2017) classification of otophysan fishes which averages 2,226.8 species (SD = 1,979.9) and 18.2 families (SD = 13.9) per order.

We hope to use this revised classification to highlight an exciting moment in the history of systematics. The emergence of a new phylogenetic perspective offers the opportunity to redefine clades, but rarely do we consider these classification schemes in the context of larger portions of the tree of life. With the emergence of the ray-finned fish tree of life, systematists have a unique opportunity to address a pivotal question: Should systematics move toward a standardized nonrank-based classification system, or if taxonomic ranks are maintained, should there be a greater attempt at consistency between major clades (de Queiroz 2007, Holt & Jønsson 2014)? While a correct approach is still subject to opinion, the translation of phylogenies to working taxonomic classifications will shape the conversational foundation for generations of comparative biologists.

## 3. SUMMARY AND PROSPECTUS

With an emergent phylogeny of all ray-finned fishes, it is tempting to think that a golden age of phylogenetics in ichthyology is ending. However, nothing could be further from the truth. A fully resolved actinopterygian tree of life will empower endless comparative investigations. Moreover, this phylogenetic perspective offers the opportunity to catalyze a new modern era of morphological phylogenetics that views molecular phylogenies as a valuable tool and not an adversary. Nearly 20 years ago, linking molecular and morphological data was proposed as the essential strategy to include extinct taxa in the tree of life (Wiens 2004), and the methodological ability to deliver this proposal has greatly increased (Heath et al. 2014). By rejecting the false dichotomy of morphology versus molecules, we move to a conversation aimed at resolving how our understanding of ray-finned fish morphology and evolution is aided by the resolution afforded by molecular phylogenies (**Figure 1**). This perspective should not only help guide the discovery of phylogenetically diagnostic morphological traits (Chanet et al. 2013, Girard et al. 2020, Wainwright et al. 2012) but also provide the foundation for understanding the genomic and developmental basis of trait evolution (Cumplido et al. 2020, Daane et al. 2019, Thompson et al. 2021). By coupling investigations of phenotype with advances in gene editing and methods by which to detect gene-trait associations, integrative studies will provide novel and unprecedented insights into the homology of characters and the development of ray-finned fish phenotypes (Colosimo et al. 2005). These possibilities are already actualized and would not have been possible without decades of research efforts by the phylogenetics community. We eagerly await these future advances in our understanding of the patterns and evolutionary processes underlying the diversification of ray-finned fishes.

## DISCLOSURE STATEMENT

The authors are not aware of any memberships, affiliations, funding, or financial holdings that may be perceived as affecting the objectivity of this review.

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# Contents

**Errata**

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