Phylogenetic Classification of Living and Fossil Ray-Finned Fishes (Actinopterygii)

Authors: Near, Thomas J., and Thacker, Christine E.

Source: Bulletin of the Peabody Museum of Natural History, 65(1) : 3-302

Published By: Peabody Museum of Natural History, Yale University

URL: https://doi.org/10.3374/014.065.0101

Phylogenetic Classification of Living and Fossil Ray-finned Fishes (*Actinopterygii*)

Thomas J. Near[1] and Christine E. Thacker[2]

[1] *Corresponding author:* Department of Ecology and Evolutionary Biology, Osborn Memorial Labs, Yale University, New Haven CT 06520-8106 USA; and Yale Peabody Museum, Yale University, New Haven CT 06520-8118 USA
—*email*: thomas.near@yale.edu
ORCID 0000-0002-7398-6670

[2] Vertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara CA 93105 USA; and Research and Collections, Department of Ichthyology, Natural History Museum of Los Angeles County, Los Angeles CA 90007 USA
—*email*: christine.e.thacker@gmail.com
ORCID 0000-0002-0700-734X

Abstract

Classification of the tremendous diversity of ray-finned fishes (*Actinopterygii*) began with the designation of taxonomic groups on the basis of morphological similarity. Starting in the late 1960s morphological phylogenetics became the basis for the classification of *Actinopterygii* but failed to resolve many relationships, particularly among lineages within the hyperdiverse *Percomorpha*. The introduction of molecular phylogenetics led to a dramatic reconfiguration of actinopterygian phylogeny. Refined phylogenetic resolution afforded by molecular studies revealed an uneven diversity among actinopterygian lineages, resulting in a proliferation of redundant group names in Linnean-ranked classifications. Here we provide an unranked phylogenetic classification for actinopterygian fishes based on a summary phylogeny of 830 lineages of ray-finned fishes that includes all currently recognized actinopterygian taxonomic families and 287 fossil taxa. We provide phylogenetic definitions for 90 clade names and review seven previously defined names. For each of the 97 clade names, we review the etymology of the clade name, clade species diversity and constituent lineages, clade diagnostic morphological apomorphies, review synonyms, and provide a discussion of the clade's nomenclatural and systematic history. The new classification is free of redundant group names and includes only one new name among the 97 clade names we review and describe, yielding a comprehensive classification that is based explicitly on the phylogeny of ray-finned fishes that has emerged in the 21st century and rests on the foundation of the previous 200 years of research on the systematics of ray-finned fishes.

Keywords

Teleostei, *Holostei*, *Ostariophysi*, *Euteleostei*, *Acanthomorpha*, *Percomorpha*, *Perciformes*, phylogeny, *PhyloCode*, taxonomy

Introduction

There are currently more than 35,085 described species of ray-finned (*Actinopterygii*) fishes (Fricke et al. 2023), comprising nearly half of the total living species diversity of vertebrates. The first classifications of the immense diversity of *Actinopterygii* were the culmination of several important and ambitious surveys of ray-finned and teleost fishes on the basis of comparative anatomy (e.g., Müller 1845a; Cope 1871a, 1871b; T. N. Gill 1872; Goodrich 1909; Jordan 1923; Regan 1929; Garstang 1931; Berg 1940; Greenwood et al. 1966) and morphological studies that were among the first to use cladistic methods (G. J. Nelson 1968, 1969c, 1973; Patterson 1973; Rosen 1973). These early efforts provided support for the monophyly of major clades of *Actinopterygii* still recognized today, including groups such as sturgeons, gars, tarpons and eels, catfishes, salmons, anglerfishes, tunas, gobies, and flatfishes. However, prior to the application of molecular data, the relationships among many of the major lineages of ray-finned fishes remained unresolved and specific phylogenetic hypotheses relied on

Bulletin of the Peabody Museum of Natural History 65(1):3–302, April 2024.

the interpretation of a few key morphological characters (e.g., Patterson 1973; Rosen 1973, 1985; Lauder and Liem 1983; Patterson 1993, 1996).

The introduction of molecular data to phylogenetics revolutionized the inference of the tree of life and brought astounding insights, including the paraphyly of *Prokaryota* (Woese and Fox 1977), the discovery of the inclusive placental mammal lineage *Afrotheria* (Stanhope et al. 1998), and the resolution of ctenophores as the sister lineage of all other metazoans (C. W. Dunn et al. 2008). In a similar way, molecular data have had an astonishing effect on the resolution of the phylogenetic relationships of *Actinopterygii* (Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Miya and Nishida 2015; Hughes et al. 2018; Ghezelayagh et al. 2022; Mu et al. 2022), with nearly every part of the ray-finned fish phylogeny modified as a result of molecular analyses (Dornburg and Near 2021). In the first years of the 21st century, morphology alone was the basis for review papers and authoritative reference texts on the relationships and classification of *Actinopterygii* (e.g., A. C. Gill and Mooi 2002; Stiassny et al. 2004; J. S. Nelson 2006), indicating the application of molecular data to the phylogenetics of fishes has lagged behind the study of other groups of vertebrates. Given the enormous diversity of *Actinopterygii*, their ecological divergence throughout nearly every available aquatic habitat, and the variety and extent of their phenotypic disparity, it is unsurprising that morphological studies have been unable to resolve many of the phylogenetic relationships within *Actinopterygii*.

Over the past 10 years molecular phylogenetics has significantly influenced the classification of *Actinopterygii* (Near, Eytan, et al. 2012; Wainwright et al. 2012; Near et al. 2013; W. L. Smith et al. 2016; Betancur-R et al. 2017; Dornburg and Near 2021). Studies based on nuclear and mitochondrial gene sequences are now complemented by those using comprehensive datasets of genomic sequences (e.g., Malmstrøm et al. 2016; Arcila et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022; Melo, Sidlauskas, et al. 2022; Glass et al. 2023). Phylogenomic data mitigate the issues that may mislead morphological studies; in particular, the data are extremely abundant and there are strategies to detect and accommodate incomplete lineage sorting, introgression, and paralogous loci (Bravo et al. 2019; Simion et al. 2020; M. L. Smith and Hahn 2022). The sheer size of genomic datasets is likely to compensate for random and systematic errors that affect phylogenetic inferences, simply by amplifying a consistent phylogenetic signal over any noise (Simion et al. 2020). Empirical support for this theory would be the repeated inference of the same phylogenetic relationships from different molecular datasets.

As phylogenetic studies of *Actinopterygii* using larger molecular datasets with inclusive taxonomic sampling became practical, a remarkable result has been the extent to which the molecular phylogenies of ray-finned fishes agree with one another (e.g., Miya et al. 2005; Near, Eytan, et al. 2012; Betancur-R et al. 2017; Chakrabarty et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022; Melo, Sidlauskas, et al. 2022). The results of independent phylogenetic analyses are not congruent in every respect, but an overall highly supported phylogeny of *Actinopterygii* has emerged from analysis of molecular data in the 21st century (Dornburg and Near 2021). The new consensus phylogeny supports traditional relationships such as the resolution of *Ostariophysi*, *Siluriformes*, *Esocidae*, *Acanthomorpha*, *Atheriniformes*, *Pleuronectoidei*, *Lophioidei*, and *Tetraodontoidei* as monophyletic groups, but includes relationships not inferred from traditional morphological studies across the entire phylogeny of *Actinopterygii* (Dornburg and Near 2021). The molecular consensus crucially provides unprecedented resolution in portions of the actinopterygian phylogeny that have been historically difficult to resolve, in particular among lineages of *Percomorpha* that formerly comprised the largest polytomy in vertebrate phylogenetics (Figure 1; G. J. Nelson 1989; A. C. Gill and Mooi 2002; Dornburg and Near 2021). Molecular phylogenies are also amenable to calibration with fossils to estimate divergence times and evolutionary rates, allowing insight into the mechanisms that generate biodiversity. The known fossil record for *Actinopterygii* is continually improving (Appendix 1). Fossil-calibrated phylogenies provide estimates of the timing of

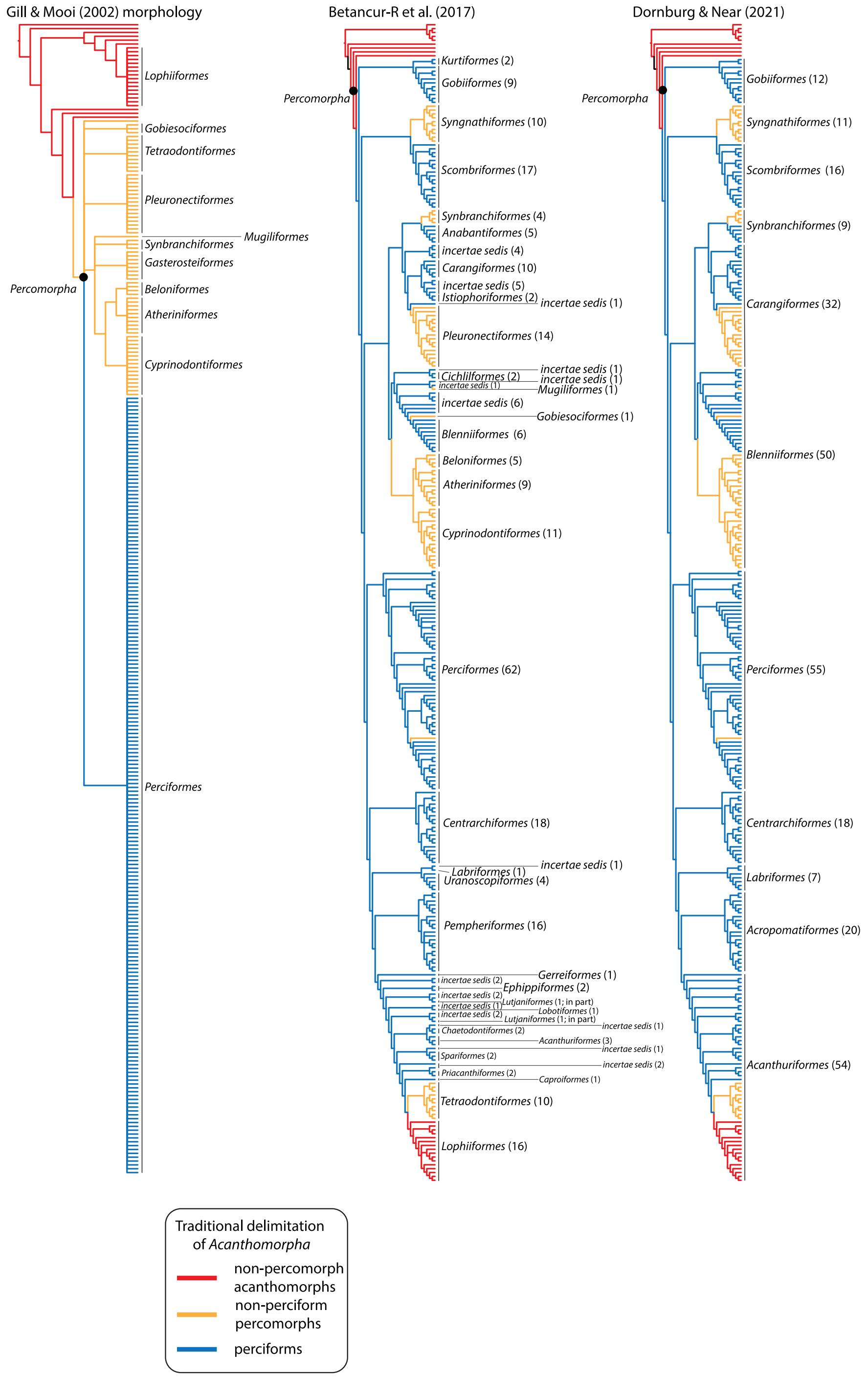

Figure 1. Comparison of phylogenies and classifications of *Acanthomorpha*. In the three phylogenies the colors of the branches indicate traditional classifications: red branches are non-percomorph acanthomorphs, orange branches are non-perciform *Percomorpha*, and blue branches are *Perciformes* (*sensu lato*). The phylogeny from A. C. Gill and Mooi (2002) is a summary hypothesis based on morphology. The phylogeny used to show the classifications of Betancur-R et al. (2017) and Dornburg and Near (2021) are based primarily on molecular studies. Numbers in parentheses indicate the number of taxonomic families.

diversification of ray-finned fishes, placing the origin of *Actinopterygii* in the Carboniferous (Giles et al. 2017, 2023) and highlighting the Eocene (56.0–33.9 Ma) as an important time in the diversification of percomorph fishes that dominate marine habitats (Ghezelayagh et al. 2022). Such inferences on the timing of lineage diversification would be impossible to resolve with morphological data alone. Instead, we may now use the time-calibrated phylogenies to understand the tempo and patterns of species diversification (e.g., Rincon-Sandoval et al. 2020; Troyer et al. 2022; Friedman and Muñoz 2023) and revisit the abundant, detailed morphological data available and interpret its evolution in the context of evolutionary patterns revealed by genomic-scale phylogenies (e.g., Nakae and Sasaki 2010; Chanet et al. 2013; M. G. Girard et al. 2020).

An important application of a robust phylogeny is to provide the framework for a classification. In the case of *Actinopterygii*, many of the lineages resolved in the 21st century molecular phylogeny had already been known and named in taxonomies based primarily on morphological inferences (e.g., Bleeker 1859; T. N. Gill 1872; Greenwood et al. 1966; J. S. Nelson 2006). Linnaean ranked classification requires the use of primary taxonomic categories: *Actinopterygii* is a Linnaean class, containing the ranks of order, family, genus, and species, each of which must be assigned for every taxon. In the Linnaean-ranked classification system of *Actinopterygii*, 28% of the approximately 515 taxonomic families are monotypic or monogeneric. In these cases, the family-group and genus names are redundant: both names refer to the same group of taxa. Consider the Salamanderfish (*Lepidogalaxias salamandroides*), which is the sister lineage of a clade containing more than 21,400 species of euteleost fishes (J. Li, Xia, et al. 2010; McDowall and Burridge 2011; Burridge et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Campbell, López, et al. 2013; Davis et al. 2016; W. L. Smith et al. 2016; Campbell, Alfaro, et al. 2017; Hughes et al. 2018; Straube et al. 2018; Rosas Puchuri 2021; Mu et al. 2022). In the Linnaean rank-based classification, *L. salamandroides* is classified as the only species in the family *Lepidogalaxiidae*, which is the only family in the order *Lepidogalaxiiformes*, which is the only order in the subcohort *Lepidogalaxii* (Betancur-R et al. 2017). In this taxonomy, *Lepidogalaxias*, *Lepidogalaxiidae*, *Lepidogalaxiiformes*, and *Lepidogalaxii* all have the same composition. Using these nested ranks to include the single species *Lepidogalaxias salamandroides* conveys no information and only lists several redundant group names.

An alternative to the Linnaean system is the unranked phylogenetically-based taxonomy outlined in the *PhyloCode* (Cantino and de Queiroz 2020). Use of the *PhyloCode* system prevents the proliferation of unnecessary and redundant group names and avoids the unsupported preconception that ranked categories have meaning apart from their exclusivity (de Queiroz and Gauthier 1990, 1992, 1994). In other words, it is easy to overlook that family-ranked taxa are not comparable to one another in any biologically or evolutionarily significant way; all a ranked taxon indicates is that any species within it are not included in any other taxon of equivalent rank. The *PhyloCode* is also strictly phylogenetic, a desirable characteristic that gives meaning to group names by explicitly tying them to clades. Clades in the *PhyloCode* are defined phylogenetically, differing from traditional Linnaean group names in they are defined in terms of ancestry and descent rather than being defined in terms of ranks and types. Each clade name is defined by at least two reference points on a phylogeny, either two taxa or a taxon and an apomorphy. The formulation of such phylogenetic definitions requires a comprehensive phylogenetic hypothesis. For *Actinopterygii*, such a hypothesis is now available, allowing for a transformation of the traditional classification of ray-finned fishes into a strictly phylogenetic framework that is as free as possible from redundant group names.

A landmark and ambitious Linnaean-ranked classification of *Actinopterygii* based on a phylogeny inferred from mtDNA and nuclear genes led to a proliferation of taxonomic orders and redundant group names (Betancur-R, Broughton, et al. 2013; Betancur-R et al. 2017). The proliferation of group names in Betancur-R et al. (2017) was a consequence of an effort to preserve traditional ordinal ranks for percomorph clades such as *Pleuronectiformes*, *Tetraodontiformes*, *Mugiliformes*, and *Cyprinodontiformes*. Because of their morphological disparity, these lineages were traditionally classified as taxonomic orders (e.g., A. C. Gill and Mooi 2002), set apart from the wastebin taxon *Perciformes* in morphology-based efforts (Figure 1). Molecular phylogenies resulted in the dramatic reallocation of lineages traditionally classified as *Perciformes* into nearly every major clade of *Percomorpha* (Figure 1), pushing traditional taxonomic orders such as *Tetraodontiformes*, *Gobiesociformes*, and *Synbranchiformes* from deeply nested positions into more apical resolutions in the phylogeny of *Percomorpha*. Within *Percomorpha*, the Betancur-R et al. (2017) classification delimits 34 taxonomic orders, each containing an average of only 7.4 taxonomic families; 13 of the 34 taxonomic orders contain only one or two families and only 10 of the orders have 10 or more families. In addition to delimiting less inclusive groups, the Betancur-R et al. (2017) classification treats 10% of all percomorph families as *incertae sedis* (Figure 1). The phylogenetic rank-free classification presented here delimits 16 major clades in *Percomorpha*, 13 of which are consistent with traditional taxonomic orders and contain an average of 21.8 lineages each that are treated as taxonomic families in rank-based classifications (Figure 1, Appendix 2; Dornburg and Near 2021; Ghezelayagh et al. 2022). The effort to maintain a handful of traditional taxonomic orders in *Percomorpha* in the Betancur-R et al. (2017) classification has resulted in a proliferation of "-iformes" group names that are neither inclusive nor phylogenetically informative (Figure 1).

Our goal in constructing a new rank-free classification of *Actinopterygii* is to build on and unify the punctuated progress made in the phylogenetics of ray-finned fishes in the 21st century (Dornburg and Near 2021). In this monograph, we consolidate and review the history of systematics and phylogenetics of the primary clades of ray-finned fishes, provide phylogenetic definitions for the names of 97 actinopterygian clades, introduce a summary phylogeny of 830 ray-finned fish lineages that includes 287 fossil taxa (Appendix 1), review information on species diversity in each clade, and provide a comprehensive list of constituent lineages for every major actinopterygian clade. We explicitly incorporate available phylogenies and whenever possible list diagnostic morphological apomorphies for each named clade. The new rank-free classification avoids redundant group names and attempts to preserve the exclusivity of clade names with -iformes, -oidei, and -oidea suffixes. For instance, clade names with an -iformes suffix are not nested in any other clade with a name ending in -iformes. In the phylogenetic trees, we list the genus name or the species binomial if a taxonomic family contains a single genus or species. In the clade accounts, we acknowledge the long history of the use of taxonomic families in ichthyology, listing all recognized taxonomic families but indicating those that are monotypic or monogeneric by identifying them with an asterisk as a redundant group name.

This new rank-free classification of *Actinopterygii* consolidates and reviews the systematic ichthyology literature of the past two centuries, builds on a consensus phylogenetic hypothesis of actinopterygian relationships, and constructs an explicit phylogenetic-based taxonomy that aims to be useful and flexible for researchers now and in the future. With this comprehensive phylogeny and classification, it is possible to investigate and communicate the overarching patterns of evolution within ray-finned fishes, which are rich in morphological complexity, ecological diversity, and biogeographic range. Combined with advances in comparative analyses that use time-calibrated molecular phylogenies, we are beginning to understand the tempo and characteristics of vertebrate evolution in aquatic habitats, across oceans and rivers, at the poles and the tropics, on coral reefs, and in environments from shallow shores to abyssal depths (e.g., Tedesco et al. 2017; Rabosky et al. 2018; Rincon-Sandoval et al. 2020; Melo, Sidlauskas, et al. 2022; E. C. Miller et al. 2022; Friedman and Muñoz 2023).

Materials and Methods

We develop a phylogeny-based classification of *Actinopterygii* following the principles of phylogenetic nomenclature outlined in the *PhyloCode* (de Queiroz and Gauthier 1990, 1992, 1994; Cantino and de Queiroz 2020), except where indicated. Articles (Art.), examples (Ex.), and recommendations (Rec.) are referred to as outlined in the *International Code of Phylogenetic Nomenclature* (*PhyloCode*) ver. 6 (Cantino and de Queiroz 2020). Following Rec. 6.1A, all scientific names of clades are italicized. This differs from the customary practice of only italicizing the genus and species names. Most of the clades presented and reviewed in this monograph are defined as minimum-crown-clades that have at minimum two internal specifiers that are both extant (Arts. 9.5 and 9.9). If there is uncertainty about the early branching history of a well-established clade, more than two specifiers are used (Art. 9.5). In a few instances, external specifiers (Art. 11.13, Ex. 1) are used to prevent the use of a clade name under specific phylogenetic hypotheses.

In following the requirements for establishing clade names (Art. 7), we provide a protologue (Art. 7.2, N. 7.2.1) for each clade name that provides everything associated with the name as it is established according to the requirements of the *PhyloCode*. The terms protologue and clade account are used interchangeably in this monograph. In this classification of *Actinopterygii* each protologue contains 10 sections.

The **definition** is the statement that explicitly identifies a clade as the referent of the taxon name and includes at least two specifiers (Art. 9.4). Original author citations are provided for each specifier.

Etymology is an attempt to trace the linguistic origin of clade names. Most of the clade names originate in ancient Greek, and we provide the original spelling following reference texts (D. W. Thompson 1947; Liddell et al. 1968). When the original spelling is ancient Greek, we provide a phonetic spelling of the word using the International Phonetic Alphabet (IPA 1999).

The **registration number** is the product of the required submission of the clade name to the official registration database (Art. 8.1). All the clade names and associated information tied to the clade definitions were submitted to the online RegNum database (Cellinese and Dell 2020), which is the official registry of clade names in *PhyloCode*. No registration number is given for the 11 clades that are not defined using the *PhyloCode*.

The **reference phylogeny** is a specific phylogenetic hypothesis that provides the basis and context for applying a clade name in the phylogenetic definition (Art. 7.2). The reference phylogenies were selected on the basis of taxonomic coverage and the inclusion of appropriate specifiers. Phylogenies resulting from an explicit and reproduceable analysis were the only ones considered (Rec. 9.13A). The reference phylogenies come from a total of 34 phylogenetic studies. Among the 97 clade accounts, the reference phylogeny for 46 clades are based on analysis of genomic data, 33 are based on analyses of Sanger-sequenced molecular data, 11 clades are defined using phylogenies inferred from combined molecular and morphological datasets, and seven clades are defined on the basis of phylogenies inferred from morphological characters alone. A synthetic phylogeny of 830 lineages of *Actinopterygii* was constructed using published phylogenetic trees in an agglomerative procedure (Beaulieu et al. 2012). All the phylogenetic studies used to construct the synthetic tree are cited among the clade accounts. The tree file in Newick is available at the Dryad data repository (Near and Thacker 2023). In the reference phylogeny section, we refer to the figure number in this monograph where the relationships of a given clade are shown and citations are provided to justify the placement of any fossil taxa in the phylogenies (Appendix 1). The absolute age intervals of the epochs, ages, and stages of the fossil record follow the Geologic Time Scale 2020 (Gradstein and Ogg 2020). In the **phylogenetics** section we provide a brief history of the systematics of the clade. Often this is the longest section of the clade account.

The **composition** of the clade includes a statement as to the current recognized species diversity and a listing of all the named major subclades of the named clade. There are no redundant group names listed in this section. If a taxonomic family in the Linnaean ranked system is monotypic or monogeneric, the species binomial or the genus name is provided. The names of fossil taxa within each named clade that are not nested in a subclade not defined in the classification are included in the phylogenetic trees and listed in the clade composition. We also highlight recent biodiversity discoveries by listing the number of new species described over the past 10 years (2013–2023).

Diagnostic apomorphies lists morphological traits that investigators have offered as diagnostic for the clade. While not required to establish a clade name in *PhyloCode*, we acknowledge the rich history of morphological phylogenetics in ichthyology that has resulted in hypothesized morphological synapomorphies for many of the clades reviewed here. In providing this information we make no judgment on the veracity of the characters but rely on dozens of studies that list morphological characters as diagnostic for the clades named and reviewed here.

A **synonym** is a name that has a spelling that is different from another name that refers to the same taxon (Art. 14.1). We differentiate three types of synonyms. Ambiguous synonyms are two names that are spelled differently for the same clade with the same taxa contained in that clade but were not given explicit phylogenetic definitions. Approximate synonyms are very close to the same clade and the content may slightly differ. Partial synonyms could be names for paraphyletic groups that exclude a part of the crown or other examples where some portion of the defined clade content is not included in the group delimited by the partial synonym.

The **comments** section provides space to discuss aspects of the phylogenetics or biology of a clade that merit highlighting. In addition, we attempt to list the earliest fossil occurrences of the clade and provide information on any molecular age estimate for the lineage.

The **constituent lineages** section provides a tabulation of all the major taxa comprising the defined clade. Any taxonomic families listed that are monotypic or monogeneric are marked with an asterisk as redundant group names. All names that are defined as clade names or listed in a protologue that have the suffix of -oidea, -idae, -inae, or -ini are valid family-group names under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014).

Our approach to constructing a rank-free classification of *Actinopterygii* necessitated a slight deviation from the principles and rules of the *PhyloCode*. While committed to maximizing the benefits of a classification that avoids redundant names, we have chosen a tempered approach that aims to accommodate traditional aspects of systematic ichthyology. Our classification is fully rank-free, but we use names with suffixes that include -formes, -oidei, and -oidea that are traditionally used for ranks of order, suborder, and superfamily. In avoiding the nesting of group names with the same suffixes, we maintain the exclusivity of those names, which requires replacement of the suffixes of several names in current usage. For example, we use *Lophioidei* and *Tetraodontoidei* in favor of *Lophiiformes* and *Tetraodontiformes* to avoid nesting these groups in *Acanthuriformes*. Because this is counter to *PhyloCode's* Principle 4 on stability, we do not use the *PhyloCode* in defining *Gadoidei*, *Atheriniformes*, *Atherinoidei*, *Belonoidei*, *Cyprinodontoidei*, *Pleuronectoidei*, *Lophioidei*, and *Tetraodontoidei*. We also do not use the *PhyloCode* in defining *Salmoniformes*, *Esocidae*, and *Gadiformes* because our delimitations of these groups would require the application of new group names.

In this classification we aim to preserve the nomenclatural history of actinopterygian systematics by retaining preexisting names for clades as much as possible. Among the 97 clade names in this classification, only one (*Oseanacephala*) is new and only seven other clade names date to the 21st century (*Acropomatiformes*, *Apogonoidei*, *Cithariniformes*, *Eupercaria*, *Ovalentaria*, *Stomiatii*, and *Zoarcoidea*). Forty-five of the group names were introduced from 1700 to 1900 CE, 19 names date from 1901 to 1950 CE, 25 group names were introduced between 1951 and 2000 CE, and 8 group names date from 2001 to 2022 CE. Seven of the 97 clade definitions were initially published in the *PhyloCode* companion volume (de Queiroz et al. 2020b; Lundberg 2020a, 2020b, 2020d; Moore and Near 2020a, 2020b, 2020c, 2020f) and are included here with any additional information to make the accounts uniform with the 90 new clade accounts.

Clade Accounts

Actinopterygii A. S. Woodward 1891:423

[J. A. Moore and T. J. Near 2020b]

Definition. Defined as a minimum-crown-clade by Moore and Near (2020b) as: "The least inclusive crown clade that contains *Polypterus bichir* Lacépède 1803, *Acipenser sturio* Linnaeus 1758, *Psephurus gladius* (Martens 1862), *Lepisosteus osseus* (Linnaeus 1758), *Amia calva* Linnaeus 1766, and *Perca fluviatilis* Linnaeus 1758."

Etymology. From the ancient Greek ἀκτίς (ˈæktɪs), meaning ray or beam, and πτερὸν (tˈɛɹɑːn), meaning fin or wing.

Registration number. 206.

Reference phylogeny. Diogo (2007, figs. 3, 4) was designated as the primary reference phylogeny by Moore and Near (2020b). See Figures 2 and 3 for a summary phylogeny of major clades in *Actinopterygii*. The placement of †*Scanilepiformes* is supported in phylogenetic analyses of morphological characters (Giles et al. 2017, 2023; Latimer and Giles 2018).

Phylogenetics. The earliest phylogenetic investigations of *Actinopterygii* involved the secondary mapping of morphological character state changes onto tree topologies that placed *Polypteridae* (bichirs and ropefish) as the sister group of *Actinopteri* (e.g., Rosen et al. 1981; Patterson 1982; Lauder and Liem 1983; Gardiner 1984). The earliest phylogenetic analyses of morphological data matrices resolved *Polypteridae* as an actinopterygian and placed several Devonian fossil taxa (e.g., †*Mimia*, †*Howqualepis*, †*Moythomasia*, and †*Kentuckia*) as crown lineage *Actinopterygii* (Gardiner and Schaeffer 1989; Coates 1999; Gardiner et al. 2005; Xu, Gao, et al. 2014; Caron et al. 2023). The status of these Devonian taxa as crown clade actinopterygians was dramatically overturned by more recent morphological phylogenetic analyses that resolve numerous Devonian-Triassic taxa as stem lineage actinopterygians and place *Polypteridae* as nested within the Triassic-aged pan-scanilepiforms or as the sister group of †*Scanilepiformes* (Giles et al. 2017, 2023; Argyriou et al. 2018, 2022; Latimer and Giles 2018; Ren and Xu 2021). From the first molecular phylogenetic studies of ray-finned fishes to the most recent phylogenomic studies (e.g., Normark et al. 1991; Hughes et al. 2018), *Actinopterygii* is resolved as monophyletic with *Polypteridae* as the sister lineage of *Actinopteri* (Inoue et al. 2003a; Kikugawa et al. 2004; Alfaro, Santini, et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; M.-Y. Chen et al. 2015; Hughes et al. 2018; Vialle et al. 2018; Wcisel et al. 2020; Bi et al. 2021). In contrast to the consistent resolution of *Polypteridae* as the sister lineage of all other living *Actinopterygii* in molecular studies, some morphological phylogenetic analyses that include fossil taxa resolve a clade with low node support containing *Polypteridae*, †*Scanilepiformes*, pan-acipenseriforms, and *Acipenseriformes* (Argyriou et al. 2018; Latimer and Giles 2018; Caron et al. 2023; Giles et al. 2023).

Composition. *Actinopterygii* includes more than 35,085 living species (Fricke et al. 2023) classified in *Polypteridae* and *Actinopteri*. Fossil taxa within *Actinopterygii* include †*Scanilepiformes* (Appendix 1; Sytchevskaya 1999; Xu and Gao 2011; Giles et al. 2017). Appendix 1 provides details of the ages and locations of the fossil scanilepiforms. Over the past 10 years 3,657 new living species of *Actinopterygii* have been described (Fricke et al. 2023), comprising 10.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Actinopterygii* include (1) cerebellum with corpus cerebelli, auricle, and valvula (Gardiner 1973; Løvtrup 1977:175), (2) teeth with apical cap of acrodin (Ørvig 1978; Rosen et al. 1981; Patterson 1982), (3) absence of superficial constrictors on gill arches (Wiley 1979), (4) presence of obliqui ventrales branchial muscle (Wiley 1979), (5) origin of coracomandibularis on branchial arch 3 (Wiley 1979), (6) adductor operculi continuous with adductor hyomandibulae (Lauder 1980), (7) adductor arcus palatini absent (Lauder 1980), (8) pelvic plate and two series of radials present (Patterson 1982), (9) anterodorsal process on scales (Patterson 1982),

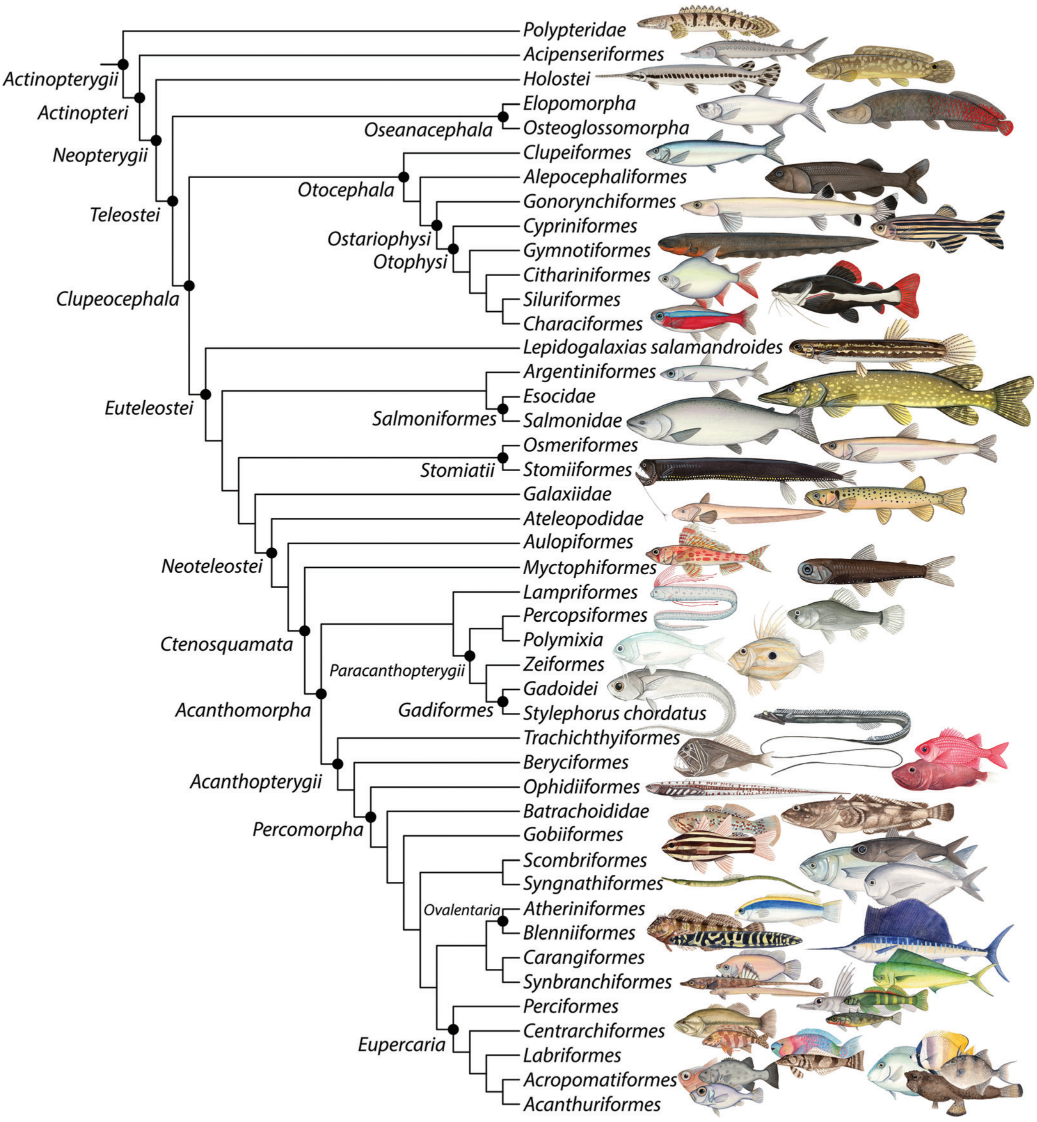

Figure 2. Phylogenetic relationships of the major living lineages of *Actinopterygii*, *Actinopteri*, *Neopterygii*, *Teleostei*, *Oseanacephala*, *Clupeocephala*, *Otocephala*, *Ostariophysi*, *Otophysi*, *Euteleostei*, *Salmoniformes*, *Stomiatii*, *Neoteleostei*, *Ctenosquamata*, *Acanthomorpha*, *Paracanthopterygii*, *Gadiformes*, *Acanthopterygii*, *Percomorpha*, *Ovalentaria*, and *Eupercaria*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts.

(10) a slender peg-and-socket articulation between scales (Patterson 1982), (11) autosphenotic ossified in postorbital process, autosphenotic and dermosphenotic fused (Patterson 1982), (12) single hyomandibular articulation above jugal canal (Patterson 1982), (13) postcleithrum present (Patterson 1982; Coates 1998), (14) prismatic ganoine on scales (Gardiner and Schaeffer 1989; Coates 1999), (15) three or more supraorbitals (Giles et al. 2017), (16) one or two infradentaries (Giles et al. 2017), (17) coronoid process of lower jaw present (Giles et al. 2017), (18) palatoquadrate with separate centers of ossification (Giles et al. 2017), (19) palate with

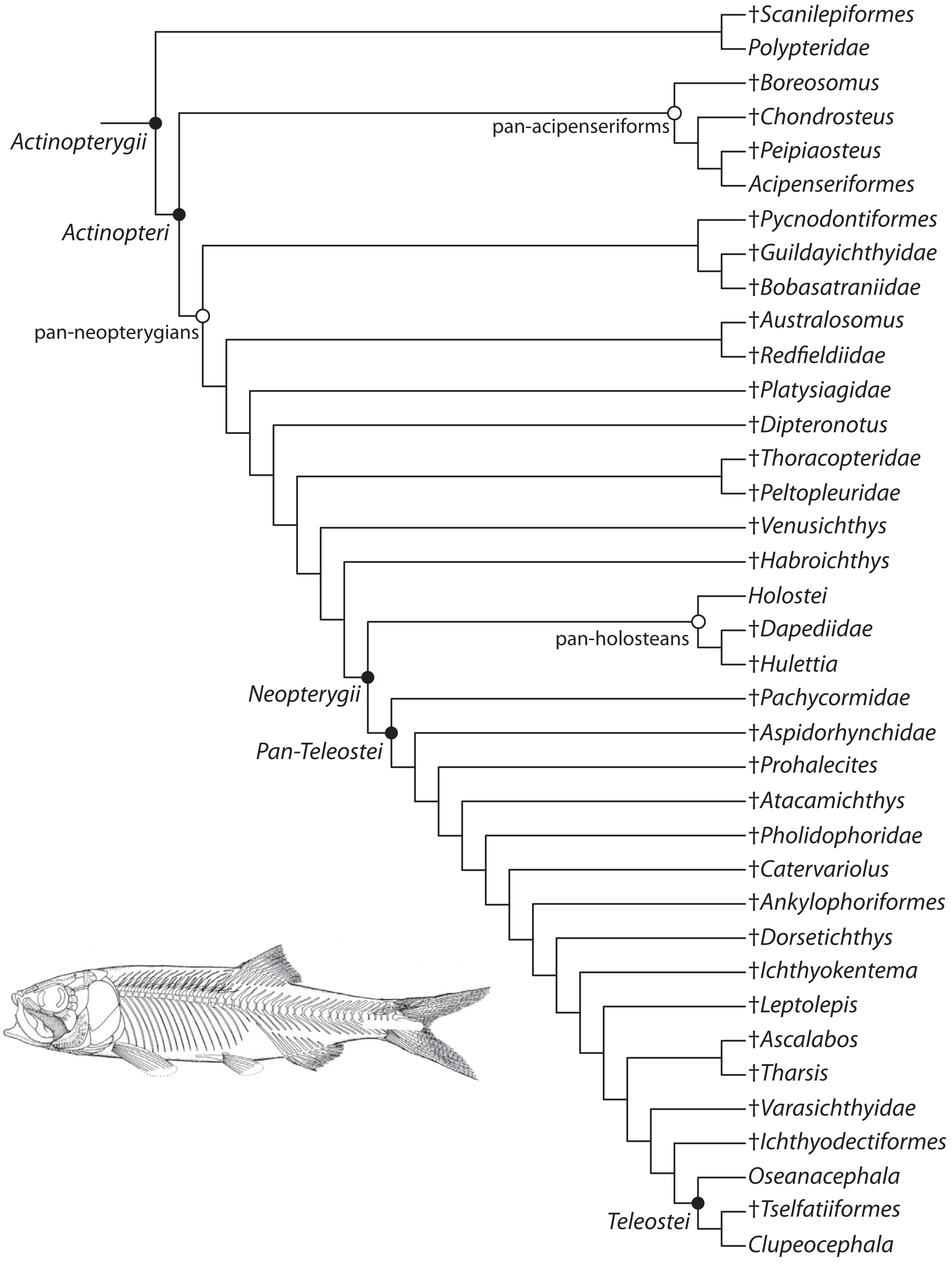

Figure 3. Phylogenetic relationships of the major living lineages and fossil taxa of *Actinopterygii*, *Actinopteri*, *Neopterygii*, *Pan-Teleostei*, and *Teleostei*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1. The clade description of *Pan-Teleostei* is presented in Moore and Near (2020e). The illustration of †*Leptolepis coryphaenoides* is reproduced with permission from Arratia (1996b).

flat dorsal margin (Giles et al. 2017), (20) narrow interorbital septum (Giles et al. 2017), (21) roof of posterior myodome perforated by palatine branch of facial nerve (Giles et al. 2017), (22) median posterior myodome present (Giles et al. 2017), (23) dermal component to basipterygoid process present (Giles et al. 2017), (24) parasphenoid extends to basioccipital (Giles et al. 2017), (25) ascending process of parasphenoid process present (Giles et al. 2017), (26) proximal segments of pectoral fin elongate with terminal segmentation (Giles et al. 2017); (27) proximal radials of dorsal fin enlarged (Giles et al. 2017); (28) constrictor mandibularis dorsalis attaches to the hyoid arch (Datovo and Rizzato 2018); and (29) constrictor mandibularis has an insertion on the lateral face of the palatoquadrate (Datovo and Rizzato 2018).

Synonyms. There are no synonyms of *Actinopterygii*.

Comments. *Actinopterygii* represents one of the major lineages of living vertebrates and along with *Sarcopterygii* comprises *Osteichthyes* (Rosen et al. 1981; Stiassny et al. 2004; Bertrand and Escrivá 2014; Moore and Near 2020d). When *Actinopterygii* was first introduced as a group name it excluded *Polypteridae* and had a composition identical to *Actinopteri* (Woodward 1891:423). Citing evidence from the morphology of scales, dermal bones of the head, the skull, nostrils, median fins, and paired fins and girdles, Goodrich (1928) considered *Polypteridae* as a group within *Actinopterygii*. By the 1980s the concept of *Actinopterygii* as comprising *Polypteridae* and *Actinopteri* was solidified in studies and reviews of morphological evidence (Rosen et al. 1981; Patterson 1982).

The earliest actinopterygian fossil taxon is †*Platysomus superbus* from the Visean (346.7–330.0 Ma) in the Carboniferous of Scotland, UK (C. D. Wilson et al. 2021). The inferred phylogenetic relationships of †*Platysomus* vary among morphological studies, but the taxon is consistently resolved as a lineage of *Actinopterygii* (Giles et al. 2017, 2023; Argyriou et al. 2018, 2022; Latimer and Giles 2018). Bayesian relaxed molecular clock age estimates for the crown age of *Actinopterygii* range between 333.5 and 384.1 million years ago, extending across the Devonian-Carboniferous boundary (Giles et al. 2017).

Constituent lineages.
Actinopteri
†*Scanilepiformes*
Polypteridae

Polypteridae C. L. Bonaparte 1835
[in Bonaparte 1840]:188–189
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade that contains *Erpetoichthys calabaricus* J. A. Smith 1865:2 and *Polypterus bichir* Lacepède 1803. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek πουλύς (pˈuːləs), meaning many, and πτερόν (tˈɛɹɑːn), meaning wing.

Registration number. 851.

Reference phylogeny. A phylogeny inferred from DNA sequences of eight concatenated Sanger-sequenced nuclear genes (Near, Dornburg, Tokita, et al. 2014, fig. 1). A phylogeny of all species of *Polypteridae* is shown in Figure 4.

Phylogenetics. All species of *Polypteridae* are included in phylogenies inferred from mtDNA and Sanger-sequenced nuclear genes (Figure 4; Suzuki et al. 2010; Near, Dornburg, Tokita, et al. 2014).

Composition. There are currently 14 living species of *Polypteridae* that includes *Erpetoichthys calabaricus* and 13 species of *Polypterus* (Moritz and Britz 2019). Over the past 10 years no new living species of *Polypteridae* have been described (Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Polypteridae* include (1) larvae with external gills that originate outside the branchial cavity (Daget 1950; Stundl et al. 2019), (2) single basibranchial (Jarvik 1980; Carvalho et al. 2013), (3) separate dorsal finlets (Daget 1950; Jarvik 1980; Gardiner and Schaeffer 1989; Coelho et al. 2018), (4) putative dorsal ribs (Britz and Bartsch 2003), (5) occipital bone

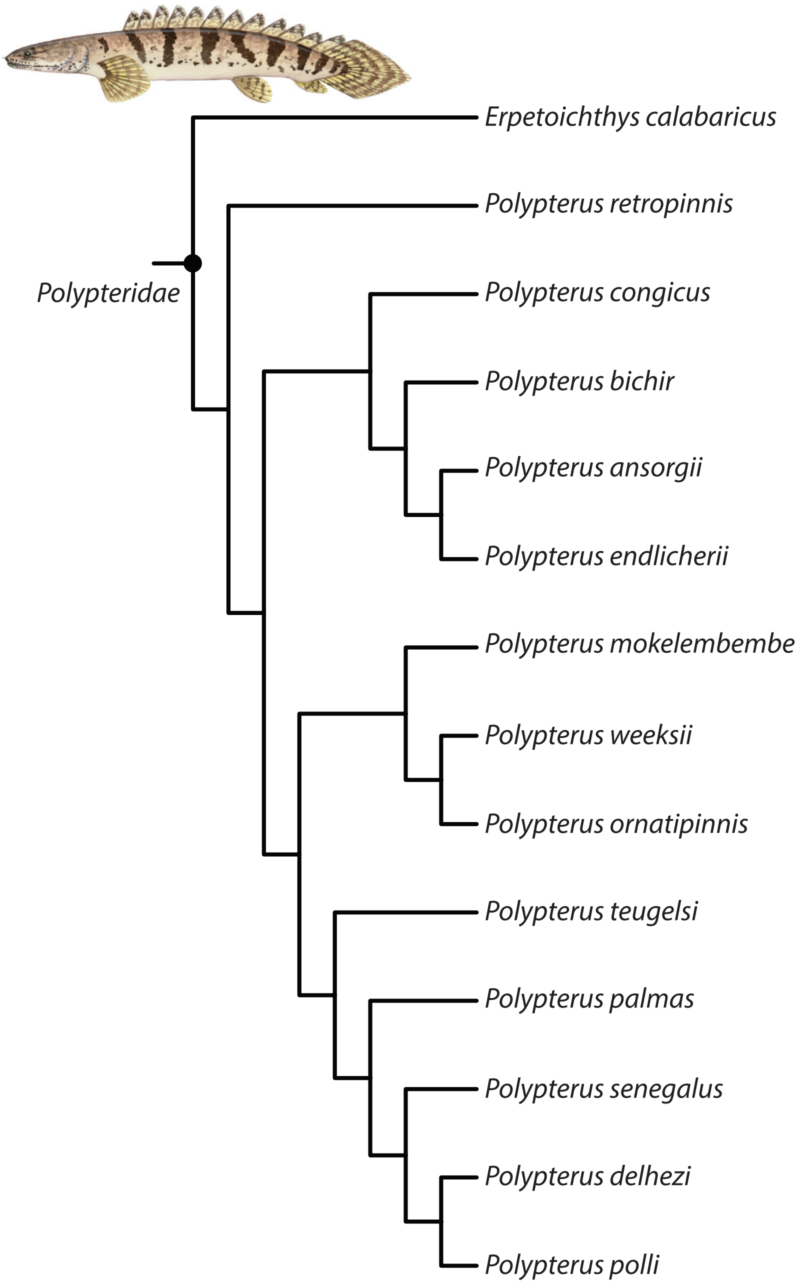

Figure 4. Phylogenetic relationships of the species of *Polypteridae*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts.

that articulates posteriorly with centrum of second vertebra (Britz and Johnson 2010), (6) spiracular canal absent (Gardiner et al. 2005), (7) ascending process of parasphenoid fused to otic region and not related to spiracle (Gardiner et al. 2005), (8) parasphenoid with aortic canal (Gardiner et al. 2005), (9) parietals absent, dermopterotics meet (Gardiner et al. 2005), (10) maxilla with superimposed infraorbital canal and dorsal arm of preopercular greatly expanded (Gardiner et al. 2005), (11) coronoid process of lower jaw composed exclusively of prearticular (Gardiner et al. 2005; Giles et al. 2017), (12) optic foramen adjacent to dorsal margin of parasphenoid (Giles et al. 2017), (13) broad interorbital septum (Giles et al. 2017), (14) lateral process present on ectopterygoid (L. Grande 2010; Giles et al. 2017), (15) four ceratobranchials (Britz and Johnson 2003; Giles et al. 2017), (16) loss of fulcra of caudal fin (Patterson 1982; Giles et al. 2017), (17) three pairs of extrascapulars (Gardiner and Schaeffer 1989; Giles et al. 2017), and (18) constrictor mandibularis dorsalis, levator arcus palatini is differentiated into partes interna and externa (Datovo and Rizzato 2018).

Synonyms. *Brachiopterygii* (G. J. Nelson 1969a, fig. 25), *Cladistia* (Rosen et al. 1981, fig. 62; Betancur-R et al. 2017:9), and *Polypteriformes* (J. S. Nelson et al. 2016:116; Betancur-R et al. 2017:9) are ambiguous synonyms of *Polypteridae*.

Comments. Bonaparte (1840) applied the group name *Polypterini* as a subfamily of *Lepidosteidae*, which is a synonym of *Lepisosteidae*. The delimitation of *Polypteridae* as containing *Polypterus* and *Erpetoichthys calabaricus* presented here was frequently used by ichthyologists in the second half of the 19th though the early 20th century (Günther 1870:326–331, 1880:364; Bridge 1904:481–485; Boulenger 1909:4; Goodrich 1909:300). We selected the name *Polypteridae* as the clade name over its synonyms because it is the name most frequently applied to a taxon approximating the named clade. *Polypteridae* is the living sister lineage of all other actinopterygians (*Actinopteri*) and results from relaxed molecular clock analyses that estimate the common ancestry of these two lineages dates to an interval between 333.5 and 384.1 million years ago (Giles et al. 2017).

In contrast to the ancient divergence of *Polypteridae* and *Actinopteri*, the earliest pan-polypterid fossils date to the Cenomanian (100.5–93.9 Ma) of the Upper Cretaceous (Daget et al. 2001; Gayet et al. 2002; Near, Dornburg, Tokita, et al. 2014), implying a gap in the fossil record of polypterids that spans at least 240 million years. All extant species of *Polypteridae* live in the freshwaters of western and central Africa, although pan-polypterid fossils are known from both Africa and South America (Gayet and Meunier 1991, 1992; Meunier and Gayet 1996; Daget et al. 2001; Otero et al. 2009). Time-calibrated multi-species coalescent analyses estimate a relatively recent time to common ancestry for the living species of *Polypteridae*, spanning the Miocene and early Oligocene between 13.6 and 24.9 million years ago (Near, Dornburg, Tokita, et al. 2014). *Polypteridae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:27).

Constituent lineages.
Erpetoichthys calabaricus
Polypterus

Actinopteri E. D. Cope 1871:587
[J. A. Moore and T. J. Near 2020]

Definition. Defined as a minimum-crown-clade by Moore and Near (2020a) as: “The least inclusive crown clade that contains *Acipenser sturio* Linnaeus 1758, *Psephurus gladius* (Martens 1862), *Lepisosteus osseus* (Linnaeus 1758), *Amia calva* Linnaeus 1766, and *Perca fluviatilis* Linnaeus 1758.”

Etymology. From the ancient Greek ἀκτίς (ˈæktɪs), meaning ray or beam, and πτερὀν (tˈɛɹɑːn), meaning fin or wing.

Registration number. 208.

Reference phylogeny. Diogo (2007, figs. 3, 4) was designated as the primary reference phylogeny by Moore and Near (2020a). See Figures 2 and 3 for summary phylogenies of major clades in *Actinopteri*. The placements of the stem-acipenseriforms †*Pycnodontiformes*, †*Guildayichthyidae*, †*Bobasatraniidae*, †*Australosomus*, †*Redfieldiidae*, †*Platysiagidae*, †*Dipteronotus*, †*Peltopleuridae*, †*Thoracopteridae*, †*Venusichthys*, and †*Habroichthys* are on the basis of phylogenetic analyses of morphological characters (L. Grande and Bemis 1991, 1996; Bemis et al. 1997; Lund 2000; Hilton and Forey 2009; Mickle et al. 2009; Hilton et al. 2011; Xu et al. 2012; Poyato-Ariza 2015; Xu and Ma 2016; Xu and Zhao 2016; Giles et al. 2017, 2023; Xu 2021; Shedko 2022; Yuan et al. 2022).

Phylogenetics. The earliest phylogenetic investigations of *Actinopteri* involved the secondary mapping of morphological character state changes onto tree topologies that placed chondrosteans (*Acipenseriformes*) and *Neopterygii* (*Holostei* and *Teleostei*) as sister lineages (Rosen et al. 1981; Patterson 1982; Lauder and Liem 1983; Gardiner 1984). Phylogenetic analyses of morphological data matrices corroborate the monophyly of *Actinopteri* (Coates 1999; Gardiner et al. 2005; Xu, Gao, et al. 2014; Poyato-Ariza 2015; Giles et al. 2017; Latimer and Giles 2018). Several molecular studies ranging from analyses of whole mtDNA genomes, samples of Sanger-sequenced nuclear genes, and phylogenomic analyses resolve *Actinopteri* as a monophyletic group (Inoue et al. 2003a; Kikugawa et al. 2004; Alfaro, Santini, et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; M.-Y. Chen et al. 2015; Hughes et al. 2018; Vialle et al. 2018; Wcisel et al. 2020; Bi et al. 2021; Mu et al. 2022).

Composition. *Actinopteri* includes 35,075 living species classified in the subclades *Acipenseriformes* and *Neopterygii*. Fossil taxa within *Actinopteri* include the pan-acipenseriforms †*Boreosomus*, †*Chondrosteus*, and †*Peipiaosteus*; and the pan-neopterygians †*Australosomus*, †*Bobasatraniidae*, †*Dipteronotus*, †*Guildayichthyidae*, †*Habroichthys*, †*Peltopleuridae*, †*Platysiagidae*, †*Pycnodontiformes*, †*Redfieldiidae*, †*Thoracopteridae*, and †*Venusichthys*. Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years 3,675 new living species of *Actinopteri* have been described (Fricke et al. 2023), comprising 10.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Actinopteri* include (1) perforated propterygium (Patterson 1982), (2) bases of marginal rays or pectoral fin embracing propterygium (Patterson 1982), (3) basal fulcra on dorsal margin of caudal fin (Patterson 1982), (4) fringing fulcra on median fins (Patterson 1982), (5) supra-angular bone present on lower jaw (G. J. Nelson 1973; Patterson 1982), (6) presence of spiracular canal in braincase (Patterson 1982), (7) swim bladder with dorsal connection to foregut (Patterson 1982), (8) hemopoietic organ above medulla (Patterson 1982), (9) diffuse pancreas (Patterson 1982), (10) olfactory rosette (Patterson 1982), (11) supratemporal fused with intertemporal forming dermopteric (Coates 1999), (12) fewer than 12 or 13 branchiostegal rays or plates (Coates 1999), (13) posterior parasphenoid expanded to cover ventral otic fissure (Coates 1999), (14) post-temporal fossa (Xu, Gao, et al. 2014), (15) basipterygoid process absent (Xu, Gao, et al. 2014), (16) quadratojugal overlaying quadrate (Xu, Gao, et al. 2014), (17) loss of presupracleithrum (Xu, Gao, et al. 2014), (18) dorsal aorta open in groove (Giles et al. 2017), (19) cerebellar corpus undivided (Giles et al. 2017), (20) cerebellar corpus with median anterior projecting portion (Giles et al. 2017), (21) hour-glass shaped medial constriction of anterior ossification of ceratohyal (Giles et al. 2017), and (22) uncinate processes on epibranchials (Giles et al. 2017).

Synonyms. *Actinopterygii* as delimited in Boulenger (1891:10), Woodward (1891:423), Dean (1895:8), McAllister (1968:18–20), G. J. Nelson (1969a:534), J. S. Nelson (1976:58; 1984:77–78) Løvtrup (1977:170–176), and Forey (1980:378) excluded *Polypteridae* and is therefore an approximate synonym of *Actinopteri*. Garstang (1931:255–256) introduced the group name *Epipneusta*, containing *Acipenseriformes*, *Holostei*, and *Teleostei*; *Epipneusta* is an approximate synonym of *Actinopteri*.

Comments. Cope's (1871b) first delimitation of *Actinopteri* included *Acipenseriformes*, *Holostei*, and *Teleostei* and is identical to the composition of the clade described here. Later Cope (1877b) modified *Actinopteri* to include only *Holostei* and *Teleostei*, but subsequent classifications used Cope's (1871b) initial concept of *Actinopteri* to include *Acipenseriformes*, *Holostei*, and *Teleostei* (Jordan 1905; Gregory 1907). After the application of phylogenetic systematics to the study of ray-finned fishes, *Actinopteri* was reintroduced to include all living actinopterygians except *Polypteridae* (Patterson 1982). The earliest fossils of *Actinopteri* are the pan-neopterygian guildayichthyids †*Discoserra pectinodon* and †*Guildayichthys carnegiei* from the Serpukhovian (330.3–323.4 Ma) in the Carboniferous of Montana, USA (Lund 2000; Mickle et al. 2009). Bayesian relaxed molecular clock analyses estimate a crown age of *Actinopteri* between 309 and 357 million years ago (Giles et al. 2017).

Constituent lineages.

Acipenseriformes
Neopterygii
†*Australosomus*
†*Bobasatraniidae*
†*Boreosomus*
†*Chondrosteus*
†*Dipteronotus*
†*Guildayichthyidae*
†*Habroichthys*
†*Peipiaosteus*
†*Peltopleuridae*
†*Platysiagidae*
†*Pycnodontiformes*
†*Redfieldiidae*
†*Thoracopteridae*
†*Venusichthys*

Acipenseriformes L. S. Berg 1940:408–409
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Acipenser sturio* Linnaeus 1758 and *Polyodon spathula* (Walbaum 1792). This is a minimum-crown-clade definition.

Etymology. *Acipenser* is the Latin name for sturgeon, which is derived from the ancient Greek ἀκκιπήσιος (D. W. Thompson 1947). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 879.

Reference phylogeny. A phylogeny inferred from a dataset of combined molecular and morphological characters (Shedko 2022, fig. 1). See Figures 2 and 3 for the relationship of *Acipenseriformes* among the major lineages of *Actinopterygii*. See Figure 5A for a summary phylogeny of the major lineages of *Acipenseriformes*. Placements of the fossil acipenseriform taxa in the phylogeny are based on the results of morphological phylogenetic analyses (L. Grande and Bemis 1991, 1996; Bemis et al. 1997; Hilton and Forey 2009; Hilton et al. 2011).

Phylogenetics. The earliest phylogenetic trees that show a monophyletic *Acipenseriformes* were inferred from a distribution of derived character states without an analysis of a coded character data matrix using an explicit optimality criterion (e.g., G. J. Nelson 1969a; Lauder and Liem 1983). Morphological and molecular phylogenies consistently resolve *Acipenseriformes* as monophyletic (e.g., L. Grande and Bemis 1996; Inoue et al. 2003a; Artyukhin 2006; Alfaro, Santini, et al. 2009; Hilton and Forey 2009; Broughton 2010; Hilton et al. 2011; Near, Eytan, et al. 2012; Giles et al. 2017, 2023; Hughes et al. 2018; Y. Shen et al. 2020; Shedko 2022).

Composition. *Acipenseriformes* includes 28 living species (Fricke et al. 2023) classified in *Acipenseridae* and *Polyodontidae*. The number of living species does not include the recently declared extinct Chinese Paddlefish, *Psephurus gladius* (H. Zhang et al. 2020). The fossil taxa †*Protopsephurus* and †*Paleopsephurus* are resolved in morphological phylogenies as pan-polyodontids, that is, outside of the crown clade *Polyodontidae* (L. Grande and Bemis 1991, 1996). †*Priscosturion* is resolved as either a pan-acipenserid or nested within *Acipenseridae* as the sister lineage of *Scaphirhynchus* (L. Grande and Hilton 2006; Hilton et al. 2011; Shedko 2022; Murray et al. 2023). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years no new living species of *Acipenseriformes* have been described (Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Acipenseriformes* include (1) loss of opercle (L. Grande and Bemis 1996; Bemis et al. 1997), (2) fewer than four branchiostegal rays (L. Grande and Bemis 1996; Bemis et al. 1997), (3) endocranium with extensive rostrum (L. Grande and Bemis 1996; Bemis et al. 1997), (4) dorsal and ventral rostral bones (L. Grande and Bemis 1996; Bemis et al. 1997; Hilton et al. 2011), (5) posttemporal bone with a ventral process (L. Grande and Bemis 1996; Bemis et al. 1997), and (6) absence of constrictor mandibularis dorsalis connection to palatoquadrate (Datovo and Rizzato 2018).

Synonyms. *Acipenseroidei* (L. Grande and Bemis 1991:113, 1996:107; Bemis et al. 1997:51–53) is an ambiguous synonym of *Acipenseriformes*.

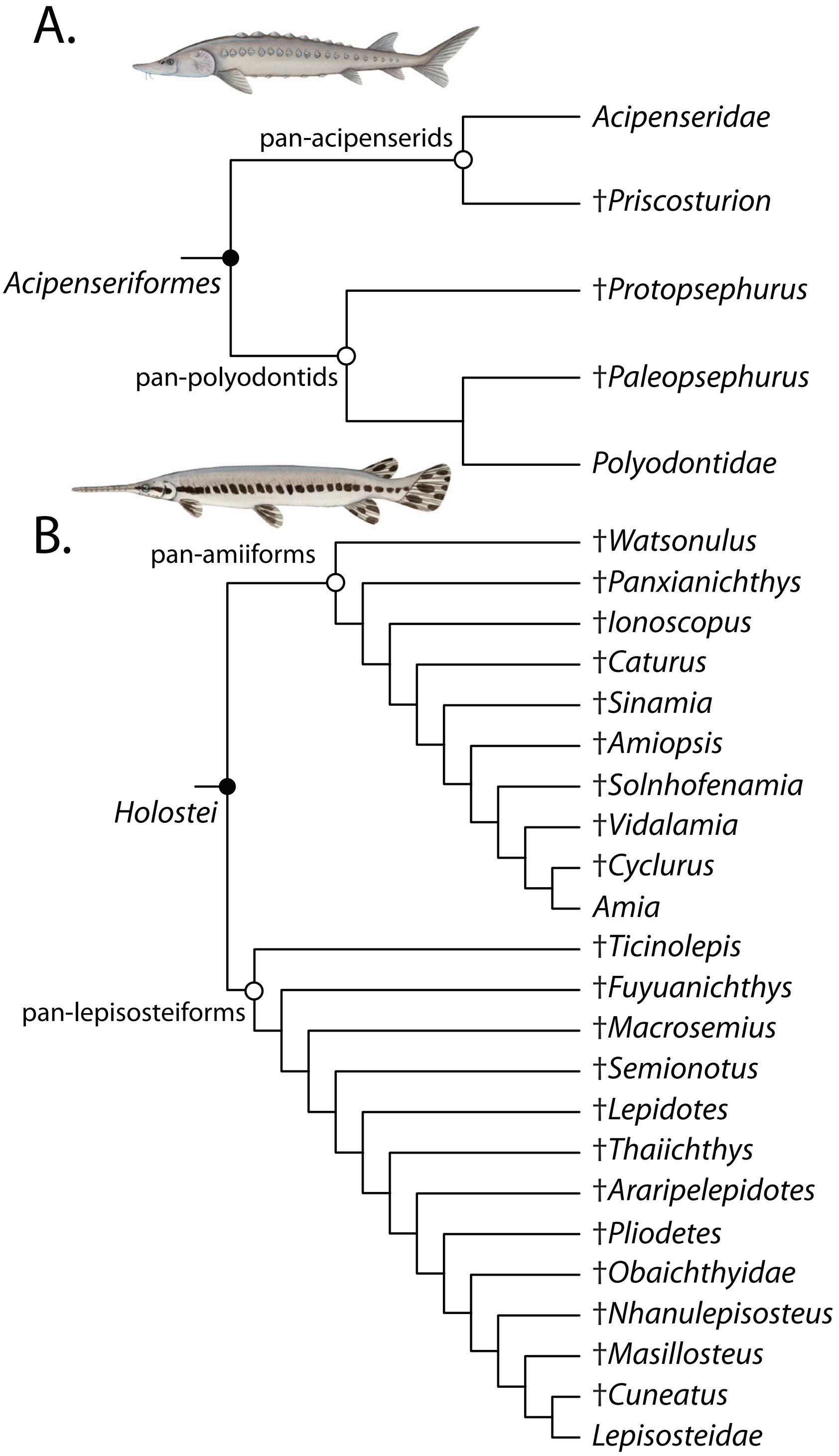

FIGURE 5. Phylogenetic relationships of the major living lineages and fossil taxa of (A) *Acipenseriformes* and (B) *Holostei*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

Comments. Berg (1940) originally included *Acipenseridae*, *Polyodontidae*, and †*Chondrostei* in *Acipenseriformes*, which we selected as the clade name over its synonyms because it is the name most frequently applied to a taxon approximating the named clade. Morphological phylogenies resolve †*Chondrostei* and †*Peipiaosteidae* as pan-acipenseriforms and are not included in *Acipenseriformes* as delimited here (L. Grande and Bemis 1991, 1996; Hilton and Forey 2009; Hilton et al. 2011). The earliest fossil *Acipenseriformes* is the pan-polyodontid †*Protopsephurus liui* from the Barremian (126.5–121.4 Ma) in the Cretaceous of China (Appendix 1). Bayesian relaxed molecular clock analyses of *Acipenseriformes* result in an average posterior crown age estimate of 126.8 million years ago, with the credible interval ranging between 120.9 and 144.5 million years ago (Hughes et al. 2018).

Constituent lineages.

Acipenseridae
Polyodontidae
†*Paleopsephurus*
†*Priscosturion*
†*Protopsephurus*

Neopterygii C. T. Regan 1923b:458
[J. A. Moore and T. J. Near 2020]

Definition. Defined as a minimum-crown-clade by Moore and Near (2020c) as: "The least inclusive crown clade containing *Lepisosteus osseus* (Linnaeus 1758), *Amia calva* Linnaeus 1766, and *Perca fluviatilis* Linnaeus 1758."

Etymology. From the ancient Greek νὲος (nˈiːo͡ʊz), meaning new, and πτερὸν (tˈɛɹɑːn), meaning fin or wing.

Registration number. 210.

Reference phylogeny. Diogo (2007, figs. 3, 4) was designated as the primary reference phylogeny by Moore and Near (2020c). See Figures 2 and 3 for summary phylogenies of the major clades in *Neopterygii*. The placements of the pan-holosteans and *Pan-Teleostei* fossil taxa in the phylogeny are on the basis of inferences from analyses of morphological characters (Patterson 1977; Patterson and Rosen 1977; Arratia 1991, 1997, 1999, 2000a, 2001, 2008, 2013, 2016, 2017; Arratia and Thies 2001; Arratia and Tischlinger 2010; Taverne 2013; Sferco et al. 2015; Giles et al. 2017, 2023; Latimer and Giles 2018; Bean and Arratia 2020; Veysey et al. 2020; Arratia et al. 2021; Bean 2021; C. Shen and Arratia 2021).

Phylogenetics. The earliest phylogenetic investigations of *Neopterygii* resulted in tree topologies that depicted *Holostei* (*Lepisosteidae* and *Amia*) plus *Teleostei* as a monophyletic group (e.g., G. J. Nelson 1969a; Patterson 1973; Wiley 1976; Lauder and Liem 1983; Wiley and Schultze 1984; Maisey 1986). Phylogenetic analyses of morphological data matrices resolve *Neopterygii* as monophyletic (Olsen 1984; Olsen and McCune 1991; Gardiner et al. 1996; Coates 1999; Cavin and Suteethorn 2006; Hurley et al. 2007; Arratia and Tischlinger 2010; L. Grande 2010; Xu and Gao 2011; Xu and Wu 2012; Xu et al. 2012; Arratia 1999, 2013; Xu, Gao, et al. 2014; Poyato-Ariza 2015; Xu and Ma 2016; Xu and Zhao 2016; Giles et al. 2017, 2023; Argyriou et al. 2018, 2022; Latimer and Giles 2018; López-Arbarello and Sferco 2018; Ren and Xu 2021; Xu 2021; Mu et al. 2022; Yuan et al. 2022).

One of the earliest molecular phylogenetic studies of ray-finned fishes used DNA sequences of small fragments of three mtDNA protein coding genes and failed to resolve *Neopterygii* as monophyletic (Normark et al. 1991). Phylogenetic analysis of complete mtDNA genome sequences strongly resolves *Neopterygii* as paraphyletic, with *Acipenseriformes* and *Holostei* as sister lineages (Inoue et al. 2003a). Molecular phylogenetic analyses of Sanger-sequenced nuclear genes, combinations of nuclear and mtDNA genes, and phylogenomic studies all resolve *Neopterygii* as monophyletic (Kikugawa et al. 2004; Alfaro, Santini, et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Broughton et al. 2013; M.-Y. Chen et al. 2015; Betancur-R et al. 2017; Hughes et al. 2018; Vialle et al. 2018; Wcisel et al. 2020).

Composition. *Neopterygii* includes more than 35,045 living species classified in *Holostei* and *Teleostei* (Near, Eytan, et al. 2012; Fricke et al. 2023). Fossil neopterygian lineages classified as *Pan-Teleostei* include †*Ankylophoriformes*, †*Ascalabos*, †*Aspidorhynchidae*, †*Atacamichthys*, †*Catervariolus*, †*Dorsetichthys*, †*Ichthyodectiformes*, †*Ichthyokentema*, †*Leptolepis*, †*Pachycormidae*, †*Pholidophoridae*, †*Prohalecites*, †*Tharsis*, and †*Varasichthyidae* (Patterson and Rosen 1977; J. Gaudant 1978; Arratia 1981; Arratia and Tischlinger 2010; Taverne 2011b, 2013; Arratia 2013; Arratia and Schultze 2024). Fossil lineages of pan-holostean neopterygians include †*Dapediidae* and †*Hulettia* (Schaeffer and Patterson 1984; Latimer and Giles 2018; López-Arbarello and Sferco 2018). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years 3,657 new living species of *Neopterygii* have been described (Fricke et al. 2023), comprising approximately 10.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Neopterygii* include (1) number of fin-rays in the anal and dorsal fins equal in number to endoskeletal supports (Patterson 1973; Patterson and Rosen 1977; Lauder and Liem 1983), (2) premaxilla with interior process that lines front part of nasal pit (Patterson 1973; Patterson and Rosen 1977), (3) vomer attached to underside of ethmoid (Patterson 1973), (4) coronoid process on articular (Patterson 1973; Patterson and Rosen 1977), (5) vertically oriented suspensorium (Patterson 1973), (6) dorsal limb of preopercle narrow (Patterson 1973), (7) symplectic present and is an outgrowth of the hyomandibular cartilage (Patterson 1973; Patterson and Rosen 1977), (8) enhanced upper pharyngeal dentition (Patterson 1973; Patterson and Rosen 1977; Lauder and Liem 1983), (9) clavicle lost or reduced to small plate lateral to cleithrum (Patterson 1973; Wiley 1976; Patterson and Rosen 1977; Lauder and Liem 1983), (10) basipterygoid process entirely composed of parasphenoid (Wiley 1976), (11) posterior commissure between the supraorbital and infraorbital canals (Wiley 1976), (12) uncinate process on first and second infrapharyngobranchials (Wiley 1976), (13) infrabranchials laterally supported (Wiley 1976), (14) differentiated dorsal gill arch musculature (Wiley 1976), (15) four basibranchial copulae (Wiley 1976), (16) quadratojugal braces the quadrate (Gardiner 1984), (17) antorbitals present (Gardiner 1984), (18) palatoquadrate disconnected from dermal cheek bones dorsally and posteriorly (Gardiner 1984), (19) hyoid facet directed posteroventrally (Gardiner and Schaeffer 1989; Coates 1999), (20) maxilla elongate and shallow (L. Grande and Bemis 1998; Hurley et al. 2007; López-Arbarello and Sferco 2018), (21) maxilla detached from preopercle (Gardiner and Schaeffer 1989; Xu, Gao, et al. 2014; López-Arbarello and Sferco 2018), (22) uppermost hypaxial caudal rays with a bundle of elongate fin ray bases that extend over several hypurals (Gardiner et al. 1996; Hurley et al. 2007), (23) ventral cranial-otic fissure closed by bone (Coates 1999), (24) canal for dorsal aorta secondarily absent (Coates 1999), (25) cerebellar corpus arches above fourth ventricle (Coates 1999), (26) presence of one or more accessory postcleithra (Arratia 1999; Hurley et al. 2007), (27) rostral-postrostral and frontal contact wholly or partially separating nasal bones (Xu, Gao, et al. 2014), (28) nasal process on premaxilla (Xu, Gao, et al. 2014), (29) four or more infraorbitals between antorbital and dermosphenotic (Xu, Gao, et al. 2014), (30) presence of mobile maxilla in cheek (Xu, Gao, et al. 2014), (31) interopercle present (Xu, Gao, et al. 2014; López-Arbarello and Sferco 2018), (32) presence of medial gular bones (Xu, Gao, et al. 2014), (33) presence of peg-like anterior process of maxilla (Xu, Gao, et al. 2014), (34) infraorbitals and suborbitals broadly overlap preopercle (Giles et al. 2017), (35) postrostral bone absent (López-Arbarello and Sferco 2018), (36) supramaxilla present (López-Arbarello and Sferco 2018), (37) subopercle with ascending process (López-Arbarello and Sferco 2018), (38) absence of a distinguishable spiracularis of the constrictor mandibularis (Datovo and Rizzato 2018), (39) posterior end of maxilla ends behind orbit (Xu 2021), and (40) posttemporals broad, nearly as wide as extrascapular (Xu 2021).

Synonyms. Cope's (1877b:293–294) revised definition of *Actinopteri*, Regan's (1904b:331–332, 1909b:76–82) delimitation of *Teleostei*, and Goodrich's (1930:xvii) composition of *Holostei* were limited to *Amia calva*, *Lepisosteidae*, and

Teleostei and are all approximate synonyms of *Neopterygii* (Moore and Near 2020c). While not a formal taxonomic name, the term "crown *Neopterygii*" is an ambiguous synonym of *Neopterygii*.

Comments. In a study of the morphology of *Lepisosteidae*, Regan (1923b:458) justified the use of a new group name (italics added to clade names): "*Holostei* and *Teleostei*, therefore are one group, for which it seems better to use the name *Neopterygii*, rather than to use *Holostei* or *Teleostei* in a new and extended sense." Among the earliest studies of actinopterygian relationships after the introduction of phylogenetic systematics, *Neopterygii* is resolved as the clade containing *Holostei* and *Teleostei* (G. J. Nelson 1969a; Patterson 1973) and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade. The oldest fossil taxon of *Neopterygii* is the pan-amiiform †*Watsonulus eugnathoides* from the Induan (251.9–249.9 Ma) in the Triassic of Madagascar (Olsen 1984; Giles et al. 2017, 2023). The crown age of *Neopterygii* estimated from Bayesian relaxed molecular clock analyses ranges from the Permian to the Carboniferous between 278 and 318 million years ago (Giles et al. 2017).

Constituent lineages.

Holostei
Teleostei
†*Ankylophoriformes*
†*Ascalabos*
†*Aspidorhynchidae*
†*Atacamichthys*
†*Catervariolus*
†*Dapediidae*
†*Dorsetichthys*
†*Hulettia*
†*Ichthyodectiformes*
†*Ichthyokentema*
†*Leptolepis*
†*Pachycormidae*
†*Pholidophoridae*
†*Prohalecites*
†*Tharsis*
†*Varasichthyidae*

Holostei J. Müller 1845a:420
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Amia calva* Linnaeus 1766 and *Lepisosteus osseus* (Linnaeus 1758), but not *Perca fluviatilis* Linnaeus 1758. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek ὅλος (hˈo͡ʊlo͡ʊz), meaning whole, entire, or complete, and ὀστέον (ˈɑːstɪən), meaning bone.

Registration number. 881.

Reference phylogeny. A phylogeny inferred from concatenated DNA sequences of 1,105 exons (Hughes et al. 2018, fig. S2). See Figures 2 and 3 for the relationship of *Holostei* among the major lineages of *Actinopterygii*. Phylogenetic relationships among the lineages of *Holostei* are shown in Figure 5B. Placements of the fossil holostean taxa in the phylogeny are on the basis of inferences from morphological analyses (Olsen 1984; Schultze and Wiley 1984; Lambers 1995; Gardiner et al. 1996; Wenz 1999; Xu and Gao 2011; López-Arbarello 2012; Xu and Wu 2012; Xu et al. 2012, 2018; Cavin et al. 2013; López-Arbarello et al. 2014, 2019, 2020; Xu. Zhao, et al. 2014; Poyato-Ariza 2015; Xu and Shen 2015; Brito et al. 2017; Sun et al. 2017; Ebert 2018; Latimer and Giles 2018; López-Arbarello and Sferco 2018; Ren and Xu 2021; Brownstein 2022; Brownstein and Lyson 2022; Brownstein et al. 2023).

Phylogenetics. The monophyly of *Holostei* was supported in one of the earliest phylogenetic systematic perspectives on the relationships of vertebrates (G. J. Nelson 1969a), reflecting pre-cladistic hypotheses that grouped *Amia* and *Lepisosteidae* (Regan 1923b; Goodrich 1930). An assessment of skeletal morphology led to the conclusion that *Holostei* is paraphyletic, with *Amia calva* as the sister lineage of *Teleostei* (Patterson 1973). Nearly every molecular phylogenetic analysis from the earliest efforts using partial-gene DNA sequences to phylogenomic analyses resolves *Holostei* as monophyletic (Normark et al. 1991; Inoue et al. 2003a; Broughton 2010; Near, Eytan, et al. 2012; Faircloth et al. 2013; Braasch et al. 2016; Hughes et al. 2018; Mu et al. 2022). In addition, a phylogenetic analysis of 70 morphological character state changes resolved *Holostei* as monophyletic (Hurley et al. 2007). A critical examination of morphology in bowfin, gars, teleosts, and several fossil lineages demonstrated that nearly all of the proposed characters supporting the hypothesis that *Amia* and teleosts share common ancestry are also present in gars (L. Grande 2010). Subsequent morphological phylogenetic analyses consistently resolve *Holostei* as monophyletic (Hurley et al. 2007; L. Grande 2010; Xu and Gao 2011; Xu and Wu 2012; Xu et al. 2012; Cavin et al. 2013; Xu, Gao, et al. 2014; Xu, Zhao, et al. 2014; Poyato-Ariza 2015; Xu and Shen 2015; Xu and Ma 2016; Xu and Zhao 2016; Giles et al. 2017, 2023; Sun et al. 2017; Argyriou et al. 2018, 2022; Latimer and Giles 2018; López-Arbarello and Sferco 2018; Xu et al. 2018, 2019; López-Arbarello et al. 2020; Ren and Xu 2021; Xu 2021; Yuan et al. 2022; Feng et al. 2023). As such, *Holostei* exemplifies one of the first conflicts in ichthyological systematics between morphological and molecular phylogenetic analyses (Patterson 1994:65–70) that was reconciled through continued morphological and genomic phylogenetic studies, in this case offering overwhelming support for the monophyly of *Holostei* (e.g., Hurley et al. 2007; L. Grande 2010; Near, Eytan, et al. 2012; Hughes et al. 2018; López-Arbarello and Sferco 2018; A. W. Thompson et al. 2021).

Composition. There are nine living species of *Holostei*, two species of *Amia*, and seven species of *Lepisosteidae* (Suttkus 1963; L. Grande 2010; Brownstein et al. 2022). There are several extinct pan-amiiform taxa that include †*Amiopsis*, †*Caturus*, †*Cyclurus*, †*Ionoscopus*, †*Panxianichthys*, †*Sinamia*, †*Solnhofenamia*, †*Vidalamia*, and †*Watsonulus*. Extinct pan-lepisosteiform lineages include †*Araripelepidotes*, †*Cuneatus*, †*Fuyuanichthys*, †*Lepidotes*, †*Macrosemius*, †*Masillosteus*, †*Nhanulepisosteus*, †*Obaichthyidae*, †*Pliodetes*, †*Semionotus*, †*Thaiichthys*, and †*Ticinolepis* (L. Grande and Bemis 1998; Wenz 1999; L. Grande 2010; López-Arbarello 2012; Xu and Wu 2012; Cavin et al. 2013; Xu, Zhao, et al. 2014; Xu and Shen 2015; López-Arbarello et al. 2016; Brito et al. 2017). Details of the ages and locations of fossil holosteans are presented in Appendix 1. Over the past 10 years no new living species of *Holostei* have been described (Fricke et al. 2023), but one species was elevated from synonymy with *Amia calva* (Brownstein et al. 2022).

Diagnostic apomorphies. Morphological apomorphies for *Holostei* include (1) posterior extent of median rostral bone in adults reduced (L. Grande 2010), (2) anterior arm on antorbital with a tube-like canal (L. Grande 2010; Xu et al. 2018), (3) adults with two vertebral centra fused into the occipital condyle (L. Grande 2010), (4) pterotic bone absent (L. Grande 2010), (5) adults with paired vomer (L. Grande 2010), (6) coronoid process of mandibula involves more than one bone (L. Grande 2010), (7) supraangular bone present (L. Grande 2010), (8) caudal region with both paired and median neural spines (L. Grande 2010), (9) normally all primary rays in caudal fin branched (L. Grande 2010), (10) fringing fulcra present on upper and lower margins of caudal fin (L. Grande 2010), (11) presence of anterior and posterior clavicle elements (L. Grande 2010), (12) four hypobranchials present (L. Grande 2010), (13) long nasal process that is tightly sutured to the frontals attaches immovable premaxilla to braincase (L. Grande 2010; Xu et al. 2018), (14) anterior portion of premaxilla pierced by olfactory foramen and lies in nasal pit (L. Grande 2010), (15) sphenotic with dermal component (L. Grande 2010; Xu et al. 2018), and (16) presence of a larval attachment organ that is a compound super-organ located at the front of the snout (Pinion et al. 2023).

Synonyms. There are no synonyms of *Holostei*.

Comments. Müller (1845a) delimited *Holostei* as including *Polypteridae* and *Lepisosteidae*. Later definitions of *Holostei* limited the group to *Amia calva*, pan-amiiforms, pan-lepisosteiforms, and *Lepisosteidae* (Regan 1923b; Goodrich 1930; L. Grande 2010). The alternative phylogenetic hypothesis that *A. calva* and *Teleostei* are sister lineages to the exclusion of *Lepisosteidae* was introduced by Patterson (1973). If future phylogenetic analyses find support for this hypothesis, the use of an external specifier in the clade definition would render *Holostei* inapplicable and *Halecostomi* would be an appropriate name for the smallest clade containing *A. calva* and *Teleostei*, but not *Lepisosteidae*. We were motivated to include an external specifier because the situation with *Holostei* and *Halecostomi* was used as an example in the *Phylonyms* volume of how to create a definition that will make a name inapplicable in the context of some phylogenies (de Queiroz et al. 2020a:xxvii). The earliest holostean is the pan-amiiform †*Watsonulus eugnathoides* from the Induan (251.9–249.9 Ma) in the Triassic of Madagascar (Olsen 1984; Giles et al. 2017, 2023). Fossil-calibrated Bayesian relaxed molecular clock analyses place the crown age of *Holostei* between 248 and 312 million years ago (Near, Eytan, et al. 2012, tbl. S1), which spans the Lower Triassic, Permian, and Upper Pennsylvanian (Carboniferous).

Constituent lineages. Redundant group names are marked with an asterisk.

*Amiidae**
Lepisosteidae
†*Amiopsis*
†*Araripelepidotes*
†*Caturus*
†*Cuneatus*
†*Cyclurus*
†*Fuyuanichthys*
†*Ionoscopus*
†*Lepidotes*
†*Macrosemius*
†*Masillosteus*
†*Nhanulepisosteus*
†*Obaichthyidae*
†*Panxianichthys*
†*Pliodetes*
†*Semionotus*
†*Sinamia*
†*Solnhofenamia*
†*Thaiichthys*
†*Ticinolepis*
†*Vidalamia*
†*Watsonulus*

Teleostei J. Müller 1845b:129

[J. A. Moore and T. J. Near 2020]

Definition. Defined as a minimum-crown-clade by Moore and Near (2020f) as: "The least inclusive crown clade that contains *Hiodon tergisus* Lesueur 1818 (*Osteoglossomorpha*), *Elops saurus* Linnaeus 1766 (*Elopomorpha*), *Engraulis encrasicolus* (Linnaeus 1758) (*Otocephala*/*Clupeomorpha*), and *Perca fluviatilis* Linnaeus 1758 (*Euteleostei*)."

Etymology. From the ancient Greek τέλειος (tˈɛlɨˌo͡ʊz), meaning perfect or complete, and ὀστέον (ˈɑːstɪən), meaning bone.

Registration number. 212.

Reference phylogeny. Diogo (2007, figs. 3, 4) was designated as the primary reference phylogeny by Moore and Near (2020f). See Figures 2 and 3 for summary phylogenies of major clades that comprise *Teleostei*. The phylogenetic placement of the fossil taxon †*Tselfatiiformes* in Figure 3 is on the basis of analysis of morphological characters (Cavin 2001).

Phylogenetics. The first phylogenetic analyses supporting the monophyly of *Teleostei* were inferred from a distribution of derived character states without an analysis of a coded character data matrix using an explicit optimality criterion (Patterson 1977; Patterson and Rosen 1977). Subsequent phylogenetic analyses of morphological characters consistently resulted in teleost monophyly (Arratia 1991, 1997, 1999, 2001, 2008, 2013, 2017; Diogo 2007; Gouiric-Cavalli and Arratia 2022). Many of these morphological studies did not include a broad sampling of teleost diversity as they were aimed at resolving relationships among *Teleostei* and stem lineages that comprise the more inclusive *Pan-Teleostei* (Moore and Near 2020e).

The earliest molecular phylogenetic studies of ray-finned fishes used DNA sequences from small fragments of mtDNA and nuclear ribosomal RNA genes and did not resolve teleosts as monophyletic or did so with low node support (Normark et al. 1991; Lê et al. 1993). Starting in the early 21st century, molecular phylogenetic analyses ranging from the use of whole mtDNA genomes to phylogenomic analyses consistently resolve *Teleostei* as monophyletic (Inoue et al. 2003a; Hurley et al. 2007; Alfaro, Santini, et al. 2009; Broughton 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Austin et al. 2015; M.-Y. Chen et al. 2015; Bian et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Vialle et al. 2018; Roth et al. 2020; Wcisel et al. 2020; Mu et al. 2022; Parey et al. 2023).

Composition. *Teleostei* contains more than 35,035 living species (Fricke et al. 2023) classified in *Oseanacephala* and *Clupeocephala*. Fossil teleosts include the †*Tselfatiiformes* (Cavin 2001). Details of the age and location of the fossil tselfatiiform taxon are presented in Appendix 1. Over the past 10 years 3,657 new living species of *Teleostei* have been described (Fricke et al. 2023), composing 10.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Teleostei* include (1) presence of endoskeletal basihyal (G. J. Nelson 1969a;

Patterson 1977; Arratia 1999, 2000c, 2008), (2) absence of a structure on ventral surface of basioccipital for cranial attachment of aortic ligament (Patterson 1975; Patterson and Rosen 1977; De Pinna 1996), (3) three hypobranchials (Patterson 1977), (4) four pharyngobranchials (Patterson 1977; De Pinna 1996), (5) seven hypurals in caudal skeleton (Patterson 1977; Patterson and Rosen 1977; De Pinna 1996), (6) base of fin rays on upper lobe of caudal fin attaches to or overlies no more than one hypural (Patterson and Rosen 1977; Arratia 1996b, 1997), (7) craniotemporal muscle present (Stiassny 1986; De Pinna 1996; Arratia 1999, 2000c; Wiley and Johnson 2010), (8) hypurals 1 and 2 laterally fused in adults (Arratia 1991), (9) absence of dorsal processes of the bases of the innermost primary caudal rays of upper lobe (Arratia 1991, 1996b, 2000c, 2008), (10) lateral forebrain bundle composed of myelinated fibers (De Pinna 1996; Wiley and Johnson 2010), (11) presence of accessory nasal sacs (X. Y. Chen and Arratia 1994; De Pinna 1996; Arratia 1999, 2000c, 2008; Wiley and Johnson 2010), (12) hyoidean artery pierces either both hypohyals or ventral hypohyal (Arratia 1999, 2000c, 2008), (13) pharyngobranchials with three ossified elements and a tooth plate-bearing cartilaginous element (Arratia 1999, 2000c, 2008; Wiley and Johnson 2010), (14) five or fewer ural neural arches modified as uroneurals (Arratia 1999, 2008; Wiley and Johnson 2010), (15) absence of notch in deep dorsal ascending margin of dentary (Arratia 2008, 2013, 2017), (16) many developed epipleural intermuscular bones in abdominal and caudal region (Arratia 2008), (17) parahypural haemal arch in adults not fused laterally to autocentrum (Arratia 2008), (18) uroneural 1 reaches anterior to preural centrum 2 (Wiley and Johnson 2010), (19) presence of an independent endoskeletal basihyal (Wiley and Johnson 2010), (20) absence of segmentum buccalis of adductor mandibulae (Datovo and Rizzato 2018), (21) presence of dilatator process on opercle (Datovo and Rizzato 2018), (22) presence of adductor crest (Datovo and Rizzato 2018), and (23) autocentrum of vertebrae with thickened lateral wall and series of ornaments including crests, grooves, and pits (Arratia 1997, 1999, 2013; Peskin et al. 2020).

Synonyms. *Teleocephala* (de Pinna 1996:159; Wiley and Johnson 2010:129–130; J. S. Nelson et al. 2016:132–133) is an ambiguous synonym of *Teleostei*. Many authors (Patterson 1977; Patterson and Rosen 1977; De Pinna 1996; Arratia 2001, 2013; Hilton 2022) use *Teleostei* as the name for a more inclusive clade that includes several stem fossil lineages (e.g., †*Ichthyodectiformes*, †*Leptolepis*, †*Pholidophorus*, and †*Varasichthyidae*), which is synonymous with *Pan-Teleostei* (Moore and Near 2020e).

Comments. Müller (1845b) introduced, named, and diagnosed *Teleostei* with a composition that is nearly identical to the delimitation presented here. Teleosts are an iconic lineage of vertebrates, but evidence for their monophyly, identification of major lineages of teleosts, and resolution of teleost phylogeny did not come into focus until the second half of the 20th century (Gosline 1965; Greenwood et al. 1966; G. J. Nelson 1969a, 1969c; Patterson 1977). The results of this research inaugurated a dramatic shift in ichthyology regarding *Teleostei*, a situation described by Patterson (1997:201) as: "An analogy is to imagine the situation in mammalogy if monotremes, marsupials, and placentals were not distinguished until 1966."

Bayesian relaxed molecular clock analyses of *Teleostei* result in an average posterior crown age estimate of 239.6 million years ago, with the credible interval ranging between 224.5 and 256.5 million years ago (Giles et al. 2017).

Constituent lineages.

Clupeocephala

Oseanacephala

†*Tselfatiiformes*

Oseanacephala C. E. Thacker and T. J. Near, new clade name

Definition. The least inclusive crown clade that contains *Anguilla rostrata* (Lesueur 1817) and *Osteoglossum bicirrhosum* (Cuvier 1829), but not *Engraulis encrasicolus* (Linnaeus 1758) or *Perca fluviatilis* Linnaeus 1758. This is a minimum-crown-clade definition with external specifiers.

Etymology. *Oseanacephala* is a partial acronym composed of the first two letters of

Osteoglossomorpha and the first letter from the remaining lineages that comprise the clade: *Elopiformes*, *Albulidae*, *Notacanthiformes*, and *Anguilliformes*. The suffix is from the ancient Greek κεφαλή (kɛfˈɑːlə), meaning the head of a human or other animal.

Registration number. 882.

Reference phylogeny. A phylogeny inferred from concatenated DNA sequences of 1,105 exons (Hughes et al. 2018, fig. S2). See Figures 2 and 3 for the resolution of living lineages of *Oseanacephala* in the phylogeny of *Actinopterygii*. See Figure 6 for the phylogenetic relationships of living and fossil lineages of *Oseanacephala*. Phylogenetic placements of the pan-osteoglossomorphs †*Jiuquanichthys* and †*Lycoptera* are on the basis of inferences from morphological analyses (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998, 2006; Hilton 2003; Murray et al. 2018).

Phylogenetics. In contrast to the substantial support for teleost monophyly from morphological and molecular phylogenetic analyses, uncertainty has remained regarding the relationships among the teleost lineages *Clupeocephala*, *Elopomorpha*, and *Osteoglossomorpha* (Hilton and Lavoué 2018; Dornburg and Near 2021; Takezaki 2021). *Taeniopaedia* was introduced as a name for the group that included *Elopomorpha* and *Clupeomorpha* (Greenwood et al. 1967), which was presented as "Division I" in the classification of teleosts (Greenwood et al. 1966). The morphological phylogeny presented in Patterson and Rosen (1977) resolved *Clupeocephala* and *Elopomorpha* as a clade supported with two traits: the presence of two uroneurals in the caudal skeleton that extend beyond ural centrum 2 and the presence of well-developed epipleural intermuscular bones. Arratia (1997) inferred a phylogeny of *Pan-Teleostei* using parsimony analyses of 131 character state changes coded from living and fossil taxa, resulting in a hypothesis where *Elopomorpha* is the sister lineage of all other teleosts.

Molecular phylogenetic analyses have resulted in all three possible relationships among *Clupeocephala*, *Elopomorpha*, and *Osteoglossomorpha* (Inoue et al. 2001; Hurley et al. 2007; Broughton 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Faircloth et al. 2013; J. N. Chen et al. 2014; Bian et al. 2016; Betancur-R et al. 2017). The earliest molecular phylogenetic studies of teleosts resolved *Elopomorpha* and *Osteoglossomorpha* as sister lineages (Lê et al. 1993), which is a frequent result in phylogenomic analyses (M.-Y. Chen et al. 2015; Bian et al. 2016; Lin et al. 2016; Hughes et al. 2018; Vialle et al. 2018; Hao et al. 2020; Roth et al. 2020; Wcisel et al. 2020; Takezaki 2021; Parey et al. 2023). Evidence from genomic organization in the form of the conservation of gene adjacency and the proportion of shared chromosomal breakpoints support monophyly of *Oseanacephala* (Parey et al. 2023).

Composition. There are currently 1,361 living species of *Oseanacephala* (Fricke et al. 2023) classified in *Elopomorpha* and *Osteoglossomorpha*. Fossil lineages of *Oseanacephala* include the pan-osteoglossomorphs †*Jiuquanichthys* and †*Lycoptera*. Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years 139 new living species of *Oseanacephala* have been described, comprising 10.2% of the living species diversity in the clade.

Diagnostic apomorphies. All lineages of *Oseanacephala* share a chromosomal rearrangement, where duplicated chromosomes 1a and 2a are fused and lineages of *Clupeocephala* are characterized by an independent fusion of duplicated chromosomes 1b and 2b (Parey et al. 2023). There are no known morphological apomorphies for *Oseanacephala*; however, fusion of the retroarticular with the angular or the articular is shared by *Elopomorpha*, *Hiodon*, and *Mormyridae* (Parey et al. 2023). The absence of this trait in *Gymnarchus niloticus*, *Notopteridae*, *Osteoglossidae*, and *Pantodon* may represent a secondary loss in these lineages of *Osteoglossomorpha* (Parey et al. 2023).

Synonyms. *Eloposteoglossocephala* (Parey et al. 2023) is an ambiguous synonym of *Oseanacephala*.

Comments. The resolution of *Oseanacephala* is completely driven by molecular phylogenetic analyses and consideration of genomic

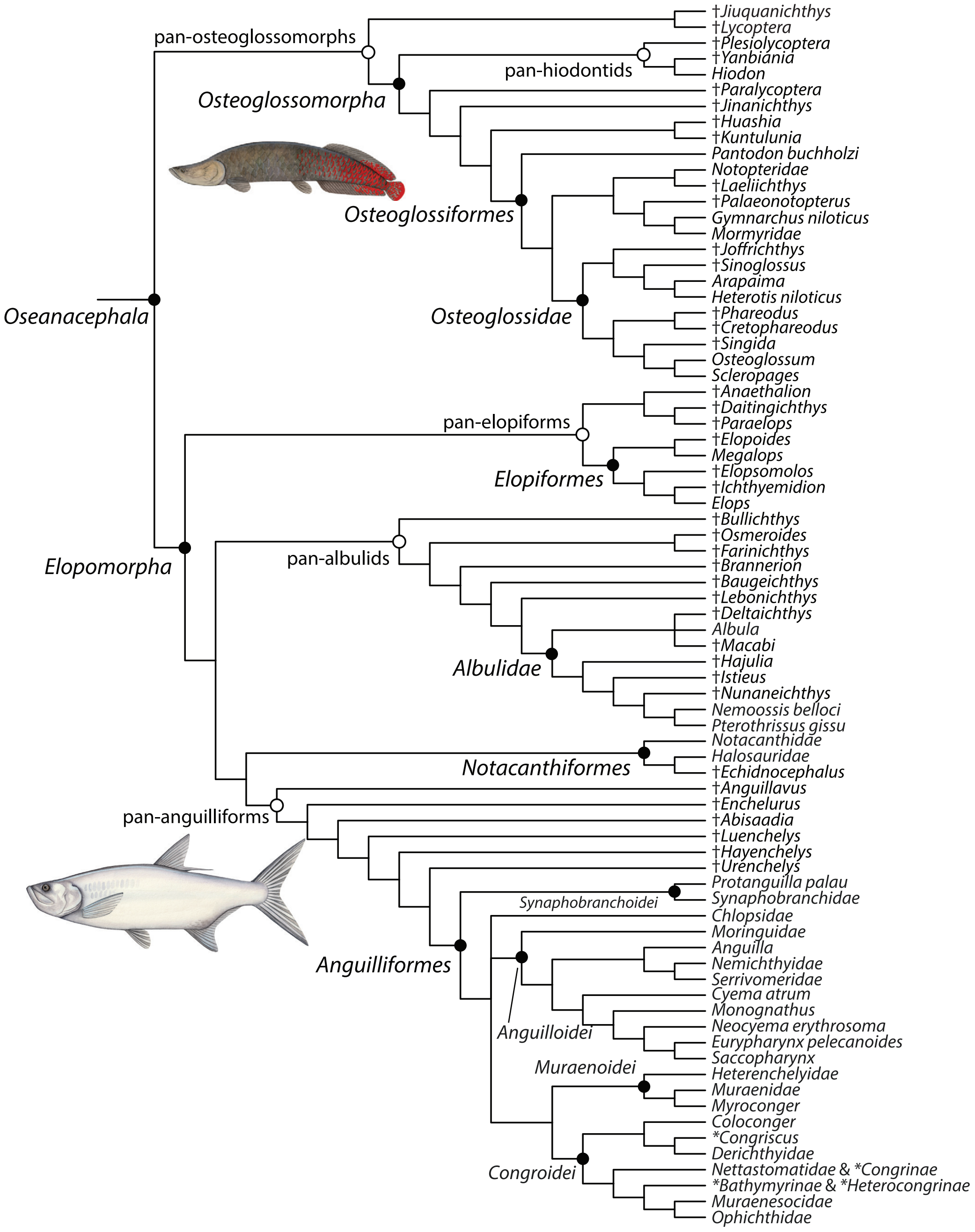

Figure 6. Phylogenetic relationships of the major living lineages and fossil taxa of *Oseanacephala*, *Osteoglossomorpha*, *Osteoglossiformes*, *Osteoglossidae*, *Elopomorpha*, *Elopiformes*, *Albulidae*, *Notacanthiformes*, *Anguilliformes*, *Synaphobranchoidei*, *Anguilloidei*, *Muraenoidei*, and *Congroidei*. Asterisk identifies lineages currently classified as *Congridae*. Lineages currently classified as *Congridae* are highlighted with an asterisk. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

organization. From the start of phylogenetic investigations of teleosts using morphology, the hypothesis that *Elopomorpha* and *Osteoglossomorpha* are sister lineages was never proposed (Patterson and Rosen 1977; Arratia 1997, 1999, 2000c). It is not clear what insight on the evolutionary diversification of teleosts is gained through the resolution of the relationships among *Clupeocephala*, *Elopomorpha*, and *Osteoglossomorpha*, but at minimum it may motivate a reexamination of jaw anatomy and bite kinematics between the bony-tongued *Osteoglossomorpha* and the complex pharyngeal jaw morphology in *Anguilliformes*. This resolution also invites investigation of potential commonalities between the robust larvae and juveniles of osteoglossomorph species and the leptocephalus larvae characteristic of *Elopomorpha*.

The earliest *Oseanacephala* fossil is the pan-elopiform †*Anaethalion zapporum* from the Kimmeridgian (154.8–149.2 Ma) in the Jurassic of Germany (Arratia 2000c). A Bayesian relaxed molecular clock analysis of *Oseanacephala* resulted in an average posterior crown age estimate of 223.98 million years ago, but no credible interval was reported (Vialle et al. 2018).

Constituent lineages.

Elopomorpha
Osteoglossomorpha
†*Jiuquanichthys*
†*Lycoptera*

Elopomorpha P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Meyers 1966:350, 354–358, 393–394

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Elops saurus* Linnaeus 1766, *Albula vulpes* (Linnaeus 1758), and *Anguilla rostrata* (Lesueur 1817). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ἔλλοψ (ɨlˈɑːps), an epithet for fish that may mean either scaly or dumb, for example, “dumb as a fish” (D. W. Thompson 1947:62; Liddell et al. 1968:537) and μορφή (mˈɔːɹ͡fiː), meaning form or shape.

Registration number. 883.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences of mitochondrial and nuclear genes and morphological characters (Dornburg et al. 2015, fig. 3). Phylogenetic relationships among living and fossil lineages of *Elopomorpha* are shown in Figure 6. The resolutions of fossil taxa in the phylogeny are on the basis of inferences from morphological characters (Arratia 1991, 1997, 1999, 2000b, 2000c, 2008, 2010b; Forey et al. 1996; Belouze 2002; Gallo and de Figueiredo 2002; Arratia and Tischlinger 2010; Forey and Maisey 2010; Mayrinck et al. 2010; de Figueiredo, Gallo, and Leal 2012; Pfaff et al. 2016; Guinot and Cavin 2018; Alves et al. 2020; Bean and Arratia 2020; Bean 2021; Hernández-Guerrero et al. 2021).

Phylogenetics. The shared presence of specialized leptocephalus larvae was the primary character that led to the delimitation of *Elopomorpha* to include *Elopiformes* (including *Albulidae*), *Notacanthiformes*, and *Anguilliformes* (Greenwood et al. 1966). The monophyly of *Elopomorpha* was challenged in several morphological and molecular inferences that included a de-emphasis on the importance of the leptocephalus larvae (Gosline 1971:100; Nybelin 1971; Hulet and Robins 1989; Filleul and Lavoué 2001; Obermiller and Pfeiler 2003); however, surveys of osteological traits, explicit phylogenetic analyses of morphological character state changes, and molecular phylogenetic analyses consistently resolve elopomorphs as monophyletic (Forey 1973a; G. J. Nelson 1973; Greenwood 1977; Patterson and Rosen 1977; Forey et al. 1996; Inoue et al. 2004; Forey and Maisey 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; J. N. Chen et al. 2014).

While analyses of morphological and molecular characters consistently resolve *Elopomorpha* as monophyletic, relationships among the elopomorph subclades vary among phylogenetic studies. *Albulidae*, containing *Albula*, *Pterothrissus*, and the recently described *Nemoossis* (Hidaka et al. 2017), is resolved as paraphyletic in some morphological and molecular studies (Forey 1973b; Inoue et al. 2004; Dornburg et al. 2015), but is monophyletic in others (Forey et al. 1996; de Figueiredo, Gallo, and Leal 2012; Alves et al. 2020). *Notacanthiformes* is resolved as either sharing common ancestry with *Albulidae* (G. J. Nelson 1973; Greenwood 1977; Patterson and Rosen 1977; C. R. Robins 1989; Inoue et al. 2004; G. D. Johnson et al. 2012) or *Anguilliformes* (Forey 1973a; Forey et al. 1996; J. N. Chen et al. 2014; Dornburg et al. 2015). There are several morphological character state changes that support *Albulidae* as the sister lineage of a clade containing *Notacanthiformes* and *Anguilliformes* (Forey et al. 1996; Datovo and Vari 2014).

Composition. *Elopomorpha* currently contains 1,107 living species (Fricke et al. 2023) classified in *Albulidae*, *Anguilliformes*, *Elopiformes*, and *Notacanthiformes*. Fossil taxa of *Elopomorpha* include the pan-elopiforms †*Anaethalion*, †*Daitingichthys*, and †*Paraelops* (Arratia 1987a; Fielitz and Bardack 1992; de Figueiredo, Gallo, and Leal 2012); the pan-albulids †*Baugeichthys*, †*Brannerion*, †*Bullichthys*, †*Farinichthys*, †*Lebonichthys*, and †*Osmeroides* (Forey et al. 1996, 2003; Filleul 2000; Gallo and de Figueiredo 2002; Forey and Maisey 2010; Mayrinck et al. 2010); and the pan-anguilliforms †*Abisaadia*, †*Anguillavus*, †*Enchelurus*, †*Hayenchelys*, †*Luenchelys*, and †*Urenchelys* (Belouze 2002; Belouze et al. 2003; Pfaff et al. 2016; Guinot and Cavin 2018). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years 124 new living species of *Elopomorpha* have been described (Fricke et al. 2023), comprising 11.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Elopomorpha* include (1) presence of the leptocephalus larval stage (Greenwood et al. 1966; Forey 1973a, 1973b; Forey et al. 1996; Inoue et al. 2004; Wiley and Johnson 2010), (2) fusion between angular and retroarticular bones of lower jaw (G. J. Nelson 1973), (3) presence of prenasal ossicles (Forey 1973a, 1973b; Forey et al. 1996; Wiley and Johnson 2010), (4) presence of pectoral splint (Forey 1973a, 1973b; Forey et al. 1996), (5) sternohyoides originates primarily on cleithrum (Greenwood 1977; Wiley and Johnson 2010), (6) spermatozoa flagellum with 9+0 axoneme arrangement and proximal centriole divided into two elongate bundles of four- and five-triplet structure (Matthei and Matthei 1975; Jamieson 1991; Wiley and Johnson 2010), (7) compound neural arch forms in a mass of cartilage over first preural and first ural centrum (Schultze and Arratia 1988; Arratia 1996a, 1997; Forey and Maisey 2010; Wiley and Johnson 2010), and (8) presence of a branchial spiracle (Forey and Maisey 2010).

Synonyms. *Elopoidei* (Gosline 1960:357) and *Elopocephalai* (Arratia 1999; Betancur-R, Broughton, et al. 2013; Betancur-R et al. 2017:13) are ambiguous synonyms of *Elopomorpha*.

Comments. Greenwood et al. (1966) introduced *Elopomorpha* as the name for a group that includes *Albulidae*, *Anguilliformes*, *Elopiformes*, and *Notacanthiformes*, and it is recognized in all subsequent classifications of *Teleostei* (e.g., G. J. Nelson 1969a; Patterson and Rosen 1977; Wiley and Johnson 2010; Betancur-R et al. 2017). *Elopomorpha* is an ancient lineage with the pan-elopid †*Elopsomolos frickhingeri* and pan-elopomorph †*Anaethalion zapporum* as the earliest known fossil taxa, both of which date from the Kimmeridgian (154.8–149.2 Ma) in the Jurassic (Arratia 2000c; Guinot and Cavin 2018). Bayesian relaxed molecular clock estimates of the crown age of *Elopomorpha* range between 157 and 200 million years ago in the Jurassic (Dornburg et al. 2015).

Constituent lineages.

Albulidae
Anguilliformes
Elopiformes
Notacanthiformes
†*Abisaadia*
†*Anaethalion*
†*Anguillavus*
†*Baugeichthys*
†*Brannerion*
†*Bullichthys*
†*Daitingichthys*
†*Enchelurus*
†*Farinichthys*
†*Hayenchelys*
†*Lebonichthys*
†*Luenchelys*
†*Osmeroides*
†*Paraelops*
†*Urenchelys*

Elopiformes P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Meyers 1966:354, 393 [T. J. Near and C. E. Thacker], converted clade name

Definition. The least inclusive crown clade that contains *Elops saurus* Linnaeus 1766 and *Megalops cyprinoides* (Broussonet 1782), but not *Albula vulpes* (Linnaeus 1758). This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek ἔλλοψ (ɪlˈɑːps), an epithet for fish that may mean either scaly or dumb, for example, "dumb as a fish" (D. W. Thompson 1947:62; Liddell et al. 1968:537). The suffix is from the Latin word *forma*, meaning form, figure, or appearance.

Registration number. 884.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences of mitochondrial and nuclear genes and morphological characters (Dornburg et al. 2015, fig. 3). Phylogenetic relationships of *Elopiformes* are presented in Figure 6. The placements of the fossil taxa in the phylogeny are on the basis of inferences from morphological characters (Arratia 2000c; de Figueiredo, Gallo, and Leal 2012; Alves et al. 2020; Hernández-Guerrero et al. 2021).

Phylogenetics. *Elopiformes* is consistently resolved as monophyletic in morphological and molecular phylogenetic studies (Forey 1973b; Demartini and Donaldson 1996; Forey et al. 1996; Filleul and Lavoué 2001; Obermiller and Pfeiler 2003; C. Wang et al. 2003; Inoue et al. 2004; Forey and Maisey 2010; de Figueiredo, Gallo, and Leal 2012; G. D. Johnson et al. 2012; K. L. Tang and Fielitz 2013; J. N. Chen et al. 2014; Dornburg et al. 2015; Poulsen et al. 2018; Alves et al. 2020; de Sousa et al. 2021; Hernández-Guerrero et al. 2021). Analyses of mtDNA sequences indicate there are multiple undescribed species masquerading as *Elops smithi* (McBride et al. 2010; Williford et al. 2022).

Composition. There are currently nine living species of *Elopiformes* classified in *Elops* and *Megalops* (Fricke et al. 2023). Fossil lineages of *Elopiformes* include the pan-megalopid †*Elopoides* and the pan-elopids †*Elopsomolos* and †*Ichthyemidion* (Forey 1973b; Poyato-Ariza 1995; Arratia 2000c). Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years no new living species of *Elopiformes* have been described (McBride et al. 2010; Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Elopiformes* include (1) medial position of posterior opening of mandibular sensory canal within lower jaw (Forey et al. 1996; Wiley and Johnson 2010), (2) presence of posteriorly expanded preopercle (Arratia 2000c), (3) presence of posteriorly expanded opercles and subopercles (Arratia 2000c), (4) presence of well-developed process on mesethmoid (Arratia 2000c), (5) presence of lateral rostral bone (Arratia 2000c), (6) presence of elongated antorbital placed anterior to infraorbital (Arratia 2000c), (7) posterior margins of infraorbitals 3 and 4 do not reach anterior margin of preopercle (Arratia 2000c), (8) anterior portion of ceratohyal not fenestrated (Arratia 2000c), (9) first ossified pleural rib occurring on the fourth or more posterior centrum (Forey and Maisey 2010), and (10) presence of constrictor mandibularis dorsalis, levator arcus palatinia, and pars temporalis (Datovo and Rizzato 2018).

Synonyms. *Elopoidei* (Greenwood et al. 1966:393) is an approximate synonym of *Elopiformes*.

Comments. Greenwood et al. (1966) applied the name *Elopiformes* to a lineage that included *Albulidae*, *Elopidae*, and *Megalopidae*, a grouping proposed by Gosline (1960) on the basis of morphology of the caudal skeleton. Subsequent phylogenetic studies consistently resolve a clade that accords with our delimitation of *Elopiformes* as the sister lineage to all other elopomorphs (Forey et al. 1996; Inoue et al. 2004). *Elopiformes* is an ancient lineage dating to the Jurassic and the pan-elopid †*Elopsomolos frickhingeri* from the Kimmeridgian (154.8–149.2 Ma) of Germany is the earliest known fossil taxon (Arratia 2000c; Dornburg et al. 2015; Guinot and Cavin 2018). Bayesian relaxed molecular clock crown age estimates for *Elopiformes* range between 82 and 175 million years ago (Near, Eytan, et al. 2012).

Constituent lineages. Redundant group names are marked with an asterisk.

*Elopidae**
*Megalopidae**
†*Elopoides*
†*Elopsomolos*
†*Ichthyemidion*

Albulidae P. Bleeker 1849:6, 12
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Albula vulpes* (Linnaeus 1758), *Nemoossis belloci* (Cadenat 1937), and *Pterothrissus gissu* Hilgendorf 1877. This is a minimum-crown-clade definition.

Etymology. *Albulae* is a Latin name for the Tiber River in Italy (Livy 1919:14–15).

Registration number. 885.

Reference phylogeny. A phylogeny resulting from a phylogenetic analysis of morphological character state changes (Forey and Maisey 2010, fig. 13). *Nemoossis belloci* (Longfin Bonefish) is not included in any phylogenetic analyses, but it is assumed it will resolve as the sister species of *Pterothrissus gissu* (Japanese Gissu) (Hidaka et al. 2017). Phylogenetic relationships of *Albulidae* (bonefishes) are shown in Figure 6. The placements of fossil taxa in the phylogeny are on the basis of inferences from morphological characters (Fielitz and Bardack 1992; Gallo and de Figueiredo 2002; de Figueiredo, Gallo, and Leal 2012; Guinot and Cavin 2018; Alves et al. 2020; Hernández-Guerrero et al. 2021; L-Recinos et al. 2023).

Phylogenetics. Classifications of *Teleostei* from the early to mid-20th century grouped *Albula* and *Pterothrissus* in either *Albulidae*, *Albuloidae*, or *Albuloidei* (Boulenger 1904b:547–549; Goodrich 1909:387–388; Berg 1940:420; Greenwood et al. 1966). Reflecting alternative classifications that grouped *Albula* and *Pterothrissus* in separate and unrelated family rank taxonomic groups (Jordan 1905:44, 46–48), it was proposed that *Pterothrissus* is the sister lineage of a clade containing *Notacanthiformes* and *Anguilliformes* on the basis of shared similarities of an elongate snout, subterminal mouth, reduced ossification of the braincase, and inwardly turned head of the maxilla (Forey 1973a). Subsequent morphological studies consistently resolve *Albulidae* as monophyletic (Greenwood 1977; Forey et al. 1996), and several morphological phylogenetic analyses incorporated fossil taxa that are either more closely related to *Albula* or to the *Pterothrissus-Nemoossis* clade (Forey and Maisey 2010; de Figueiredo, Gallo, and Leal 2012; Guinot and Cavin 2018; Alves et al. 2020; Hernández-Guerrero et al. 2021; L-Recinos et al. 2023). Molecular phylogenies differ in their support for the monophyly of *Albulidae*. Analyses of mitochondrial DNA and concatenated nuclear genes each result in paraphyly of *Albulidae*, with *Pterothrissus* resolved as the sister lineage of *Notacanthiformes* (Inoue et al. 2004; G. D. Johnson et al. 2012; Dornburg et al. 2015); however, other phylogenetic studies using mitochondrial DNA result in the resolution of a monophyletic *Albulidae* (C. Wang et al. 2003; K. L. Tang and Fielitz 2013; Poulsen et al. 2018).

Composition. *Albulidae* currently contains 13 living species classified in *Albula*, *Nemoossis*, and *Pterothrissus* (Hidaka et al. 2017; Fricke et al. 2023). Fossil taxa of *Albulidae* include †*Deltaichthys*, †*Hajulia*, †*Istieus*, †*Macabi*, and †*Nunaneichthys* (Forey and Maisey 2010; de Figueiredo, Gallo, and Leal 2012; Guinot and Cavin 2018; Alves et al. 2020; Hernández-Guerrero et al. 2021; L-Recinos et al. 2023). Details of the ages and locations of the fossil taxa are presented in Appendix 1. There were no new living species of *Albulidae* described over the past 10 years, but there remains at least one undescribed species of *Albula* (Pickett et al. 2020).

Diagnostic apomorphies. Morphological apomorphies for *Albulidae* include (1) presence of subepiotic fossa (Forey et al. 1996; Wiley and Johnson 2010), (2) ectopterygoid with dorsal process (Forey et al. 1996; Wiley and Johnson 2010), (3) presence of fenestration within hyomandibular and metapterygoid suture that allows levator arcus palatine to pass through and insert on medial surface of palate (Forey et al. 1996; Wiley and Johnson 2010), and (4) sternohyoideus originating mainly on cleithrum (Forey et al. 1996).

Synonyms. *Albuloidae* (Berg 1940:420), *Albuloidei* (Greenwood et al. 1966:393; Forey 1973a:94), and *Albuliformes* (Forey et al. 1996:184; J. S. Nelson et al. 2016; Betancur-R et al. 2017:14) are all ambiguous synonyms of *Albulidae*.

Comments. When Bleeker (1849) introduced the name *Albulidae*, there was only one taxon, *Albula*, classified in the group (Günther 1868:468). Shortly after the description of *Pterothrissus* (Hilgendorf 1877), several classifications of teleosts grouped *Albula* and *Pterothrissus* in *Albulidae* (Boulenger 1904b:547–549; Goodrich 1909:387–388). *Albulidae* was selected as the clade name over its synonyms because they are redundant group names relative to *Albulidae* in ranked taxonomies. *Albulidae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:64).

The earliest fossil taxa in *Albulidae* is †*Nunaneichthys mexicanus* from the Albian-Cenomanian (100.5–93.9 Ma) in the Cretaceous from Mexico (Hernández-Guerrero et al. 2021). There are no molecular divergence time estimates for *Albulidae.*

Constituent lineages.

Albula
Nemoossis
Pterothrissus
†*Deltaichthys*
†*Hajulia*
†*Istieus*
†*Macabi*
†*Nunaneichthys*

Notacanthiformes E. S. Goodrich 1909:416
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Notacanthus chemnitzii* Bloch 1788 and *Halosaurus ovenii* J. Y. Johnson 1864. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek νῶτον (nˈo͞otən), meaning of the back, and ἄκανθα (ækˈænθə), meaning thorn or spine. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 886

Reference phylogeny. A phylogeny resulting from analysis of a concatenated dataset of DNA sequences from mitochondrial and nuclear genes and morphological characters (Barros-García et al. 2018, fig. 1b). Phylogenetic relationships of *Notacanthiformes* are presented in Figure 6. The placement of the fossil lineage †*Echidnocephalus* in the phylogeny is based on inferences from morphological characters (Forey et al. 1996; Arratia 2010b; Guinot and Cavin 2018).

Phylogenetics. Classifications of teleost fishes from the early 20th century grouped *Notacanthidae* (deep-sea spiny eels) and *Halosauridae* (halosaurs) with the pan-aulopiform †*Dercetidae* and *Fierasfer*, which is a synonym of the ophiid *Carapus* (Boulenger 1904b; Goodrich 1909:416–419). Regan (1909b) removed †*Dercetidae* and *Fierasfer* and limited the group *Heteromi* to *Notacanthidae* and *Halosauridae*. *Notacanthiformes*, comprising *Notacanthidae* and *Halosauridae*, was identified as one of the major lineages of *Elopomorpha* (Greenwood et al. 1966) and subsequent phylogenetic analyses have supported notacanthiform monophyly (Forey et al. 1996; Inoue et al. 2004; J. N. Chen et al. 2014; Dornburg et al. 2015; Barros-García et al. 2018; Poulsen et al. 2018). There is less certainty on the relationships of *Notacanthiformes* among major lineages of *Elopomorpha*. Some phylogenetic analyses of morphological and molecular characters place *Notacanthiformes* as the sister lineage of *Albulidae* (Greenwood 1977; Patterson and Rosen 1977; C. R. Robins 1989; C. Wang et al. 2003; Inoue et al. 2004; G. D. Johnson et al. 2012; Near, Eytan, et al. 2012), but other studies resolve *Notacanthiformes* and *Anguilliformes* as sister lineages (Forey 1973a; Forey et al. 1996; Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; J. N. Chen et al. 2014; Dornburg et al. 2015). Forey et al. (1996) identified 14 morphological synapomorphies for a clade containing *Notacanthiformes* and *Anguilliformes*; many of these traits are character losses in the context of their evolution within *Elopomorpha* (Wiley and Johnson 2010).

Composition. There are currently 28 living species of *Notacanthiformes* (Fricke et al. 2023) classified in *Notacanthidae* and *Halosauridae*. Fossil lineages of *Notacanthiformes* include the pan-halosaurid †*Echidnocephalus* (Forey et al. 1996; Arratia 2010b). Details of the age and location of †*Echidnocephalus* are presented in

Appendix 1. Over the past 10 years one new species of *Notacanthiformes* has been described (Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Notacanthiformes* include (1) complete separation of parmalaris from remaining muscles of adductor mandibulae (Greenwood 1977; Datovo and Vari 2014), (2) nodule between maxillary head and palatine (Greenwood 1977; Wiley and Johnson 2010), (3) presence of posteriorly directed spine on maxilla (Forey et al. 1996; Wiley and Johnson 2010), and (4) pelvic fins connected by membrane (Forey et al. 1996; Wiley and Johnson 2010).

Synonyms. *Heteromi* (T. N. Gill 1893:133; Regan 1909a:82–83) and *Halosauri* (Garstang 1931:258) are approximate synonyms of *Notacanthiformes*.

Comments. Greenwood et al. (1966) limited *Notacanthiformes* to *Notacanthidae* and *Halosauridae*. The name *Notacanthiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest notacanthiform fossil taxon is the pan-halosaurid †*Echidnocephalus troscheli* from the Campanian (83.2–72.2 Ma) in the Cretaceous of Germany (Forey et al. 1996; Arratia 2010b). Bayesian relaxed molecular clock age estimates of *Notacanthiformes* result in an average posterior crown age estimate between 70 and 125 million years ago (Dornburg et al. 2015).

Constituent lineages.

Halosauridae

Notacanthidae

†*Echidnocephalus*

Anguilliformes E. S. Goodrich 1909:403
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Myroconger compressus* Günther 1870, *Gymnothorax formosus* Bleeker 1864b, *Protanguilla palau* Johnson, Ida, and Sakaue in G. D. Johnson et al. 2012, *Synaphobranchus kaupi* J. Y. Johnson 1862, *Conger oceanicus* (Mitchill 1818a), and *Anguilla anguilla* (Linnaeus 1758). This is a minimum-crown-clade definition.

Etymology. From the Latin *Anguilla*, meaning eel, and *forma*, meaning form, figure, or appearance.

Registration number. 887.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences from three nuclear genes and two mitochondrial protein coding genes (Santini, Kong, et al. 2013, fig. 2). Phylogenetic relationships of *Anguilliformes* are presented in Figure 6.

Phylogenetics. Species classified as *Anguilliformes* were initially grouped with unrelated eel-like species in *Apodes* of Linnaeus (1758:242). By the middle of the 19th century, a taxonomic group comprising the modern *Anguilliformes* was established (Bleeker 1864c). Greenwood et al. (1966) delimited two groups within *Anguilliformes*, *Anguilloidei* for the typical eels and *Saccopharyngoidei* containing the morphologically bizarre deep-sea lineages that included *Saccopharynx* (swallowers), *Eurypharynx pelecanoides* (Pelican Eel), and *Monognathus* (onejaw gulpers). The saccopharyngoids are so morphologically unique that it has been proposed they were a divergent lineage not closely related to any living osteichthyans (Tchernavin 1947). The saccopharyngoid traits include the absences of ventral fins, pelvic girdle, opercular bones, and branchiostegals (Böhlke 1966; Bertelsen et al. 1989). The saccopharyngoids were included with all other eels in Boulenger's (1904b:599–605) *Apodes* and in Goodrich's (1909:403–408) *Anguilliformes*. In a classification of teleosts, Regan (1909b) grouped anguilloids and saccopharyngoids in *Apodes*, but he later put *Saccopharynx* in T. N. Gill and Ryder's (1883) *Lyomeri*, established to accommodate the saccopharyngoid *Eurypharynx pelecanoides* (Regan 1912a, 1912e). On the basis of comparative morphology, C. R. Robins (1989) countered the classification of *Anguilliformes* presented in Greenwood et al. (1966) and vigorously promoted the hypothesis that anguilloids and saccopharyngoids are distantly related. The delimitation of the saccopharyngoids was later expanded to include the bobtail snipe eels *Cyema atrum* and *Neocyema erythrosoma* (Raju 1974; Castle 1977).

Subsequent to the delimitation of *Elopomorpha* (Greenwood et al. 1966), there is broad support for the monophyly of *Anguilliformes* in morphological and molecular phylogenetic studies (Forey 1973a; Forey et al. 1996; Inoue et al. 2003b, 2004, 2010; Obermiller and Pfeiler 2003; C. Wang et al. 2003; López et al. 2007; G. D. Johnson et al. 2012; Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; J. N. Chen et al. 2014; Dornburg et al. 2015; Poulsen et al. 2018). The use of morphological characters to investigate phylogenetic relationships of *Anguilliformes* is challenged by difficulties in constructing inclusive data matrices due to limited knowledge on anguilliform anatomy and the reductive nature of eel skeletons (Forey et al. 1996). The situation is improving with detailed studies of gill arch musculature (Springer and Johnson 2015), the pharyngeal jaw apparatus (G. D. Johnson 2019), and the pectoral girdle (da Silva and Johnson 2018). A recent phylogenetic analysis of *Congroidei* using 42 coded characters from the pectoral girdle demonstrates the potential for explicit phylogenetic analysis of morphological traits in resolving relationships within *Anguilliformes* (da Silva et al. 2019).

Despite the historic challenges of using morphology to investigate anguilliform phylogeny, parsimony analysis of a data matrix of morphological character state changes resulted in the nesting of saccopharyngoids within the anguilloids (Forey et al. 1996). The paraphyly of anguilloids relative to saccopharyngoids is reflected in several molecular phylogenetic analyses (Inoue et al. 2003b, 2004, 2010; Santini, Kong, et al. 2013; J. N. Chen et al. 2014; Dornburg et al. 2015; Poulsen et al. 2018). The issue of the phylogenetic affinities of saccopharyngoids is effectively settled, as evidenced by a proposed set of taxonomic groupings in *Anguilliformes* that do not include *Saccopharyngiformes* or *Saccopharyngoidei*, classifying them with the anguilloid lineages *Anguillidae* (freshwater eels), *Moringuidae* (spaghetti eels), *Nemichthyidae* (snipe eels), and *Serrivomeridae* (sawtooth eels) (K. L. Tang and Fielitz 2013). Molecular phylogenetic analyses resolve *Anguilliformes* into four clades: *Synaphobranchoidei*, *Muraenoidei*, *Congroidei*, and *Anguilloidei* (K. L. Tang and Fielitz 2013). Several currently recognized taxa within *Anguilliformes* are non-monophyletic in molecular phylogenetic analyses, including *Chlopsidae* (false morays), *Coloconger* (shottail eels), *Congridae* (conger eels), *Cyematidae* (bobtail snipe eels), *Derichthyidae* (narrowneck eels), and *Nettastomatidae* (Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; Poulsen et al. 2018; Lü et al. 2019; K. Zhang, Zhu, et al. 2021; Huang et al. 2023).

Composition. *Anguilliformes* currently contains 1,057 species (Fricke et al. 2023) classified in *Anguilloidei*, *Chlopsidae*, *Congroidei*, *Muraenoidei*, and *Synaphobranchoidei* (K. L. Tang and Fielitz 2013). Over the past 10 years 122 new living species of *Anguilliformes* have been described, comprising 11.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Anguilliformes* include (1) symplectic fused with quadrate (Forey et al. 1996; Wiley and Johnson 2010), (2) absence of first pharyngobranchial, gill arches displaced posteriorly and free from the neurocranium (Forey et al. 1996; Wiley and Johnson 2010; Espíndola et al. 2023), (3) absence of pelvic girdle and pelvic fins (Forey et al. 1996; Wiley and Johnson 2010), (4) body scales absent or embedded with a basket-weave pattern (C. R. Robins 1989; Wiley and Johnson 2010; G. D. Johnson et al. 2012; Espíndola et al. 2023), (5) ceratohyal with elongated anterior end (C. R. Robins 1989; Wiley and Johnson 2010), (6) anterior branchiostegals curve behind and above opercle (C. R. Robins 1989; Wiley and Johnson 2010; G. D. Johnson et al. 2012; Espíndola et al. 2023), (7) endopterygoid absent (G. D. Johnson et al. 2012; Espíndola et al. 2023), (8) single hypohyal or hypohyal absent (G. D. Johnson et al. 2012; Espíndola et al. 2023), (9) dorsal and anal fins confluent with caudal fin (G. D. Johnson et al. 2012; Espíndola et al. 2023), (10) fewer than eight caudal fin rays in each lobe (G. D. Johnson et al. 2012; Espíndola et al.

2023), (11) posttemporal absent (G. D. Johnson et al. 2012; Espíndola et al. 2023), (12) epurals absent (G. D. Johnson et al. 2012; Espíndola et al. 2023), (13) absence of levator internus 3 (Springer and Johnson 2015; Espíndola et al. 2023), (14) presence of musculus pharyngobranchialis 2-epibranchialis 1 (Springer and Johnson 2015; Espíndola et al. 2023), (15) presence of a single pharyngoclavicularis (Springer and Johnson 2015; Espíndola et al. 2023), (16) presence of rectus ventralis 3 and 4 (Springer and Johnson 2015; Espíndola et al. 2023), (17) absence of rectus communis (Springer and Johnson 2015; Espíndola et al. 2023), (18) levator internus 2 insertion includes upper tooth plate 4 (Springer and Johnson 2015; Espíndola et al. 2023), (19) hypobranchial 3 either absent or entirely cartilaginous (Springer and Johnson 2015; Espíndola et al. 2023), (20) absence of accessory element at distal end of ceratobranchial 4 (Springer and Johnson 2015; Espíndola et al. 2023), (21) adductor mandibulae originates on parietal (Espíndola et al. 2023), and (22) adductor mandibulae lacks segmentum mandibularis (Espíndola et al. 2023).

Synonyms. *Apodes* (Kaup 1856:1; Boulenger 1904b:600–605; Regan 1912e:377–379; Jordan 1923:130; Trewavas 1932:655–656) and *Muraeni* (Bleeker 1864c:113) are approximate synonyms of *Anguilliformes*. *Encheli* is a partial synonym of *Anguilliformes* (Garstang 1931:257).

Comments. The composition of *Anguilliformes* in Goodrich (1909:370, 403–404) is very close to that delimited here and in Greenwood et al. (1966), the differences being the addition of lineages discovered after these important studies (e.g., Castle 1977; G. D. Johnson et al. 2012). The name *Anguilliformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

While there are several fossil lineages of pan-anguilliforms from the Cretaceous, the earliest fossil *Anguilliformes* are from the Ypresian (56.0–48.1 Ma) in the Eocene of Italy (Bannikov 2014b; Carnevale et al. 2014; Pfaff et al. 2016). Relaxed molecular clock analyses estimate the crown age of *Anguilliformes* between 84 and 116 million years ago (Santini, Kong, et al. 2013).

Constituent lineages.

Anguilloidei
Chlopsidae
Congroidei
Muraenoidei
Synaphobranchoidei

Synaphobranchoidei P. Bleeker 1864a:13
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Synaphobranchus kaupi* J. Y. Johnson 1862, *Simenchelys parasitica* Gill in Bean and Goode 1879, and *Protanguilla palau* Johnson, Ida, and Sakaue in G. D. Johnson et al. 2012. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek σύν (sˈɪn), meaning together; ἁφή (ɐfˈɛ), meaning a joint or a fastening; and βραγχίον (bɹˈækiə͡n), Latinized as *branchium*, meaning a fish gill.

Registration number. 888.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences from three nuclear genes and two mitochondrial protein coding genes (Santini, Kong, et al. 2013, fig. 2). Phylogenetic relationships of *Synaphobranchoidei* are presented in Figure 6.

Phylogenetics. Molecular phylogenetic analyses consistently resolve *Protanguilla palau* (Cave Eel) and species of *Synaphobranchidae* (cutthroat eels) as a monophyletic group (Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; Poulsen et al. 2018). Some investigators contend that morphological character state changes support *Protanguilla* as the sister lineage of all other *Anguilliformes* (G. D. Johnson et al. 2012; Espíndola et al. 2023), but this inference is on the basis of the distribution of several key morphological traits and not the result of an explicit phylogenetic analysis of coded character state changes.

Composition. *Synaphobranchoidei* currently contains 53 species (Fricke et al. 2023) classified in *Synaphobranchidae* and *Protanguilla* (K. L. Tang and Fielitz 2013). Over the past

10 years 15 new living species of *Synaphobranchoidei* have been described (Fricke et al. 2023), comprising 28.3% of the living species diversity in the clade.

Diagnostic apomorphies. The leptocephalus larvae of species of *Synaphobranchidae* are unique among all other lineages of *Anguilliformes* in possessing vertically or diagonally elongated eyes (C. H. Robins and Robins 1989). The morphology of the larvae of *Protanguilla palau* is not known.

Synonyms. There are no synonyms of *Synaphobranchoidei*.

Comments. Bleeker (1864a,13) applied *Synaphobranchoidei* as a ranked taxonomic family to classify *Synaphobranchus kaupi*. Given the resolution of *Synaphobranchidae* and *Protanguilla* as sister lineages in molecular phylogenies (Santini, Kong, et al. 2013; Poulsen et al. 2018), K. L. Tang and Fielitz (2013, tbl. II) revised the classification of *Anguilliformes* with a new delimitation of *Synaphobranchoidei* that is the basis of the definition presented here. Bayesian relaxed molecular clock analysis estimates the crown age of *Synaphobranchoidei* between 55 and 108 million years ago (Santini, Kong, et al. 2013).

Constituent lineages. Redundant group names are marked with an asterisk.

*Protanguillidae** *Synaphobranchidae*

Anguilloidei P. Bleeker 1859:xxxiii
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Anguilla anguilla* (Linnaeus 1758), *Moringua microchir* Bleeker 1853a, and *Serrivomer beanii* T. N. Gill and Ryder 1883. This is a minimum-crown-clade definition.

Etymology. From the Latin *Anguilla*, meaning eel.

Registration number. 889.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences from three nuclear genes and two mitochondrial protein coding genes (Santini, Kong, et al. 2013, fig. 2). See Figure 6 for a phylogeny of the major lineages of *Anguilloidei*.

Phylogenetics. Several molecular phylogenetic analyses result in the monophyly of *Anguilloidei*, with *Moringuidae* resolved as the sister lineage of all other anguilloids (Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; Poulsen et al. 2018). The lineages previously classified as *Lyomeri*, *Saccopharyngiformes*, or *Saccopharyngoidei* are nested in *Anguilloidei*, but analyses differ on the monophyly of a group containing *Monognathidae*, *Cyematidae*, *Saccopharyngidae*, *Neocyematidae*, and *Eurypharyngidae* (Santini, Kong, et al. 2013; Poulsen et al. 2018).

Composition. *Anguilloidei* currently contains 81 species (Fricke et al. 2023) classified in *Anguillidae*, *Cyema*, *Eurypharynx*, *Monognathidae*, *Moringuidae*, *Nemichthyidae*, *Neocyema*, *Saccopharyngidae*, and *Serrivomeridae*. Over the past 10 years no new living species of *Anguilloidei* have been described (Fricke et al. 2023).

Diagnostic apomorphies. There are no known morphological apomorphies for *Anguilloidei*.

Synonyms. *Lyomeri* (T. N. Gill and Ryder 1883:263–264; Jordan 1923:134; Garstang 1931:257; Böhlke 1966:603–610), *Saccopharyngiformes* (Berg 1940:439–440; McAllister 1968:88–89; C. R. Robins 1989:13–15), and *Saccopharyngoidei* (Greenwood et al. 1966:393; J. S. Nelson 2006:125; J. S. Nelson et al. 2016:149–150) are all partial synonyms of *Anguilloidei*.

Comments. Bleeker (1864c) applied *Anguilloidei* as a ranked taxonomic family to a group containing *Anguilla anguilla* and the fossil taxon †*Paranguilla tigrina*. Greenwood et al. (1966) classified all *Anguilliformes* that were not in their *Saccopharyngoidei* into *Anguilloidei*. On the basis of the resolution of clades in molecular phylogenetic analyses, K. L. Tang and Fielitz (2013) revised the classification of *Anguilliformes* with a new delimitation of *Anguilloidei* that is the basis of the definition presented here. Bayesian relaxed molecular clock analysis estimates the crown age of *Anguilloidei* between approximately 64 and 90 million years ago (Santini, Kong, et al. 2013).

Constituent lineages. Redundant group names are marked with an asterisk.

*Anguillidae**
*Cyematidae**
*Eurypharyngidae**
*Monognathidae**
Moringuidae
Nemichthyidae
*Neocyematidae**
*Saccopharyngidae**
Serrivomeridae

Muraenoidei L. J. F. J. Fitzinger 1832:332 [T. J. Near and C. E. Thacker], converted clade name

Definition. The least inclusive clade that contains *Muraena helena* Linnaeus 1758, *Myroconger compressus* Günther 1870, and *Pythonichthys microphthalmus* (Regan 1912d). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek μύραινα (mjʊ͡ɹˈeɪ͡nə) that is the name of the Mediterranean Moray, *Muraena helena* (D. W. Thompson 1947:162–165).

Registration number. 890.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of the mitochondrial 12S and 16S rRNA genes (K. L. Tang and Fielitz 2013, fig. 1). Phylogenetic relationships among the lineages of *Muraenoidei* are presented in Figure 6.

Phylogenetics. Molecular phylogenetic analyses resolve *Muraenoidei* as monophyletic, with *Myroconger* (thin eels) and *Muraenidae* (moray eels) as sister clades relative to *Heterenchelyidae* (Inoue et al. 2010; G. D. Johnson et al. 2012; Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; Poulsen et al. 2018). Alternatively, a morphological analysis results in paraphyly of *Muraenoidei*, with the chlopsid *Xenoconger fryeri* (Fryer's False Moray) resolved as the sister lineage of *Muraenidae* relative to *Myroconger* (D. G. Smith 1984).

Composition. *Muraenoidei* currently contains 238 species (Fricke et al. 2023) classified in *Heterenchelyidae* (mud eels), *Muraenidae*, and *Myroconger* (K. L. Tang and Fielitz 2013). Over the past 10 years 23 new living species of *Muraenoidei* have been described (Fricke et al. 2023), composing 9.7% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Muraenoidei* include (1) frontals not fused (J. S. Nelson et al. 2016), (2) reduction in gill arch elements (J. S. Nelson et al. 2016), (3) reduction of lateral line (J. S. Nelson et al. 2016), and (4) normal-sized eyes (J. S. Nelson et al. 2016).

Synonyms. There are no synonyms of *Muraenoidei*.

Comments. Müller (1845b) used *Muraenoidei* as a family group name in his classification of *Teleostei*. *Muraenoidei* was later treated as a suborder containing *Chlopsidae* (false morays), *Muraenidae*, and *Myrocongridae* (C. R. Robins 1989). Given the resolution of a clade containing *Heterenchelyidae*, *Muraenidae*, and *Myroconger* in molecular phylogenies (Inoue et al. 2010; G. D. Johnson et al. 2012; Santini, Kong, et al. 2013; Poulsen et al. 2018), K. L. Tang and Fielitz (2013, table II) revised the classification of *Anguilliformes* with a new delimitation of *Muraenoidei* that is the basis of the definition presented here. Bayesian relaxed molecular clock analysis estimates the crown age of *Muraenoidei* ranges between 60 and 90 million years ago (Santini, Kong, et al. 2013).

Constituent lineages. Redundant group names are marked with an asterisk.

Heterenchelyidae
Muraenidae
*Myrocongridae**

Congroidei P. Bleeker 1864a:18 [T. J. Near and C. E. Thacker], converted clade name

Definition. The least inclusive crown clade that contains *Conger conger* (Linnaeus 1758), *Conger oceanicus* (Mitchill 1818a), *Derichthys serpentinus* T. N. Gill 1884b, *Heteroconger hassi* (Klausewitz and Eibl-Eibesfeldt 1959), and *Ophichthys zophochir* Jordan and Gilbert 1882a. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek γόγγρος (ɡˈɔŋɡɹoʊ͡z), meaning conger eel, Latinized to *conger* (D. W. Thompson 1947:49–50).

Registration number. 891.

Reference phylogeny. A phylogeny inferred from a concatenated dataset of DNA sequences from three nuclear genes and two mitochondrial protein coding genes (Santini, Kong, et al. 2013, fig. 2). Although *Conger conger* is not included in the reference phylogeny, it resolves with other species of *Conger* in molecular phylogenetic analyses (J. N. Chen et al. 2014, figs. 1, 2). The relationships among the lineages of *Congroidei* are shown in Figure 6.

Phylogenetics. The lineages delimited here in *Congroidei* are consistently resolved as monophyletic in molecular phylogenetic analyses (Inoue et al. 2010; G. D. Johnson et al. 2012; Santini, Kong, et al. 2013; K. L. Tang and Fielitz 2013; Poulsen et al. 2018). Despite the strong support for monophyly of *Congroidei*, the phylogenetics is complicated by the nonmonophyly of *Derichthyidae* (narrowneck eels) and *Congridae* (conger eels) in the analyses. Molecular studies support monophyly of a lineage containing *Colocongridae* (shorttail eels), *Congriscus* (*Congridae*), and *Derichthyidae* (López et al. 2007; Santini, Kong, et al. 2013; Poulsen et al. 2018); however, *Nessorhamphus* (*Derichthyidae*) and *Congriscus* are sister lineages, and *Derichthys* is resolved as sister to *Colocongridae* (worm eels) (Santini, Kong, et al. 2013). There is poor support for many of these nodes in the molecular phylogenies, but a morphological analysis provides strong support for the monophyly of *Derichthyidae* and resolution of a clade containing *Colocongridae*, *Congriscus*, and *Derichthyidae* (da Silva et al. 2019). Species of *Nettastomatidae* (duckbill eels) and the *Congridae* subclade *Congrinae* form a clade (Santini, Kong, et al. 2013; Poulsen et al. 2018), but *Nettastomatidae* and *Congrinae* are both paraphyletic. The *Congridae* subclades *Bathymyrinae* and *Heterocongrinae* are resolved as a clade (Santini, Kong, et al. 2013; Poulsen et al. 2018), but *Bathymyrinae* is rendered paraphyletic by *Heteroconger* (Santini, Kong, et al. 2013). *Muraenesocidae* (pike congers) and *Ophichthidae* (snake eels) are both monophyletic and resolved as sister lineages (Santini, Kong, et al. 2013; Poulsen et al. 2018).

Composition. *Congroidei* currently contains 660 species (Fricke et al. 2023) classified in *Congridae*, *Coloconger*, *Derichthyidae*, *Muraenesocidae*, *Nettastomatidae*, and *Ophichthidae*. Over the past 10 years 81 new living species of *Congroidei* have been described (Fricke et al. 2023), comprising 12.3% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Congroidei*.

Synonyms. There are no synonyms for *Congroidei*.

Comments. Bleeker (1864a:18) applied *Congroidei* as a taxonomic family. Classifications of *Anguilliformes* in the 20th century delimited *Congroidei* as a more inclusive group than given here on the basis of the presence of fused frontal bones in the skull (C. R. Robins 1989; J. S. Nelson 1994). Given the results of molecular phylogenetic analyses (Santini, Kong, et al. 2013; Poulsen et al. 2018), K. L. Tang and Fielitz (2013, table II) revised the classification of *Congroidei* to include *Chlopsidae*, *Congridae*, *Derichthyidae*, *Muraenesocidae*, *Nettastomatidae*, and *Ophichthidae*, which is not followed here. Bayesian relaxed molecular clock analysis estimates the crown age of *Congroidei* between 64 and 90 million years ago (Santini, Kong, et al. 2013).

Constituent lineages. Redundant group names are marked with an asterisk.

*Colocongridae**
Congridae
Derichthyidae
Muraenesocidae
Nettastomatidae
Ophichthidae

Osteoglossomorpha P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Meyers 1966:350, 354–358, 393–394

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Hiodon tergisus* Lesueur 1818, *Pantodon buchholzi* Peters 1876, *Notopterus notopterus* (Pallas 1769), and *Osteoglossum bicirrhosum* (Cuvier 1829). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ὀστέον (ˈɑːstɪən), meaning bone; γλῶσσα (glˈɔsə), meaning tongue; and μορφή (mˈɔːɹ͡fiː), meaning form or shape.

Registration number. 892.

Reference phylogeny. A phylogeny inferred from DNA sequences of 546 exons (Peterson et al. 2022, fig. 1e). Phylogenetic relationships of the major living lineages and fossil taxa of *Osteoglossomorpha* are shown in Figure 6. The placements of the fossil lineages in the phylogeny are based on analyses of morphological characters (J.-Y. Zhang 1998, 2006; G.-Q. Li and Wilson 1999; Xu and Chang 2009).

Phylogenetics. Several studies prior to the mid-1960s hinted at a close relationship among what are now considered the lineages of *Osteoglossomorpha* (Ridewood 1904, 1905; Garstang 1931; Gregory 1933:161–175; Gosline 1960, 1961; Greenwood 1963), but it was Greenwood et al. (1966) that named the group and solidified evidence for its monophyly. The monophyly of *Osteoglossomorpha* is supported in several morphological and molecular phylogenetic analyses and *Hiodon* (mooneyes) and *Osteoglossiformes* are consistently resolved as sister groups (G.-Q. Li and Wilson 1996, 1999; G.-Q. Li, Wilson, et al. 1997; J.-Y. Zhang 1998; Hilton 2003; Inoue et al. 2003a, 2009; Lavoué and Sullivan 2004; M. V. H. Wilson and Murray 2008; Santini et al. 2009; Xu and Chang 2009; Lavoué, Miya, Arnegard, et al. 2012; Betancur-R, Broughton, et al. 2013; Hilton and Lavoué 2018; Murray et al. 2018; Brito et al. 2020; Peterson et al. 2022).

Composition. *Osteoglossomorpha* currently contains 254 living species (Fricke et al. 2023) classified in *Hiodon* and *Osteoglossiformes*. There are several fossil lineages of *Osteoglossomorpha* that include pan-hiodontids †*Plesiolycoptera* and †*Yanbiania* (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998) and the pan-osteoglossiforms †*Paralycoptera*, †*Jinanichthys*, †*Huashia*, and †*Kuntulunia* (Jiangyong 1990; G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998, 2006; Xu and Chang 2009; Murray et al. 2018). Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years 15 new living species of *Osteoglossomorpha* have been described (Fricke et al. 2023), comprising 5.9% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Osteoglossomorpha* include (1) primary bite between parasphenoid and basihyal; however, this trait is an apomorphy for a more inclusive pan-osteoglossomorphs (Greenwood et al. 1966; G.-Q. Li and Wilson 1996), (2) supramaxilla absent (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 2006; Xu and Chang 2009), (3) fourth and fifth infraorbitals fused (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998), (4) last uroneural much shorter than first uroneural (J.-Y. Zhang 1998), (5) rectangular-shaped infraorbital bone (G.-Q. Li and Wilson 1999), (6) seven pelvic-fin rays (J.-Y. Zhang 2006), (7) nasal bones tubular and strongly curved (Hilton 2003), (8) supraorbital sensory canal ending in frontal bone (Hilton 2003; M. V. H. Wilson and Murray 2008), (9) ascending process of premaxilla not developed or slightly developed (Hilton 2003; M. V. H. Wilson and Murray 2008), (10) autopalatine bone absent (M. V. H. Wilson and Murray 2008), (11) supraorbital absent (Mirande 2017), (12) complete absence of epurals (Mirande 2017), (13) bony epipleurals absent (Mirande 2017), and (14) intestine coils to the left of the stomach (Mirande 2017).

Synonyms. *Osteoglossi* is a partial (Garstang 1931:256–257) and an ambiguous (Gosline 1960:358) synonym of *Osteoglossomorpha*. *Osteoglossoidei* (Gosline 1960:358) is an ambiguous synonym of *Osteoglossomorpha*.

Comments. The earliest fossil osteoglossomorphs include the pan-osteoglossiforms †*Paralycoptera*, †*Jinanichthys*, and †*Huashia* that date from the Aptian (121.4–113.2 Ma) in the Cretaceous of China. Bayesian relaxed molecular clock analyses of *Osteoglossomorpha* result in an average posterior crown age estimate of 234.4 million years ago, with the credible interval ranging between 212.4 and 259.0 million years ago (Peterson et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Hiodontidae**
Osteoglossiformes
†*Huashia*
†*Jinanichthys*
†*Kuntulunia*
†*Paralycoptera*
†*Plesiolycoptera*
†*Yanbiania*

Osteoglossiformes P. H. Greenwood 1963:408
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Pantodon buchholzi* Peters 1876, *Notopterus notopterus* (Pallas 1769), and *Osteoglossum bicirrhosum* (Cuvier 1829). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ὀστέον (ˈɑːstɪən), meaning bone, and γλῶσσα (glˈɔsə), meaning tongue. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 896.

Reference phylogeny. A phylogeny inferred from DNA sequences of 546 exons (Peterson et al. 2022, fig. 1e). Phylogenetic relationships among the major lineages of *Osteoglossiformes* are shown in Figure 6. The placements of the fossil taxa †*Palaeonotopterus* and †*Laeliichthys* in the phylogeny are based on analyses of morphological characters (Cavin and Forey 2001; Murray et al. 2018; Brito et al. 2020).

Phylogenetics. The monophyly of *Osteoglossiformes* is supported in several morphological and molecular phylogenetic analyses (Taverne 1979, 1998; G.-Q. Li and Wilson 1996, 1999; G.-Q. Li, Wilson, et al. 1997; Hilton 2003; Lavoué and Sullivan 2004; J.-Y. Zhang 2006; M. V. H. Wilson and Murray 2008; Inoue et al. 2009; Xu and Chang 2009; Lavoué et al. 2011; Lavoue, Miya, Arnegard, et al. 2012; Lavoué 2015, 2016; Murray et al. 2018; Brito et al. 2020; Peterson et al. 2022). Within *Osteoglossiformes*, there is consistent support for the monophyly of a lineage consisting of *Notopteridae* (featherfin knifefishes) and the clade *Mormyroidea*, which contains *Mormyridae* (elephantfishes) and *Gymnarchus niloticus* (Aba) (Taverne 1979, 1998; G.-Q. Li and Wilson 1996, 1999; G.-Q. Li, Wilson, et al. 1997; Lavoué and Sullivan 2004; M. V. H. Wilson and Murray 2008; Inoue et al. 2009; Lavoué et al. 2011; Lavoue, Miya, Arnegard, et al. 2012; Lavoué 2015, 2016; Murray et al. 2018; Peterson et al. 2022).

Morphological phylogenies differ on the resolution of *Osteoglossidae* (bonytongues) with *Pantodon buchholzi* (Butterflyfish) as either the sister lineage of all other osteoglossids (Bonde 1996; M. V. H. Wilson and Murray 2008; Xu and Chang 2009) or nested within *Osteoglossidae* as the sister lineage of a clade containing *Osteoglossum* and *Scleropages* (Taverne 1979, 1998; G.-Q. Li and Wilson 1996, 1999; G.-Q. Li, Grande, et al. 1997; G.-Q. Li, Wilson, et al. 1997; Hilton 2003; Brito et al. 2020). Most molecular phylogenies resolve *Pantodon* as distantly related to other *Osteoglossidae* as the sister lineage of all other *Osteoglossiformes* (Lavoué and Sullivan 2004; Inoue et al. 2009; Lavoué et al. 2011; Lavoue, Miya, Arnegard, et al. 2012; Lavoué 2015, 2016; Hughes et al. 2018; Peterson et al. 2022).

Mormyridae is the most species-rich lineage of *Osteoglossiformes*, with at least 227 species classified in 22 genera (Fricke et al. 2023). Biodiversity discovery is active in mormyrids, as 11% of the living species diversity in the clade was described over the past 10 years (Sullivan et al. 2016; Fricke et al. 2023). Molecular phylogenies inferred from Sanger-sequenced nuclear and mitochondrial genes do not confidently resolve relationships within *Mormyridae*, but do strongly indicate that *Brienomyrus*, *Hippopotamyrus*, *Marcusenius*, and *Pollimyrus* are paraphyletic (Sullivan et al. 2000, 2016; Levin and Golubtsov 2018). Phylogenomic analyses of *Mormyridae* result in resolved and well-supported phylogenies where *Hippopotamyrus* and *Marcusenius* are paraphyletic, but *Pollimyrus* is monophyletic (Peterson et al. 2022). The Cretaceous fossil taxon †*Palaeonotopterus greenwoodi* is resolved as the sister lineage of *Mormyroidea* (*Mormyridae* and *Gymnarchus*) in phylogenetic analyses of morphological characters (Hilton 2003; Murray et al. 2018; Brito et al. 2020).

Morphological and molecular phylogenetic analyses resolve a monophyletic *Notopteridae* (e.g., Inoue et al. 2009; Brito et al. 2020). Within notopterids, the Asian (*Chitala* and *Notopterus*) and African (*Papyrocranus* and *Xenomystus*) lineages are each monophyletic and resolved as sister clades (Inoue et al. 2009). Morphological phylogenetic analyses resolved the Cretaceous fossil taxon †*Laeliichthys ancestralis* from Brazil as the sister lineage of *Arapaiminae* (*Heterotis* and *Arapaima*) (G.-Q. Li and Wilson 1996, 1999; Taverne 1998); however, a more recent morphological analysis places †*Laeliichthys* as the sister lineage of *Notopteridae* (Brito et al. 2020).

Composition. *Osteoglossiformes* currently contains 254 living species (Fricke et al. 2023) that include *Pantodon buchholzi*, *Gymnarchus niloticus*, and species classified in *Mormyridae*, *Notopteridae*, and *Osteoglossidae* (Hilton 2003). Fossil taxa include the pan-mormyroid †*Palaeonotopterus* and pan-notopterid †*Laeliichthys* (Silva Santos 1985; Lundberg 1993; Forey 1997; Cavin and Forey 2001; Murray et al. 2018; Brito et al. 2020). The ages and locations of †*Palaeonotopterus* and †*Laeliichthys* are given in Appendix 1. Over the past 10 years 15 new living species of *Osteoglossiformes* have been described (Fricke et al. 2023), comprising 5.9% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Osteoglossiformes* include (1) 15 or fewer primary branched caudal fin rays (G.-Q. Li and Wilson 1996; G.-Q. Li, Grande, et al. 1997; G.-Q. Li, Wilson, et al. 1997; Hilton and Britz 2010), (2) two or fewer uroneurals in caudal skeleton (G.-Q. Li and Wilson 1996; Wiley and Johnson 2010), (3) nasal bone gutter-like or subrectangular (G.-Q. Li and Wilson 1996; G.-Q. Li, Grande, et al. 1997; G.-Q. Li, Wilson, et al. 1997), (4) six or fewer hypurals in caudal skeleton (G.-Q. Li, Grande, et al. 1997; Xu and Chang 2009), (5) dorsal hypurals and ural centrum 2 fused (G.-Q. Li, Wilson, et al. 1997; M. V. H. Wilson and Murray 2008; Hilton and Britz 2010; Wiley and Johnson 2010), (6) epurals absent (Hilton 2003; M. V. H. Wilson and Murray 2008; Hilton and Britz 2010), (7) bony elements associated with second ventral gill arch present as processes on second hypobranchial (Xu and Chang 2009), (8) presence of one ossified pair of hypohyals (Xu and Chang 2009), and (9) palatine and ectopterygoid fused (Xu and Chang 2009).

Synonyms. There are no synonyms of *Osteoglossiformes*.

Comments. The first delimitation of *Osteoglossiformes* included *Hiodon* and excluded *Mormyridae* (Greenwood et al. 1966:394). The hypothesis that *Hiodon* was nested in the clade delimited here as *Osteoglossiformes* was supported in several studies (G. J. Nelson 1968; Greenwood 1973; Lauder and Liem 1983). The delimitation of *Osteoglossiformes* that includes all living species of *Osteoglossomorpha* except *Hiodon tergisus and H. alosoides* was first proposed by Taverne (1979), and this hypothesis is corroborated in nearly all subsequent morphological and molecular phylogenetic analyses (e.g., G.-Q. Li and Wilson 1996; Lavoué and Sullivan 2004; Peterson et al. 2022).

The earliest fossil taxon of *Osteoglossiformes* is the pan-notopterid †*Laeliichthys ancestralis* from the Barremian (126.5–121.4 Ma) in the Cretaceous of Brazil (Silva Santos 1985; Brito et al. 2020). Bayesian relaxed molecular clock analyses of *Osteoglossiformes* result in an average posterior crown age estimate of 197.7 million years ago, with the credible interval ranging between 174.4 and 221.6 million years ago (Peterson et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Gymnarchidae**
Mormyridae
Notopteridae
Osteoglossidae
*Pantodontidae**
†*Laeliichthys*
†*Palaeonotopterus*

Osteoglossidae C. L. Bonaparte 1845:387
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Osteoglossum bicirrhosum* (Cuvier 1829) and *Heterotis niloticus* (Cuvier 1829), but not *Pantodon buchholzi* Peters 1876. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek ὀστέον (ˈɑːstɪən), meaning bone, and γλῶσσα (ɡlˈɔsə), meaning tongue.

Registration number. 897.

Reference phylogeny. A phylogeny inferred from DNA sequences of complete mitochondrial genomes (Lavoué 2015, fig. 2). Phylogenetic relationships among the living lineages and fossil taxa of *Osteoglossidae* are presented in Figure 6. The placements of the fossil taxa in the phylogeny are on the basis of inferences from morphological characters (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998, 2006; Hilton 2003; Xu and Chang 2009; Murray et al. 2018).

Phylogenetics. Morphological and molecular analyses differ on the phylogenetic resolution of *Pantodon buchholzi* and *Osteoglossidae*. All morphological analyses resolve *Pantodon* either as the sister lineage of all other *Osteoglossidae* (G. J. Nelson 1969b; Greenwood 1973; Bonde 1996; M. V. H. Wilson and Murray 2008; Murray et al. 2018) or as the sister lineage of *Osteoglossinae* (G. J. Nelson 1968; Taverne 1979, 1998; G.-Q. Li and Wilson 1996, 1999; G.-Q. Li, Grande, et al. 1997; G.-Q. Li, Wilson, et al. 1997; Taverne 1998; J.-Y. Zhang 2006; Murray et al. 2018), which is a clade containing *Osteoglossum* and *Scleropages* (Hilton and Lavoué 2018). Molecular analyses agree with morphological studies in resolving two sets of sister lineages within *Osteoglossidae*: *Osteoglossinae* (*Osteoglossum* and *Scleropages*) and *Arapaiminae* (*Arapaima* and *Heterotis*); however, most molecular phylogenies place *Pantodon* as the sister lineage of all other *Osteoglossiformes*, distantly related to *Osteoglossidae* (Lavoué and Sullivan 2004; Inoue et al. 2009; Lavoué et al. 2011; Lavoue, Miya, Arnegard, et al. 2012; Lavoué 2015, 2016; Hughes et al. 2018; Peterson et al. 2022).

Composition. *Osteoglossidae* currently contains 12 living species (D. J. Stewart 2013a, 2013b; Fricke et al. 2023) that include *Heterotis niloticus* (African Arowana) and species classified in *Arapaima*, *Osteoglossum*, and *Scleropages*. Fossil lineages of *Osteoglossidae* include the pan-arapaimines †*Joffrichthys* and †*Sinoglossus* and the pan-osteoglossines †*Cretophareodus*, †*Phareodus*, and †*Singida* (G.-Q. Li and Wilson 1996, 1999; J.-Y. Zhang 1998, 2006; Hilton 2003; Xu and Chang 2009; Murray et al. 2018). The ages and locations of the fossil osteoglossids are given in Appendix 1. Over the past 10 years no new living species of *Osteoglossidae* have been described (Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Osteoglossidae* include (1) six hypurals in caudal skeleton (G.-Q. Li and Wilson 1996), (2) opercle oval or kidney- shaped (G.-Q. Li and Wilson 1996; G.-Q. Li, Grande, et al. 1997), (3) palatoquadrate area behind and below orbit completely covered by infraorbitals (G.-Q. Li and Wilson 1996; G.-Q. Li, Grande, et al. 1997; Hilton 2003; J.-Y. Zhang 2006; M. V. H. Wilson and Murray 2008; Forey and Hilton 2010), (4) ventral part of preopercle does not reach level of orbit (G.-Q. Li, Wilson, et al. 1997; M. V. H. Wilson and Murray 2008), (5) basipterygoid process present (G.-Q. Li, Wilson, et al. 1997; Hilton 2003), (6) no connection between swim bladder and ear (G.-Q. Li, Wilson, et al. 1997; Forey and Hilton 2010), (7) supraorbital canal ending in frontal (G.-Q. Li and Wilson 1999; Forey and Hilton 2010), (8) extrascapular bone reduced and irregularly shaped (Hilton 2003; M. V. H. Wilson and Murray 2008; Forey and Hilton 2010), (9) nasal bones flat and broad (Hilton 2003; Forey and Hilton 2010), tooth plates of basibranchial and basihyal continuous (Hilton 2003), (10) subopercle small and anterior to opercle (Hilton 2003; J.-Y. Zhang 2006; Forey and Hilton 2010), (11) scales with reticulate furrows present over entire scale (Hilton 2003; Forey and Hilton 2010), (12) infraorbitals 3 and 4 fused (J.-Y. Zhang 2006), (13) temporal fossa present, bordered by epioccipital and pterotic (Xu and Chang 2009), and (14) first parapophysis expanded (Forey and Hilton 2010).

Synonyms. There are no synonyms of *Osteoglossidae*.

Comments. Bonaparte's (1845) introduction of the name *Osteoglossidae* was in a list of taxonomic names in a classification of fishes with no comment. Günther's (1868:377–380) delimitation of *Osteoglossidae* is identical to that presented here.

Osteoglossidae is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:64). The earliest fossil taxon included in *Osteoglossidae* is †*Cretophareodus alberticus* from the Campanian (83.2–72.2 Ma) in the Cretaceous of Canada (G.-Q. Li 1996; Arbour et al. 2009). Bayesian relaxed molecular clock analyses of *Osteoglossidae* result in an average posterior crown age estimate of 96.6 million years ago, with the credible interval ranging between 78.6 and 112.7 million years ago (Peterson et al. 2022).

Constituent lineages.

Arapaima
Heterotis
Osteoglossum
Scleropages
†*Cretophareodus*
†*Joffrichthys*
†*Phareodus*
†*Singida*
†*Sinoglossus*

Clupeocephala P. H. Greenwood 1973:326

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Clupea harengus* Linnaeus 1758 (*Otocephala*, *Clupeiformes*), *Engraulis encrasicolus* (Linnaeus 1758) (*Otocephala*, *Clupeiformes*), *Cyprinus carpio* Linnaeus 1758 (*Otocephala*, *Cypriniformes*), *Lepidogalaxias salamandroides* Mees 1961 (*Euteleostei*), and *Perca fluviatilis* Linnaeus 1758 (*Euteleostei*, *Perciformes*). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek *κλουπαῖα* (klˈuːpiə͡), a name with an obscure origin for an uncertain number of fish species used by ancient authors such as Plutarch (D. W. Thompson 1947:117–118) and *κεφαλή* (kɛfˈɑːlə), meaning the head of a human or other animal.

Registration number. 898.

Reference phylogeny. A phylogeny inferred from DNA sequences sampled from 1,105 exons (Hughes et al. 2018, fig. S2). Phylogenetic relationships among the major living lineages and fossil taxa of *Clupeocephala* are shown in Figure 7. The resolutions of the fossil taxa in the phylogeny are on the basis of inferences from morphology (Taverne 1981; Gayet 1994; Fielitz 2002; de Figueiredo and Gallo 2004; de Figueiredo 2005; Gallo et al. 2009; de Figueiredo, Gallo, and Delarmelina, et al. 2012a; Guinot and Cavin 2018).

Phylogenetics. *Clupeocephala* was identified as the clade containing all living teleosts to the exclusion of *Elopomorpha* and *Osteoglossomorpha* (Patterson and Rosen 1977). Monophyly of *Clupeocephala* is consistently supported; however, the delimitation of lineages within the clade and hypotheses of their relationships vary among molecular and morphological phylogenetic analyses (Lê et al. 1993; Lecointre 1995; G. D. Johnson and Patterson 1996; Lecointre and Nelson 1996; Arratia 1997, 2018; Ishiguro et al. 2003; Lavoué et al. 2005; Poulsen et al. 2009; Near, Eytan, et al. 2012; Faircloth et al. 2013; Hughes et al. 2018; Straube et al. 2018; Musilova et al. 2019; Roth et al. 2020; Mu et al. 2022). In addition to morphological and molecular phylogenetic analyses, the conservation of gene adjacency in the genome and the proportion of shared chromosomal breakpoints support monophyly of *Clupeocephala* (Parey et al. 2023).

Composition. *Clupeocephala* currently contains more than 33,675 living species (Fricke et al. 2023) classified in *Otocephala* and *Euteleostei* (Near, Eytan, et al. 2012; Dornburg and Near 2021). Fossil lineages of *Clupeocephala* include the pan-euteleosts †*Avitosmerus*, †*Beurlenichthys*, †*Erichalcis*, †*Gaudryella*, †*Ghabouria*, †*Helgolandichthys*, †*Parawenzichthys*, †*Santanasalmo*, †*Scombroclupeoides*, †*Wenzichthys*, and †*Tchernovichthys* (Taverne 1981; Gayet 1994; Fielitz 2002; de Figueiredo 2005; Gallo et al. 2009; de Figueiredo, Gallo, and Delarmelina, et al. 2012; Guinot and Cavin 2018). Details of the ages and locations of fossil lineages are presented in Appendix 1. Over the past 10 years there have been 3,518 new living species of *Clupeocephala* described, comprising 10.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Clupeocephala* include (1)

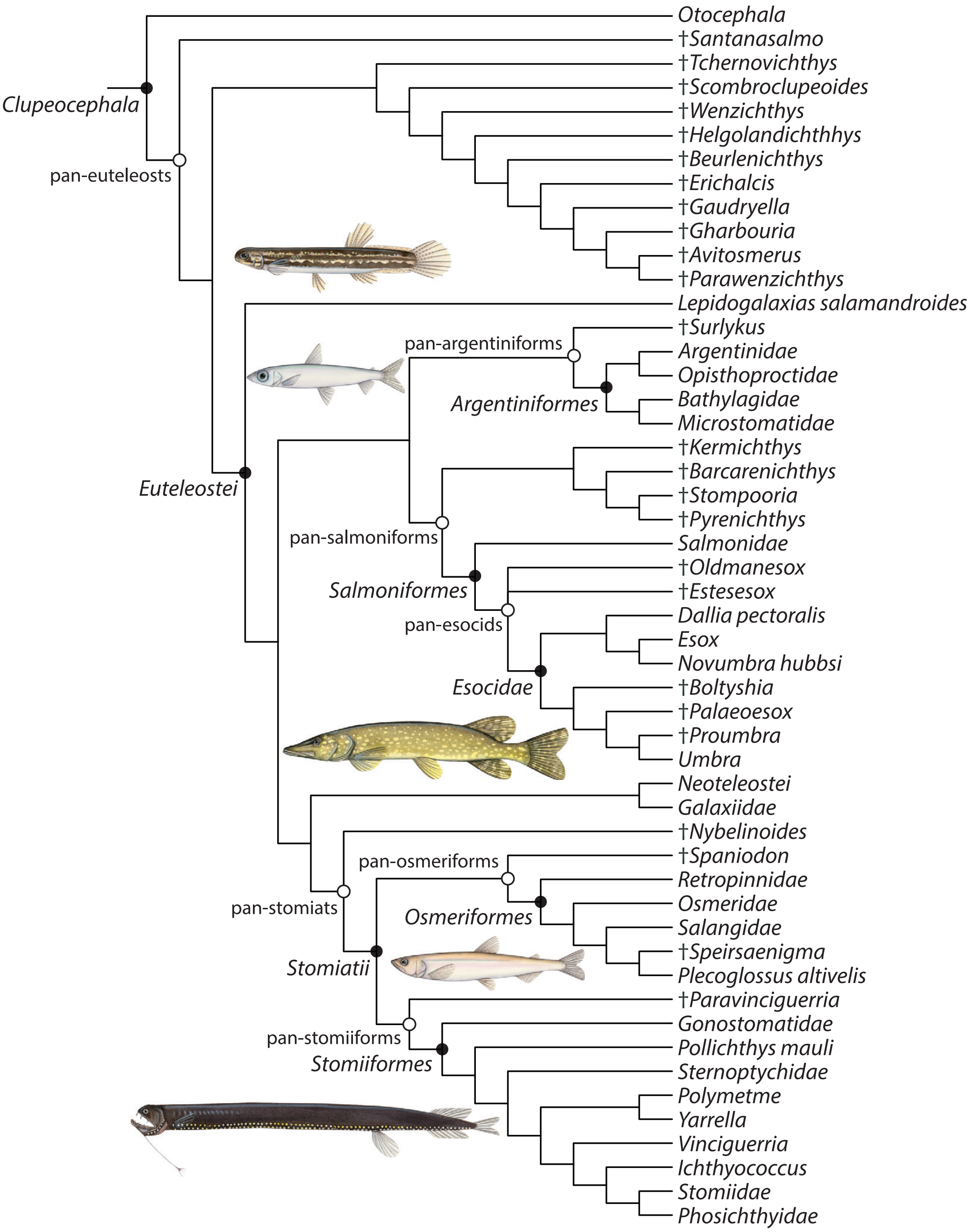

FIGURE 7. Phylogenetic relationships of the major living lineages and fossil taxa of *Clupeocephala*, *Euteleostei*, *Argentiniformes*, *Salmoniformes*, *Esocidae*, *Stomiatii*, *Osmeriformes*, and *Stomiiformes*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

autopalatine bone ossifies early in ontogeny (Arratia 2010a), (2) hypohyals pierced by hyoidean arteries (Arratia 2010a), (3) tooth plate of cartilaginous fourth pharyngobranchial element forms by the growth of only one tooth plate (Arratia 2010a), (4) uroneurals not inclined toward horizontal plane, but aligned at different angles (Arratia 2010a), (5) angular and articular bones fused (Arratia 2010a), (6) retroarticular bone excluded from articular facet of quadrate (Arratia 2010a), (7) absence of tooth plates on pharyngobranchial 1 (Arratia 2010a), (8) absence of tooth plates on pharyngobranchial 2 (Arratia 2010a), (9) absence of tooth plates on pharyngobranchial 3 (Arratia 2010a), (10) six or fewer hypurals (Arratia 2010a), and (11) fusion of duplicated chromosomes 2a and 2b (Parey et al. 2023).

Synonyms. There are no synonyms of *Clupeocephala*.

Comments. In defining *Clupeocephala* as all living teleosts to the exclusion of *Elopomorpha* and *Osteoglossomorpha*, Patterson and Rosen (1977) provided a resolution to the long-standing uncertainly regarding the relationships of *Clupeiformes* that was left unresolved in Greenwood et al. (1966). The composition of *Clupeocephala* has not changed subsequent to its introduction by Patterson and Rosen (1977). The earliest fossil taxon in *Clupeocephala* that is not an otocephalan is the pan-euteleost †*Tchernovichthys exspectatum* from the Hauterivian (132.6–126.5 Ma) in the Cretaceous of Israel (Gayet 1994). Bayesian relaxed molecular clock analyses of *Clupeocephala* result in an average posterior crown age estimate of 224.8 million years ago, with the credible interval ranging between 210.8 and 236.6 million years ago (Hughes et al. 2018).

Constituent lineages.

Euteleostei
Otocephala
†*Avitosmerus*
†*Beurlenichthys*
†*Erichalcis*
†*Gaudryella*
†*Ghabouria*
†*Helgolandichthys*
†*Parawenzichthys*
†*Santanasalmo*
†*Scombroclupeoides*
†*Tchernovichthys*
†*Wenzichthys*

Otocephala G. D. Johnson and C. Patterson 1996:315

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Engraulis encrasicolus* (Linnaeus 1758) (*Clupeiformes*), *Gonorynchus greyi* (Richardson 1845) (*Gonorynchiformes*), and *Cyprinus carpio* Linnaeus 1758 (*Cypriniformes*). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ὠτός (hˈo͡ʊtˈo͡ʊz), meaning of the ear (the genitive declension of ὀύς), and ϰεφαλή (kɛfˈɑːlə), meaning the head of a human or other animal.

Registration number. 899.

Reference phylogeny. A maximum likelihood phylogeny inferred from DNA sequences sampled from whole mitochondrial genomes (Poulsen et al. 2009, fig. 2). Phylogenetic relationships among the major lineages of *Otocephala* are shown in Figure 8. The placement of the fossil lineages †*Ellimmichthyiformes*, †*Santanaclupea*, and †*Tischlingerichthys* in the phylogeny reflects inferences based on morphology (Arratia 1997; Taverne 1997a; Forey 2004; Zaragüeta-Bagils 2004; Diogo 2007; Alvarado-Ortega et al. 2008; Mayrinck et al. 2015a; Vernygora et al. 2016; Vernygora 2020; Marramà et al. 2023).

Phylogenetics. The first phylogenies supporting monophyly of *Clupeocephala* resolved *Clupeiformes* and *Euteleostei* as sister groups, with *Ostariophysi* included in *Euteleostei* (Patterson and Rosen 1977). The monophyly of *Otocephala* as a group containing *Ostariophysi* and *Clupeiformes* to the exclusion of *Euteleostei* was a discovery resulting from early molecular phylogenetic analyses of gnathostomes (Lê et al. 1993), but subsequently supported in several morphological phylogenetic analyses and reviews of morphological synapomorphies (Arratia 1996b, 1997, 1999; G. D. Johnson and Patterson 1996; Lecointre and Nelson 1996). Phylogenetic analyses of DNA sequences from whole mitochondrial genomes resulted in an unexpected expansion of *Otocephala* to include the deep-sea *Alepocephaliformes* (Ishiguro et al.

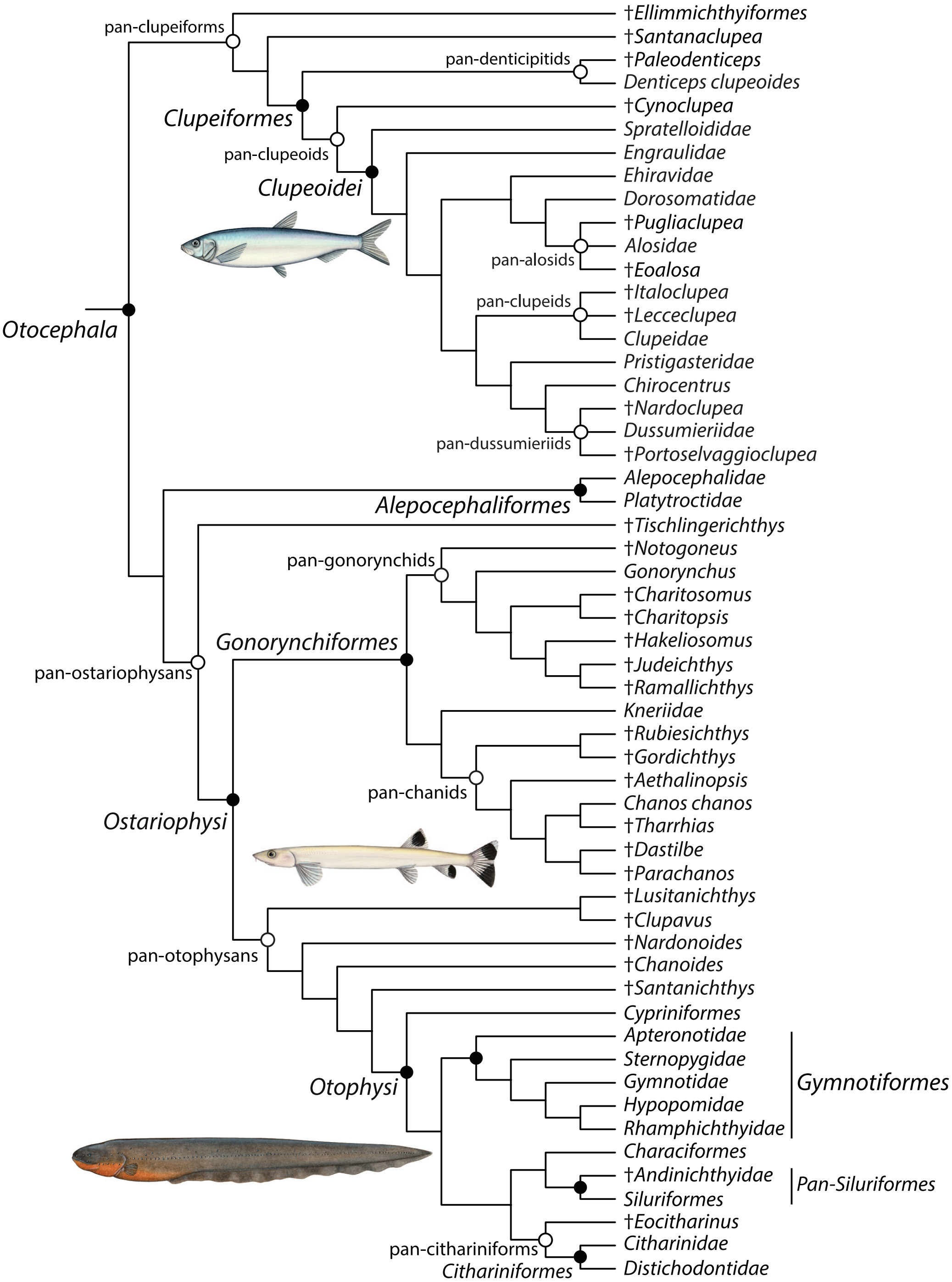

FIGURE 8. Phylogenetic relationships of the major living lineages and fossil taxa of *Otocephala*, *Clupeiformes*, *Clupeoidei*, *Alepocephaliformes*, *Ostariophysi*, *Gonorynchiformes*, *Otophysi*, *Gymnotiformes*, *Pan-Siluriformes*, and *Characiformes*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1. The clade description of *Pan-Siluriformes* is presented in Lundberg (2020c).

2003; Lavoué et al. 2005, 2007; Lavoué, Miya, Kawaguchi, et al. 2008), historically classified within *Euteleostei* as *Argentiniformes* (e.g., Greenwood and Rosen 1971; A. C. Gill and Mooi 2002; J. S. Nelson 2006:192–194). The monophyly of the expanded *Otocephala* and the resolution of *Alepocephaliformes* and *Ostariophysi* as sister lineages is supported in molecular phylogenetic analyses of nuclear genes, combinations of mitochondrial and nuclear genes, and a phylogenomic analysis of DNA sequences sampled from more than 800 exons (Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013; Straube et al. 2018). Investigations of morphological characters identify apomorphies consistent with the delimitation of *Otocephala* presented here (Arratia 2018; Straube et al. 2018).

Composition. *Otocephala* currently contains 12,270 living species (Fricke et al. 2023) classified in *Alepocephaliformes*, *Clupeiformes*, and *Ostariophysi*. Fossil lineages of *Otocephala* include the pan-clupeiforms †*Ellimmichthyiformes* and †*Santanaclupea* and the pan-ostariophysan †*Tischlingerichthys* (L. Grande 1985; Maisey 1993; Arratia 1997; M.-M. Chang and Maisey 2003; Zaragüeta-Bagils 2004; Alvarado-Ortega et al. 2008, 2020; de Figueiredo 2009; Murray and Wilson 2013; Vernygora 2020; Marramà et al. 2023). Over the past 10 years 1,729 new living species of *Otocephala* have been described (Fricke et al. 2023), comprising 14.1% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Otocephala* include (1) parietals fused with extrascapulars, with an uncertain distribution in *Alepocephaliformes* (Lecointre and Nelson 1996; Arratia 2018; Straube et al. 2018), (2) anterior part of swim bladder with silvery peritoneum (Fink and Fink 1996; Straube et al. 2018), but *Alepocephaliformes* lack a swim bladder (Arratia 2018; Straube et al. 2018), and (3) haemal spines anterior of preural centrum 2 fuse with their centra from an early point in development (Arratia 2018; Straube et al. 2018).

Synonyms. *Otomorpha* (Wiley and Johnson 2010:134; Betancur-R et al. 2017:14–15) and *Ostarioclupeomorpha* (Arratia 1997:155) are ambiguous synonyms of *Otocephala*.

Comments. G. D. Johnson and Patterson (1996) applied the group name *Otocephala* to the clade containing *Clupeiformes* and *Ostariophysi*, which was initially discovered in one of the earliest molecular data to investigate teleost phylogeny (Lê et al. 1993). Molecular phylogenetic analyses led to the expansion of *Otocephala* to include *Alepocephaliformes* (Ishiguro et al. 2003; Near, Eytan, et al. 2012; Straube et al. 2018). The name *Otocephala* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil otocephalan lineages include the pan-ostariophysan †*Tischlingerichthys* from the Tithonian (149.2–143.1 Ma) in the Jurassic of Germany (Arratia 1997, 2001). Bayesian relaxed molecular clock analyses of *Otocephala* result in an average posterior crown age estimate of 194.5 million years ago, with the credible interval ranging between 179.7 and 211.2 million years ago (Hughes et al. 2018).

Constituent lineages.
Alepocephaliformes
Clupeiformes
Ostariophysi
†*Ellimmichthyiformes*
†*Santanaclupea*
†*Tischlingerichthys*

Clupeiformes E. S. Goodrich 1909:386
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Denticeps clupeoides* Clausen 1959, *Clupea harengus* Linnaeus 1758, and *Engraulis encrasicolus* (Linnaeus 1758). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek *κλουπαῖα* (klˈuːpi͡ə), a name with an obscure origin for an uncertain number of fish species used by ancient authors such as Plutarch (D. W. Thompson 1947:117–118). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 900.

Reference phylogeny. A phylogeny inferred from DNA sequences of 1,165 exons (Q. Wang et al. 2022, fig. 2). Phylogenetic relationships among the living and fossil lineages of *Clupeiformes* are shown in Figure 8. The fossil lineages †*Cynoclupea* and †*Paleodenticeps* are placed in the phylogeny on the basis of inferences from morphology (Greenwood 1960, 1968; Malabarba and Di Dario 2017; Vernygora 2020).

Phylogenetics. Greenwood et al. (1966) delimited *Clupeiformes* to include *Denticeps clupeoides* and *Clupeoidei*, which is reflected in subsequent classifications (G. J. Nelson 1970b; L. Grande 1985; Lavoué, Konstantinidis, et al. 2014; J. S. Nelson et al. 2016:164–172; Betancur-R et al. 2017). A consistent result in morphological and molecular phylogenetic analyses of *Clupeiformes* is the resolution of *Clupeoidei* and *Denticeps* as sister groups (G. J. Nelson 1967, 1970b; Patterson and Rosen 1977; L. Grande 1985; Lavoué et al. 2007; de Pinna and Di Dario 2010; Lavoué, Konstantinidis, et al. 2014; Straube et al. 2018; Vernygora 2020; Milec et al. 2022; Q. Wang et al. 2022).

Composition. *Clupeiformes* currently contains 448 living species that include *Denticeps clupeoides* and species classified in *Clupeoidei* (Lavoué, Konstantinidis, et al. 2014; Q. Wang et al. 2022; Fricke et al. 2023). Fossil lineages of *Clupeiformes* include the pan-clupeoid †*Cynoclupea* (Malabarba and Di Dario 2017) and the pan-denticipitid †*Paleodenticeps* (Greenwood 1960). Details of the ages and locations of †*Cynoclupea* and †*Paleodenticeps* fossil taxa are given in Appendix 1. Over the past 10 years 43 new living species of *Clupeiformes* have been described (Fricke et al. 2023), comprising 9.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Clupeiformes* include (1) presence of abdominal scutes (Whitehead 1962; Patterson 1970; L. Grande 1985; Wiley and Johnson 2010), (2) diverticulum of swim bladder penetrates exoccipital, expanding to form ossified bulla in prootic or pterotic (Greenwood et al. 1966; L. Grande 1985; Wiley and Johnson 2010), (3) presence of recessus lateralis where infraorbital canal merges with preopercular canal (Greenwood et al. 1966; Greenwood 1968; L. Grande 1982, 1985; T. Grande and de Pinna 2004; Zaragüeta-Bagils 2004), (4) supraoccipital completely separates parietals (Whitehead 1962; Patterson 1970; L. Grande 1982, 1985; Zaragüeta-Bagils 2004), (5) absence of basipterygoid process of parasphenoid (Zaragüeta-Bagils 2004), (6) third preural centrum with thin haemal spine (Zaragüeta-Bagils 2004), and (7) presence of sensory cephalic canal branch that originates at junction between extrascapular bone and recessus lateralis (Di Dario and de Pinna 2006).

Synonyms. *Clupeomorpha* (Greenwood et al. 1966:358−-361) and *Clupei* (Wiley and Johnson 2010:134–135; Betancur-R et al. 2017:15) are ambiguous synonyms of *Clupeiformes*.

Comments. When first delimited, *Clupeiformes* was a "purely artificial assemblage of lowly organised (*sic*) families (Goodrich 1909:386)" and included clupeiforms as well as lineages now classified as *Elopomorpha*, *Osteoglossomorpha*, *Salmonidae*, *Gonorynchiformes*, *Alepocephaliformes*, and *Stomiiformes*. Greenwood et al. (1966) dismantled the groups *Isospondyli* and *Malacopterygii* (e.g., Boulenger 1904a; Bigelow 1963), limiting *Clupeiformes* to *Clupeoidei* and *Denticeps*. The name *Clupeiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Clupeiformes* is the pan-clupeoid †*Cynoclupea* from the Barremian-Aptian (129.4–113.0 Ma) in the Cretaceous of Brazil, which was initially placed as the sister lineage of a clade containing *Chirocentridae* and *Engraulidae* (Malabarba and Di Dario 2017). However, *Engraulidae* is the sister lineage of all other *Clupeoidei*, and *Chirocentridae* shares common ancestry with *Pristigasteridae* (Vernygora 2020). The shared character states with both *Engraulidae* and *Pristigasteridae* indicate †*Cynoclupea* is best resolved as a pan-clupeoid (Malabarba and Di Dario 2017). Bayesian relaxed molecular clock analyses of *Clupeiformes* result in an average posterior crown age estimate of 130.8 million years ago, with the credible interval ranging between 125.5 and 138.9 million years ago (Q. Wang et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Clupeoidei
*Denticipitidae**
†*Cynoclupea*
†*Paleodenticeps*

Clupeoidei P. Bleeker 1849:6

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Spratelloides gracilis* (Temminck and Schlegel 1846), *Clupea harengus* Linnaeus 1758, and *Engraulis encrasicolus* (Linnaeus 1758), but not *Denticeps clupeoides* Clausen 1959. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek *ϰλουπαῖα* (klˈuːpi͡ə), a name with an obscure origin for an uncertain number of fish species used by ancient authors such as Plutarch (D. W. Thompson 1947:117–118).

Registration number. 901.

Reference phylogeny. A phylogeny inferred from DNA sequences of 1,165 exons (Q. Wang et al. 2022, fig. 2). See Figure 8 for a phylogeny of the living and fossil lineages comprising *Clupeoidei*. The placements of fossil lineages in the phylogeny are based on inferences from morphology (Taverne 2002, 2004, 2007a, 2007b, 2011a; Marramà and Carnevale 2018).

Phylogenetics. Greenwood et al. (1966) grouped all living species of *Clupeiformes* in *Clupeoidei* except *Denticeps clupeoides*. On the basis of gill arch morphology, G. J. Nelson (1967, 1970b) delimited four lineages of *Clupeoidei*: *Chirocentridae* (wolf herrings), *Clupeidae* (shads and sardines), *Engraulidae* (anchovies), and *Pristigasteridae* (longfin herrings). Analyses of morphological characters and molecular phylogenetic studies consistently support the monophyly of *Clupeoidei* (L. Grande 1985; Di Dario 2004; Lavoué et al. 2007, 2013; Li and Ortí 2007; Lavoué, Miya, Kawaguchi, et al. 2008; de Pinna and Di Dario 2010; Bloom and Lovejoy 2014; Lavoué, Konstantinidis, et al. 2014; Bloom and Egan 2018; Egan et al. 2018; Milec et al. 2022; Q. Wang et al. 2022); however, the traditional delimitation of *Clupeidae* is not resolved as monophyletic (e.g., Lavoué, Konstantinidis, et al. 2014; Egan et al. 2018; Vernygora 2020). The lack of clupeid monophyly has prompted the recognition of the lineages *Alosidae* (shads), *Dorosomatidae* (gizzard shads), *Dussumieriidae* (round herrings), *Ehiravidae* (ehiravines), and *Spratelloididae* (small round herrings) (Bloom and Egan 2018; Vernygora 2020; Q. Wang et al. 2022). Traditionally, *Dussumieriidae* included *Dussumieria* and *Etrumeus* (Whitehead 1985; J. S. Nelson et al. 2016:170), but phylogenomic analysis resolves *Dussumieria* and *Chirocentrus* as sister lineages and *Etrumeus* as the sister lineage of all sampled species of *Clupeidae* (Q. Wang et al. 2022).

Molecular phylogenies inferred from combinations of Sanger-sequenced mitochondrial and nuclear genes and phylogenomic analysis of 1,165 exons resolve *Spratelloididae* as the sister lineage of all other *Clupeoidei* (Bloom and Egan 2018; Egan et al. 2018; Q. Wang et al. 2022). Morphological characters seem to support *Chirocentridae* and *Engraulidae* as sister groups (Di Dario 2009; Malabarba and Di Dario 2017; Vernygora 2020, figs. 6, 7), but molecular phylogenies place *Chirocentrus* as the sister lineage to *Pristigasteridae* (Bloom and Egan 2018; Egan et al. 2018; Vernygora 2020, figs. 6–9). A morphological phylogenetic analysis of 175 characters sampled from 101 clupeiform species resulted in unresolved relationships with poor node support (Vernygora 2020, figs. 6, 7).

Composition. *Clupeoidei* currently contains 447 living species (Fricke et al. 2023) classified in *Alosidae*, *Chirocentrus*, *Clupeidae*, *Dorosomatidae*, *Dussumieria*, *Ehiravidae*, *Engraulidae*, *Pristigasteridae*, and *Spratelloididae* (Q. Wang et al. 2022). Fossil clupeoids include the pan-clupeids †*Italoclupea* and †*Lecceclupea* (Taverne 2007a, 2011a), the pan-dussumieriids †*Nardoclupea* and †*Portoselvaggioclupea* (Taverne 2002, 2007b), and the pan-alosids †*Eoalosa* and †*Pugliaclupea* (Taverne 2004; Marramà and Carnevale 2018). Details regarding the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years 43 new living species of *Clupeoidei* have been described (Fricke et al. 2023), comprising 9.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Clupeoidei* include (1) first uroneural and first preural fused (L. Grande 1985; Zaragüeta-Bagils 2004), (2) relative size of first ural centrum reduced (L. Grande 1985; Zaragüeta-Bagils 2004), (3) absence of lateral line scales (L. Grande 1985; Vernygora 2020), (4) parhypural and first ural centrum separated (L. Grande 1985; Zaragüeta-Bagils 2004), (5) absence of a complete series of ventral scutes between isthmus and anus (Zaragüeta-Bagils 2004), (6) ventral limb of hyomandibula and quadrate separated by metapterygoid (Di Dario 2009; Vernygora 2020), (7) single row of gill rakers on first through third arches (de Pinna and Di Dario 2010), (8) close proximity of dorsal gill arch elements to the midline (de Pinna and Di Dario 2010), (9) second and third infrapharyngobranchials produced anteriorly as a narrow long process (de Pinna and Di Dario 2010), and (10) presence of notch on third hypural (Vernygora 2020).

Synonyms. There are no synonyms of *Clupeoidei*.

Comments. *Clupeoidei* is among the most economically important lineages of fishes (FAO 2020). The generation of phylogenomic datasets that include hundreds of clupeoid species is a major priority for future teleost phylogenetics. This priority goes beyond the inherent interest in resolving this portion of the tree of life and is justified by the clade's economic importance and growing conservation concerns (FAO 2020; Birge et al. 2021).

Fossil taxa phylogenetically nested within crown subclades of *Clupeoidei* include †*Knightia eocaena* in *Clupeidae*, †*Chasmoclupea aegyptica* and †*Trollichthys bolcensis* in *Spratelloididae*, and †*Eoengraulis fasoloi* in *Engraulidae* (Vernygora 2020). The earliest fossil lineage of *Clupeoidei* is †*Audenaerdia casieri* with an uncertain phylogenetic resolution with *Clupeidae* or *Alosidae* from the Santonian (85.7–83.2 Ma) in the Cretaceous (Taverne 1997a, 1997b). The earliest *Clupeoidei* fossil lineages with a more confident phylogenetic resolution include the pan-clupeids †*Italoclupea* and †*Lecceclupea* (Taverne 2007a, 2011a), the pan-dussumieriids †*Nardoclupea* and †*Portoselvaggioclupea* (Taverne 2007b), and the pan-alosid †*Pugliaclupea* (Taverne 2004) from the Campanian-Maastrichtian (83.26–66.0 Ma) in the Cretaceous. Bayesian relaxed molecular clock analyses of *Clupeoidei* result in an average posterior crown age estimate of 91.4 million years ago, with the credible interval ranging between 76.1 and 107.3 million years ago (Q. Wang et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Alosidae
*Chirocentridae**
Clupeidae
Dorosomatidae
Dussumieriidae
Ehiravidae
Engraulidae
Pristigasteridae
Spratelloididae
†*Eoalosa*
†*Italoclupea*
†*Lecceclupea*
†*Nardoclupea*
†*Portoselvaggioclupea*
†*Pugliaclupea*

Alepocephaliformes N. B. Marshall 1962:265
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Alepocephalus rostratus* Risso 1820, *Alepocephalus bairdii* Goode and Bean 1879, *Bathylaco nigricans* Goode and Bean 1896, and *Platytroctes apus* Günther 1878b. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek λεπῐ́ς (lˈɛpɪs), meaning the scale of a fish, with the prefix "a" meaning without scales and κεφαλή (kɛfˈɑːlə) meaning the head of a human or other animal. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 902.

Reference phylogeny. A phylogeny of *Alepocephaliformes* inferred from DNA sequences of complete mitochondrial genomes (Poulsen et al. 2009, fig. 3). Although *Alepocephalus rostratus* is not included in the reference phylogeny, it clusters with *Xenodermichthys copei* as the only sampled species of *Alepocephaliformes* in a DNA barcoding study (Landi et al. 2014, fig. S1). Phylogenetic relationships of *Alepocephaliformes* are shown in Figure 8.

Phylogenetics. The phylogenetic placement of *Alepocephaliformes* within *Teleostei* has shifted substantially over the past century, previously being grouped with *Clupeiformes* (Gregory and Conrad 1936), a delimitation of *Salmoniformes* that includes *Salmonidae*, *Argentiniformes*, *Galaxiidae*, *Osmeriformes*, *Stomiiformes*, and *Esocidae* (Greenwood et al. 1966; Markle 1976), and *Osmeriformes* (Gosline 1969). Greenwood and Rosen (1971) hypothesized *Alepocephaliformes* and *Argentiniformes* are sister lineages on the basis of a modified posterior pharyngobranchial structure they named the crumenal organ, which was the basis for the resolution of this clade in subsequent morphological studies (Begle 1992; G. D. Johnson and Patterson 1996). However, Ahlstrom et al. (1984) rejected the hypothesized common ancestry of *Alepocephaliformes* and *Argentiniformes* because alepocephaliform species hatch from larger eggs and exhibit direct development; additionally, the two lineages share no unique ontogenetic characters. Molecular phylogenetic analyses consistently resolve *Alepocephaliformes* in a clade with *Clupeiformes* and *Ostariophysi* (Ishiguro et al. 2003; Lavoué, Miya, Poulsen, et al. 2008; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Straube et al. 2018), prompting the classification of these three clades in *Otocephala*.

Two morphological analyses of relationships within *Alepocephaliformes* result in very different phylogenetic trees, with all alepocephaliforms classified as *Alepocephalidae* (slickheads) in Begle (1992) and the resolution of *Alepocephalidae* and *Platytroctidae* (tubeshoulders) in G. D. Johnson and Patterson (1996). Molecular phylogenetic analyses of DNA sequences from whole mitochondrial genomes or combinations of mitochondrial and nuclear genes resolve *Alepocephalidae* and *Platytroctidae* each as monophyletic groups (Lavoué, Miya, Poulsen, et al. 2008; Poulsen et al. 2009; Betancur-R et al. 2017; Rabosky et al. 2018; Poulsen 2019), but one molecular analysis resulted in *Platytroctidae* nested within *Alepocephalidae* (Betancur-R et al. 2017).

Composition. There are currently 142 living species of *Alepocephaliformes* classified in *Alepocephalidae* and *Platytroctidae* (Fricke et al. 2023). Over the past 10 years two new living species of *Alepocephaliformes* have been described, accounting for 1.4% of the living species diversity in the clade.

Diagnostic apomorphies. The apomorphies of *Alepocephaliformes* are uncertain because of the reductive nature of morphological characters in the lineages and the fact that all morphological phylogenetic analyses assumed a relationship with *Argentiniformes* (Begle 1992; G. D. Johnson and Patterson 1996). Morphological apomorphies for *Alepocephaliformes* include (1) separation of parietals by supraoccipital (Greenwood and Rosen 1971; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (2) absence of posttemporal fossa (Gosline 1969; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (3) presence of branchiostegal cartilages (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (4) reduction of dorsal portion of opercle (Begle 1992; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (5) forward extension of ossified epipleural series to third vertebra (Patterson and Johnson 1995; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (6) absence of urodermal (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), and (7) presence of single postcleithrum (Markle 1976; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010).

Synonyms. *Alepocephaloidei* (Bleeker 1859:xxx; Wiley and Johnson 2010:141), *Alepocephaloidea* (Greenwood and Rosen 1971:39–40; Begle 1992:351; G. D. Johnson and Patterson 1996:312), and *Alepocephali* (Betancur-R et al. 2017:15) are ambiguous synonyms of *Alepocephaliformes*. *Alepocephaloidei* and *Bathylaconoidei* (Greenwood et al. 1966:394) are approximate synonyms of *Alepocephaliformes*.

Comments. Marshall (1962:265) applied the name *Alepocephaliformes* to the lineage comprising *Alepocephalidae* and *Searsiidae*, a synonym of *Platytroctidae* (Parr 1951; Van der Laan et al. 2014:58). Long considered a subclade of *Argentiniformes* (Greenwood and Rosen 1971; Begle 1992; G. D. Johnson and Patterson 1996), *Alepocephaliformes* is now placed with

Clupeiformes and *Ostariophysi* in *Otocephala* (Near, Eytan, et al. 2012; Arratia 2018; Straube et al. 2018). The name *Alepocephaliformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The fossil record of *Alepocephaliformes* is relatively poor when compared with other lineages of *Otocephala*. The earliest skeletal fossils of *Alepocephaliformes* date to the Rupelian (33.9–28.1 Ma) in the Oligocene and the earliest otoliths are from the Ypresian (56.0–47.8 Ma) in the Eocene (Přikryl and Carnevale 2019). A maximum likelihood relaxed molecular clock analysis of *Alepocephaliformes* resulted in a crown age estimate of 38.8 million years ago (Rabosky et al. 2018).

Constituent lineages.
Alepocephalidae *Platytroctidae*

Ostariophysi M. Sagemehl 1885:22 (as *Ostariophysen*) [Lundberg 2020]

Definition. Defined as a minimum-crown-clade in Lundberg (2020a) as: "The crown clade originating in the most recent common ancestor of *Gonorynchus* (originally *Cyprinus*) *gonorynchus* (Linnaeus 1766), *Cyprinus carpio* Linnaeus 1758 (*Cypriniformes*), *Charax* (originally *Salmo*) *gibbosus* (Linnaeus 1758) (*Characiformes*), *Gymnotus carpio* Linnaeus 1758 (*Gymnotiformes*; *Gymnotoidei* on the reference phylogeny), and *Silurus glanis* Linnaeus 1758 (*Siluriformes*; *Siluroidei* on the reference phylogeny)."

Etymology. From the ancient Greek ὀστάριον (ho͡ʊstˈɑːɹ͡ɹi͡ən), meaning little bone, and φῦσα (fˈuːsə), meaning bladder.

Registration number. 196.

Reference phylogeny. Fink and Fink (1981, fig. 1) was designated as the reference phylogeny by Lundberg (2020a). Phylogenetic relationships of the living and fossil lineages of *Ostariophysi* are presented in Figure 8. The placement of the pan-otophysan fossil lineages †*Chanoides*, †*Clupavus*, †*Lusitanichthys*, †*Nardonoides*, and †*Santanichthys* are on the basis of inferences from morphology (Patterson 1984a; Taverne 1995; Diogo et al. 2008; Diogo 2009; Malabarba and Malabarba 2010; Mayrinck 2011).

Phylogenetics. The monophyly of *Ostariophysi* as a lineage that includes *Gonorynchiformes* and *Otophysi* was first inferred from the morphology of the caudal skeleton and cervical vertebrae (Rosen and Greenwood 1970), a conclusion not universally accepted at the time (T. R. Roberts 1973). Subsequent summaries and phylogenetic analyses of morphological characters consistently resolve *Ostariophysi* as monophyletic (Fink and Fink 1981, 1996; Patterson 1984a, 1984b, 1994; Arratia 1999, 2000a, 2008, 2010b; Diogo et al. 2008). Early molecular phylogenetic analyses of whole mitochondrial genomes resolved *Gonorynchiformes* and *Clupeiformes* as sister lineages (Ishiguro et al. 2003; Saitoh et al. 2003; Peng et al. 2006). However, the monophyly of *Ostariophysi* is supported in all subsequent molecular phylogenetic studies that include analyses of whole mitochondrial genomes (Lavoué et al. 2005, 2007, 2010; Jondeung et al. 2007; Lavoué, Miya, Poulsen, et al. 2008; Poulsen et al. 2009; Nakatani et al. 2011; Davis et al. 2013), collections of Sanger-sequenced mitochondrial or nuclear genes (Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013), and phylogenomic datasets (Arcila et al. 2017; Chakrabarty et al. 2017; Dai et al. 2018; Hughes et al. 2018; Straube et al. 2018; Mu et al. 2022).

Composition. *Ostariophysi* currently contains 11,682 species (Fricke et al. 2023) classified in *Gonorynchiformes* and *Otophysi*. Fossil ostariophysans include the pan-otophysans †*Chanoides*, †*Clupavus*, †*Lusitanichthys*, †*Nardonoides*, and †*Santanichthys* (Patterson 1984a; Fink and Fink 1996; Cavin 1999; Filleul and Maisey 2004; Diogo et al. 2008; Malabarba and Malabarba 2010; Mayrinck 2011; Mayrinck et al. 2015b). Details regarding the ages and locations of the fossil taxa are listed in Appendix 1. Over the past 10 years there have been 1,686 new living species of *Ostariophysi* described (Fricke et al. 2023), comprising 14.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Ostariophysi* include (1) sacculi and lagena situated posteriorly and along the midline (Rosen and Greenwood 1970; Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (2) swim bladder divided into small anterior and large posterior chamber (Rosen and Greenwood 1970; Fink and Fink 1981, 1996; Wiley and Johnson 2010), (3) anterior chamber of swim bladder covered with silvery peritoneal tunic (Rosen and Greenwood 1970; Fink and Fink 1981, 1996; Lundberg 2020a), (4) peritoneal tunic covering anterior chamber of swim bladder attached to two most anterior pleural ribs (Rosen and Greenwood 1970; Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (5) absence of basisphenoid (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (6) absence of dermopalatine (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (7) absence of supramaxillae (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (8) dorsal mesentery suspending swim bladder thickened anterodorsally (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (9) absence of supraneural or accessory neural arch anterior to first vertebra (Fink and Fink 1981, 1996; Lundberg 2020a), (10) presence of expanded anterior neural arches that form roof over neural canal (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (11) absence of neural arch anterior to arch of first vertebral centrum (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), (12) haemal spines anterior to second preural centrum fused to centrum (Fink and Fink 1981, 1996), (13) presence of Schreckstoff pheromone, an alarm substance produced by epidermal cells, stimulating a fright reaction in conspecifics (Pfeiffer 1977; Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020a), and (14) absence of supraneural 1 and its cartilaginous precursor (Hoffmann and Britz 2006; Wiley and Johnson 2010).

Synonyms. There are no synonyms of *Ostariophysi*.

Comments. Sagemehl (1885:22) applied the name *Ostariophysen* to a group consisting of *Cypriniformes*, *Gymnotiformes*, *Siluriformes*, *Characiformes*, and *Citharíniformes*, which are classified here as *Otophysi*. This more exclusive definition of *Ostariophysi* was maintained for nearly a century (Boulenger 1904b:573–596; Goodrich 1909:371; Regan 1911d, 1911e; Jordan 1923:134–153; Greenwood et al. 1966; Gosline 1971:120–124). Citing several shared morphological traits, Rosen and Greenwood (1970) expanded *Ostariophysi* to include *Gonorynchiformes* and placed *Cypriniformes*, *Gymnotiformes*, *Siluriformes*, and *Characiformes* (*sensu lato*) in *Otophysi*. The earliest fossil *Ostariophysi* is the pan-otophysan †*Santanichthys diasii* from the Aptian-Albian (121.4–100.5 Ma) in the Cretaceous of Brazil. Bayesian relaxed molecular clock analyses of *Ostariophysi* result in an average posterior crown age estimate of 160.6 million years ago, with the credible interval ranging between 154.2 and 169.6 million years ago (Hughes et al. 2018).

Constituent lineages.

Gonorynchiformes
Otophysi
†*Chanoides*
†*Clupavus*
†*Lusitanichthys*
†*Nardonoides*
†*Santanichthys*

Gonorynchiformes P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Myers 1966:374 [T. J. Near and C. E. Thacker], converted clade name

Definition. The least inclusive crown clade that contains *Gonorynchus gonorynchus* (Linnaeus 1766), *Gonorynchus greyi* (Richardson 1845), *Chanos chanos* [Fabricius in Niebuhr (ex Forsskål) 1775], and *Kneria paucisquamata* Poll and Stewart 1975. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek γωνία (ɡˈo͡ʊniə), meaning angle, and ῥυγχος (ɹˈuːɡko͡ʊz), meaning snout or beak. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 903.

Reference phylogeny. A time-calibrated phylogeny inferred from morphological characters and nine Sanger-sequenced nuclear genes (Near, Dornburg, and Friedman 2014, fig. 4). Although *Gonorynchus gonorynchus* is not included in the reference phylogeny, it resolves in a clade with four other species of *Gonorynchus*, including *G. greyi*, in a phylogenetic analysis of morphological characters (T. Grande 1999, fig. 10). Phylogenetic relationships among living and fossil lineages of *Gonorynchiformes* are shown in Figure 8. The placement of fossil lineages in the phylogeny is on the basis of analyses of morphological characters (Gayet 1993; T. Grande 1994, 1996; T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010; Near, Dornburg, and Friedman 2014; Ribeiro, Poyato-Ariza, et al. 2018).

Phylogenetics. The first studies of relationships within *Gonorynchiformes* differed as to the earliest divergences in the clade. Greenwood et al. (1966) hypothesized that *Gonorynchus* was the likely sister lineage to all other gonorynchiforms, but Rosen and Greenwood (1970) argued that *Chanos* is the least morphologically specialized lineage of *Gonorynchiformes* and presented a classification reflecting this hypothesis.

Phylogenetic analyses using morphological characters have frequently included fossil lineages and all resolve *Chanos* as the living sister lineage of all other *Gonorynchiformes* (Patterson 1984b; Blum 1991; Gayet 1993; T. Grande 1994, 1996; T. Grande and Poyato-Ariza 1995, 1999; Poyato-Ariza 1996b; G. D. Johnson and Patterson 1997; Poyato-Ariza et al. 2010; Amaral and Brito 2012; Amaral et al. 2013; Ribeiro, Poyato-Ariza, et al. 2018). A diversity of molecular phylogenetic analyses of mtDNA, Sanger-sequenced nuclear genes, and phylogenomic datasets resolve *Gonorynchus* as the sister lineage of all other *Gonorynchiformes* (Lavoué et al. 2005; Lavoué, Miya, Moritz, et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Davis et al. 2013; Chakrabarty et al. 2017; Straube et al. 2018). Morphological and molecular phylogenetic analyses consistently support *Phractolaemus ansorgii* and all other species of *Kneriidae* as sister taxa (T. Grande 1994; G. D. Johnson and Patterson 1997; T. Grande and Poyato-Ariza 1999; Lavoué et al. 2005; Lavoué, Miya, Moritz, et al. 2012; Davis et al. 2013; Near, Dornburg, and Friedman 2014). Relationships among the five living species of *Gonorynchus* were resolved in a phylogenetic analysis of 12 morphological characters (T. Grande 1999).

Composition. *Gonorynchiformes* currently contains 40 living species (Fricke et al. 2023; Kalumba et al. 2023) that include *Chanos chanos* and species classified in *Gonorynchus* and *Kneriidae* (T. Grande and Poyato-Ariza 1999). Fossil lineages of *Gonorynchiformes* include the pan-chanids †*Aethalionopsis*, †*Dastilbe*, †*Gordichthys*, †*Parachanos*, †*Rubiesichthys*, and †*Tharrhias* (Poyato-Ariza 1994, 1996a; Fara et al. 2010). Fossil pan-gonorynchid lineages include †*Charitopsis*, †*Charitosomus*, †*Hakeliosomus*, †*Judeichthys*, †*Notogoneus*, and †*Ramallichthys* (L. Grande and Grande 1999; Fara et al. 2010). Details of the ages and locations of the fossil taxa are given in Appendix 1. One new living species of *Gonorynchiformes* has been described over the past 10 years, comprising 2.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gonorynchiformes* include (1) bone and cartilage of interorbital septum reduced where orbitosphenoid absent (Fink and Fink 1981, 1996; Patterson 1984b; T. Grande and Poyato-Ariza 1995; Poyato-Ariza et al. 2010; Wiley and Johnson 2010), (2) parietals reduced in size to canal-bearing ossicles (Rosen and Greenwood 1970; Fink and Fink 1981; Patterson 1984b; Poyato-Ariza et al. 2010; Wiley and Johnson 2010), (3) middle region of suspensorium, bounded by articular condyle for quadrate and hyomandibular, longer relative to height of suspensorium and opercular series (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (4) premaxilla thin and flat (Fink and Fink 1981, 1996; Patterson 1984b), (5) presence of bilateral pouches in branchial chamber located posterior to fourth epibranchial (Greenwood et al. 1966; Fink and Fink 1981, 1996; Wiley and Johnson 2010), (6) absence of teeth on fifth ceratobranchial (Fink and Fink 1981, 1996; Patterson 1984b; T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010; Wiley and Johnson 2010), (7) anterior neural arch large, forming tight joint with exoccipital or exoccipital and supraoccipital

(Fink and Fink 1981, 1996; Patterson 1984b; T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010; Wiley and Johnson 2010), (8) presence of epicentral bones, also referred to as cephalic ribs (Patterson and Johnson 1995; Fink and Fink 1996; T. Grande and Poyato-Ariza 1999; Wiley and Johnson 2010), (9) absence of Baudelot's ligament (Patterson and Johnson 1995; Fink and Fink 1996; Wiley and Johnson 2010), (10) presence of exceptionally long esophagus (Fink and Fink 1996; Wiley and Johnson 2010), (11) pterosphenoids either slightly reduced, not articulating anteroventrally but in close proximity anterodorsally or greatly reduced and well-separated both anteroventrally and anterodorsally (T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010), (12) parietals partially or completely separated by supraoccipital (T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010), (13) ascending process of premaxilla absent (T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010), (14) maximum height of dentary at midpoint or at anterior region close to symphysis (T. Grande and Poyato-Ariza 1999), (15) fewer than five infraorbitals (T. Grande and Poyato-Ariza 1999), (16) anterior neural arches slightly in contact with adjacent arches or exhibit overlapping lateral contact with adjacent arches (T. Grande and Poyato-Ariza 1999), (17) rib on third vertebral centrum wider and shorter than posterior ribs (T. Grande and Poyato-Ariza 1999; Poyato-Ariza et al. 2010), and (18) premaxilla, maxilla, and dentary without teeth (Poyato-Ariza et al. 2010).

Synonyms. *Gonorhynchoidei* (Gosline 1960:357, 1971:113–114), *Anotophysi* (Rosen and Greenwood 1970:23), and *Anotophysa* (Betancur-R et al. 2017:15) are ambiguous synonyms of *Gonorynchiformes*.

Comments. Gosline (1960, 1971:113–114) was the first investigator to delimit a group containing *Gonorynchus*, *Chanos chanos*, *Cromeria*, *Kneria*, and *Phractolaemus ansorgii*, which he named *Gonorhynchoidei* (*sic*). Greenwood et al. (1966) included the kneriid *Grasseichthys gabonensis* and named the group *Gonorynchiformes*. The name *Gonorynchiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Gonorynchiformes* is the pan-chanid †*Rubiesichthys gregalis* from the Berriasian and Valanginian (143.1–132.6 Ma) in the Cretaceous of Spain (Poyato-Ariza 1996a). Bayesian relaxed molecular clock analyses of *Gonorynchiformes* using fossil tip-dating result in an average posterior crown age estimate of 219.8 million years ago, with the credible interval ranging between 201.7 and 240.0 million years ago (Near, Dornburg, and Friedman 2014).

Constituent lineages. *Phractolaemus ansorgii* is classified here as a species of *Kneriidae*. Redundant group names are marked with an asterisk.

*Chanidae**
*Gonorynchidae**
Kneriidae
†*Aethalionopsis*
†*Charitopsis*
†*Charitosomus*
†*Dastilbe*
†*Gordichthys*
†*Hakeliosomus*
†*Judeichthys*
†*Notogoneus*
†*Parachanos*
†*Ramallichthys*
†*Rubiesichthys*
†*Tharrhias*

Otophysi W. Garstang 1931:253, 256 [Lundberg 2020]

Definition. Defined as a minimum-crown-clade in Lundberg (2020a) as: "The crown clade originating in the most recent common ancestor of *Cyprinus carpio* Linnaeus 1758 (*Cypriniformes*), *Charax* (originally *Salmo*) *gibbosus* (Linnaeus 1758) (*Characiformes*), *Gymnotus carpio* Linnaeus 1758 (*Gymnotiformes*; *Gymnotoidei* on the reference phylogeny), and *Silurus glanis* Linnaeus 1758 (*Siluriformes*; *Siluroidei* on the reference phylogeny)."

Etymology. From the ancient Greek ὠτός (hˈo͡ʊtˈo͡ʊz), meaning belonging to the ear, and φῦσα (fˈuːsə), meaning bladder.

Registration number. 197.

Reference phylogeny. Fink and Fink (1981, fig. 1) was designated as the primary reference phylogeny by Lundberg (2020a). Phylogenetic relationships of the major lineages of *Otophysi* are presented in Figure 8. The placements of the pan-siluriform †*Andinichthyidae* and the pan-citharinid †*Eocitharinus* in the phylogeny are based on inferences from morphology (Arratia and Gayet 1995; Gayet and Meunier 2003; Murray 2003; Guinot and Cavin 2018).

Phylogenetics. Phylogenetic analyses of morphological characters resolve *Otophysi* as monophyletic and place *Cypriniformes* as the sister group of a clade containing *Characiformes* (*sensu lato*), *Siluriformes*, and *Gymnotiformes* (Fink and Fink 1981, 1996; Arratia 1992; Diogo et al. 2008). The monophyly of *Otophysi* is consistently supported by molecular phylogenetic studies, including analyses of whole mitochondrial genomes (Lavoué et al. 2005; Jondeung et al. 2007; Poulsen et al. 2009; Nakatani et al. 2011), collections of Sanger-sequenced mitochondrial or nuclear genes (Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013), and phylogenomic datasets (Arcila et al. 2017; Chakrabarty et al. 2017; Dai et al. 2018; Hughes et al. 2018; Straube et al. 2018; Faircloth et al. 2020). Within *Otophysi*, morphological and molecular phylogenies are incongruent with regards to the relationships of *Characiformes* (*sensu lato*), *Siluriformes*, and *Gymnotiformes*. Specifically, the traditional delimitation of *Characiformes* that includes *Citharіniformes* is not resolved as monophyletic relative to *Siluriformes* or *Gymnotiformes* in phylogenetic studies ranging from the early single locus analyses in the mid-1990s to phylogenomic analyses in the early 21st century (Ortí and Meyer 1996, 1997; Nakatani et al. 2011; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013; Chakrabarty et al. 2017; Dai et al. 2018; Hughes et al. 2018, fig. S2; Faircloth et al. 2020; Simion et al. 2020; Melo, Sidlauskas, et al. 2022; Yang et al. 2023).

Composition. *Otophysi* currently contains more than 11,640 species (Fricke et al. 2023) classified in *Characiformes*, *Citharіniformes*, *Cypriniformes*, *Gymnotiformes*, and *Siluriformes*. Fossil otophysans include the *Pan-Siluriformes* lineage †*Andinichthyidae* (Gayet 1988a, 1990; Arratia and Gayet 1995; Gayet and Meunier 1998, 2003; Bogan et al. 2018) and the pan-citharіniform †*Eocitharinus macrognathus* (Murray 2003). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years there have been 1,683 new living species of *Otophysi* described (Fricke et al. 2023), comprising 14.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Otophysi* include (1) axe-shaped endochondral portion of metapterygoid (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (2) first or first and second anterior supraneurals with ventral expansion that forms synchondral joint with neural arches (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (3) scaphium and claustrum of Weberian apparatus present (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (4) reduction of second neural arch that is modified into intercalarium (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (5) centra of anterior vertebrae shortened (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (6) fusion of first two parapophyses and centra (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (7) presence of the tripus, a bone that is an element of the Weberian apparatus and is likely a modified pleural rib (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (8) presence of the os suspensorium (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (9) pelvic bone bifurcated (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (10) presence of compound terminal vertebrae (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (11) hypural 2 fused with compound centrum (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (12) the sinus impar of inner ear present (Fink and Fink 1981, 1996; Wiley and Johnson 2010), (13) loss of supradorsal 2 and all supradorsals posterior to vertebra 4 (Hoffmann and Britz 2006; Wiley and Johnson 2010), and (14) fusion of supradorsals 3 and 4 with supraneural 2 and 3 cartilages to form neural complex (Hoffmann and Britz 2006; Wiley and Johnson 2010).

Synonyms. *Ostariophysen* (Sagemehl 1885:22), *Ostariophysi* (Boulenger 1904b:573–596; Goodrich 1909:371; Regan 1911d:13–15, 1911e:554; Jordan 1923:134–153; Greenwood et al. 1966:380–382, 395–396; Gosline 1971:120–124), and *Plectospondyli* (Cope 1871a:454; Jordan

1923:134–153) are approximate synonyms of *Otophysi*. *Cypriniformes* is an ambiguous synonym of *Otophysi* (Bertin and Arambourg 1958:2285–2287; McAllister 1968:67–78).

Comments. Garstang (1931) delimited a more inclusive *Otophysi* that in addition to *Siluriformes* and *Characiformes* included *Osteoglossiformes*, *Elopiformes*, and *Clupeiformes*. Sagemehl (1885) applied the name *Ostariophysen* to a group now delimited as *Otophysi*. Rosen and Greenwood (1970) expanded *Ostariophysi* to include *Gonorynchiformes*, and placed *Cypriniformes*, *Gymnotiformes*, *Siluriformes*, and *Characiformes* (*sensu lato*) in *Otophysi*. The name *Otophysi* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

Bayesian relaxed molecular clock analyses of *Otophysi* result in an average posterior crown age estimate of 146.9 million years ago, with the credible interval ranging between 137.9 and 156.5 million years ago (Hughes et al. 2018).

Constituent lineages.

Characiformes
Cithariniformes
Cypriniformes
Gymnotiformes
Siluriformes
†*Andinichthyidae*
†*Eocitharinus*

Cypriniformes E. S. Goodrich 1909:371
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Catostomus catostomus* (Forster 1773), *Gyrinocheilus pustulosus* Vaillant 1902, *Cobitis taenia* Linnaeus 1758, *Cyprinus carpio* Linnaeus 1758, and *Paedocypris progenetica* Kottelat et al. 2006. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κυπρῖνος (kuːpɹˈiːno͡ʊz), frequently applied to the European Carp, *Cyprinus carpio* (D. W. Thompson 1947:135–136). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 904.

Reference phylogeny. A phylogeny of 1,703 species of *Cypriniformes* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Although the reference phylogeny does not include *Paedocypris progenetica*, the species resolves within the cyprinoid clade *Danionidae* (danionins) in phylogenetic analysis of mtDNA, combined mtDNA and nuclear gene sequences, and morphological characters (Rüber et al. 2007; Fang et al. 2009; K. L. Tang et al. 2010; Britz, Conway, et al. 2014). Phylogenetic analysis of DNA sequences of nuclear genes resolves *Paedocypris* as the sister lineage of *Cyprinoidei* or *Cypriniformes* (Mayden and Chen 2010; Stout et al. 2016; Malmstrøm et al. 2018). Phylogenetic relationships of living and fossil lineages of *Cypriniformes* are shown in Figure 9. The resolution of †*Jianghanichthys* in the phylogeny is based on analysis of morphological characters (J. Liu et al. 2015).

Phylogenetics. Greenwood et al. (1966) argued for monophyly of *Cypriniformes* on the basis of morphological characters from the pharyngeals, skull, oral jaws, vertebrae, and Weberian apparatus. X.-W. Wu et al. (1981) mapped morphological character changes onto a phylogeny that included *Cyprinoidei* and the cobitoid subclade *Balitoridae* (hillstream loaches) as sister lineages, a relationship that is not supported in any subsequent study of cypriniform phylogeny. Analysis of discretely coded morphological characters consistently resolves *Cyprinoidei* as the sister lineage of a clade containing *Gyrinocheilus* (algae eaters), *Catostomidae* (suckers), and *Cobitoidei* (Siebert 1987; Conway and Mayden 2007; Conway 2011). Inferred relationships differ among morphological analyses, with *Gyrinocheilus* and *Catostomidae* as successive sister lineages to *Cobitoidei* (Siebert 1987; Conway and Mayden 2007) or *Gyrinocheilus* and *Catostomidae* resolved as a clade that is the sister lineage of *Cobitoidei* (Conway 2011; Mabee et al. 2011; Britz, Conway, et al. 2014). Morphological phylogenetic analyses that include the Eocene-aged †*Jianghanichthys* result in a set of 116 most parsimonious trees. The strict consensus of these trees resolves the most recent common ancestor of

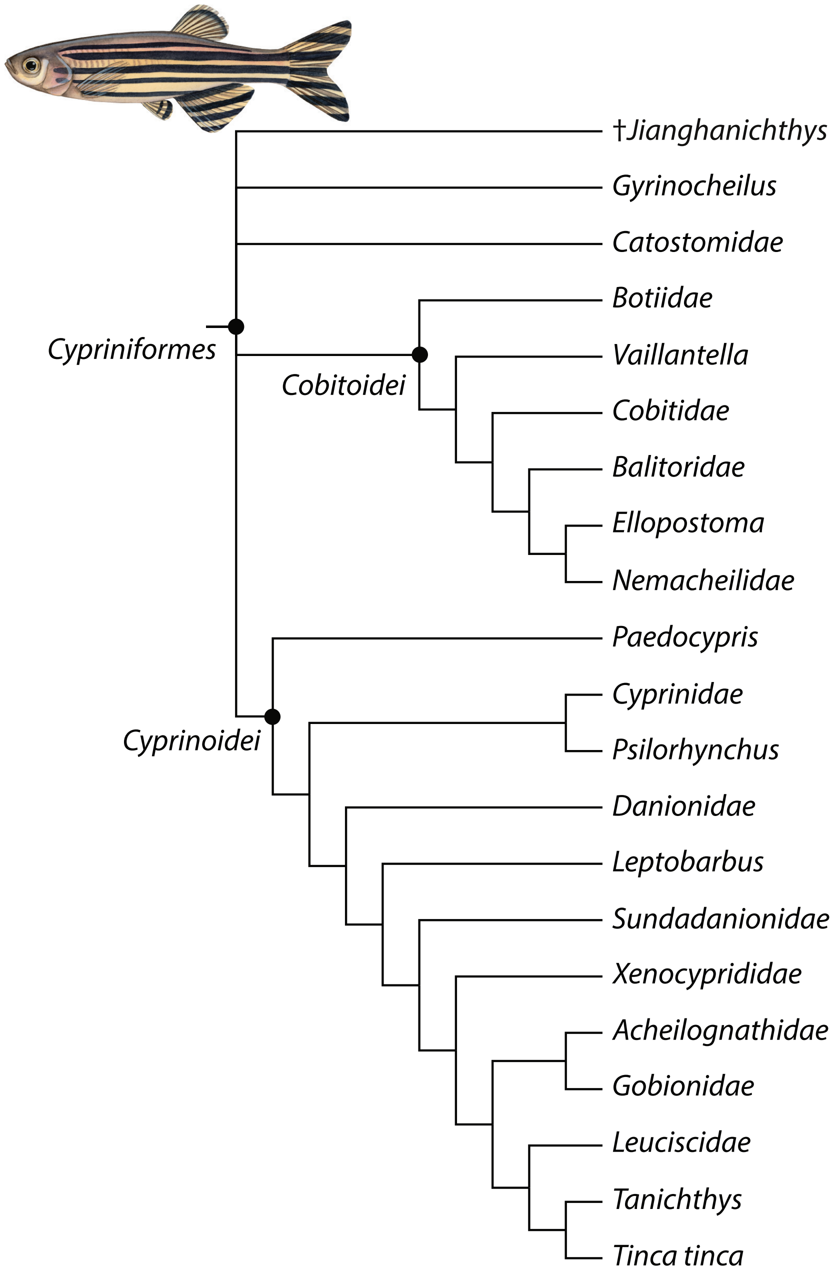

FIGURE 9. Phylogenetic relationships of the major living lineages and fossil taxa of *Cypriniformes*, *Cobitoidei*, and *Cyprinoidei*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

Cypriniformes as a polytomy subtending *Gyrinocheilus*, *Catostomidae*, *Cobitoidei*, *Cyprinoidei*, and †*Jianghanichthys* (J. Liu et al. 2015).

The monophyly of *Cypriniformes* is supported in a range of molecular phylogenetic studies that include analyses of whole mitochondrial genomes (Saitoh et al. 2006, 2011; Jondeung et al. 2007; He, Gu, et al. 2008; Poulsen et al. 2009; Nakatani et al. 2011), trees inferred from collections of Sanger-sequenced mitochondrial or nuclear genes (Mayden et al. 2008, 2009; Mayden and Chen 2010; Betancur-R et al. 2017; Hirt et al. 2017; Luo et al. 2023), and analysis of phylogenomic datasets (Stout et al. 2016; Hughes et al. 2018). Molecular phylogenetic analyses uniformly resolve *Catostomidae*, *Cobitoidei*, *Cyprinoidei*, and *Gyrinocheilus* as monophyletic (Šlechtová et al. 2007; W.-J. Chen et al. 2009; Mayden and Chen 2010; Stout et al. 2016; Hirt et al. 2017; Tao et al. 2019); however, molecular analyses result in five different hypotheses of relationships among these four lineages (Saitoh et al. 2006; Šlechtová et al. 2007; W.-J. Chen et al. 2008; Mayden et al. 2008; Bohlen and Šlechtová 2009; Mayden and Chen 2010; Stout et al. 2016; Hirt et al. 2017; Tao et al. 2019).

Composition. *Cypriniformes* currently contains 4,827 living species (Fricke et al. 2023) classified in *Catostomidae*, *Cobitoidei*, *Cyprinoidei,* and *Gyrinocheilus* (Mayden and Chen 2010; Conway 2011; Tan and Armbruster 2018). †*Jianghanichthys* is the only fossil taxon of *Cypriniformes* that is not a lineage of *Catostomidae*, *Cobitoidei*, or *Cyprinoidei* (J. Liu et al. 2015). The age and location of †*Jianghanichthys* is presented in Appendix 1. Over the past 10 years 661 new living species of *Cypriniformes* have been described (Fricke et al. 2023), comprising 13.7% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Cypriniformes* include (1) kinethmoid present (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (2) preethmoid present (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (3) dorsomedial autopalatine process present (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010), (4) autopalatime-endopterygoid articulation present (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (5) loss of ectopterygoid-autopalatine overlap (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010), (6) premaxilla extends furthest dorsally adjacent to midline (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (7) presence of ankylosed teeth on ceratobranchial 5 (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (8) lateral process of second vertebral centrum is elongate and projects into somatic musculature (Fink and Fink 1981, 1996; Conway et al. 2010; Wiley and Johnson 2010; Conway 2011), (9) absence of pharyngobranchial uncinate processes (Siebert 1987; Conway 2011), (10) three branchiostegal rays (Conway et al. 2010; Conway 2011; Mabee et al. 2011), and (11) teeth on ceratobranchial 5 arranged in a single row (Mabee et al. 2011).

Synonyms. *Eventognathi* (T. N. Gill 1861a:8–9; Gregory 1907:477–478; Jordan 1923:139–145), *Cyprinidae* (Boulenger 1904b:581–586; Goodrich 1909:375–376), *Cyprinoidei* (Berg 1940:444–446; Greenwood et al. 1966:384–386, 396; X.-W. Wu et al. 1981:572), *Cyprinoidea* (McAllister 1968:70–71), *Cyprinoidae* (Gosline 1971:121), and *Cypriniphysae* (Betancur-R et al. 2017) are ambiguous synonyms of *Cypriniformes*.

Comments. The taxa delimited here as *Cypriniformes* were grouped together in several pre-phylogenetic classifications (T. N. Gill 1893; Boulenger 1904b:581–586; Gregory 1907:477–478; Goodrich 1909:375–376; Regan 1911d; Jordan 1923:139–145; Berg 1940). The name *Cypriniformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade. Despite the strong support for cypriniform monophyly, relationships among the constituent lineages are not well-resolved, and there are disparate hypotheses on the phylogenetic placement of *Paedocypris* (Britz and Conway 2011; Britz, Conway, et al. 2014; Tan and Armbruster 2018).

The earliest fossil *Cypriniformes* is †*Jianghanichthys hubeiensis* from the early Eocene (56.0–47.8 Ma) of China (J. Liu et al. 2015). Bayesian relaxed molecular clock analyses of *Cypriniformes* result in an average posterior crown age estimate of 97.2 million years ago, with the credible interval ranging between 84.9 and 115.3 million years ago (Hughes et al. 2018).

Constituent lineages. Redundant group names are marked with an asterisk.

Catostomidae
Cobitoidei
Cyprinoidei
*Gyrinocheilidae**
†*Jianghanichthys*

Cobitoidei L. J. F. J. Fitzinger 1832:332
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Botia almorhae* Gray 1831 and *Cobitis taenia* Linnaeus 1758. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κωβῖτις (cobitis), which is an adjective of the gudgeon *Gobio gobio* (Linnaeus 1758), translating to "like a gudgeon" (D. W. Thompson 1947:139; Kottelat 2012).

Registration number. 905.

Reference phylogeny. A phylogeny of 1,703 species of *Cypriniformes* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Phylogenetic relationships of the major lineages of *Cobitoidei* are presented in Figure 9.

Phylogenetics. Analysis of morphological characters results in the resolution of a clade containing *Catostomidae*, *Cobitoidei*, and *Gyrinocheilus* (Siebert 1987; Conway and Mayden 2007; Conway 2011; Britz, Conway, et al. 2014), which had been called *Cobitidoidea* (Siebert 1987) and *Cobitoidea* (Sawada 1982; Conway et al. 2010; Simons and Gidmark 2010; J. S. Nelson et al. 2016:186). Morphological and molecular phylogenetic analyses consistently resolve *Cobitoidei* as monophyletic (Siebert 1987; Saitoh et al. 2006; Q. Tang et al. 2006; Šlechtová et al. 2007; Mayden et al. 2008, 2009; Bohlen and Šlechtová 2009; W.-J. Chen et al. 2009; Mayden and Chen 2010; Conway 2011; Britz, Conway, et al. 2014; Stout et al. 2016; Rabosky et al. 2018; Luo et al. 2023), but some molecular analyses resolve *Cobitoidea* as paraphyletic (W.-J. Chen et al. 2009; Stout et al. 2016).

Phylogenetic inferences of relationships within *Cobitoidei* are broadly congruent between morphological and molecular studies (e.g., Saitoh et al. 2006; Šlechtová et al. 2007; W.-J. Chen et al. 2009; Conway 2011; Mabee et al. 2011; Tao et al. 2019) with *Botiidae* (bottid loaches) placed as the sister lineage of all other *Cobitoidei* and resolution of a clade containing *Cobitidae* (loaches), *Balitoridae* (hillstream loaches), and *Nemacheilidae* (stone loaches) (Q. Tang et al. 2006; Mayden et al. 2008; Bohlen and Šlechtová 2009; Mayden and Chen 2010; S. Liu et al. 2012; Stout et al. 2016; Luo et al. 2023). Molecular phylogenies place *Barbucca* (fire-eyed loaches) and *Serpenticobitis* (serpent loaches) in *Balitoridae* (Šlechtová et al. 2007; Bohlen and Šlechtová 2009; Rabosky et al. 2018), *Ellopostoma* (enigmatic loaches) as the sister lineage of *Nemacheilidae*, *Balitoridae*, or a clade containing *Balitoridae* and *Nemacheilidae* (Bohlen and Šlechtová 2009; W.-J. Chen et al. 2009; Rabosky et al. 2018; Luo et al. 2023), and *Vaillantella* (longfin loaches) as the sister lineage of the cobitoid clade that contains *Cobitidae*, *Ellopostoma*, *Balitoridae*, and *Nemacheilidae* (Q. Tang et al. 2006; Šlechtová et al. 2007; Bohlen and Šlechtová 2009; W.-J. Chen et al. 2009; S. Liu et al. 2012; Stout et al. 2016; Rabosky et al. 2018).

Composition. There are currently 1,361 species of *Cobitoidei* (Fricke et al. 2023) classified in *Balitoridae*, *Botiidae*, *Cobitidae*, *Ellopostoma*, *Nemacheilidae*, and *Vaillantella* (Šlechtová et al. 2007; Bohlen and Šlechtová 2009; W.-J. Chen et al. 2009; Tan and Armbruster 2018). Over the past 10 years there have been 266 new living species of *Cobitoidei* described (Fricke et al. 2023), comprising 19.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological synapomorphies for *Cobitoidei* include (1) presence of transversus ventralis V process on ceratobranchial 5 (Siebert 1987; Conway 2011), (2) presence of second preethmoid (Conway 2011), (3) anteriormost edge of orbitosphenoid contacts ethmoid complex (Conway 2011), (4) presence of preautopalatine (Conway 2011), (5) presence of cleithral-occipital ligament (Conway 2011), and (6) third and fourth lateral line ossifications much larger than other lateral line ossifications (Conway 2011).

Synonyms. *Cobitidoidea* (Siebert 1987:43) and *Cobitoidea* (Sawada 1982:212) are approximate synonyms of *Cobitoidei*.

Comments. *Cobitoidei* was the name applied to the paraphyletic group that included all non-cyprinoid cypriniforms to the exclusion of *Catostomidae* (Kottelat 2012). Given the uncertainty in the phylogenetic relationships among major lineages of *Cypriniformes* (Figure 9), we apply the group name *Cobitoidei* to all non-cyprinoid cypriniforms to the exclusion of *Gyrinocheilus* and *Catostomidae*.

Cobitoidei are frequently classified with *Catostomidae* and *Gyrinocheilus* (Siebert 1987; Conway et al. 2010; J. S. Nelson et al. 2016:186) or with *Gyrinocheilus* to the exclusion of *Catostomidae* (Kottelat 2012). Some classifications of ray-finned fishes include *Barbuccidae*, *Gastromyzontidae*, and *Serpenticobitidae* as taxonomic families of *Cobitoidei* (Kottelat 2012; J. S. Nelson et al. 2016:191–193; Betancur-R et al. 2017; Tan and Armbruster 2018). Along with many other researchers, we include *Barbucca*, *Gastromyzontinae*, and *Serpenticobitis* in *Balitoridae* (Q. Tang et al. 2006; Šlechtová et al. 2007; Bohlen and Šlechtová 2009; W.-J. Chen et al. 2009; S. Liu et al. 2012; Z. S. Randall and Page 2015; Tao et al. 2019). This inclusive delimitation of *Balitoridae* is both consistent with phylogenetic relationships and reduces the number of redundant group names in the classification of *Cobitoidei*, as both *Barbuccidae* and *Serpenticobitidae* contain a single genus and ranking these clades as equivalent to *Gastromyzontidae* and *Balitoridae* conveys no information about their phylogenetic relationships.

The cobitoid fossil record is sparse and limited to Asia and Europe (Conway et al. 2010). The earliest fossil cobitoids are †*Cobitis longipectoralis* from the late early Miocene (18 Ma) and †*C. nanningensis* from the early-middle Oligocene in China (G.-J. Chen et al. 2010, 2015). Relaxed molecular clock analyses estimate the age of *Cobitoidei* to be between 50 and 78 million years ago (Hughes et al. 2018).

Constituent lineages. Redundant group names are marked with an asterisk.

Balitoridae
Botiidae
Cobitidae
*Ellopostomatidae**
Nemacheilidae
*Vaillantellidae**

Cyprinoidei L. J. F. J. Fitzinger 1832:332
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Cyprinus carpio* Linnaeus 1758, *Danio rerio* (Hamilton 1822), *Leuciscus leuciscus* (Cuvier 1816), and *Paedocypris progenetica* Kottelat et al. 2006. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κυπρῖνος (kuːpɹˈiːno͡ʊz), frequently applied to the European Carp, *Cyprinus carpio* (D. W. Thompson 1947:135–136).

Registration number. 906.

Reference phylogeny. A phylogeny of 1,703 species of *Cypriniformes* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Although the reference phylogeny does not include *Paedocypris progenetica*, the species resolves within the cyprinoid clade *Danionidae* (danionins) in phylogenetic analysis of mtDNA, combined mtDNA and nuclear gene sequences, and morphological characters (Rüber et al. 2007; Fang et al. 2009; K. L. Tang et al. 2010; Britz, Conway, et al. 2014). Phylogenetic analysis of DNA sequences of nuclear genes resolves *Paedocypris* as the sister lineage of *Cyprinoidei* or *Cypriniformes* (Mayden and Chen 2010; Stout et al. 2016; Malmstrøm et al. 2018). Phylogenetic relationships among the major clades of *Cyprinoidei* are presented in Figure 9.

Phylogenetics. Inference of the phylogenetics of *Cyprinoidei* is challenged by the high diversity of species in the clade; incongruent relationships of miniature species classified in *Paedocypris*, *Sundadanio*, and *Fangfangia* (Mayden and Chen 2010; Britz et al. 2011; Britz, Conway, et al. 2014); and phylogenetic resolution of the southeast Asian *Tanichthys* (cardinal minnows) and the European *Tinca tinca* (Tench) (Conway et al. 2010; Simons and Gidmark 2010; Tan and Armbruster 2018). Despite the remaining problems in the phylogeny of *Cyprinoidei*, incremental resolution of their relationships over the past 30 years has led to the elevation of 11 taxonomic families that were all classified as *Cyprinidae* (carps) for over 100 years (T. N. Gill 1872, 1893; Hensel 1970; W.-J. Chen and Mayden 2009; Tan and Armbruster 2018).

Phylogenetic analysis of *Cyprinoidei* using morphological characters resolves *Cyprinidae* as the sister lineage of all other cyprinoid lineages and *Danionidae* (dianions) as the sister lineage of a clade containing *Acheilognathidae* (bitterlings), *Gobionidae* (gudgeons), *Leuciscidae* (true minnows), and *Xenocyprididae* (Cavender and Coburn 1992; Conway 2011). In addition, *Tinca tinca* has uncertain resolution and *Psilorhynchus* (torrent minnows) is the sister lineage of all other *Cyprinoidei* (Cavender and Coburn 1992; Conway 2011). Analysis of a dataset that expands the character matrix from Conway (2011) resolves the cyprinoid miniature lineages *Paedocypris* and *Sundadanio* in a clade with *Danionella* (Britz, Conway, et al. 2014).

There are many molecular phylogenetic studies of *Cyprinoidei* that collectively include all known major lineages. The types of molecular data include whole mtDNA genomes (Saitoh et al. 2006; He, Gu, et al. 2008; Mayden et al. 2008; Chen et al. 2023; Hao et al. 2023), individual mtDNA or nuclear genes (e.g., Cunha et al. 2002; X. Z. Wang et al. 2007; He, Mayden, et al. 2008), combinations of mtDNA and nuclear genes (e.g., W.-J. Chen and Mayden 2009; Mayden and Chen 2010; Tao et al. 2019), and phylogenomic datasets (Stout et al. 2016; Hughes et al. 2018). Molecular phylogenies consistently nest *Psilorhynchus* within *Cyprinoidei* as the sister lineage of *Cyprinidae* (Šlechtová et al. 2007; He, Gu, et al. 2008; W.-J. Chen and Mayden 2009; Mayden and Chen 2010; K. L. Tang et al. 2013; Hirt et al. 2017; Rabosky et al. 2018; Tao et al. 2019), resolve a clade containing *Acheilognathidae*, *Gobionidae*, *Leptobarbus*, *Leuciscidae*, *Sundadanio*, *Tanichthys*, *Tinca tinca*, and *Xenocyprididae* (W.-J. Chen and Mayden 2009; Fang et al. 2009; Mayden and Chen 2010; K. L. Tang et al. 2013; Stout et al. 2016; Hirt et al. 2017; Rabosky et al. 2018), and a lineage that includes *Acheilognathidae*, *Gobionidae*, *Leuciscidae*, *Tanichthys*, *Tinca tinca*, and *Xenocyprididae* (Saitoh et al. 2006; Rüber et al. 2007; X. Z. Wang et al. 2007, 2012; W.-J. Chen et al. 2008; He, Mayden, et al. 2008; Mayden et al. 2008, 2009; W.-J. Chen and Mayden 2009; Fang et al. 2009; Mayden and Chen 2010; K. L. Tang et al. 2013; Tao et al. 2013, 2019; Stout et al. 2016; Hirt et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; F. Chen et al. 2023; Hao et al. 2023). The relationships of *Tinca tinca* and *Tanichthys* vary among studies, with some resolving these two lineages as closely related (Fang et al. 2009; Mayden and Chen 2010; K. L. Tang et al. 2013) and sharing phylogenetic affinities with *Leuciscidae* (X. Z. Wang et al. 2007, 2012; Stout et al. 2016; Rabosky et al. 2018) or *Xenocyprididae* (Rüber et al. 2007; Tao et al. 2013; Hirt et al. 2017; Tao et al. 2019).

Phylogenetic analysis of mtDNA, combined mtDNA and nuclear gene sequences, and morphological characters resolve *Paedocypris* within the cyprinoid subclade *Danionidae* (Rüber et al. 2007; Fang et al. 2009; K. L. Tang et al. 2010, 2013; Britz, Conway, et al. 2014); however, analysis of nuclear gene datasets places this taxon as the sister lineage of *Cyprinoidei* or *Cypriniformes* (Mayden and Chen 2010; Stout et al. 2016; Malmstrøm et al. 2018). Gene trees inferred from each of the six loci examined by Mayden and Chen (2010) exhibit six different phylogenetic resolutions of *Paedocypris*: nested in *Cyprinidae*, the sister lineage of *Cyprinidae*, the sister lineage of *Cypriniformes*, the sister lineage of *Catostomidae*, the sister lineage of *Gyrinocheilus*, and nested within *Danionidae* (Britz, Conway, et al. 2014). It is possible that the disparate phylogenetic placements of *Paedocypris* among molecular datasets are the result of long branch attraction related to the dramatically reduced size of its genome (Britz, Conway, et al. 2014; Malmstrøm et al. 2018).

Composition. There are currently more than 3,375 living species of *Cyprinoidei* (Fricke et al. 2023) that includes *Tinca tinca* and species in *Acheilognathidae*, *Cyprinidae*, *Danionidae*, *Gobionidae*, *Leptobarbus* (sultan barbs), *Leuciscidae*, *Paedocypris*, *Psilorhynchus*, *Sundadanio*, *Tanichthys*, *Tinca*, and *Xenocyprididae*. Over the past 10 years 395 new living species of *Cyprinoidei* have been described (Fricke et al. 2023), comprising 11.7% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Cyprinoidei* include (1) absence of uncinate process on epibranchials 1 and 2 (Siebert 1987; Cavender and Coburn 1992; Conway et al. 2010), (2) pharyngobranchial 1 absent (Siebert 1987; Cavender and Coburn 1992; Conway et al. 2010), (3) pharyngobranchial 3 overlaps pharyngobranchial 2 (Siebert 1987; Cavender and Coburn 1992; Conway et al. 2010), (4) presence of well-developed subtemporal fossae (Siebert 1987; Cavender and Coburn 1992; Conway et al. 2010), (5) anterior opening of trigeminal-facial chamber positioned between prootic and pterosphenoid, (6) loss of contact between infraorbital 5 and supraorbital (Cavender and Coburn 1992; Conway et al. 2010), and (7) presence of opercular canal (Cavender and Coburn 1992; Conway et al. 2010).

Synonyms. *Cyprinidae* (T. N. Gill 1872:18, 1893:132; Siebert 1987:43; Howes 1991b:8–17; Cavender and Coburn 1992:296–300; J. S. Nelson 2006:139–143; Simons and Gidmark 2010:419–425) and *Cyprinoidea* (Greenwood et al. 1966:396; Conway 2011, fig. 43; J. S. Nelson et al. 2016:181) are ambiguous synonyms of *Cyprinoidei*.

Comments. The lineages of *Cyprinoidei* were long classified as *Cyprinidae* and highlighted as one of the most species-rich taxonomic families of vertebrates (T. N. Gill 1872; Jordan 1923; Greenwood et al. 1966; Howes 1991b; J. S. Nelson et al. 2016:181); however, the disassembly of *Cyprinidae sensu lato* into 12 taxonomic families was the result of a desire to preserve the Linnaean taxonomic family rank of the monogeneric *Psilorhynchidae* (Hora 1925) that is phylogenetically nested within *Cyprinoidei* (W.-J. Chen and Mayden 2009; Tan and Armbruster 2018). The name *Cyprinoidei* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade. While it is appropriate to view the changing classification of *Cyprinoidei* as an outcome of greater resolution of their phylogenetic relationships, the uncertainty as to the phylogeny of the miniature lineages *Paedocypris*, *Sundadanio*, and *Fangfangia* (Britz, Conway, et al. 2014) remains one of the most important issues in vertebrate phylogeny.

The earliest fossil taxon of *Cyprinoidei* is †*Palaeogobio zhongyuanensis*, classified in *Gobionidae* from the early middle Eocene (approximately 47 Ma) of China (Zhou 1990; M.-M. Chang and Chen 2008). An interesting set of cyprinoid fossils from the Sangkarewang Formation in Sumatra, Indonesia is classified in *Cyprinidae* and *Danionidae*; however, the age of the formation is only tentatively assigned to the middle Eocene (Murray 2019, 2020). Bayesian relaxed molecular clock analyses of the crown age of *Cyprinoidei* result in a credible interval ranging between 67 and 98 million years ago (Hirt et al. 2017).

Constituent lineages. Redundant group names are marked with an asterisk.

Acheilognathidae
Cyprinidae
Danionidae
Gobionidae
*Leptobarbidae**
Leuciscidae
*Paedocyprididae**
*Psilorhynchidae**
Sundadanionidae
*Tanichthyidae**
*Tincidae**
Xenocyprididae

Gymnotiformes C. T. Regan 1911d:23
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Gymnotus carapo* Linnaeus 1758, *Gymnotus pantherinus* (Steindachner 1908), *Apteronotus albifrons* (Linnaeus 1766), and *Sternopygus macrurus* (Bloch and Schneider 1801). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek γυμνός (d͡ʒˈɪmno͡ʊz), meaning naked, and νῶτον (nˈa͡ʊtən), meaning back. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 907.

Reference phylogeny. A phylogeny inferred from DNA sequences of 966 ultraconserved element (UCE) loci (Alda et al. 2019). Although *Gymnotus carapo* is not included in the reference phylogeny, it resolves in a clade with five other species of *Gymnotus*, including *G. pantherinus*, in a phylogenetic analysis of Sanger-sequenced mitochondrial and nuclear genes (Tagliacollo et al. 2016, figs. 2–4). Phylogenetic relationships among the major lineages of *Gymnotiformes* are presented in Figure 8.

Phylogenetics. There is substantial morphological evidence supporting the monophyly of *Gymnotiformes*, which is consistently corroborated in molecular phylogenetic analyses (e.g., Fink and Fink 1981, 1996; Nakatani et al. 2011; W.-J. Chen et al. 2013; Arcila et al. 2017). Phylogenetic relationships among the five major lineages of *Gymnotiformes* differ among analyses of morphological characters (Triques 1993; Gayet et al. 1994; Albert 2001), short Sanger-sequenced fragments of mtDNA genes (Alves-Gomes et al. 1995), combined analyses of morphology and DNA sequences of mtDNA and nuclear genes (Albert and Crampton 2005; Tagliacollo et al. 2016), and phylogenomic datasets (Arcila et al. 2017; Alda et al. 2019). The phylogenies differ as to the resolution of the sister lineage of all other *Gymnotiformes*: analyses of morphology and combined molecular and morphological datasets place *Gymnotidae* (nakedback knifefishes) as the sister lineage of all other *Gymnotiformes* (Albert 2001; Albert and Crampton 2005; Tagliacollo et al. 2016) and phylogenies inferred from alternative morphological datasets and phylogenomic datasets composed of exons and UCEs resolve *Apteronotidae* (ghost knifefishes) as the sister to all other *Gymnotiformes* (Triques 1993; Gayet et al. 1994; Arcila et al. 2017; Alda et al. 2019). Coalescent-based species tree analysis of UCE loci results in a phylogenetic tree in which lineages that produce a pulse-type electrical signal [*Gymnotidae*, *Hypopomidae* (bluntnose knifefishes), and *Rhamphichthyidae* (sand knifefishes)] are a monophyletic group that is the sister group of a clade comprising lineages that produce a wave-type electrical signal [*Apteronotidae* and *Sternopygidae* (glass knifefishes)] (Alda et al. 2019).

Morphological studies imply that *Gymnotiformes* and *Siluriformes* share a common ancestor relative to other major clades of *Otophysi* (Fink and Fink 1981, 1996); however, no unconstrained phylogenetic analysis of molecular data supports this relationship (Dimmick and Larson 1996; Ortí and Meyer 1996; Nakatani et al. 2011; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013; Arcila et al. 2017; Chakrabarty et al. 2017; Hughes et al. 2018; Melo, Sidlauskas, et al. 2022). The phylogeny of *Otophysi* inferred from molecular data suggests that the passive electroreception and its associated specialized neural anatomy, cytology, and physiology in *Gymnotiformes* and *Siluriformes* has multiple evolutionary origins or multiple losses within the clade (Fink and Fink 1996; Albert et al. 1998).

Composition. There are currently 272 living species of *Gymnotiformes* (Fricke et al. 2023) classified in *Apteronotidae*, *Gymnotidae*, *Hypopomidae*, *Rhamphichthyidae*, and *Sternopygidae* (Ferraris et al. 2017). Over the past 10 years 68 new living species of *Gymnotiformes* have been described (Fricke et al. 2023), comprising 25% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gymnotiformes* include (1) absence of palatine ossification and palatine cartilage with flexure permitting mobility (Fink and Fink 1981; Albert 2001), (2) mesopterygoid with vertical strut that usually articulates with orbitosphenoid (Fink and Fink 1981), (3) claustrum of Weberian apparatus absent as a separate ossified element (Fink and Fink 1981; Albert 2001), (4) anterior and posterior parts of Baudelot's ligament attach to cleithrum (Fink and Fink 1981), (5) pelvic girdle and pelvic fin absent (Fink and Fink 1981; Albert 2001), (6) dorsal fin absent (Fink and Fink 1981; Albert 2001), (7) presence of elongate anal fin (Fink and Fink 1981; Albert 2001), (8) anal fin rays articulate directly with proximal radials and distal radials are reduced (Fink and Fink 1981; Albert 2001), (9) caudal skeleton reduced to single element and caudal fin reduced or absent (Mago-Leccia and Zaret 1978; Fink and Fink

1981; Albert 2001), (10) anus placed ventral or anterior to pectoral fin origin (Fink and Fink 1981; Albert 2001), (11) absence of maxillary teeth (Albert 2001), (12) articular surface of maxilla on stalk (Albert 2001), (13) levator posterior muscle not differentiated, (14) lateral margins of parasphenoid not extending to a horizontal with trigeminal foramen (Albert 2001), (15) dorsal telencephalic area with large dorsalis centralis and small dorsalis medialis (Albert 2001), (16) eye in adults covered by epidermis (Albert 2001), (17) Schreckstoff club cells and fright response absent (Albert 2001), (18) ampullary organs organized into rosettes (Albert 2001), (19) ectopterygoid absent (Albert 2001), (20) metapterygoid triangular in shape (Albert 2001), (21) sixth epibranchial with elongate ascending process, and (22) presence of electric organs composed of rows of modified elongate myofibrils (Albert 2001).

Synonyms. *Gymnonoti* (T. N. Gill 1872:18; Jordan 1923:138), *Gymnotidae* (Boulenger 1904b:579–581), *Gymnotoidei* (Goodrich 1909:376–377; Berg 1940:443–444; Greenwood et al. 1966:383–384; Fink and Fink 1981:303), *Gymnotoidea* (McAllister 1968:69; Rosen and Greenwood 1970:23), and *Gymnotoidae* (Gosline 1971:121) are ambiguous synonyms of *Gymnotiformes*.

Comments. The group name *Gymnotiformes* has long been applied to the clade as defined above (Regan 1911d; Mago-Leccia 1978; J. S. Nelson 1984:154–156; Fink and Fink 1996; Betancur-R et al. 2017) and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The fossil record of *Gymnotiformes* is limited to a handful of fragmentary fossils, including †*Humboldtichthys kirschbaumi* from the Miocene of Bolivia (Gayet et al. 1994; Gayet and Meunier 2000; Albert and Fink 2007). A morphological phylogenetic analysis places the holotype specimen of †*H. kirschbaumi* within *Sternopygidae* (Albert and Fink 2007). Bayesian relaxed molecular clock analyses of *Gymnotiformes* result in an average posterior crown age estimate of 62.4 million years ago, with the credible interval ranging between 46.0 and 81.6 million years ago (Hughes et al. 2018).

Constituent lineages.
Apteronotidae
Gymnotidae
Hypopomidae
Rhamphichthyidae
Sternopygidae

Citharinifomes J. M. Mirande 2017:342
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Citharinus citharus* (Geoffroy St. Hilaire 1809) and *Distichodus mossambicus* Peters 1852. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κῐθᾰρα (kɪθˈɑːɹ͡ɪə), meaning harp or lute. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 908.

Reference phylogeny. A phylogeny inferred from a maximum likelihood analysis of DNA sequences from two mtDNA genes and two nuclear genes (Arroyave et al. 2013, fig. 4). Phylogenetic relationships of *Characiformes* are shown in Figure 8.

Phylogenetics. Analyses of morphological and molecular characters consistently support the monophyly of *Citharinifomes* (Vari 1979; Ortí and Meyer 1997; Buckup 1998; Calcagnotto et al. 2005; Arroyave and Stiassny 2011; Arroyave et al. 2013; Arcila et al. 2017, 2018; Lavoué et al. 2017; Rabosky et al. 2018; Betancur-R. et al. 2019; Burns and Sidlauskas 2019; Melo, Sidlauskas, et al. 2022).

Composition. There are currently 117 species of *Citharinifomes* (Fricke et al. 2023) classified in *Citharinidae* (citharinids) and *Distichodontidae* (distichodontids). Over the past 10 years nine new living species of *Citharinifomes* have been described (Fricke et al. 2023), comprising 7.7% of the living species diversity in the clade.

Diagnostic apomorphies. Vari (1979) listed 14 morphological synapomorphies that support monophyly of *Citharinifomes*; however, eight of these character states are either ancestral within *Otophysi* or are secondarily derived in some lineages of *Characiformes* (Fink and Fink 1981). Morphological character states consistent with the monophyly of *Cithariniformes* include (1) second and third vertebrae with ventral elaborations and ventral expansion of os suspensorium (Vari 1979), (2) bicuspidate teeth (Vari 1979), (3) postcleithra 2 and 3 fused (Vari 1979), (4) hypurals 1 and 2 fused (Vari 1979), (5) absences of lateral wings on supraethmoid (Vari 1979), and (6) large and ventrally ovate third posttemporal fossa bordered by epioccipital and exoccipital (Vari 1979).

<u>Synonyms.</u> *Citharinidae* (Regan 1911d:21–22; J. S. Nelson 1994:142–143) and *Citharinoidei* (Buckup 1993:138; J. S. Nelson et al. 2016:194–195; Betancur-R et al. 2017:17) are ambiguous synonyms of *Cithariniformes*.

<u>Comments.</u> *Cithariniformes* was a group name applied to the clade containing *Citharinidae* and *Distichodontidae* (Mirande 2017, table 3), but long classified as a lineage of *Characiformes* (Vari 1979; Fink and Fink 1981, 1996; Buckup 1998; Betancur-R et al. 2017). Molecular phylogenetic analyses consistently resolve *Characiformes*, *Siluriformes*, and *Gymnotiformes* as a clade to the exclusion of *Cithariniformes* (Nakatani et al. 2011; Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013; Chakrabarty et al. 2017; Hughes et al. 2018, fig. S2; Faircloth et al. 2020; Melo, Sidlauskas, et al. 2022; Yang et al. 2023). It is unknown whether the seven morphological apomorphies identified by Fink and Fink (1981) supporting the hypothesis that *Cithariniformes* and *Characiformes* share common ancestry are present in a wider range of characiform taxa; their study did not include species of *Acestrorhynchus* (needlejaws), *Gasteropelecidae* (freshwater hatchetfishes), *Iguanodectidae* (tetras), *Serrasalmidae* (pacus), or *Triportheidae* (elongate hatchetfishes). The monophyly of both *Cithariniformes* and *Characiformes* is validated in phylogenetic analyses of morphological data matrices that use an explicit optimality criterion (Buckup 1998; de Pinna et al. 2018). However, the relationships of these two lineages relative to *Siluriformes* and *Gymnotiformes* have not been investigated using morphological phylogenetic analyses that seek a tree or set of trees with an optimal distribution of character state changes.

The earliest *Cithariniformes* fossil is a tooth identified as a species of *Distichodus* from the Lower Nawata formation at Lothagam, Kenya dated to approximately 7.5 million years ago (McDougall and Feibel 1999; K. M. Stewart 2001, 2003). Bayesian relaxed molecular clock analyses of *Cithariniformes* result in an average posterior crown age estimate of 119.7 million years ago, with the credible interval ranging between 93.2 and 149.3 million years ago (Melo, Sidlauskas, et al. 2022).

<u>Constituent lineages.</u>
Citharinidae
Distichodontidae

Siluriformes O. P. Hay 1929:25
[Lundberg 2020]

<u>Definition.</u> Defined as a minimum-crown-clade in Lundberg (2020d) as: “The crown clade originating in the most recent common ancestor of *Loricaria cataphracta* Linnaeus 1758 (*Loricarioidei*), *Diplomystes* (originally *Silurus*) *chilensis* (Molina 1782) (*Diplomystidae*), and *Silurus glanis* Linnaeus 1758 (*Siluroidei*).”

<u>Etymology.</u> From the ancient Greek σίλουρος (sɪlˈʊ͡ɹo͡ʊz), which is the name applied to several species of catfishes in Europe and Egypt, including the Wels Catfish, *Silurus glanis* (D. W. Thompson 1947:233–237). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

<u>Registration number.</u> 199.

<u>Reference phylogeny.</u> Sullivan et al. (2006, figs. 1, 2) was designated as the primary reference phylogeny by Lundberg (2020d). Phylogeny of the living and fossil lineages of *Siluriformes* is presented in Figure 10. The placements of the fossil lineages †*Bachmannia* and †*Hypsidoris* are on the basis of inferences from morphology (L. Grande 1987; L. Grande and de Pinna 1998; Azpelicueta and Cione 2011).

<u>Phylogenetics.</u> There are several reviews on the phylogenetics of *Siluriformes* prior to the application of molecular data (de Pinna 1998;

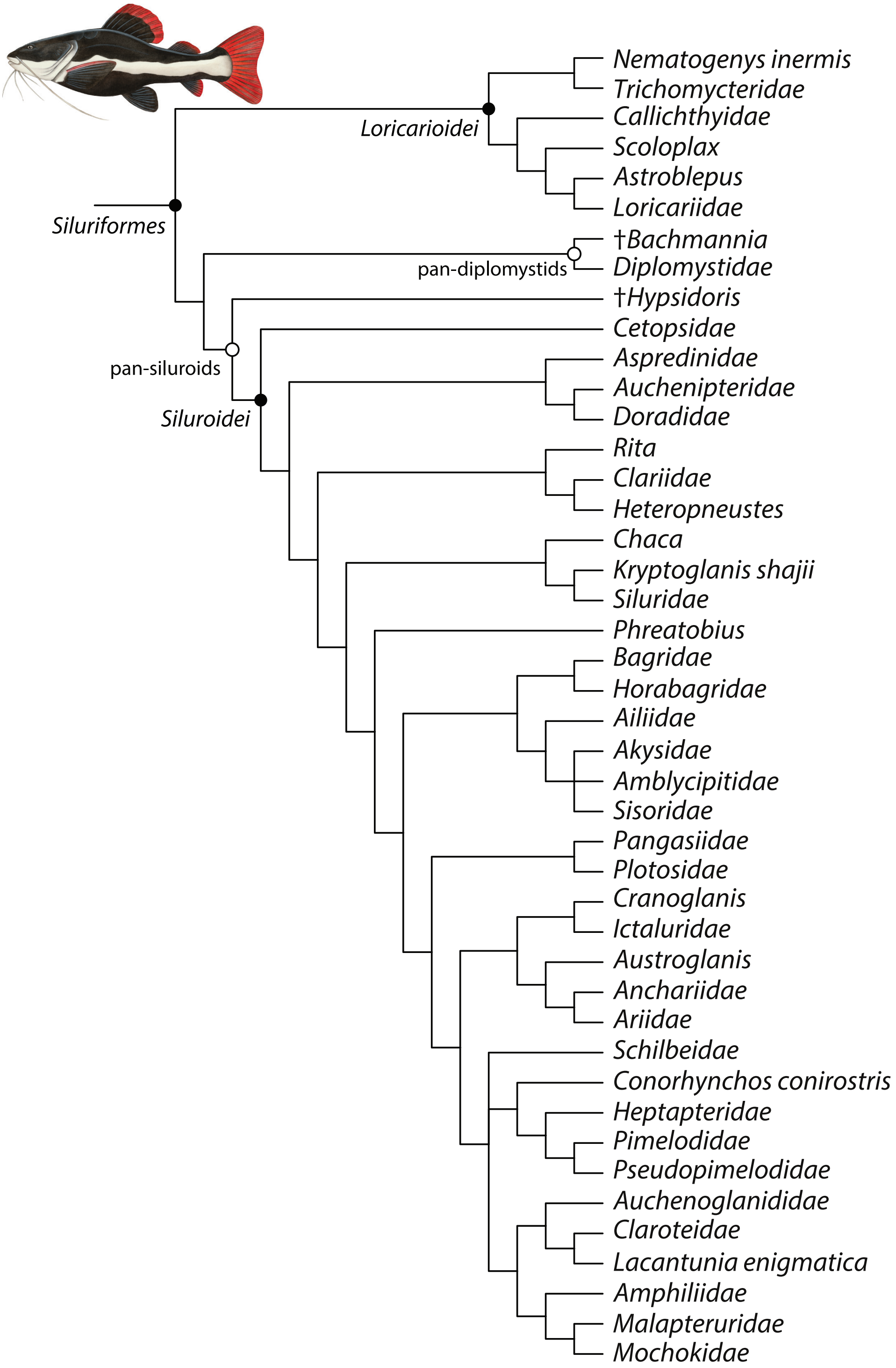

FIGURE 10. Phylogenetic relationships of the major living lineages and fossil taxa of *Siluriformes*, *Loricarioidei*, and *Siluroidei*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

Diogo 2003, 2004; Teugels 2003). The monophyly of *Siluriformes* is supported in analyses of morphological characters (Fink and Fink 1981, 1996; Mo 1991; Arratia 1992; de Pinna 1993; Diogo 2004) and in all molecular phylogenetic studies, which includes analyses of whole mitochondrial genomes (Jondeung et al. 2007; Poulsen et al. 2009; Nakatani et al. 2011; Schedel et al. 2022; Duong et al. 2023), collections of Sanger-sequenced mitochondrial or nuclear genes (Betancur-R, Broughton, et al. 2013; W.-J. Chen et al. 2013), and phylogenomic datasets (Arcila et al. 2017; Chakrabarty et al. 2017; Hughes et al. 2018).

The first explicit phylogenetic studies of relationships within *Siluriformes* were morphological analyses aimed at determining the relationships among the *Loricarioidei* (Howes 1983; Schaefer 1990) and the relationships of the Eocene fossil taxon †*Hypsidoris* (L. Grande 1987; L. Grande and de Pinna 1998). More inclusive morphological phylogenetic studies aimed at including representatives of all the taxonomic families of *Siluriformes* place *Diplomystidae* (velvet catfishes) as the sister lineage of all other catfishes (Mo 1991; de Pinna 1993, 1998); support the monophyly of *Loricarioidei*; and do not resolve *Siluroidei* as monophyletic (Mo 1991; de Pinna 1993, 1998). A subsequent morphological analysis roots the phylogeny on *Diplomystidae* and resolves both *Loricarioidei* and *Siluroidei* as monophyletic (Diogo 2004, fig. 3.124); however, this study was critiqued on issues involving character state polarity and homology (Schaefer 2006). The Eocene fossil taxa †*Bachmannia* and †*Hypsidoris* are resolved as the sister lineages of *Diplomystidae* and *Siluroidei*, respectively (L. Grande 1987; L. Grande and de Pinna 1998; Azpelicueta and Cione 2011).

Molecular phylogenetic analyses of *Siluriformes* consistently resolve *Loricarioidei* as the sister lineage of a clade containing *Diplomystidae* and *Siluroidei* (Sullivan et al. 2006; Lundberg et al. 2007; Nakatani et al. 2011; W.-J. Chen et al. 2013; Kappas et al. 2016; Arcila et al. 2017; Rivera-Rivera and Montoya-Burgos 2017, 2018; Schedel et al. 2022). In molecular phylogenetic studies, the monophyly of *Loricarioidei* and *Siluroidei* are strongly supported (e.g., Sullivan et al. 2006; Nakatani et al. 2011; Arcila et al. 2017; Schedel et al. 2022). Molecular evolutionary rate heterogeneity among lineages is proposed as a mechanism for the incongruence between morphological and molecular phylogenies with regard to the placement of *Loricarioidei* in contrast to *Diplomystidae* as the sister lineage of all other *Siluriformes* (Rivera-Rivera and Montoya-Burgos 2018).

Composition. *Siluriformes* currently contains 4,188 species (Fricke et al. 2023) classified in *Loricarioidei*, *Diplomystidae*, and *Siluroidei*. *Siluriformes* includes the pan-diplomystid †*Bachmannia* and the pan-siluroid †*Hypsidoris* (L. Grande 1987; L. Grande and de Pinna 1998; Gayet and Meunier 2003; Azpelicueta and Cione 2011). Details of the ages and locations of the siluriform fossil taxa are presented in Appendix 1. Over the past 10 years 628 new living species of *Siluriformes* have been described (Fricke et al. 2023), comprising 15% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Siluriformes* include (1) parietal bones absent (Fink and Fink 1981, 1996; Arratia 1992, 2003a; Wiley and Johnson 2010; Lundberg 2020d), (2) autopalatine bone separate from suspensorium (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020d), (3) ectopterygoid and endopterygoid reduced and not articulating with metapterygoid, quadrate, and hyomandibular (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (4) metapterygoid anterodorsal to quadrate (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (5) symplectic and posterior process of quadrate absent (Fink and Fink 1981, 1996; Arratia 2003a; Wiley and Johnson 2010; Lundberg 2020d), (6) preopercle and interopercle shortened (Fink and Fink 1981, 1996; Wiley and Johnson 2010; Lundberg 2020d), (7) subopercles absent (Fink and Fink 1981, 1996; Arratia 1992, 2003a; Wiley and Johnson 2010; Lundberg 2020d), (8) complex centrum formed by fusion of centra 2, 3, and 4 (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (9) third and fourth neural arches fused to each other and to complex centrum (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (10) parapophysis of second vertebral centrum absent (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (11) transformator process of Weberian apparatus tripus separated posteriorly by width of the complex centrum (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010), (12) parapophysis of fourth vertebral centrum expanded and articulating with posttemporal supracleithrum (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (13) parapophysis of fourth vertebral centrum fused to complex centrum (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010), (14) os suspensorium of Weberian apparatus consisting of only an anterior horizontal process (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010), (15) suspensorium of pectoral girdle consisting of single ossified element including the supracleithrum, an ossified Baudelot's ligament, and posttemporal (Fink and Fink 1981, 1996; Arratia 1992; Wiley and Johnson 2010; Lundberg 2020d), (16) Baudelot's ligament distally bifurcated (Fink and Fink 1981, 1996), (17) dorsal fin with two tightly bound anterior spines (Lundberg et al. 2007; Lundberg 2020d), (18) skin naked with no bony-ridge scales that are present in most other lineages of *Teleostei* (Fink and Fink 1981, 1996; Lundberg 2020d), (19) palatoquadrate with separate pars autopalatine (Arratia 1992), (20) posterior palatoquadrate fused with symplectic cartilage (Arratia 1992), (21) articulation of autopalatine and vomer at midpoint of autopalatine (Arratia 1992), (22) articulation of autopalatine and lateral ethmoid at mid length of autopalatine (Arratia 1992), (23) entopterygoid not the main support for the eye (Arratia 1992), (24) retroarticular and anguloarticular fused (Arratia 1992), (25) Meckel cartilage with coronoid process (Arratia 1992), (26) upper pharyngeal tooth plate with retractor muscles (de Pinna 1993), (27) first pharyngobranchial lies parallel to first epibranchial (de Pinna 1993), (28) second pharyngobranchial elongated and rod-like (de Pinna 1993), (29) first basibranchial absent (de Pinna 1993), (30) intermuscular epineural and epipleural bones absent (Arratia 2003b; Lundberg 2020d), (31) maxillary bears a fleshy barbel (Lundberg 2020d), (32) basihyal absent (Lundberg 2020d), (33) postcleithra absent (Lundberg 2020d), and (34) pectoral fin with single spine with rotating and locking joint that articulates with cleithrum (Lundberg 2020d).

Synonyms. *Siluridae* (Swainson 1838:325–360; Günther 1864a:1–2), *Siluri* (Bleeker 1858:13–43), *Nematognathi* (T. N. Gill 1861a:11; Eigenmann and Eigenmann 1890:5; Jordan 1923:145–153), *Siluroidei* (Goodrich 1909:377–384; Bertin and Arambourg 1958:2302–2304; McAllister 1968:71–78), and *Siluroidea* (Regan 1911e) are ambiguous synonyms of *Siluriformes*.

Comments. The lineages delimited here as *Siluriformes* were grouped together in several pre-Darwinian and pre-cladistic classifications of teleosts (Bleeker 1858; Günther 1864a; Boulenger 1904b), with a degree of sophistication exemplified by placing *Diplomystidae* apart from all other groups of *Siluriformes* based on the presence of a toothed maxillary (Goodrich 1909:380; Regan 1911e). The monophyly of *Siluriformes* is consistently supported, from the first phylogenetic treatments of fishes to recent molecular analyses (Greenwood et al. 1966; Fink and Fink 1981; Nakatani et al. 2011; Arcila et al. 2017; Hughes et al. 2018). Remaining problems in the phylogenetics of *Siluriformes* include the incongruence among morphological and molecular studies regarding *Diplomystidae* or *Loricarioidei* as the sister lineage of all other *Siluriformes* (Mo 1991; de Pinna 1993; Arcila et al. 2017; Rivera-Rivera and Montoya-Burgos 2018) and the slight morphological support for the monophyly of *Siluroidei* (Diogo 2004; Lundberg et al. 2014).

The earliest fossils of *Siluriformes* that are not *Loricarioidei* or *Siluroidei* are Campanian (83.2–72.2 Ma) and Maastrichtian (72.2–66.0 Ma) pectoral spines identified as *Diplomystidae* from Argentina and Bolivia (Cione 1987; Arratia and Cione 1996; Gayet and Meunier 1998). Bayesian relaxed molecular clock analyses of *Siluriformes* result in an average posterior crown age estimate of 121.4 million years ago, with the credible interval ranging between 111.3 and 131.7 million years ago (Hughes et al. 2018).

Constituent lineages.

Diplomystidae	†*Bachmannia*
Loricarioidei	†*Hypsidoris*
Siluroidei	

Loricarioidei P. Bleeker 1858:37
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Nematogenys inermis* (Guichenot 1848), *Loricaria cataphracta* Linnaeus 1758, *Loricaria simillima* Regan 1904a, and *Trichomycterus guianense* (Eigenmann 1909). This is a minimum-crown-clade definition.

Etymology. From the Latin *lorica*, a coat of chain mail armor, in reference to the bony plates on the body of many species in this clade.

Registration number. 909.

Reference phylogeny. A phylogeny inferred from DNA sequences of two nuclear genes (Sullivan et al. 2006, fig. 1). Although *Loricaria cataphracta* is not included in the reference phylogeny, it resolves with other species of *Loricaria* in molecular phylogenetic analyses (Covain et al. 2016, fig. 7; Moreira et al. 2017, fig. 3). Phylogenetic relationships among the major lineages of *Loricarioidei* are presented in Figure 10.

Phylogenetics. Morphological and molecular phylogenetic analyses consistently support the monophyly of *Loricarioidei* (Howes 1983; Schaefer 1990; Mo 1991; de Pinna 1993, 1998; Diogo 2004; Sullivan et al. 2006; Lundberg et al. 2007; Covain et al. 2016; Arcila et al. 2017; Moreira et al. 2017; Schedel et al. 2022). Within *Loricarioidei*, morphological and molecular analyses resolve two primary clades: *Trichomycteridae* (pencil catfishes) and *Nematogenys inermis* (Mountain Catfish) form a monophyletic group that is the sister lineage of a clade containing *Callichthyidae* (callichthyid armored catfishes), *Astroblepus* (climbing catfishes), and *Loricariidae* (suckermouth armored catfishes) (Mo 1991; de Pinna 1993, 1998; Arcila et al. 2017).

Composition. *Loricarioidei* currently contains 1,773 species (Ferraris 2007; Fricke et al. 2023) that includes *Nematogenys inermis* and species classified in *Astroblepus*, *Callichthyidae*, *Loricariidae*, *Nematogenys*, *Scoloplax* (spiny dwarf catfishes), and *Trichomycteridae* (Sullivan et al. 2006). There have been 391 new living species of *Loricarioidei* described over the past 10 years (Fricke et al. 2023), comprising 22.1% of the living species diversity of the clade.

Diagnostic apomorphies. Morphological apomorphies for *Loricarioidei* include (1) odontodes present (Baskin 1973; Howes 1983; Schaefer and Lauder 1986; Schaefer 1990; de Pinna 1998), (2) encapsulated swim bladder present (Howes 1983; Schaefer and Lauder 1986; Schaefer 1990), (3) median processes of exoccipitals do not meet at midline (de Pinna 1998), (4) absence of anterior cartilages on arms of basipeterygium (de Pinna 1998), (5) bifid cusps on oral jaw teeth (de Pinna 1998), and (6) autopalatine compressed dorsoventrally with dorsal process that forms surface of articulation with neurocranium (Diogo 2004).

Synonyms. *Loricarioidea* (Schaefer and Lauder 1986, fig. 1; de Pinna 1998:292–294, fig. 6) is an ambiguous synonym of *Loricarioidei*.

Comments. On the basis of the results of morphological and molecular phylogenetic studies (e.g., Schaefer 1990; Sullivan et al. 2006), the group name *Loricarioidei* was applied to the clade containing *Loricariidae*, *Astroblepus*, *Scoloplax*, *Callichthyidae*, *Trichomycteridae*, and *Nematogenys* (Sullivan et al. 2006).

The earliest phylogenetic analyses within *Siluriformes* aimed to resolve relationships among lineages of *Loricarioidei* (Howes 1983; Schaefer 1990). The results of morphological and molecular phylogenetic analyses of relationships within *Loricarioidei* are broadly congruent (e.g., de Pinna 1993; Arcila et al. 2017).

The earliest fossil *Loricarioidei* is the callichthyid †*Corydoras revelatus* from the Late Paleocene (58.5 Ma) of Argentina (Marshall et al. 1997; Lundberg et al. 1998; Reis 1998). Relaxed molecular clock analyses estimate the crown age of *Loricarioidei* at approximately 90 million years ago (Rabosky et al. 2018).

Constituent lineages. Redundant group names are marked with an asterisk.

*Astroblepidae**
Callichthyidae
Loricariidae
*Nematogenyidae**
*Scoloplacidae**
Trichomycteridae

Siluroidei P. Bleeker 1858:34
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Silurus glanis* Linnaeus 1758, *Cetopsis coecutiens* (Lichtenstein 1819), and *Pimelodus maculatus* Lacepède 1803, but not *Loricaria simillima* Regan 1904a or *Diplomystes nahuelbutaensis* Arratia 1987b. This is a minimum-crown-clade definition with external specifiers.

Etymology. From the ancient Greek σίλουρος (sɪlˈʊ͡ɹo͡ʊz), which is the name applied to several species of catfishes in Europe and Egypt, including the Wels Catfish, *Silurus glanis* (D. W. Thompson 1947:233–237).

Registration number. 910.

Reference phylogeny. A phylogeny of 752 species of *Siluroidei* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Phylogenetic relationships among the major lineages of *Siluroidei* are presented in Figure 10.

Phylogenetics. The first phylogenetic studies to resolve *Siluroidei* as monophyletic include analyses of 440 morphological characters and DNA sequences of two nuclear genes (Diogo 2004, fig. 3.124; Sullivan et al. 2006). Molecular phylogenetic analyses consistently support the monophyly of *Siluroidei*; however, relationships among deeper nodes are typically unresolved and poorly supported (Sullivan et al. 2006; Lundberg et al. 2007; Kappas et al. 2016; Arcila et al. 2017; Rivera-Rivera and Montoya-Burgos 2018; K. Zhang, Liu, et al. 2021; Schedel et al. 2022; Duong et al. 2023). Despite the lack of strong resolution along the backbone of the siluroid phylogeny, there are several well-supported conclusions from morphological and molecular phylogenetic analyses. For example, *Cetopsidae* (whale catfishes) are either deeply branching or specifically placed as the sister lineage of all other *Siluroidei* in many phylogenetic studies (Mo 1991; de Pinna 1993; Diogo 2004; Lundberg et al. 2007; Q. Wang et al. 2015; Arcila et al. 2017; Rivera-Rivera and Montoya-Burgos 2018; K. Zhang, Liu, et al. 2021; Schedel et al. 2022; Duong et al. 2023). Phylogenies inferred from both morphological and molecular datasets result in the polyphyly of the traditional delimitation of *Schilbeidae* (butter catfishes) distributed in freshwater habitats of Africa and Asia (Mo 1991; de Pinna 1993; Hardman 2005; Sullivan et al. 2006; Schedel et al. 2022), with Asian lineages subsequently classified in *Ailiidae* (Asian schilbeids) (J. Wang et al. 2016; X. Li and Zhou 2018). Phylogenetic analyses consistently support the common ancestry of several groupings of siluroid lineages: *Aspredinidae* (banjo catfishes), *Auchenipteridae* (driftwood catfishes), and *Doradidae* (thorny catfishes) (Sullivan et al. 2006, 2008; Nakatani et al. 2011; Q. Wang et al. 2015; Arcila et al. 2017; Rabosky et al. 2018; Rivera-Rivera and Montoya-Burgos 2018; Cui et al. 2020; K. Zhang, Liu,et al. 2021; Schedel et al. 2022; Duong et al. 2023); *Clariidae* (airbreathing catfishes) and *Heteropneustes* (airsac catfishes) (Mo 1991; Diogo 2004; Hardman 2005; Sullivan et al. 2006; Nakatani et al. 2011; Q. Wang et al. 2015; J. Wang et al. 2016; Rabosky et al. 2018; Cui et al. 2020; K. Zhang, Liu, et al. 2021; Schedel et al. 2022; Duong et al. 2023); the Madagascar endemic *Anchariidae* (Malagasy catfishes) and the marine *Ariidae* (sea catfishes) (de Pinna 1993; Sullivan et al. 2006; J. Wang et al. 2016); and the east Asian *Cranoglanis* (armorhead catfishes) and the North American *Ictaluridae* (bullhead catfishes) (Diogo 2004; Hardman 2005; Sullivan et al. 2006; Nakatani et al. 2011; Q. Wang et al. 2015; Kappas et al. 2016; J. Wang et al. 2016; Rabosky et al. 2018; Cui et al. 2020; Schedel et al. 2022; Duong et al. 2023).

An important result from the earliest inclusive molecular phylogenetic analyses of *Siluroidei* was the resolution of two inclusive clades: Big Asia [*Ailiidae*, *Akysidae* (stream catfishes), *Amblycipitidae* (torrent catfishes), *Bagridae* (bagrid catfishes), *Horabagridae* (sun catfishes), and *Sisoridae* (sisorid catfishes)] and Big Africa [*Amphiliidae* (loach catfishes), *Claroteidae* (claroteids), *Lacantunia enigmatica* (Chiapas Catfish), *Malapteruridae* (electric catfishes), *Mochokidae* (squeakers), and *Schilbeidae*], which highlighted freshwater habitats in Asia and Africa as important areas of siluroid diversification (Sullivan et al. 2006; Lundberg et al. 2007). Molecular phylogenetic analyses resolve the enigmatic *Conorhynchos conirostris* (Anteater Catfish), which is currently not classified in a Linnean-ranked taxonomic family (Eschmeyer and Fricke 2023), in a clade with other South American freshwater lineages that includes *Heptapteridae* (threebarbeled catfishes), *Pimelodidae* (long-whiskered catfishes), and *Pseudopimelodidae* (bumblebee catfishes) (Sullivan et al. 2006, 2013; G. S. C. Silva et al. 2021). An analysis of a supermatrix of 27 nuclear and mitochondrial genes places this South American siluroid lineage in the Big Africa clade (Rabosky et al. 2018; J. Chang et al. 2019).

Morphological and molecular studies provide insight into the phylogenetic relationships of the enigmatic South African lineage *Austroglanis* (rock catfishes) and two species discovered and described in the early 21st century, *Lacantunia enigmatica* and *Kryptoglanis shajii* (Subterranean Catfish) (Skelton et al. 1984; Rodiles-Hernández et al. 2005; Vincent and Thomas 2011; Britz, Kakkassery, et al. 2014). *Austroglanis* was initially classified in *Bagridae* (Skelton et al. 1984), but morphological and molecular analyses place this lineage in a clade that contains *Cranoglanis*, *Ictaluridae*, and *Anchariidae* or as the sister lineage of *Pangasiidae* (Diogo 2004; Rabosky et al. 2018; Schedel et al. 2022). *Lacantunia enigmatica* was discovered in the Rio Usumacinta basin in Chiapas, Mexico and *Kryptoglanis shajii* was discovered from subterranean waters in Kerala, India (Rodiles-Hernández et al. 2005; Vincent and Thomas 2011). Both species were each classified in monotypic taxonomic families, *Lacantuniidae* and *Kryptoglanidae* (Rodiles-Hernández et al. 2005; Britz, Kakkassery, et al. 2014). Molecular analyses resolve *L. enigmatica* and the African freshwater *Claroteidae* as sister lineages (Lundberg et al. 2007; Rabosky et al. 2018). Morphological characters suggest *K. shajii* is closely related to *Siluridae* (Lundberg et al. 2014).

Composition. There are currently 2,408 living species of *Siluroidei* (Ferraris 2007; Fricke et al. 2023) that includes *Conorhynchos conirostris*, *Kryptoglanis shajii*, *Lacantunia enigmatica*, *Rita* (ritas), and species classified in *Ailiidae*, *Akysidae*, *Amblycipitidae*, *Amphiliidae*, *Anchariidae*, *Ariidae*, *Aspredinidae*, *Auchenipteridae*, *Auchenoglanididae* (auchenoglanids), *Austroglanis*, *Bagridae*, *Cetopsidae*, *Chaca* (squarehead catfishes), *Clariidae*, *Claroteidae*, *Cranoglanis*, *Doradidae*, *Heptapteridae*, *Heteropneustes*, *Horabagridae*, *Ictaluridae*, *Malapteruridae*, *Mochokidae*, *Pangasiidae* (shark catfishes), *Phreatobius* (underground catfishes), *Pimelodidae*, *Plotosidae* (eeltail catfishes), *Pseudopimelodidae*, *Schilbeidae*, *Siluridae*, and *Sisoridae*. Over the past 10 years 236 new living species of *Siluroidei* have been described (Fricke et al. 2023), comprising 9.8% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Siluroidei* include (1) protractor hyoideus differentiated into pars dorsalis, ventralis, and lateralis (Diogo 2004), (2) articulatory surface of autopalatine for neurocranium directed mesially (Diogo 2004), (3) coronomeckelian bone reduced (Diogo 2004), (4) barbels located on anterior rim of posterior nostril (Lundberg et al. 2014), and (5) parasphenoid positioned along anterior margin of trigeminofacial foramen (Lundberg et al. 2014).

Synonyms. There are no synonyms of *Siluroidei*.

Comments. *Siluriformes* is a clade that was long recognized as a taxonomic group and its composition was unchanged in post-Darwinian and phylogenetic classifications, but *Siluroidei* is a subclade discovered as a result of phylogenetic analyses in the first 10 years of the 21st century (Diogo 2004; Sullivan et al. 2006). Work remains in resolving the phylogenetic relationships among the lineages of *Siluroidei*, with initial phylogenomic analyses showing considerable potential (Arcila et al. 2017).

The earliest fossils of *Siluroidei* are Campanian (83.2–72.2 Ma) and Maastrichtian (72.2–66.0

Ma) pectoral spines and fragments of skull bones of *Ariidae* in Argentina (Cione 1987; Arratia and Cione 1996; Gayet and Meunier 1998). Relaxed molecular clock analyses estimate the crown age of *Siluroidei* between 100 and 105 million years ago (Lundberg et al. 2007).

Constituent lineages. Redundant group names are marked with an asterisk.

Ailiidae
Akysidae
Amblycipitidae
Amphiliidae
Anchariidae
Ariidae
Aspredinidae
Auchenipteridae
Auchenoglanididae
*Austroglanididae**
Bagridae
Cetopsidae
*Chacidae**
Clariidae
Claroteidae
Conorhynchos
*Cranoglanididae**
Doradidae
Heptapteridae
*Heteropneustidae**
Horabagridae
Ictaluridae
*Kryptoglanidae**
*Lacantuniidae**
Malapteruridae
Mochokidae
Pangasiidae
*Phreatobiidae**
Pimelodidae
Plotosidae
Pseudopimelodidae
*Ritidae**
Schilbeidae
Siluridae
Sisoridae

Characiformes C. T. Regan 1911d:15
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Crenuchus spilurus* Günther 1863a, *Alestes inferus* Stiassny, Schelly, and Mamonekene 2009, *Charax gibbosus* (Linnaeus 1758), and *Charax metae* Eigenmann 1922, but not *Citharinus congicus* Boulenger 1897. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek χάραξ (kˈɑːɹ͡ɹæks) as a name for species of *Sparidae* that exhibit teeth on the oral jaws (D. W. Thompson 1947:284–285). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 911.

Reference phylogeny. A phylogeny of 293 species of *Characiformes* inferred from DNA sequences of 1,288 ultraconserved element (UCE) loci (Melo, Sidlauskas, et al. 2022, fig. 1). Although *Charax gibbosus* is not included in the reference phylogeny, it resolves in a clade with three other species of *Charax* in a phylogenetic analysis of morphological characters (Mattox and Toledo-Piza 2012, fig. 41). See Figure 11 for the phylogenetic relationships among the major lineages of *Characiformes*.

Phylogenetics. The first phylogenetic studies of *Characiformes* utilized morphological characters to investigate relationships among the subclades *Curimatidae* (toothless characiforms), *Prochilodontidae* (flannelmouth characiforms), *Anostomidae* (toothed headstanders) (Vari 1983), *Ctenoluciidae* (pike characids), *Lebiasinidae* (pencilfishes), *Hepsetus* (African pikes), and *Erythrinidae* (trahiras) (Vari 1995). Phylogenetic analyses of molecular and morphological matrices consistently support the monophyly of *Characiformes* relative to *Cithariniformes* and other otophysans (Ortí 1997; Ortí and Meyer 1997; Buckup 1998; Calcagnotto et al. 2005; Hubert et al. 2005a, 2005b; Mirande 2009; Oliveira et al. 2011; Arcila et al. 2017, 2018; de Pinna et al. 2018; Betancur-R. et al. 2019; Burns and Sidlauskas 2019; Melo, Sidlauskas, et al. 2022). There is extensive incongruence among phylogenetic analyses of *Characiformes*; the analysis of multiple morphological datasets results in different phylogenies (Buckup 1998; Mirande 2009), different trees are inferred from different molecular datasets (e.g., Ortí and Meyer 1997; Oliveira et al. 2011), and there are substantial differences between phylogenies inferred from morphological and molecular datasets (e.g., Vari 1995; Mirande 2009; Betancur-R. et al. 2019; Melo, Sidlauskas, et al. 2022). Two sets of relationships that are congruent between phylogenies inferred from morphological and molecular datasets are the resolution of the phenotypically unique *Tarumania walkerae* (Muck Fish) as the sister lineage of all other species of *Erythrinidae* (Arcila et al. 2018; de Pinna et al. 2018; Melo, de Pinna, et al. 2022) and the monophyly of *Anostomoidea* that contains *Anostomidae*, *Chilodontidae* (headstanders), *Curimatidae*, and *Prochilodontidae* (Vari 1983; Buckup 1998;

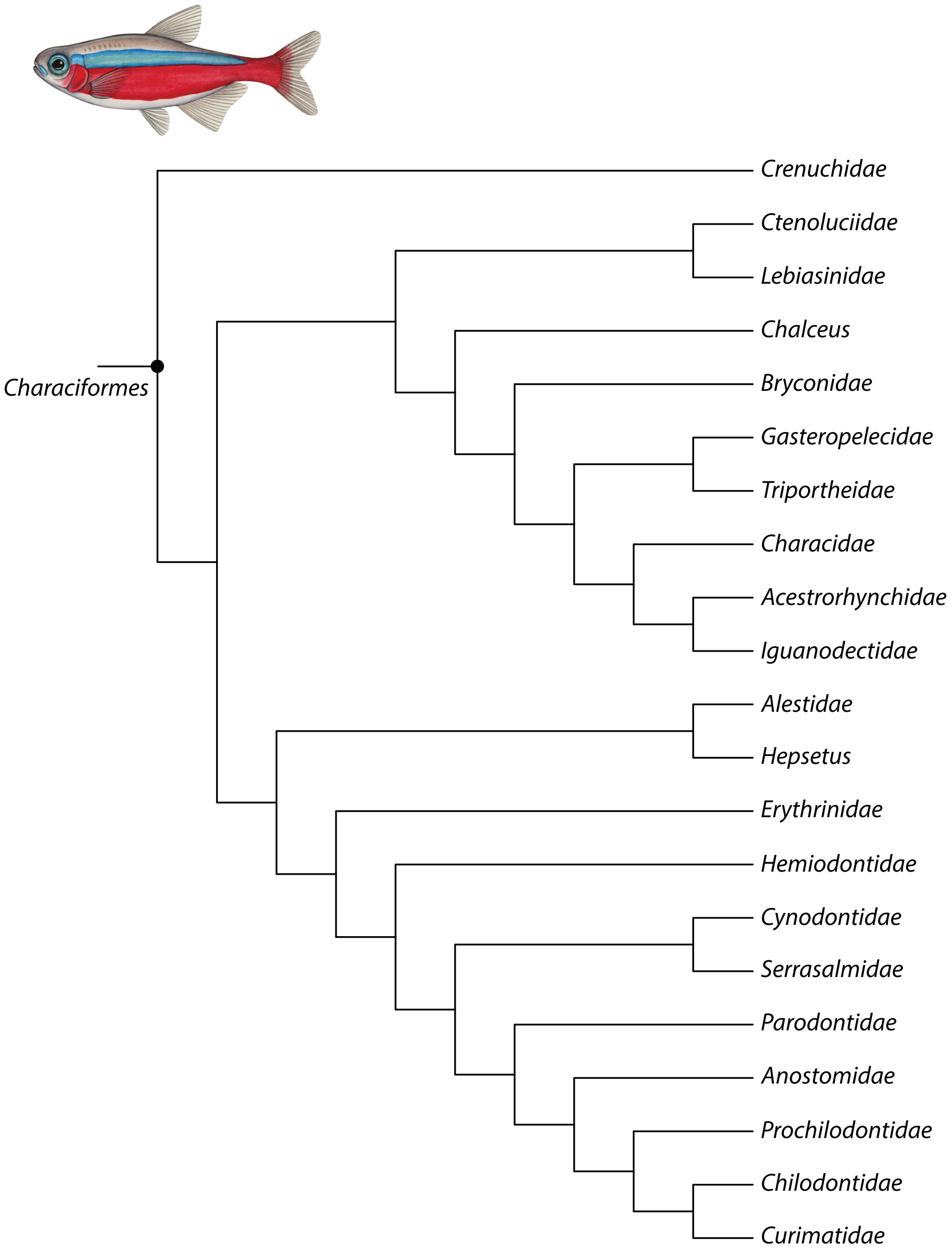

FIGURE 11. Phylogenetic relationships of the major living lineages and fossil taxa of *Characiformes*. Filled circles identify the common ancestor of clades, with formal names defined in the clade accounts.

Oliveira et al. 2011; Dillman et al. 2016; Arcila et al. 2017, 2018; Melo et al. 2018; Betancur-R. et al. 2019; Burns and Sidlauskas 2019; Melo, Sidlauskas, et al. 2022).

Molecular phylogenetic studies with dense taxon sampling using either collections of Sanger-sequenced mtDNA and nuclear genes or phylogenomic datasets exhibit adequate congruence to highlight several consistent results. *Crenuchidae* (South American darters) is the sister lineage of all other *Characiformes* (Oliveira et al. 2011; Arcila et al. 2017, 2018; Betancur-R. et al. 2019; Burns and Sidlauskas 2019; Melo, de Pinna, et al. 2022; Melo, Sidlauskas, et al. 2022). The lineage *Chalceus* (toucanfishes) was traditionally classified in *Alestidae* (African tetras) (Zanata and Vari 2005; Mirande 2009, 2010), but is resolved as the sister lineage of a clade containing *Acestrorhynchidae* (needlejaws), *Bryconidae* (South American trouts), *Characidae* (tetras), *Gasteropelecidae* (freshwater hatchetfishes), *Iguanodectidae* (tetras), and *Triportheidae* (elongate hatchetfishes) (Arroyave and Stiassny 2011; Oliveira et al. 2011; Arcila et al. 2017, 2018; Betancur-R. et al. 2019; Burns and Sidlauskas 2019; Melo, Sidlauskas, et al. 2022). The predatory lineages *Ctenoluciidae* and *Hepsetidae* are sister lineages in a morphological phylogeny (Buckup 1998); however, molecular phylogenies resolve a monophyletic group containing both African characiform lineages *Hepsetidae* and *Alestidae* (Oliveira et al. 2011; Arcila et al. 2017, 2018; Betancur-R. et al. 2019; Melo, de Pinna, et al. 2022; Melo, Sidlauskas, et al. 2022). The traditional delimitation of the species-rich *Characidae* (Lima et al. 2003; Mirande 2009, 2010) is not monophyletic in molecular phylogenies, prompting the elevation of *Acestrorhynchidae*, *Bryconidae*, *Iguanodectidae*, and *Triportheidae*; *Characidae* was restricted to species lacking a supraorbital (Lucena and Menezes 1998; Mirande 2009; Oliveira et al. 2011).

Composition. *Characiformes* currently contains 2,238 species (Fricke et al. 2023) classified in *Acestrorhynchidae*, *Alestidae*, *Anostomidae*, *Bryconidae*, *Chalceus*, *Characidae*, *Chilodontidae*, *Crenuchidae*, *Ctenoluciidae*, *Curimatidae*, *Cynodontidae* (dogtooth characins), *Erythrinidae*, *Gasteropelecidae*, *Hemiodontidae*, *Hepsetus*, *Iguanodectidae*, *Lebiasinidae*, *Parodontidae* (scrapetooths), *Prochilodontidae*, *Serrasalmidae* (pacus), and *Triportheidae*. Over the past 10 years 317 new living species of *Characiformes* have been described (Fricke et al. 2023), comprising 14.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological synapomorphies of *Characiformes* include (1) fourth neural arch fused to vertebra (Fink and Fink 1981; Buckup 1998), (2) synchondral joint between third and fourth neural arches reduced or absent (Fink and Fink 1981; Buckup 1998), (3) pelvic girdle slightly emarginate anteriorly (Fink and Fink 1981), (4) medial portion of joint between mesethmoid and vomer either flat or covered by midsagittal osseus or cartilaginous crest (Buckup 1998), and (5) A_1 and A_2 muscles of adductor mandibulae completely separated at their origins (Datovo and Castro 2012).

Synonyms. *Heterognathi* (T. N. Gill 1893:131; Jordan 1923:134–138), *Characoidei* (Greenwood et al. 1966:383–384), and *Characoidea* (McAllister 1968:69; Rosen and Greenwood 1970:23; T. R. Roberts 1973:377) are approximate synonyms of *Characiformes*. *Characoidei* (Buckup 1998, table 3; Betancur-R et al. 2017:17) is an ambiguous synonym of *Characiformes*.

Comments. As delimited here, *Characiformes* resolves as a monophyletic group in morphological and molecular phylogenetic analyses (e.g., Buckup 1998; Melo, Sidlauskas, et al. 2022). *Characiformes* and *Citharinformes* were classified together in a more inclusive *Characiformes* from the mid-19th century to the present day (Günther 1864a; Betancur-R et al. 2017). Molecular phylogenetic analyses consistently fail to resolve *Characiformes* and *Citharinformes* as a monophyletic group relative to other clades of *Otophysi*. The phylogenies of *Characiformes* inferred from phylogenomic datasets are not only resolving relationships among the most inclusive lineages in the clade (Arcila et al. 2017; Betancur-R. et al. 2019; Melo, Sidlauskas, et al. 2022), but also illuminating the effect of Gondwanan fragmentation on the distribution of characiforms in South America and Africa (Melo, Sidlauskas, et al. 2022). South American characiforms are paraphyletic relative to the clade containing the African *Alestidae* and *Hepsetidae*. The relaxed molecular clock age estimate for the divergence of African characiforms is consistent with the timing of the separation of South America and Africa (Melo, Sidlauskas, et al. 2022), validating *Characiformes* as an iconic example of continental-drift-driven vicariance in the diversification of freshwater lineages (Lundberg 1993; Ortí and Meyer 1997).

The earliest fossil *Characiformes* are from the Maastrichtian (72.2–66.0 Ma) in Bolivia and include intermediate teeth and skeletal fragments identified as species of *Acestrorhynchidae*, *Characidae*, and *Serrasalmidae* (Gayet et al. 2001, 2003). Isolated teeth from the Cenomanian (100.5–93.9 Ma) of Morocco are often cited as the earliest characiform fossils (Dutheil 1999; Malabarba and Malabarba 2010), but these teeth may be attributed to pan-lepisosteiforms (Cavin 2017:105). Bayesian relaxed molecular clock analyses of *Characiformes* result in an average posterior crown age estimate of 129.4 million years ago, with the credible interval ranging between 110.0 and 148.7 million years ago (Melo, Sidlauskas, et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk. *Tarumania walkerae* is classified here as a species of *Erythrinidae.*

Acestrorhynchidae
Alestidae
Anostomidae
Bryconidae
*Chalceidae**
Characidae
Chilodontidae
Crenuchidae
Ctenoluciidae
Curimatidae
Cynodontidae
Erythrinidae
Gasteropelecidae
Hemiodontidae
*Hepsetidae**
Iguanodectidae
Lebiasinidae
Parodontidae
Prochilodontidae
Serrasalmidae
Triportheidae

Euteleostei P. H. Greenwood, G. S. Myers, D. E. Rosen, and S. H. Weitzman 1967:227

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Lepidogalaxias salamandroides* Mees 1961, *Salmo salar* Linnaeus 1758, and *Perca fluviatilis* Linnaeus 1758, but not *Clupea harengus* Linnaeus 1758. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek εὖ (ˌiːjˈuː), meaning good or well; τέλειος (tˈɛlɨˌo͡ʊz), meaning perfect or complete; and ὀστέον (ˈɑːstɪən), meaning bone.

Registration number. 912.

Reference phylogeny. A phylogeny inferred from a phylogenomic dataset composed of DNA sequences from more than 1,100 exons (Hughes et al. 2018, fig. S2). Phylogenetic relationships among the major living and fossil lineages of *Euteleostei* are presented in Figure 7. The placement of the pan-argentiniform †*Surlykus*; the pan-salmoniforms †*Barcarenichthys*, †*Kermichthys*, †*Pyrenichthys*, and †*Stompooria*; the pan-stomiat †*Nybelinoides*; and the pan-osmeriform †*Spaniodon* are on the basis of inferences from morphology (Taverne 1982, 1992; Gayet and Lepicard 1985; Gayet 1988b; Anderson 1998; Fielitz 2002; Taverne and Filleul 2003; Guinot and Cavin 2018; Schrøder and Carnevale 2023).

Phylogenetics. *Euteleostei* is resolved as monophyletic in molecular phylogenetic studies that range from analysis of whole mtDNA genomes (J. Li, Xia, et al. 2010; Campbell, López, et al. 2013) to DNA sequences from multiple nuclear and mtDNA genes (Burridge et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Davis et al. 2016), and phylogenomic datasets (Campbell, Alfaro, et al. 2017; Hughes et al. 2018; Straube et al. 2018; Rosas Puchuri 2021). A phylogenetic analysis of 42 morphological characters resolves the otocephalan lineage *Alepocephaliformes* nested within *Euteleostei* as the sister lineage of *Argentiniformes*, nests *Stomiiformes* in *Neoteleostei*, and places *Esocidae* (pikes and mudminnows) as the sister lineage of *Neoteleostei* (G. D. Johnson and Patterson 1996). A supertree analysis that utilized phylogenies resulting from morphological and molecular studies as input trees resolved *Salmoniformes* as the sister lineage of a clade named *Zoroteleostei* that includes all other euteleosts (M. V. H. Wilson and Williams 2010). The phylogenies of *Euteleostei* presented in G. D. Johnson and Patterson (1996) and Wilson and Williams (2010) are incongruent with trees inferred from molecular phylogenetic analyses (e.g., J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Hughes et al. 2018).

One of the most remarkable results from molecular phylogenetic analyses of fishes is the resolution of the unique and enigmatic freshwater *Lepidogalaxias salamandroides* (Salamanderfish) as the sister lineage of all other *Euteleostei* (J. Li, Xia, et al. 2010; McDowall and Burridge 2011; Burridge et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Campbell, López, et al. 2013; Davis et al. 2016; W. L. Smith et al. 2016; Campbell, Alfaro, et al. 2017; Hughes et al. 2018; Straube et al. 2018; Rosas Puchuri 2021; Mu et al. 2022). Within euteleosts, molecular studies consistently resolve three sets of sister lineages: *Salmonidae* (salmons and trouts) and *Esocidae* (includes *Umbridae*); *Stomiiformes* and *Osmeriformes*; and a lineage containing *Galaxiidae* (galaxiids) and *Neoteleostei* (Burridge et al. 2012; Near, Eytan, et al. 2012; Davis et al. 2016; Straube et al. 2018; Rosas Puchuri 2021). The phylogenetic relationships of *Argentiniformes* remain unresolved, with molecular studies resulting in four different hypotheses: as the sister lineage of the clade containing *Salmonidae* and *Esocidae* (C. H. Li et al. 2008; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Campbell, López, et al. 2013; Hughes et al. 2018; Straube et al. 2018; Rosas Puchuri 2021); the sister lineage of a clade containing *Galaxiidae*, *Salmonidae*, and *Esocidae* (Betancur-R, Broughton, et al. 2013); the sister lineage of a clade containing *Stomiiformes*, *Osmeriformes*, and *Galaxiidae* (Burridge et al. 2012); or as the sister lineage of a clade containing *Stomiiformes*, *Osmeriformes*, *Galaxiidae*, and *Neoteleostei* (Campbell, Alfaro, et al. 2017; Rosas Puchuri 2021).

Composition. *Euteleostei* currently consists of more than 21,405 species (Fricke et al. 2023) that include *Lepidogalaxias salamandroides* and species classified in *Salmoniformes*, *Stomiatii*, *Argentiniformes*, *Galaxiidae*, and *Neoteleostei*. Fossil taxa include the pan-argentiniform †*Surlykus*, the pan-stomiat †*Nybelinoides* (Taverne 1982), and the pan-salmoniforms †*Kermichthys* (Taverne 1992), †*Barcarenichthys* (Gayet 1988b, 1989), †*Stompooria* (Anderson 1998), and †*Pyrenichthys* (Gayet and Lepicard 1985). Details of the locations and ages of the fossil taxa are presented in Appendix 1. Over the past 10 years 1,789 new living species of *Euteleostei* have been described (Fricke et al. 2023), comprising 8.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Euteleostei* include (1) presence of stegural, a membranous outgrowth of uroneural 1 (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (2) caudal median cartilages present (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), and (3) unique supraneural shape (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010). The first two of these proposed synapomorphies for *Euteleostei* are also present in *Alepocephaliformes*, which is nested in *Otocephala* and distantly related to *Euteleostei* (Figure 2).

Synonyms. *Protacanthopterygii* (Greenwood et al. 1966:366–387, 394–396; Wiley and Johnson 2010:141–143; Betancur-R et al. 2017:18), *Zoroteleostei* (M. V. H. Wilson and Williams 2010:404; J. S. Nelson et al. 2016:251), and *Osmeromorpha* (J. S. Nelson et al. 2016:252) are partial synonyms of *Euteleostei*. *Euteleosteomorpha* (Wiley and Johnson 2010:140; Betancur-R et al. 2017:18) is an ambiguous synonym of *Euteleostei*.

Comments. Along with *Osteoglossomorpha*, *Elopomorpha*, and *Otocephala*, *Euteleostei* is one of the four major clades of *Teleostei* (Dornburg and Near 2021). On its initial delimitation, *Euteleostei* included *Ostariophysi* (Greenwood et al. 1966, 1967), which was accepted in subsequent studies and classifications (Rosen 1973, 1974; Travers 1981; W. L. Fink and Weitzman 1982; Lauder and Liem 1983; W. L. Fink 1984a; J. S. Nelson 1984:117–119, 1994:124–125; Sanford 1990; Begle 1992). On the basis of the morphology of the teleost skull occipital region, Rosen (1985) suggested that ostariophysans, esocoids, and argentinoids are not euteleosts. Within *Euteleostei*, the presence of acellular bone was proposed as a synapomorphy for a clade containing *Esocidae*, *Osmeriformes*, and *Neoteleostei* (L. R. Parenti 1986). With the consistent resolution of *Otocephala* as a clade that includes *Ostariophysi* and *Clupeiformes* in molecular and morphological phylogenetic analyses (e.g., Lê et al. 1993; Lecointre and Nelson 1996; Arratia 1997; Near, Eytan, et al. 2012; Straube et al. 2018), classifications no longer include *Ostariophysi* in *Euteleostei* and thus closely match the composition of the clade to which we are applying that name (J. S. Nelson 2006:189; Wiley and Johnson 2010; J. S. Nelson et al. 2016:241; Betancur-R et al. 2017; Dornburg and Near 2021).

The earliest fossil *Euteleostei* is the panstomiat †*Nybelinoides brevis* from the Barremian and Aptian (126.5–113.2 Ma) of Belgium (Appendix 1; Taverne 1982; Guinot and Cavin 2018). Bayesian relaxed molecular clock analyses of *Euteleostei* result in an average posterior crown age estimate of 210.5 million years ago, with the credible interval ranging between 196.4 and 223.8 million years ago (Hughes et al. 2018).

<u>Constituent lineages.</u> Redundant group names are marked with an asterisk.

Argentiniformes
Galaxiidae
*Lepidogalaxiidae**
Neoteleostei
Salmoniformes
Stomiatii
†*Barcarenichthys*
†*Kermichthys*
†*Nybelinoides*
†*Pyrenichthys*
†*Stompooria*
†*Surlykus*

Argentiniformes G. D. Johnson and C. Patterson 1996:315

[T. J. Near and C. E. Thacker],
converted clade name

<u>Definition.</u> The least inclusive crown clade that contains *Argentina sphyraena* Linnaeus 1758 and *Microstoma microstoma* (Risso 1810). This is a minimum-crown-clade definition.

<u>Etymology.</u> From the ancient Greek ἀργύρεος (ˈɑːɹ͡ɡjʊɹɪˌo͡ʊz), meaning silvery. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

<u>Registration number.</u> 913.

<u>Reference phylogeny.</u> A phylogeny inferred from DNA sequences of 1,133 exons (Rosas Puchuri 2021, fig. 3.1). The phylogenetic relationships of the major lineages of *Argentiniformes* are presented in Figure 7.

<u>Phylogenetics.</u> Over the past century *Argentiniformes* was classified with combinations of *Salmonidae* (salmons and trouts), *Alepocephaliformes*, *Galaxiidae* (galaxiids), *Osmeriformes*, *Stomiiformes*, *Esocidae* (pikes and mudminnows), and *Myctophiformes* (Gosline 1960; Greenwood et al. 1966; G. J. Nelson 1970a). Greenwood and Rosen (1971) hypothesized that *Argentiniformes* and *Alepocephaliformes* are sister lineages as evidenced by the presence of a modified posterior pharyngobranchial structure they named the crumenal organ, which was the basis for the resolution of this clade in subsequent morphological studies (Begle 1992; G. D. Johnson and Patterson 1996). Molecular phylogenetic analyses consistently resolve *Argentiniformes* and *Alepocephaliformes* as distantly related: *Alepocephaliformes* is related to *Clupeiformes* and *Ostariophysi* in *Otocephala* and *Argentiniformes* is phylogenetically nested in *Euteleostei* (Figure 2; Ishiguro et al. 2003; Lavoué, Miya, Poulsen, et al. 2008; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Davis et al. 2016; Campbell, Alfaro, et al. 2017; Hughes et al. 2018; Straube et al. 2018; Rosas Puchuri 2021).

Morphological and molecular phylogenetic analyses consistently support the monophyly of *Argentiniformes* (Begle 1992; Patterson and Johnson 1995; Ishiguro et al. 2003; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Straube et al. 2018; Schrøder and Carnevale 2023). Phylogenetic analysis of morphological characters resolves *Argentinidae* (argentines) as the sister lineage of all other *Argentiniformes*, with *Bathylagidae* (deep-sea smelts) and *Opisthoproctidae* (barreleyes) as sister taxa (Rosen 1974) or *Bathylagidae* and *Microstomatidae* (pencilsmelts) as sister taxa (Patterson and Johnson 1995). Molecular phylogenetic analyses resolve the four major lineages of *Argentiniformes* into two sets of sister lineages: one clade containing *Argentinidae* and *Opisthoproctidae* and the other including *Bathylagidae* and *Microstomatidae* (J. Li, Xia, et al. 2010; Rosas Puchuri 2021).

<u>Composition.</u> There are currently 100 living species of *Argentiniformes* (Fricke et al. 2023) classified in *Argentinidae*, *Bathylagidae*,

Microstomatidae, and *Opisthoproctidae*. Over the past 10 years there have been eight new living species of *Argentiniformes* described (Fricke et al. 2023), comprising 8.0% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Argentiniformes* include (1) metapterygoid reduced in size (Begle 1992; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (2) endopterygoid teeth absent (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (3) parietal carrying commissural sensory canal (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (4) premaxilla without teeth (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (5) maxilla without teeth (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (6) supramaxillae absent (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (7) basibranchials 1-3 without teeth (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (8) epibranchial 4 with distinct levator process (G. D. Johnson and Patterson 1996), (9) pharyngobranchial 2 without teeth (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (10) pharyngobranchial 3 without teeth (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), and (11) supraneurals develop in "pattern 2" (G. D. Johnson and Patterson 1996).

Synonyms. *Argentinoidei* (Greenwood et al. 1966:394; Wiley and Johnson 2010:141) and *Argentinoidea* (Greenwood and Rosen 1971:39; J. S. Nelson 1984:160–162, 1994:179–181; Begle 1992:351; Johnson and Patterson 1996:309) are ambiguous synonyms of *Argentiniformes*.

Comments. Subsequent to the resolution of *Alepocephaliformes* within *Otocephala* (e.g., Ishiguro et al. 2003), classifications of *Actinopterygii* consistently use the group name *Argentiniformes* for the clade containing *Argentinidae*, *Bathylagidae*, *Microstomatidae*, and *Opisthoproctidae* (Davis et al. 2016; J. S. Nelson et al. 2016:252–254; Betancur-R et al. 2017; Dornburg and Near 2021).

The earliest fossils of *Argentiniformes* are otoliths from the Maastrichtian (72.2–66.0 Ma) of Maryland, USA, identified as *Argentinidae* and †*Argentina voigti* from Bavaria, Germany (Nolf and Stringer 1996; Schwarzhans 2010; Schwarzhans and Jagt 2021; Stringer and Schwarzhans 2021). The earliest skeletal argentiniform fossil is †*Glossanodon musceli* from the Rupelian (33.9–27.3 Ma) of the Czech Republic and Poland (Paucă 1929; Gregorová 2011; Přikryl et al. 2016). Relaxed molecular clock analyses estimate the crown age of *Argentiniformes* between 34.5 and 76.5 million years ago (Near, Eytan, et al. 2012).

Constituent lineages.

Argentinidae	*Microstomatidae*
Bathylagidae	*Opisthoproctidae*

Salmoniformes P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Myers 1966:394

Definition. The least inclusive crown clade that contains *Salmo salar* Linnaeus 1758 and *Esox lucius* Linnaeus 1758. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. *Salmo* is Latin for *Salmo trutta*, dating to Pliny (N.H. 9.68) in the first century CE (Andrews 1955). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Reference phylogeny. A phylogeny inferred from a phylogenomic dataset consisting of DNA sequences from more than 1,100 exons (Hughes et al. 2018, fig. S2). Phylogenetic relationships of the major lineages of *Salmoniformes* are presented in Figure 7. The placements of the fossil taxa †*Oldmanesox* and †*Estesesox* in the phylogeny follow inferences from morphology (Brinkman et al. 2014).

Phylogenetics. Morphological studies result in a disparate set of phylogenetic relationships for *Salmonidae* (trouts and salmons) and *Esocidae* (pikes and mudminnows). *Salmonidae* are resolved as the sister lineage of *Osmeriformes* (Rosen 1974; G. D. Johnson and Patterson 1996); *Galaxiidae* (Rosen 1974); *Neoteleostei* (Lauder and Liem 1983; W. L. Fink 1984a); a clade containing *Osmeriformes*, *Argentiniformes*, and *Alepocephaliformes* (Sanford 1990); or unresolved among euteleosts (W. L. Fink and Weitzman 1982; Begle 1991, 1992). Morphological studies place *Esocidae* as the sister lineage of a clade containing *Argentiniformes*, *Galaxiidae*, *Salmonidae*, and *Osmeriformes* (Rosen 1974); a clade containing *Salmonidae* and *Osmeriformes* (Rosen 1974); the sister lineage of all other *Euteleostei* (W. L. Fink and Weitzman 1982; W. L. Fink 1984a; Sanford 1990; Begle 1991, 1992); or as the sister lineage of *Neoteleostei* (G. D. Johnson and Patterson 1996). One set of morphological studies resolves *Salmonidae* and *Esocidae* as sister lineages (R. R. G. Williams 1987; M. V. H. Wilson and Williams 2010), a result that is congruent with molecular phylogenetic analyses (Ishiguro et al. 2003; Lopez et al. 2004; Osinov and Lebedev 2004; C. H. Li et al. 2008; Davis 2010; J. Li, Xia, et al. 2010; Burridge et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Campbell, López, et al. 2013; Faircloth et al. 2013; Davis et al. 2014, 2016; Campbell, Alfaro, et al. 2017; Hughes et al. 2018; Straube et al. 2018; Musilova et al. 2019; Harvey et al. 2021; Rosas Puchuri 2021; Mu et al. 2022).

Composition. *Salmoniformes* includes 275 species classified in *Salmonidae* and *Esocidae* (Fricke et al. 2023). Fossil taxa include the Cretaceous pan-esocids †*Estesesox* from the Campanian and Maastrichtian (83.2–66.0 Ma) of Montana, USA, and †*Oldmanesox* from the Campanian (83.2–72.2 Ma) of Alberta, Canada (M. V. H. Wilson et al. 1992). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years 30 new living species of *Salmoniformes* have been described, comprising 10.9% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Salmoniformes* include (1) hyomandibular with unique process that extends towards the symplectic and metapterygoid (R. R. G. Williams 1987; M. V. H. Wilson and Williams 2010), (2) absence of distinct ligament connecting adductor mandibulae and maxilla-mandibular ligament (R. R. G. Williams 1987; M. V. H. Wilson and Williams 2010), and (3) absence of caudal scutes, median bony plates that form anterior to procurrent caudal fin rays [caudal scutes are also absent in *Alepocephaliformes*] (G. D. Johnson and Patterson 1996).

Synonyms. *Protacanthopterygii* (M. V. H. Wilson and Williams 2010:404; J. S. Nelson et al. 2016:243–251) is an ambiguous synonym of *Salmoniformes*.

Comments. The earliest fossil *Salmoniformes* are the western North American pan-esocids †*Oldmanesox* from the Campanian (83.6–72.1 Ma) and †*Estesesox* from the Campanian and Maastrichtian (72.1–66.0 Ma) (M. V. H. Wilson et al. 1992; Brinkman et al. 2014). Bayesian relaxed molecular clock analyses of *Salmoniformes* result in an average posterior crown age estimate of 82.8 million years ago, with the credible interval ranging between 76.8 and 88.3 million years ago (Hughes et al. 2018).

Constituent lineages.

Esocidae	†*Estesesox*
Salmonidae	†*Oldmanesox*

Esocidae C. S. Rafinesque 1815:89

Definition. The least inclusive crown clade that contains *Esox lucius* Linnaeus 1758 and *Umbra krameri* Walbaum 1792. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. *Isox* is Latin, possibly Celtic or Basque in origin, which was the name for *Salmo salar* dating to Pliny (N.H. 9.44) in the first century CE (D. W. Thompson 1947:95; Andrews 1955).

Reference phylogeny. A phylogeny inferred from analysis of DNA sequences of 53 ultraconserved element (UCE) loci (Campbell, Alfaro, et al. 2017, fig. 1). Phylogenetic relationships of living and fossil lineages of *Esocidae* are presented in Figure 7. Placements of the fossil taxa †*Boltyshia*, †*Palaeoesox*, and †*Proumbra* in the phylogeny are on the basis of inferences from morphology (J. Gaudant 2012).

Phylogenetics. Relationships inferred from morphology place *Esox* as the sister lineage to a clade previously classified as *Umbridae* that contains *Umbra*, *Dallia*, and *Novumbra* (Cavender 1969; G. J. Nelson 1972; M. V. H. Wilson and Veilleux 1982); however, a study of meristic and morphometric traits noted the lack of morphological evidence for the monophyly of *Umbridae* (Reist 1987). To date, there is no phylogenetic investigation of *Esocidae* that employs explicit analysis of coded morphological character states. Molecular phylogenetic analyses consistently resolve *Umbridae* as paraphyletic, with *Umbra* placed as the sister lineage of all other *Esocidae* (Lopez et al. 2000, 2004; Burridge et al. 2012; Near, Eytan, et al. 2012; Campbell, López, et al. 2013; Campbell, Alfaro, et al. 2017; Marić et al. 2017; Pan et al. 2021). Several molecular phylogenetic studies are aimed at resolving relationships among species of *Esox* and providing a basis for species discovery and delimitation in the clade (T. Grande et al. 2004; Denys et al. 2014, 2018).

Composition. There are currently 13 living species of *Esocidae* (T. Grande et al. 2004; Lucentini et al. 2011; Denys et al. 2014; Kuehne and Olden 2014; Fricke et al. 2023). The species *Dallia admirabilis* Chereshnev and *D. delicatissima* are synonyms of *Dallia pectoralis* Bean (Campbell and Lopéz 2014; Dyldin et al. 2020). Fossil taxa of *Esocidae* include †*Novumbra oregonensis* from the Rupelian (33.90–27.82 Ma) in Oregon (Cavender 1969; Woodburne 2004), several species of *Esox* (M. V. H. Wilson 1980; L. Grande 1999), and the pan-umbrines †*Boltyshia*, †*Palaeoesox*, and †*Proumbra* (J. Gaudant 2012). Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years one new species of *Esocidae* has been described (Fricke et al. 2023), comprising 7.7% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Esocidae* include (1) ethmoidal and antorbital canals present as pitlines (G. J. Nelson 1972; Rosen 1974), (2) presence of mandibulopreopercular, subnasal, and opercular pitlines (G. J. Nelson 1972; Rosen 1974), (3) presence of paired elongate proethmoids (Rosen 1974; G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (4) basibranchial tooth plate in two parts (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (5) second pharyngobranchial conical in shape with tip enclosed in bone (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), (6) single upper pharyngeal tooth plate composed of upper fourth upper pharyngeal (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010), and (7) presence of a single postcleithrum (G. D. Johnson and Patterson 1996; Wiley and Johnson 2010).

Synonyms. *Esociformes* (J. S. Nelson 1994:176–178, 2006:204–206; G. D. Johnson and Patterson 1996:316; López et al. 2004, fig. 2; J. S. Nelson et al. 2016:248–251; Betancur-R et al. 2017:18; Pan et al. 2021, fig. 1), *Esocoidei* (Berg 1940:429; Gosline 1960:358; Greenwood et al. 1966:394; G. J. Nelson 1972:32; J. S. Nelson 1984:157–159; Wiley and Johnson 2010:142), and *Esocoidea* (Rosen 1974:311) are ambiguous synonyms of *Esocidae*. *Umbridae* (Greenwood et al. 1966:394; G. J. Nelson 1972:32–33; Rosen 1974:311; J. S. Nelson 1984:158_159, 1994:177–178) and *Esocinae* (López et al. 2000:429) are partial synonyms of *Esocidae*.

Comments. As a consequence of molecular phylogenetic analyses (e.g., López et al. 2000, 2004; Campbell, Alfaro, et al. 2017), the classification of esociform fishes was modified by the inclusion of *Dallia* and *Novumbra* into *Esocidae* with *Esox* and limiting *Umbridae* to *Umbra* (J. S. Nelson 2006:205–206; J. S. Nelson et al. 2016:251). This change makes *Umbra* and *Umbridae* redundant group names. Historically, *Esocidae* and *Umbridae* were classified as *Esocoidei* (e.g., Wiley and Johnson 2010) or *Esociformes* (e.g., Betancur-R et al. 2017); however, these group names are redundant with *Esocidae* as delimited here. *Esocidae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:64).

The earliest fossil *Esocidae* is †*Esox tiemani* from Tiffanian (60.2–56.8 Ma) North American Land Mammal Age dated rocks in Alberta, Canada (M. V. H. Wilson 1980; L. Grande 1999; Speijer et al. 2020, fig. 28.12) or †*Boltyshia brevicauda* from the Thanetian (59.2–56.0 Ma) in Ukraine (Cavagnetto and Gaudant 2000; J. Gaudant 2012). Bayesian relaxed molecular clock analyses of *Esocidae* result in an average posterior age estimate of 88.6 million years ago, with the credible interval ranging between 85.1 and 95.6 million years ago (Campbell, López, et al. 2013).

Constituent lineages.

Esox
Dallia
Novumbra
Umbra
†*Boltyshia*
†*Palaeoesox*
†*Proumbra*

Stomiatii R. Betancur-R, R. E. Broughton,
E. O. Wiley, K. Carpenter, J. A. López,
C. Li, N. I. Holcroft, D. Arcila, M. Sanciangco,
J. C. Cureton II, F. Zhang, T. Buser,
M. A. Campbell, J. A. Ballesteros,
A. Roa-Varón, S. Willis, W. C. Borden,
T. Rowley, P. C. Reneau, D. J. Hough, G. Lu,
T. Grande, G. Arratia, and G. Ortí 2013: app. 2
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Osmerus mordax* (Mitchill 1814) and *Stomias boa* (Risso 1810). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek στὀμᾰ (stˈo͡ʊmə), meaning mouth.

Registration number. 920.

Reference phylogeny. A phylogeny inferred from nine Sanger-sequenced nuclear genes (Near, Eytan, et al. 2012, fig. S1). Phylogenetic relationships of the living and fossil lineages of *Stomiatii* are presented in Figure 7. The placements of the pan-stomiiform †*Paravinciguerria* and the pan-osmeriform †*Spaniodon* are on the basis of inferences from morphology (Taverne and Filleul 2003; Carnevale and Rindone 2011).

Phylogenetics. A pre-phylogenetic morphological study proposed that *Stomiiformes* and *Osmeridae* exhibit a "relatively close relationship" (Weitzman 1967:523). Subsequent morphological studies resulted in varied and incongruent phylogenetic hypotheses among major lineages of *Euteleostei* and did not resolve *Stomiatii* as monophyletic (e.g., W. L. Fink 1984a; Rosen 1985; G. D. Johnson and Patterson 1996; Wilson and Williams 2010). Molecular phylogenetic analyses of *Euteleostei* consistently resolve *Stomiatii* as a monophyletic lineage that includes *Osmeriformes* and *Stomiiformes* (Davis 2010; J. Li, Xia, et al. 2010; Burridge et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Campbell, López, et al. 2013; Davis et al. 2014, 2016; W. L. Smith et al. 2016; Campbell, Alfaro, et al. 2017; Malmstrøm et al. 2017; Hughes et al. 2018; Straube et al. 2018; Musilova et al. 2019; Rosas Puchuri 2021; Mu et al. 2022).

Composition. There are currently 500 living species of *Stomiatii* (Fricke et al. 2023) classified in *Osmeriformes* and *Stomiiformes*. Fossil lineages of *Stomiatii* include the pan-osmeriform †*Spaniodon* and the pan-stomiiform †*Paravinciguerria* (Appendix 1; Taverne and Filleul 2003; Carnevale and Rindone 2011). Over the past 10 years 31 new living species of *Stomiatii* have been described (Fricke et al. 2023), comprising 6.2% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological synapomorphies for *Stomiatii* (Betancur-R et al. 2017; Straube et al. 2018).

Synonyms. *Stomiati* (Betancur-R et al. 2017:18) is a variant spelling of *Stomiatii*.

Comments. *Stomiatii* is a group name applied to the clade containing *Osmeriformes* and *Stomiiformes* (Betancur-R, Broughton, et al. 2013).

The earliest fossil *Stomiatii* is the pan-stomiiform †*Paravinciguerria praecursor* from the Cenomanian (100.5–93.9 Ma) of Morocco and Sicily (Appendix 1; Khalloufi et al. 2010; Carnevale and Rindone 2011). Bayesian relaxed molecular clock analyses of *Stomiatii* result in an average posterior crown age estimate of 115.4 million years ago, with the credible interval ranging between 81.1 and 147.6 million years ago (Hughes et al. 2018).

Constituent lineages.

Osmeriformes
Stomiiformes
†*Paravinciguerria*
†*Spaniodon*

Stomiiformes W. L. Fink and S. H. Weitzman 1982:32

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Stomias boa* (Risso 1810), *Gonostoma denudatum* Rafinesque 1810b, *Sternoptyx diaphana* Hermann 1781, and *Vinciguerria nimbaria* (Jordan and Williams in Jordan and Starks 1895). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek στὀμᾰ (stˈo͡ʊmə), meaning mouth. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 922.

Reference phylogeny. A phylogeny of 99 species of *Stomiiformes* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Phylogenetic relationships among the major lineages of *Stomiiformes* are presented in Figure 7.

Phylogenetics. Morphological phylogenetic studies consistently support the monophyly of *Stomiiformes* (Rosen 1973; Weitzman 1974; W. L. Fink and Weitzman 1982; W. L. Fink 1984b; Harold and Weitzman 1996; Harold 1998). Aside from phylogenies with limited taxon sampling (Harold and Weitzman 1996; Harold 1998), there is no morphological phylogenetic analysis of *Stomiiformes* that includes a comprehensive taxon sampling of the major lineages in the clade. Morphological phylogenetic analyses are aimed at stomiiform subclades: *Sternoptychidae* (marine hatchetfishes) (Harold 1993, 1994; Harold and Weitzman 1996), *Gonostomatidae* (bristlemouths) (Harold and Weitzman 1996; Harold 1998), and *Stomiidae* (barbeled dragonfishes) (W. L. Fink 1984b; W. L. Fink 1985). Weitzman (1974:338) introduced *Phosichthyidae* (lightfishes) to contain *Pollichthys mauli* (Stareye Lightfish), *Phosichthys argenteus* (Silver Lightfish), and *Vinciguerria*, *Yarrella*, *Polymetme*, *Ichthyococcus*, and *Woodsia*. There are no morphological apomorphies identified for *Phosichthyidae* and the group is resolved as paraphyletic in morphological studies (W. L. Fink 1984b; Harold and Weitzman 1996).

Molecular phylogenetic analyses resolve *Stomiiformes* as monophyletic (Miya et al. 2003; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Davis et al. 2014, 2016; W. L. Smith et al. 2016; Rosas Puchuri 2021). A small number of molecular phylogenetic analyses include a sampling of the major lineages of *Stomiiformes* (Davis et al. 2014; Kenaley et al. 2014; Rabosky et al. 2018; Rosas Puchuri 2021). In analyses of DNA sequence data, the phosichthyid *Vinciguerria* is resolved as the sister lineage of all other *Stomiiformes* (Kenaley et al. 2014; Betancur-R et al. 2017; Rosas Puchuri 2021); however, analysis of translated amino acid sequences from more than 1,000 exons places *Vinciguerria* as nested well within *Stomiiformes* (Rosas Puchuri 2021). In molecular phylogenies, *Stomiidae*, *Gonostomatidae*, and *Sternoptychidae* are each resolved as monophyletic, but *Phosichthyidae* is deeply paraphyletic (Davis et al. 2014; Kenaley et al. 2014; Rabosky et al. 2018; Rosas Puchuri 2021). The former lineages of *Phosichthyidae* that include *Pollichthys mauli*, *Polymetme*, *Yarrella*, *Vinciguerria*, and *Ichthyococcus* do not resolve with other lineages that are delimited in named Linnaean taxonomic families (Figure 7; Rabosky et al. 2018; Rosas Puchuri 2021), and there are no available family-group names to accommodate any of these genera (Van der Laan et al. 2014). We delimit *Phosichthyidae* to include *Phosichthys argenteus* and species of *Woodsia*.

Composition. There are currently 458 living species of *Stomiiformes* (Fricke et al. 2023), including *Pollichthys mauli* and species classified in *Ichthyococcus*, *Polymetme*, *Vinciguerria*, *Yarrella*, *Gonostomatidae*, *Phosichthyidae*, *Sternoptychidae*, and *Stomiidae*. Over the past 10 years there have been 31 new living species of *Stomiiformes* described (Fricke et al. 2023), comprising 6.8% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Stomiiformes* include (1) single broad termination of the second epibranchial that articulates with the second and third pharyngobranchials (Rosen 1973; W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (2) unique structure of the photophores (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (3) type 3 tooth attachment (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (4) medial section of adductor mandibulae divided into two sections, dorsal section inserting directly onto the maxilla and ventral portion inserting on primordial ligament (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (5) unique crossing pattern of ethmoid-premaxillary ligament (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (6) greatly enlarged posterior branchiostegal rays (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (7) some branchiostegal rays articulating with ventral hypohyals (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (8) rete mirabile located at posterior of swim bladder (W. L. Fink and Weitzman 1982; Wiley and Johnson 2010), (9) part of obliquus dorsalis 4 attached to fourth pharyngobranchial (Springer and Johnson 2004; Wiley and Johnson 2010), and (10) adductor 5 attaches to fourth epibranchial (Springer and Johnson 2004; Wiley and Johnson 2010).

Synonyms. *Stomiatoidei* (Jordan 1923:126–127; Gregory and Conrad 1936:25–27; Gosline 1960:358; Greenwood et al. 1966:372–373, 394; McAllister 1968:48–52; Weitzman 1974:338), *Stomiatoidea* (Beebe and Crane 1939:69), *Stenopterygii* (Rosen 1973:509), *Stomiatiformes* (Rosen 1973:509; Wiley and Johnson 2010:144; Betancur-R et al. 2017:144), and *Stomiatia* (Wiley and Johnson 2010:144) are ambiguous synonyms of *Stomiiformes*.

Comments. Prior to the development of phylogenetic systematics, lineages of *Stomiiformes* were consistently recognized as a natural group in taxonomic classifications (Regan 1923a; Gregory and Conrad 1936, fig. 3; Beebe and Crane 1939; Gosline 1960). The group name *Stomiiformes* has been applied to this clade since the early 1980s (W. L. Fink and Weitzman 1982; J. S. Nelson 1984:172–177, 1994:196–201, 2006:207–212; Near, Eytan, et al. 2012; Davis et al. 2016; J. S. Nelson et al. 2016:259–264; Dornburg and Near 2021), which is why it is selected as the clade name over its synonyms. While consistently resolved as monophyletic in phylogenetic analyses of *Teleostei* (e.g., Davis et al. 2014; Rabosky et al. 2018), relationships within *Stomiiformes* are not consistent among molecular analyses and there is no morphological phylogenetic study that includes a robust sampling of the major lineages in the clade. The lack of a robust understanding of the phylogenetic relationships within *Stomiiformes* is reflected by the deep paraphyly of *Phosichthyidae*, which prevents the establishment of a ranked Linnaean classification where the taxonomic families reflect monophyletic groups. The lineages not currently placed in Linnaean families are listed with generic names in the classification outlined in Appendix 2 and in the constituent lineages section below.

The earliest fossil *Stomiiformes* is †*Eosternoptyx discoidalis*, a species of *Sternoptychidae* from the Bartonian-aged (41.2–37.7 Ma) deposit in the Pabdeh Formation, Iran (Afsari et al. 2014). Relaxed molecular clock analyses estimate the crown age of *Stomiiformes* to be between 63 and 120 million years ago (Kenaley et al. 2014).

Constituent lineages.
Gonostomatidae
Ichthyococcus
Phosichthyidae
Pollichthys
Polymetme
Stomiidae
Sternoptychidae
Vinciguerria
Yarrella

Osmeriformes D. P. Begle 1991:46
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Osmerus eperlanus* (Linnaeus 1758), *Osmerus mordax* (Mitchill 1814), and *Retropinna semoni* (Weber 1895). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ὀσμή (hˈoʊ̑smeɪ̑), meaning odor. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 925.

Reference phylogeny. A phylogeny inferred from DNA sequences of nine nuclear genes (Near, Eytan, et al. 2012, fig. S1). Although *Osmerus eperlanus* is not included in the reference phylogeny, it resolves in a clade with other species of *Osmerus* in a molecular phylogenetic analysis (Ilves and Taylor 2009, fig. 3). Phylogenetic relationships of living and fossil lineages of *Osmeriformes* are presented in Figure 7. Placement of the fossil taxon †*Speirsaenigma* in the phylogeny is on the basis of a phylogenetic analysis of morphological characters (M. V. H. Wilson and Williams 1991).

Phylogenetics. Among the multiple morphological studies of relationships among lineages of *Euteleostei* (McDowall 1969, 1984; G. J. Nelson 1970a; W. L. Fink and Weitzman 1982; W. L. Fink 1984a; Sanford 1990; Begle 1991; G. D. Johnson and Patterson 1996), only Rosen (1974:311) proposed a grouping of *Osmeridae* (smelts), *Plecoglossus altivelis* (Ayu), *Salangidae* (noodlefishes), and *Retropinnidae* (southern smelts) that is consistent with the current delimitation of *Osmeriformes*. Molecular phylogenetic analyses consistently resolve *Osmeriformes* as monophyletic (Waters et al. 2002; López et al. 2004; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Rabosky et al. 2018; Straube et al. 2018). Phylogenies inferred from morphology nest *Plecoglossus* and *Salangidae* within *Osmeridae* (Howes and Sanford 1987; G. D. Johnson and Patterson 1996); however, molecular studies resolve *Osmeridae* as monophyletic and the sister lineage of a clade containing *Plecoglossus* and *Salangidae* (Ilves and Taylor 2009; J. Li, Xia, et al. 2010; Burridge et al. 2012; Near, Eytan, et al. 2012; Rosas Puchuri 2021).

Composition. There are currently 42 living species of *Osmeriformes* (Fricke et al. 2023) that includes *Plecoglossus altivelis* and species classified in *Osmeridae*, *Salangidae*, and *Retropinnidae*. Fossil taxa of *Osmeriformes* include †*Speirsaenigma lindoei* from the Thanetian (59.2–56.0 Ma) in Alberta, Canada (Appendix 1; M. V. H. Wilson and Williams 1991; Lofgren et al. 2004). Over the past 10 years no new living species of *Osmeriformes* have been described.

Diagnostic apomorphies. In an effort to identify morphological apomorphies consistent with the monophyly of *Osmeriformes*, we used maximum parsimony as executed in Mesquite v. 3.70 (Maddison and Maddison 2021) to map 112 morphological character state changes reported in G. D. Johnson and Patterson (1996, app. 1) onto a phylogeny of *Euteleostei* that matches the tree in Figure 7. Relationships within *Osmeridae* and *Retropinnidae* matched those inferred in molecular phylogenetic analyses (Waters et al. 2002; Ilves and Taylor 2009). There is one character state change identified in the mapping exercise that appears as an unambiguous apomorphy; however, several other character state changes exhibit a pattern that is compelling for the hypothesis of osmeriform monophyly. The six characters include (1) pelvic girdle with ventral condyle (McDowall 1969, 1984; G. D. Johnson and Patterson 1996), (2) vomer without shaft [species of *Salangidae* have a vomer with a shaft and *Plecoglossus* lacks a vomer] (G. D. Johnson and Patterson 1996), (3) fifth epibranchial fused with fourth epibranchial at both ends [species of *Plecoglossus*, *Prototroctes*, and *Stokellia* have fifth epibranchial that is free or fused with fourth epibranchial only at its lower end] (G. D. Johnson and Patterson 1996), (4) epineural bones or ligaments originate on the centrum of several anterior vertebrate [the epineural bones or ligaments originate on the neural arch in species of *Prototroctes* and *Retropinna*] (G. D. Johnson and Patterson 1996), (5) cleithrum with narrow columnar process [cleithrum in species of *Salangidae* lacks a process] (McDowall 1969; G. D. Johnson and Patterson 1996), and (6) presence of an enlarged first pectoral radial that partially covers the scapula [the first pectoral radial is unmodified in species of *Mallotus* and *Salangidae*] (G. D. Johnson and Patterson 1996).

Synonyms. *Osmeroidea* (Rosen 1974:311) is an ambiguous synonym of *Osmeriformes*. *Osmeroidei* (G. D. Johnson and Patterson 1996:307; Wiley and Johnson 2010:142) is a partial synonym of *Osmeriformes*.

Comments. When first applied as a group name, *Osmeriformes* was delimited as a polyphyletic group that included *Plecoglossus*, *Osmeridae*, *Salangidae*, *Retropinnidae*, *Argentiniformes*, *Alepocephaliformes*, *Lepidogalaxias*, and *Galaxiidae* (Begle 1991; J. S. Nelson 1994:178–189); the paraphyletic group containing *Plecoglossus*, *Osmeridae*, *Salangidae*, *Retropinnidae*, *Lepidogalaxias*, and *Galaxiidae* (J. S. Nelson 2006:194–199); and the monophyletic group as delimited here (Davis et al. 2016; J. S. Nelson et al. 2016:256–259; Betancur-R et al. 2017; Rosas Puchuri 2021). The name *Osmeriformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Osmeriformes* is the pan-plecoglossid †*Speirsaenigma lindoei* from the Thanetian (59.2–56.0 Ma) in Alberta, Canada (M. V. H. Wilson and Williams 1991; Lofgren et al. 2004). Relaxed molecular clock analyses estimate the age of *Osmeriformes* to be between 80.0 and 125.7 million years ago (Near, Eytan, et al. 2012).

Constituent lineages. Redundant group names are marked with an asterisk.

Osmeridae
*Plecoglossidae**
Retropinnidae
Salangidae
†*Speirsaenigma*

Neoteleostei G. J. Nelson 1969a:534
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Ateleopus japonicus* Bleeker 1853b (*Ateleopodidae*), *Alepisaurus ferox* Lowe 1833 (*Aulopiformes*), *Scopelengys tristis* Alcock 1890 (*Myctophiformes*), and *Micropterus salmoides* (Lacépède 1802) (*Centrarchiformes*), but not *Osmerus mordax* (Mitchill 1814) (*Osmeriformes*). This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek νέος (nˈiːo͡ʊz), meaning new; τέλειος (tˈɛlɨˌo͡ʊz), meaning perfect or complete; and ὀστέον (ˈɑːstɪən), meaning bone.

Registration number. 926.

Reference phylogeny. A phylogeny inferred from DNA sequences of nine concatenated Sanger-sequenced nuclear genes (Near, Eytan, et al. 2012, fig. S1). See Figures 2 and 12 for the phylogeny of lineages comprising *Neoteleostei*.

Phylogenetics. When initially delimited, *Neoteleostei* was represented in phylogenetic trees of the major lineages of vertebrates as a clade including *Atherinoidei*, *Myctophiformes*, *Paracanthopterygii* (*sensu lato*), and *Acanthopterygii* (G. J. Nelson 1969a). *Neoteleostei* was expanded to include *Stomiiformes* on the basis of three morphological synapomorphies (Rosen 1973); however, two of these traits were subsequently rejected on the basis of homology and phylogenetic incongruence (W. L. Fink and Weitzman 1982). The monophyly of a *Neoteleostei* that includes *Stomiiformes* was widely accepted in reviews of actinopterygian phylogeny and classification (Lauder and Liem 1983; Stiassny 1986; G. D. Johnson 1992; J. S. Nelson 1994, 2006; A. C. Gill and Mooi 2002; Stiassny et al. 2004; Wiley and Johnson 2010).

Molecular phylogenetic studies resolve *Neoteleostei* as a monophyletic group to the exclusion of *Stomiiformes* (Davis 2010; J. Li, Xia, et al. 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Davis et al. 2014, 2016; W. L. Smith et al. 2016; Malmstrøm et al. 2017; Hughes et al. 2018; Musilova et al. 2019; Mu et al. 2022). Within *Neoteleostei* molecular phylogenies resolve either *Ateleopodidae* (jellynose fishes) (e.g., Near, Eytan, et al. 2012), *Aulopiformes* (e.g., Hughes et al. 2018), or a clade containing *Ateleopodidae* and *Aulopiformes* (Mu et al. 2022) as the sister lineage of all other *Neoteleostei*. Morphology of the dorsal gill arch musculature suggests that *Ateleopodidae* forms a clade with *Aulopiformes* (Springer and Johnson 2004; Wiley and Johnson 2010). The uncertainty in the phylogenetic relationships of *Ateleopodidae* is a challenge to the delimitation of *Eurypterygii*, which is a hypothesized clade that includes *Aulopiformes* and *Ctenosquamata* (G. D. Johnson 1992). There is no morphological phylogenetic analysis of discretely coded morphological character state changes aimed at resolving relationships among the lineages of *Neoteleostei*.

Composition. Currently there are more than 20,460 living species of *Neoteleostei* (Fricke

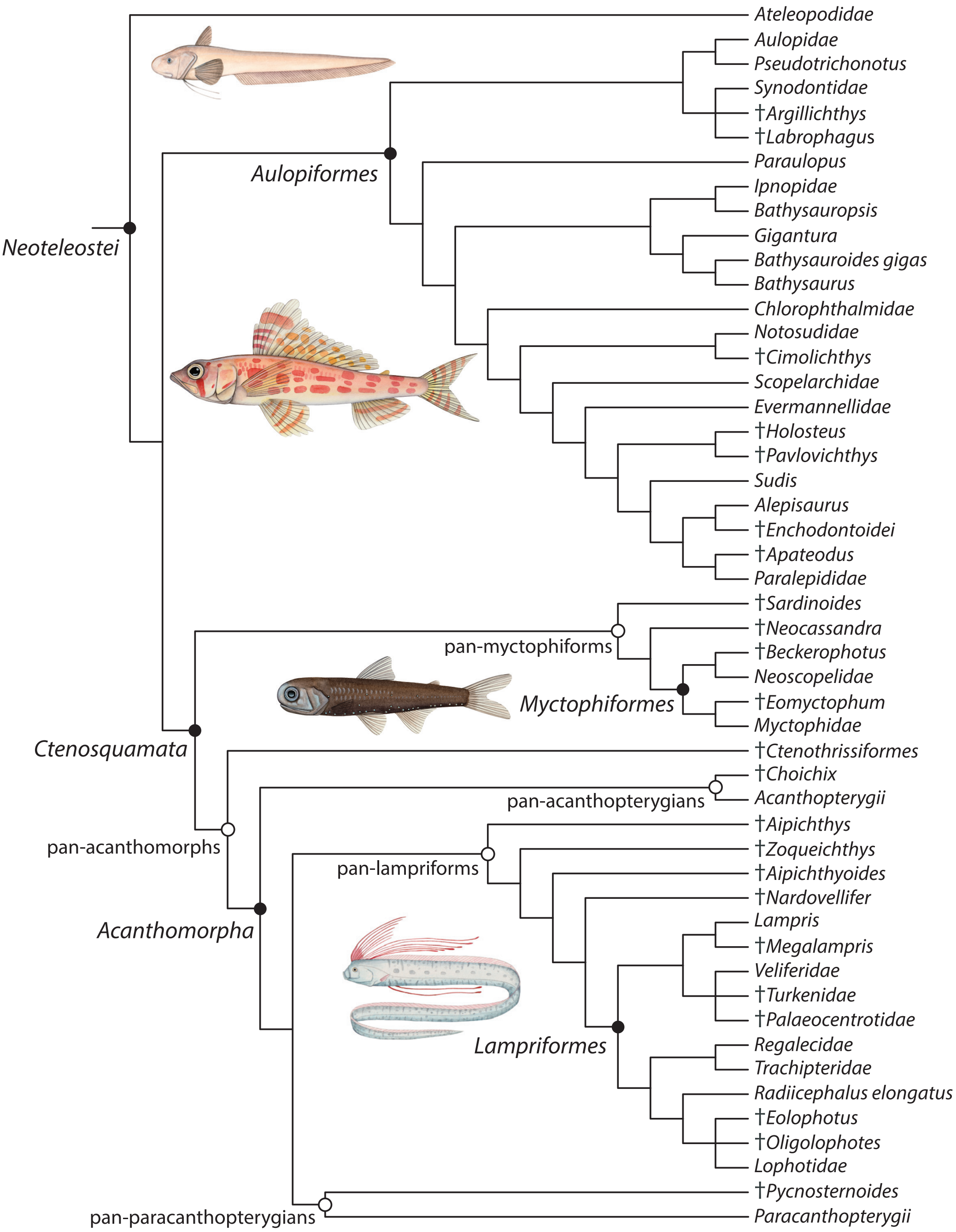

FIGURE 12. Phylogenetic relationships of the major living lineages and fossil taxa of *Neoteleostei*, *Aulopiformes*, *Ctenosquamata*, *Myctophiformes*, *Acanthomorpha*, and *Lampriformes*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

et al. 2023) classified in *Ateleopodidae*, *Aulopiformes*, and *Ctenosquamata*. Over the past 10 years there have been 1,707 new living species of *Neoteleostei* described (Fricke et al. 2023), comprising 8.3% of the living species diversity in the clade.

Diagnostic apomorphies. The morphological apomorphies proposed for *Neoteleostei* considered a delimitation of the clade that includes *Stomiiformes*. The apomorphies include (1) presence of retractor dorsalis (Rosen 1973; G. D. Johnson 1992; Olney et al. 1993; Wiley and Johnson 2010), (2) third internal levator inserts on fifth upper pharyngeal tooth plate (G. D. Johnson 1992; Olney et al. 1993; Wiley and Johnson 2010), (3) type 4 tooth attachment (G. D. Johnson 1992; Olney et al. 1993; Wiley and Johnson 2010), (4) transversus dorsalis attaches to second epibranchial (Springer and Johnson 2004; Wiley and Johnson 2010), and (5) presence of transversus epibranchialis 2 (Springer and Johnson 2004; Wiley and Johnson 2010).

Synonyms. There are no synonyms of *Neoteleostei*.

Comments. The monophyly of *Neoteleostei* is one of the key discoveries in the early efforts of applying phylogenetic systematics to the relationships of ray-finned fishes (G. J. Nelson 1969a; Rosen 1973). There have been slight modifications to the original delimitation of *Neoteleostei*, but the integrity of the clade remains largely intact (Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013). *Neoteleostei* is consistently applied as the group name for the clade as delimited here (Near, Eytan, et al. 2012; Davis et al. 2016; J. S. Nelson et al. 2016:264; Betancur-R et al. 2017; Hughes et al. 2018). *Neoteleostei* contains more than 58% of the living species diversity of ray-finned fishes and composes the dominant group of vertebrates occupying marine habitats.

The earliest fossil *Neoteleostei* is the aulopiform †*Atolvorator longipectoralis* from the Barremian (126.5–121.4 Ma) in the Cretaceous of Brazil (Gallo and Coelho 2008; Newbrey and Konishi 2015). Bayesian relaxed molecular clock analyses of *Neoteleostei* result in an average posterior crown age estimate of 161.0 million years ago, with the credible interval ranging between 152.2 and 172.0 million years ago (Hughes et al. 2018).

Constituent lineages.
Ateleopodidae
Aulopiformes
Ctenosquamata

Aulopiformes D. E. Rosen 1973:509
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Aulopus filamentosus* (Bloch 1792a) and *Alepisaurus ferox* Lowe 1833. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek αὐλωπίας (ɔːlˈo͡ʊpi͡əz) of unknown origin, a name applied to species of *Scombridae* by ancient Mediterranean authors (D. W. Thompson 1947:20–21). The suffix is from the Latin *forma*, meaning form, figure, or appearance.

Registration number. 928.

Reference phylogeny. A phylogeny inferred from a combined dataset of mitochondrial and nuclear gene DNA sequences and 138 morphological characters (Davis 2010, fig. 7). Phylogenetic relationships of living and fossil lineages of *Aulopiformes* are presented in Figure 12. The fossil taxa are placed in the phylogeny on the basis of analyses of morphological characters (Fielitz 2004; Davis and Fielitz 2010; Marramà and Carnevale 2017; Beckett, Giles, et al. 2018).

Phylogenetics. In pre-phylogenetic classifications, *Aulopiformes* and *Myctophiformes* were grouped together in *Iniomi* or a more inclusive *Myctophiformes* (e.g., Regan 1911a; Greenwood et al. 1966; Gosline 1971). *Aulopiformes* was first delimited as a monophyletic group in one of the earliest efforts to resolve the phylogenetic relationships of *Euteleostei* (Rosen 1973). Several phylogenetic analyses using morphological characters inferred paraphyly of *Aulopiformes* (R. K. Johnson 1982; Rosen 1985; Hartel and Stiassny 1986); however, subsequent morphological and molecular studies resolved the lineage as monophyletic

(G. D. Johnson 1992; Baldwin and Johnson 1996; Sato and Nakabo 2002; Fielitz 2004; Davis 2010; Fielitz and González-Rodríguez 2010). The most comprehensive phylogeny of *Aulopiformes* is one resulting from analysis of combined morphological and molecular characters (Davis 2010). Incongruence in the phylogenies inferred from the combined morphological and molecular dataset and those based solely on morphological characters involve the relationships of *Alepisaurus* (lancetfishes and daggertooths), *Bathysauropsis* (black lizardfishes), *Chlorophthalmidae* (greeneyes), *Evermannellidae* (sabertooth fishes), *Ipnopidae* (deep-sea tripod fishes), *Notosudidae* (waryfishes), *Paralepididae* (barracudinas), and *Sudis* (Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010). Analysis of morphological characters resolves the phylogenetic relationships of fossil lineages of *Aulopiformes* that include †*Argillichthys*, †*Apateodus*, †*Cimolichthys*, †*Enchodontoidei*, †*Holosteus*, †*Labrophagus*, and †*Pavlovichthys* (Fielitz 2004; Davis and Fielitz 2010; Fielitz and González-Rodríguez 2010; H. M. A. Silva and Gallo 2011; Cavin et al. 2012; Marramà and Carnevale 2017; Beckett, Giles, et al. 2018; Díaz-Cruz et al. 2020, 2021).

Composition. There are 298 living species of *Aulopiformes* (Fricke et al. 2023), including *Alepisaurus, Bathysauroides gigas* (Pale Deepsea Lizardfish) and species classified in *Bathysaurus*, *Bathysauropsis*, *Gigantura* (telescopefishes), *Paraulopus* (cucumberfishes), *Pseudotrichonotus* (sand-diving lizardfishes), *Sudis*, *Aulopidae* (flagfins), *Chlorophthalmidae*, *Evermannellidae*, *Ipnopidae*, *Notosudidae*, *Paralepididae*, *Scopelarchidae* (pearleyes), and *Synodontidae* (lizardfishes). Fossil taxa of *Aulopiformes* include †*Apateodus*, †*Cimolichthys*, †*Argillichthys*, †*Labrophagus*, †*Enchodontoidei*, †*Holosteus*, and †*Pavlovichthys* (Fielitz and González-Rodríguez 2010; Marramà and Carnevale 2017; Beckett, Giles, et al. 2018; Díaz-Cruz et al. 2020, 2021). Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years 25 new species of *Aulopiformes* have been described (Fricke et al. 2023), comprising 8.4% of the species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Aulopiformes* include (1) presence of elongate uncinate process on second epibranchial (Rosen 1973; Sato and Nakabo 2002; Davis 2010; Beckett, Giles, et al. 2018), (2) cartilaginous condyle on dorsal surface of third pharyngobranchial does not articulate with second epibranchial (G. D. Johnson 1992; Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010; Wiley and Johnson 2010), (3) fourth epibranchial with enlarged proximal end capped with a large band of cartilage and uncinate process at middle portion (Sato and Nakabo 2002; Davis 2010; Beckett, Giles, et al. 2018), (4) presence of fifth epibranchial (Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010; Beckett, Giles, et al. 2018), (5) ventral portion of palatine not expanded laterally (Sato and Nakabo 2002; Davis 2010), (6) posterior placement of the palatine cartilaginous facet for articulation with lateral ethmoid (Sato and Nakabo 2002; Davis 2010), (7) epipleurals extend anteriorly to at least second vertebrae (Patterson and Johnson 1995; Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010; Wiley and Johnson 2010), (8) one or more epipleurals displaced dorsally into horizontal septum (Patterson and Johnson 1995; Baldwin and Johnson 1996; Davis 2010; Wiley and Johnson 2010), (9) some ribs ossify in membrane bone (Baldwin and Johnson 1996; Davis 2010), (10) proximal portion of principal caudal-fin rays with modified segment (Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010), (11) medial process of pelvic girdle joined with cartilage (Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010; Wiley and Johnson 2010), (12) presence of two adductor profundus elements, (13) absence of swim bladder (R. K. Johnson 1982; Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010; Wiley and Johnson 2010), and (14) presence of head spines on larvae (Baldwin and Johnson 1996; Sato and Nakabo 2002; Davis 2010).

Synonyms. *Scopeliformes* (Gosline 1961:10–11), *Cyclosquamata* (Rosen 1973:509; Betancur-R et al. 2017:19), and *Aulopa* (Wiley and Johnson 2010:144) are ambiguous synonyms of *Aulopiformes*. *Iniomi* is a partial synonym of *Aulopiformes* (Gosline et al. 1966:1-2).

Comments. *Aulopiformes* has been consistently used as the group name for the clade outlined in the definition (Rosen 1973; W. L. Fink 1984a; Davis 2010; Wiley and Johnson 2010; Davis et al. 2016; J. S. Nelson et al. 2016:266–276) and is chosen as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

Eight of the 15 taxonomic families of *Aulopiformes* contain either a single species or a single genus (Davis 2010). Future efforts aimed at reducing group names in the phylogenetic-based classification of *Aulopiformes* could place *Harpadon*, *Pseudotrichonotus*, *Saurida*, *Synodus*, and *Trachinocephalus* into *Aulopidae*; *Bathysaurus* and *Bathysauroides gigas* into *Giganturidae*; and *Bathysauropsis* into *Ipnopoidae*.

The earliest fossil *Aulopiformes* is †*Atolvorator longipectoralis* from the Barremian (129.4–121.4 Ma) in Brazil (Gallo and Coelho 2008; Newbrey and Konishi 2015). The phylogenetic affinities of †*Atolvorator* within *Aulopiformes* are unresolved (Gallo and Coelho 2008). Bayesian relaxed molecular clock analyses of *Aulopiformes* result in an average posterior crown age estimate of 140 million years ago, with the credible interval ranging between 127 and 156 million years ago (Davis and Fielitz 2010).

Constituent lineages. Redundant group names are marked with an asterisk.

*Alepisauridae**
Aulopidae
*Bathysauridae**
*Bathysauroididae**
*Bathysauropsidae**
Chlorophthalmidae
Evermannellidae
*Giganturidae**
Ipnopidae
Notosudidae
Paralepididae
*Paraulopidae**
*Pseudotrichonotidae**
Scopelarchidae
*Sudidae**
Synodontidae
†*Apateodus*
†*Argillichthys*
†*Cimolichthys*
†*Enchodontoidei*
†*Holosteus*
†*Labrophagus*
†*Pavlovichthys*

Ctenosquamata D. E. Rosen 1973
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Scopelengys tristis* Alcock 1890 and *Micropterus salmoides* (Lacépède 1802). This is a minimum-crown-clade definition.

Etymology. Derived from the ancient Greek κτείς (tˈiːnɪs), meaning comb, and the Latin *squama*, meaning scale.

Registration number. 929.

Reference phylogeny. A phylogeny inferred from DNA sequences of nine concatenated Sanger-sequenced nuclear genes (Near, Eytan, et al. 2012, figs. 1, S1). Phylogenetic relationships of the major lineages of *Ctenosquamata* are presented in Figures 2 and 12. The placement of the fossil taxa †*Ctenothrissiformes*, †*Sardinoides*, and †*Neocassandra* are on the basis of analysis and inferences from morphological characters (M. Gaudant 1978b, 1979; Prokofiev 2006a; Dietze 2009; Davesne et al. 2016).

Phylogenetics. In a groundbreaking study of euteleost phylogeny on the basis of osteology and musculature of the jaws, pharyngobranchials, and caudal skeleton, Rosen (1973) introduced the group name *Ctenosquamata* for the clade containing *Myctophiformes* and *Acanthomorpha*. Rosen (1973) argued that *Myctophiformes*, comprising *Myctophidae* and *Neoscopelidae*, was more closely related to *Acanthomorpha*, in contrast to traditional classifications that grouped *Aulopiformes* with *Myctophiformes* (e.g., Regan 1911a; Jordan 1923:153–156; Berg 1940:437–438; Gosline et al. 1966; R. K. Johnson 1982). In a study of occipital anatomy, Rosen (1985) later rejected the monophyly of *Ctenosquamata*, proposing a phylogeny in which *Myctophidae* (lanternfishes) and *Acanthomorpha* share a common ancestry to the exclusion of *Neoscopelidae* (blackchins). Johnson (1992) convincingly pointed out problems in the interpretation of character variation in Rosen (1985) and reviewed evidence for the monophyly of *Ctenosquamata*.

The monophyly of *Ctenosquamata* is supported in phylogenetic analyses of discretely coded morphological characters (Stiassny 1996; Wiley et al. 1998; Dietze 2009). Manual cladistic solutions representing ctenosquamate monophyly (Lauder and Liem 1983; Stiassny

1986) and other summary phylogenies of ray-finned fishes and teleosts depict monophyly of *Ctenosquamata* (W. L. Fink and Weitzman 1982; Rosen 1982; W. L. Fink 1984a; G. J. Nelson 1989; G. D. Johnson 1992; C. D. Roberts 1993; Yamaguchi 2000; A. C. Gill and Mooi 2002; Springer and Johnson 2004). Phylogenetic analysis of morphological characters resolves the Late Cretaceous †*Ctenothrissiformes* and *Acanthomorpha* as sister lineages (Davesne et al. 2016; Cantalice et al. 2021), a result consistent with a pre-cladistic study (Patterson 1964). Studies by M. Gaudant (1978b, 1979) hypothesized that †*Ctenothrissiformes* are stem lineage ctenosquamates.

Molecular phylogenetic analyses consistently resolve *Ctenosquamata* as monophyletic (Wiley et al. 1998; Alfaro, Santini, et al. 2009; Davis 2010; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Poulsen et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2014, 2016; Denton 2014; Malmstrøm et al. 2016; W. L. Smith et al. 2016; Mirande 2017; Hughes et al. 2018; Martin et al. 2018; Mu et al. 2022; J.-F. Wang et al. 2023). In a maximum parsimony analysis of complete mtDNA genomic sequences, the ateleopid lineages *Ateleopus* and *Ijimaia* are nested in *Ctenosquamata* (Miya et al. 2001, 2003), but subsequent analyses using model based phylogenetic analysis of complete mtDNA genomic sequences result in ctenosquamate monophyly (Poulsen et al. 2013; J.-F. Wang et al. 2023).

<u>Composition.</u> *Ctenosquamata* includes more than 21,150 living species (Fricke et al. 2023) classified in *Acanthomorpha* and *Myctophiformes.* Fossil taxa of *Ctenosquamata* include the pan-acanthomorph †*Ctenothrissiformes* (Patterson 1964; M. Gaudant 1978b; Davesne et al. 2016) and the pan-myctophiforms †*Sardinoides monasteri* and †*Neocassandra mica* (Prokofiev 2006a; Dietze 2009). Details on the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years there have been 1,681 new living species of *Ctenosquamata* described (Fricke et al. 2023), comprising 8.3% of the living species diversity in the clade.

<u>Diagnostic apomorphies.</u> Morphological apomorphies for *Ctenosquamata* include (1) absences of fifth upper pharyngeal tooth plates and associated third levatores interni (G. D. Johnson 1992; Olney et al. 1993; Stiassny 1996; Wiley and Johnson 2010), (2) two or fewer branchiostegal rays on posterior ceratohyal (McAllister 1968; Stiassny 1996; Wiley and Johnson 2010), (3) loss of craniotemporalis musculature (Stiassny 1986, 1996; Wiley and Johnson 2010), (4) absence of supraorbital bones (Stiassny 1996; Wiley and Johnson 2010), and (5) presence of single and medially fused neural arch on first vertebral centrum (Stiassny 1996; Wiley and Johnson 2010).

<u>Synonyms.</u> There are no synonyms of *Ctenosquamata*.

<u>Comments.</u> The earliest fossil *Ctenosquamata* includes several pan-lampriforms, pan-acanthopterygians, pan-holocentrids, pan-trachichthyiforms, pan-percomorphs, and †*Ctenothrissa signifer* from the Cenomanian (100.5–93.2 Ma) in the Cretaceous of Lebanon (Bannikov and Bacchia 2005; Davesne et al. 2016). Bayesian relaxed molecular clock analyses of *Ctenosquamata* result in an average posterior crown age estimate of 149.7 million years ago, with the credible interval ranging between 141.8 and 159.1 million years ago (Hughes et al. 2018).

<u>Constituent lineages.</u>
Acanthomorpha
Myctophiformes
†*Ctenothrissiformes*
†*Neocassandra*
†*Sardinoides*

Myctophiformes C. T. Regan 1911a:121

[T. J. Near and C. E. Thacker],
converted clade name

<u>Definition.</u> The least inclusive crown clade that contains *Neoscopelus macrolepidotus* J. Y. Johnson 1863 and *Myctophum punctatum* Rafinesque 1810b. This is a minimum-crown-clade definition.

<u>Etymology.</u> From the ancient Greek μυκτήρ (mˈuːktɚ), meaning nose, and ὀφίς (ˈo͡ʊfiz), meaning snake. The suffix is from the Latin *forma*, meaning form, figure, or appearance.

<u>Registration number.</u> 930.

Reference phylogeny. A phylogeny inferred from a combined analysis of phylogenomic data (UCEs), Sanger-sequenced mtDNA and nuclear genes, and morphology (Martin et al. 2018, fig. 4). Phylogenetic relationships of living and fossil lineages of *Myctophiformes* are presented in Figure 12. The placements of fossil taxa in the phylogeny are on the basis of inferences from morphology (Prokofiev 2006a; Dietze 2009).

Phylogenetics. The first phylogenies of *Myctophiformes* inferred from morphological characters included nearly every genus (Paxton et al. 1984; Stiassny 1996), but did not include outgroups to test monophyly of the taxon. A phylogenetic analysis that sampled 60 morphological characters from taxa representing *Acanthomorpha*, *Aulopiformes*, *Myctophidae* (lanternfishes), *Neoscopelidae* (blackchins), and *Stomiiformes* resolves *Myctophiformes* as monophyletic (Dietze 2009). The monophyly of *Myctophiformes* is supported in morphological analyses (Stiassny 1986, 1996; Yamaguchi 2000). A combined analysis of morphology, mtDNA, Sanger-sequenced nuclear genes, and next-generation sequenced UCE loci strongly supports the monophyly of *Myctophiformes* (Martin et al. 2018). One analysis of partial mtDNA rRNA genes resolves *Myctophiformes* as paraphyletic (Colgan et al. 2000); however, all other phylogenetic analyses of molecular data result in myctophiform monophyly (e.g., Miya et al. 2001, 2003; Davis 2010; Near, Eytan, et al. 2012, 2013; Poulsen et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2014, 2016; Denton 2014; W. L. Smith et al. 2016; Martin et al. 2018).

Composition. *Myctophiformes* currently contains 258 living species (Paxton and Hulley 1999a, 1999b; Fricke et al. 2023), classified in *Myctophidae* and *Neoscopelidae*. Fossil lineages of *Myctophiformes* include the pan-neoscopelid †*Beckerophotus* and the pan-myctophid †*Eomyctophum*. Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years there was one new species of *Myctophiformes* described (Fricke et al. 2023), comprising 0.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Myctophiformes* include (1) median dorsal keel present on mesethmoid (Stiassny 1986, 1996; Wiley and Johnson 2010), (2) median maxilla-premaxillary ligaments (VIII) insert on the contralateral buccal elements (Stiassny 1986, 1996; Wiley and Johnson 2010), (3) large tooth plate fused to proximal end of fourth ceratobranchial (Stiassny 1996; Wiley and Johnson 2010), (4) absence or reduction of first levator externus (Stiassny 1996; Wiley and Johnson 2010), (5) parapophyses on first vertebral centrum are cone-like and enlarged and meet at ventral midline (Stiassny 1986, 1996; Wiley and Johnson 2010), (6) adipose fin support inserted ventrally into supracarinalis posterior muscle mass (Stiassny 1996; Wiley and Johnson 2010), (7) presence of tranversus paryngobranchiales 2a and 2b (Springer and Johnson 2004; Wiley and Johnson 2010), (8) single fused extrascapular (Martin et al. 2018), and (9) narrow pubic plate (Martin et al. 2018).

Synonyms. *Myctophata* (Wiley and Johnson 2010:146; Betancur-R et al. 2017:19) and *Scopelomorpha* (Rosen and Patterson 1969:460; Rosen 1973:509; J. S. Nelson et al. 2016:276) are ambiguous synonyms of *Myctophiformes*. *Myctophoidei* (Greenwood et al. 1966:395) is a partial synonym of *Myctophiformes*.

Comments. Prior to Rosen's (1973) proposal limiting *Myctophiformes* to *Myctophidae* and *Neoscopelidae*, earlier classifications considered *Myctophiformes* or *Iniomi* to include *Aulopiformes*, *Myctophidae*, and *Neoscopelidae* (e.g., Regan 1911a; Greenwood et al. 1966; Gosline 1971). Scientists questioned the reality of *Iniomi* as early as the late 19th century (e.g., T. N. Gill 1893). In the first 10 years after Rosen (1973) some authors continued to recognize this heterogeneous concept of *Myctophiformes* (R. K. Johnson 1982; Okiyama 1984). Convincing evidence for the delimitation of *Myctophiformes* followed here came from detailed and thorough morphological analyses (Stiassny 1986, 1996). Essentially all molecular analyses have supported the monophyly of *Myctophiformes* (e.g., Near, Eytan, et al. 2012; Poulsen et al. 2013; Davis et al. 2014), demonstrating that as much as molecular phylogenies dramatically affect teleost classifications, they are also corroborative for well-supported but contentious hypotheses proposed as a result of analysis of morphological data. The name *Myctophiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Myctophiformes* are two pan-myctophids: the otolith taxon †*Eokrefftia prediaphus* from the Thanetian (59.2–56.0 Ma) of South Australia and the skeletal taxon †*Eomyctophum broncus* from the Ypresian (56.0–48.1 Ma) of New Zealand (Schwarzhans 2019; Schwarzhans and Carnevale 2021). Bayesian relaxed molecular clock analyses of *Myctophiformes* result in an average posterior crown age estimate of 69.0 million years ago, with the credible interval ranging between 60.1 and 78.7 million years ago (Near et al. 2013).

Constituent lineages.
Myctophidae
Neoscopelidae
†*Beckerophotus*
†*Eomyctophum*

Acanthomorpha D. E. Rosen 1973:510
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Lampris guttatus* (Brünnich 1788), *Polymixia lowei* Günther 1859, *Percopsis omiscomaycus* (Walbaum 1792), *Zeus faber* Linnaeus 1758, *Stylephorus chordatus* Shaw 1791, *Gadus morhua* Linnaeus 1758, *Diretmus argenteus* Johnson 1864, *Beryx decadactylus* Cuvier 1829 in Cuvier and Valenciennes (1829a), *Carapus bermudensis* (Jones 1874), and *Micropterus salmoides* (Lacépède 1802). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ᾰ̓́κανθα (ækˈænθə), meaning thorn or spine, and μορφή (mˈɔːɹ͡fiː), meaning form or shape.

Registration number. 931.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S1–S25). Phylogenetic relationships among the major living and fossil lineages of *Acanthomorpha* are presented in Figures 2 and 12. Phylogenetic placements of fossil taxa are on the basis of inferences from morphological analyses (Davesne et al. 2014, 2016; Delbarre et al. 2016; Cantalice et al. 2021).

Phylogenetics. Phylogenetic analyses of discretely coded morphological character state changes resolve *Acanthomorpha* as monophyletic (Stiassny 1986; Stiassny and Moore 1992; G. D. Johnson and Patterson 1993; Davesne et al. 2016; Cantalice et al. 2021). Relationships within acanthomorphs differ among morphological analyses, but several studies resolve *Lampriformes* as the sister lineage to all other acanthomorphs and *Holocentridae* as the sister lineage of *Percomorpha* (Stiassny and Moore 1992; Olney et al. 1993; Davesne et al. 2016; Cantalice et al. 2021).

Molecular phylogenetic analyses using mtDNA, nuclear genes, or combinations of the two and phylogenomic analyses consistently resolve *Acanthomorpha* as monophyletic (W.-J. Chen et al. 2003; Miya et al. 2003, 2005; W. L. Smith and Wheeler 2006; Alfaro, Santini, et al. 2009; Santini et al. 2009; Davis 2010; Near, Eytan, et al. 2012, 2013; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; Malmstrøm et al. 2016; W. L. Smith et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Musilova et al. 2019; Roth et al. 2020; Ghezelayagh et al. 2022; Mu et al. 2022). However, relationships among the major lineages of *Acanthomorpha* vary across studies. Phylogenomic analyses consistently resolve three major clades: *Lampriformes*, *Paracanthopterygii*, and *Acanthopterygii* (Alfaro et al. 2018; Hughes et al. 2018; Musilova et al. 2019; Ghezelayagh et al. 2022). Trees inferred from phylogenomic analyses of exons resolve *Lampriformes* as the sister lineage of *Acanthopterygii* (Hughes et al. 2018; Musilova et al. 2019; Roth et al. 2020), while phylogenomic analyses of UCE loci and a set of 82 exons place *Lampriformes* as the sister lineage of *Paracanthopterygii* (Alfaro et al. 2018; Ghezelayagh et al. 2022; Mu et al. 2022). Bayesian concordance factors estimated using UCE data find that resolution of *Lampriformes* as sister of *Paracanthopterygii* is supported by the greatest proportion of sampled loci; however, the 95% highest posterior density of the concordance factors overlaps with that of the phylogeny that resolves *Lampriformes* and *Acanthopterygii* as sister lineages (Ghezelayagh et al. 2022), suggesting relationships among lineages of *Acanthomorpha* are not confidently resolved.

Composition. *Acanthomorpha* currently includes more than 19,895 living species (Fricke et al. 2023), classified in the subclades *Lampriformes*, *Paracanthopterygii*, and *Acanthopterygii*. Fossil lineages include the pan-lampriforms †*Aipichthys*, †*Aipichthyoides*, †*Nardovelifer*, and †*Zoqueichthys* (Patterson 1964; Alvarado-Ortega and Than-Marchese 2012; Murray and Wilson 2014; Davesne et al. 2016; Delbarre et al. 2016; Cantalice et al. 2021); the pan-paracanthopterygian †*Pycnosteroides* (Patterson 1964, 1993; Davesne et al. 2016; Cantalice et al. 2021); and the pan-acanthopterygian †*Choichix* (Cantalice et al. 2021). Details of the ages and locations of the fossil taxa are given in Appendix 1. Over the past 10 years 1,680 new species of *Acanthomorpha* have been described (Fricke et al. 2023), comprising 8.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Acanthomorpha* include (1) anterior facets on the first vertebral centrum that articulate with the exoccipital condyles (Rosen 1985; G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (2) maxillo-rostroid ligament originates from inner portion of maxillary median process and inserts onto rostral cartilage (Stiassny 1986; Olney et al. 1993; Wiley and Johnson 2010), (3) spina occipitalis extends ventrally, forming dorsal margin of the foramen magnum (Stiassny 1986; Olney et al. 1993), (4) anterior extension of lateral ethmoid located close to, or sutured with, lateral process projecting from ventral stalk of vomer (Stiassny 1986; Olney et al. 1993; Davesne et al. 2016; Cantalice et al. 2021), (5) upper limb of posttemporal bound to epioccipital with a reduced posttemporal-epioccipital ligament (Stiassny 1986; Olney et al. 1993), (6) distal ossification of medial pelvic process (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (7) separated medial and anterior infracarinales muscles (G. D. Johnson and Patterson 1993; Stiassny 1993; Wiley and Johnson 2010), (8) presence of unsegmented, bilaterally fused dorsal and anal fin spines (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010; Davesne et al. 2016; Cantalice et al. 2021), (9) absence of median caudal cartilages (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), and (10) antorbital bone absent (Cantalice et al. 2021).

Synonyms. *Acanthomorphata* (Wiley and Johnson 2010:127, 146–147; Betancur-R et al. 2017:20) is an ambiguous synonym of *Acanthomorpha*.

Comments. *Acanthomorpha*, or spiny-rayed fishes, comprise one of the major inclusive lineages of teleost fishes and the name *Acanthomorpha* is here defined as applying to the clade originating in their most recent common ancestor. Since the recognition and delimitation of *Acanthomorpha* by Rosen (1973), the major living lineages that comprise this taxon have not changed. The discovery of support for acanthomorph monophyly and the phylogenetic relationships of its constituent lineages (Stiassny 1986; G. D. Johnson and Patterson 1993; Near, Eytan, et al. 2012) remains an active area of research. Recent Sanger sequencing and phylogenomic studies provide unprecedented taxon sampling and resolution for acanthomorph phylogenetic relationships (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Alfaro et al. 2018; Ghezelayagh et al. 2022).

The earliest fossils of *Acanthomorpha* date to the Cenomanian (100.5–93.9 Ma) (Patterson 1993; Friedman 2010; Murray 2016). Bayesian relaxed molecular clock analyses of *Acanthomorpha* result in an average posterior crown age estimate of 144.8 million years ago, with the credible interval ranging between 136.9 and 152.3 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Acanthopterygii
Lampriformes
Paracanthopterygii
†*Aipichthyoides*
†*Aipichthys*
†*Choichix*
†*Nardovelifer*
†*Pycnosteroides*
†*Zoqueichthys*

Lampriformes G. C. Steyskal 1980:171
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Lampris guttatus* (Brünnich 1788), *Metavelifer multiradiatus* (Regan 1907a), and *Regalecus russelii* (Cuvier 1816), but not *Stylephorus chordatus* Shaw 1791. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek λαμπρός (lˈæmpɹo͡ʊz) meaning bright, brilliant, or radiant. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 932.

Reference phylogeny. A phylogeny of *Lampriformes* inferred from analysis of seven Sanger-sequenced nuclear genes (Brownstein and Near 2023, fig. 4). Phylogenetic relationships of the living and fossil lineages of *Lampriformes* are presented in Figure 12. The placements of the fossil lampriform taxa in the phylogeny are on the basis of inferences from morphology (Bannikov 1999; Gottfried et al. 2006; Brownstein and Near 2023).

Phylogenetics. The phylogenetic relationships within *Lampriformes* have been investigated with analyses of morphological and molecular datasets (Oelschläger 1983; Olney et al. 1993; Wiley et al. 1998; T. R. Roberts 2012; Martin 2015). The morphological phylogenies presented in Olney et al. (1993) and Martin (2015), and the molecular phylogeny in Wiley et al. (1998) are congruent in the resolution of *Veliferidae* (velifers) as the sister lineage of all other *Lampriformes* and *Lampris* (opahs) as the sister lineage of a clade containing *Lophotidae* (crestfishes), *Radiicephalus* (tapertails), *Regalecidae* (oarfishes), and *Trachipteridae* (ribbonfishes). A molecular phylogeny inferred from mtDNA and nuclear genes resolves a clade containing *Lampris* and *Veliferidae* that is the sister lineage of all other *Lampriformes* (Rabosky et al. 2018; J. Chang et al. 2019), which is consistent with the classification that grouped *Lampris* and *Veliferidae* in *Bathysomi* and all other lineages of lampriforms in *Taeniosomi* (Regan 1907b). A series of morphological phylogenetic analyses that included multiple species of *Lampriformes* were aimed at investigating the relationships of several pan-lampriform fossil taxa (Davesne et al. 2014, 2016; Delbarre et al. 2016; Cantalice et al. 2021).

The two earliest morphological phylogenetic analyses of Oelschläger (1983) and Olney et al. (1993) include *Stylephorus chordatus* as this species was long classified with lineages of *Lampriformes* (Günther 1861:306; Regan 1908, 1924; Starks 1908; Goodrich 1909:475–477; Jordan 1923; Greenwood et al. 1966; McAllister 1968; J. S. Nelson 2006). Molecular phylogenetic analyses consistently resolve *Lampriformes* as monophyletic to the exclusion of *Stylephorus*, which is resolved as the sister lineage of all other *Gadiformes* (Miya et al. 2007; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Alfaro et al. 2018; Hughes et al. 2018; Ghezelayagh et al. 2022). Morphological phylogenetic analyses aimed at relationships among lineages of *Acanthomorpha* are congruent with molecular phylogenies in resolving *Lampriformes* and *Stylephorus* as distantly related (Davesne et al. 2016).

Composition. There are currently 30 living species of *Lampriformes* (Fricke et al. 2023) classified in *Lampris*, *Lophotidae*, *Radiicephalus*, *Regalecidae*, and *Veliferidae*. Fossil taxa of *Lampriformes* include the species of *Veliferidae* †*Veronavelifer sorbini*; the pan-veliferids †*Palaeocentrotus boeggildi*, †*Turkmene finitimus*, and †*Danatinia casca* (Bannikov 1990, 1999, 2014a); the species of *Lophotidae* †*Babelichthys olneyi* (Davesne 2017); the pan-lophotids †*Protolophotus elami*, †*Eolophotes lenis*, and †*Oligolophotes fragosus* (Walters 1957; Bannikov 1999; Davesne 2017); and the pan-lamprid †*Megalampris keyesi* (Gottfried et al. 2006). Details of the ages and locations for the fossil taxa are given in Appendix 1. In the last 10 years, four new living species of *Lampriformes* have been described (Underkoffler et al. 2018; Koeda and Ho 2019; Fricke et al. 2023), comprising 13.3% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Lampriformes* include (1) second ural centrum free from fused first ural and preural centra and fused posteriorly to upper hypural plate (Patterson 1968; Wiley and Johnson 2010; Davesne et al. 2014, 2016; Delbarre et al. 2016; Cantalice et al. 2021), (2) anterior palatine process and anterior palatomaxillary ligament absent (Olney et al. 1993; Wiley and Johnson 2010; Davesne et al. 2014), (3) mesethmoid posterior to lateral ethmoids (Olney et al. 1993; Wiley and Johnson 2010), (4) elongate ascending processes of premaxillae and large rostral cartilage insert into frontal vault or cradle (Olney et al. 1993; Wiley and Johnson 2010; Davesne et al. 2014, 2016; Cantalice et al. 2021), (5) first dorsal fin pterygiophore inserts anterior to first neural spine (Olney et al. 1993; Wiley and Johnson 2010; Davesne et al. 2014, 2016; Cantalice et al. 2021), (6) postcleithrum composed of a single bone (Otero and Gayet 1996; Davesne et al. 2014, 2016; Delbarre et al. 2016; Cantalice et al. 2021), (7) premaxillary free of dentition (Delbarre et al. 2016), (8) dentary free of dentition (Delbarre et al. 2016), (9) endopterygoid free of dentition (Delbarre et al. 2016), and (10) condylar articulation between anterior ceratohyal and ventral hypohyal (Davesne et al. 2016; Cantalice et al. 2021).

Synonyms. *Allotriognathi* is an ambiguous (Regan 1907b:638–640; Garstang 1931:259) and a partial (Jordan 1923:165–166) synonym of *Lampriformes*. *Atelaxia* (Starks 1908:1) is a partial synonym of *Lampriformes*. *Lampridiformes* (Goodrich 1909:475–477; Walters and Fitch 1960:442; Greenwood et al. 1966:398; McAllister 1968:106–108; J. S. Nelson 1976:179–180; Lauder and Liem 1983:166; Olney et al. 1993:137; Springer and Johnson 2004:80–81; Wiley and Johnson 2010:127, 147), *Lampridacea* (Wiley and Johnson 2010:127, 147), *Lamprimorpha* (J. S. Nelson et al. 2016:280), and *Lampripterygii* (Betancur-R et al. 2017:20) are ambiguous synonyms of *Lampriformes*.

Comments. *Lampriformes* is the group name most frequently applied to the clade as defined here in several classifications of acanthomorphs (Davis et al. 2016; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil taxa of *Lampriformes* include †*Danatinia casca* and †*Turkmene finitimus* from the Ypresian (56.0–48.1 Ma) of Turkmenistan (Bannikov 1999). Bayesian relaxed molecular clock analyses of *Lampriformes* result in an average posterior crown age estimate of 58.1 million years ago, with the credible interval ranging between 55.8 and 69.7 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Lampridae**
Lophotidae
*Radiicephalidae**
Regalecidae
Trachipteridae
Veliferidae
†*Eolophotes*
†*Megalampris*
†*Oligolophotes*
†*Palaeocentrotidae*
†*Turkmenidae*

Paracanthopterygii P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Myers 1966:352, 396–397 [T. J. Near and C. E. Thacker], converted clade name

Definition. The least inclusive crown clade that contains *Percopsis omiscomaycus* (Walbaum 1792) (*Percopsiformes*) and *Gadus morhua* Linnaeus 1758 (*Gadiformes*). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek παρά (pˈæɹə) meaning beside, ἄκανθα (ækˈænθə) meaning thorn or spine, and πτερὸν (tˈɛɹɑːn) meaning fin or wing.

Registration number. 933.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S1). Phylogenetic relationships of the living lineages and fossil taxa of *Paracanthopterygii* are presented in Figure 13. Placements of the fossil taxa in the phylogeny are on the basis of inferences from morphology (Tyler and Santini 2005; Alvarado-Ortega and Than-Marchese 2012; Murray and Wilson 2014; Davesne et al. 2016, 2017; Cantalice et al. 2021; Schrøder et al. 2022).

Phylogenetics. *Paracanthopterygii* was first delimited as a named group in Greenwood et al.

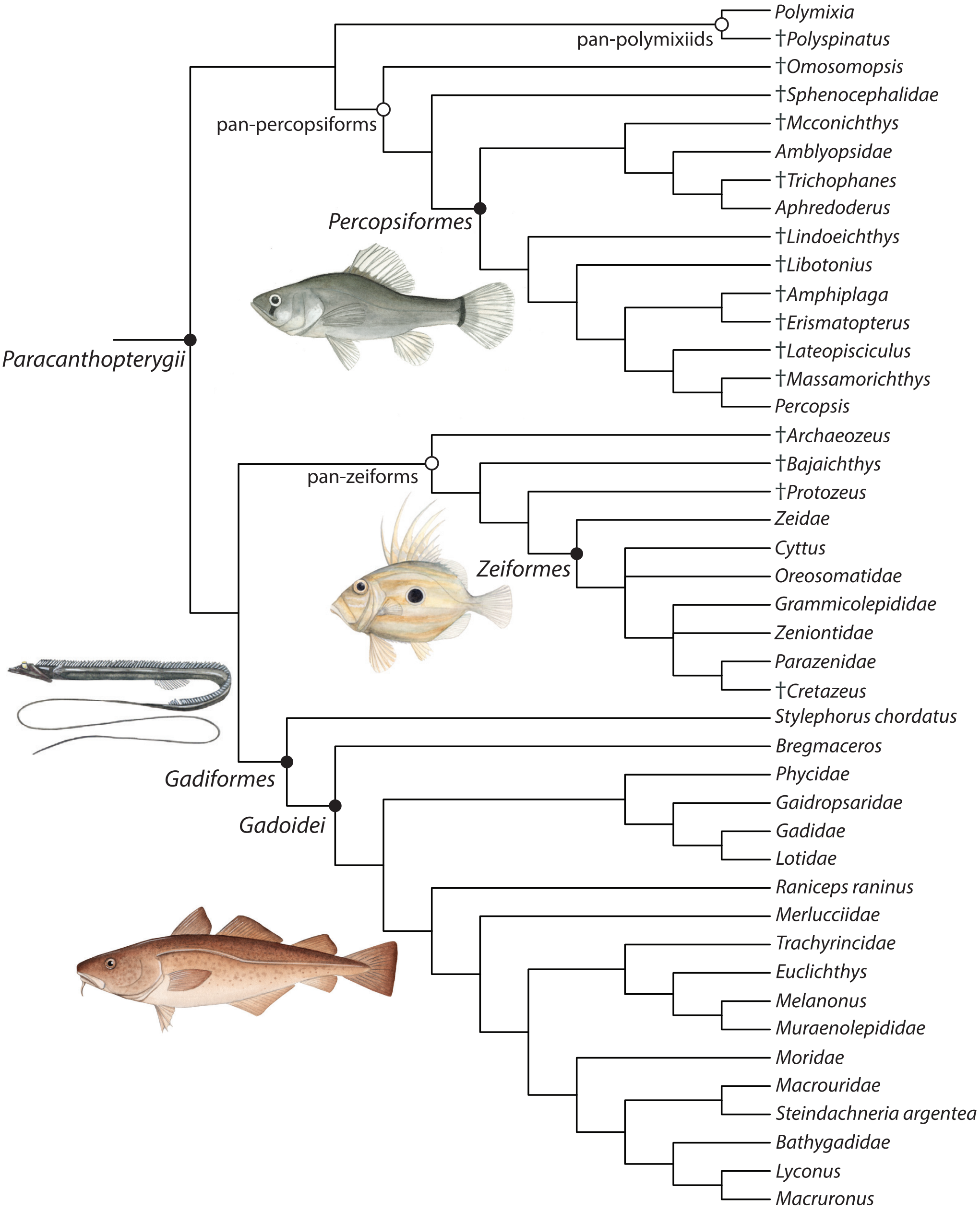

Figure 13. Phylogenetic relationships of the major living lineages and fossil taxa of *Paracanthopterygii*, *Percopsiformes*, *Zeiformes*, *Gadiformes*, and *Gadoidei*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

(1966). Among teleosts there is no other taxonomic group that has had a more fluid history of hypotheses aimed at its composition (Rosen and Patterson 1969; Patterson and Rosen 1989; A. C. Gill 1996; T. Grande et al. 2013). The varied delimitations of *Paracanthopterygii* before the advent of molecular phylogenetics included *Myctophiformes* (Fraser 1972) and the percomorphs *Ophidiiformes*, *Batrachoididae*, *Gobiesocoidei*, *Lophioidei*, and *Zoarcoidei*

(Rosen and Patterson 1969; Fraser 1972; Lauder and Liem 1982; Patterson and Rosen 1989). All of the premolecular delimitations of *Paracanthopterygii* excluded *Zeiformes* because they were considered a lineage of *Acanthopterygii* (Greenwood et al. 1966; Rosen 1984; Patterson and Rosen 1989; G. D. Johnson and Patterson 1993), despite inferences from morphology that argued for common ancestry of zeiforms and paracanthopterygians (M. Gaudant 1979; Gayet 1980b).

The delimitation of *Paracanthopterygii* that includes *Gadiformes*, *Percopsiformes*, *Polymixia*, and *Zeiformes* was first proposed as a result of phylogenetic analyses of whole mtDNA genomes (Miya et al. 2003, 2005), and supported in subsequent molecular studies (W. L. Smith and Wheeler 2006; B. Li et al. 2009; T. Grande et al. 2013; W.-J. Chen Santini, et al. 2014; Malmstrøm et al. 2016; Alfaro et al. 2018; Hughes et al. 2018; Musilova et al. 2019; Roth et al. 2020; Roa-Varón et al. 2021; Ghezelayagh et al. 2022; Mu et al. 2022; J.-F. Wang et al. 2023) as well as a phylogenetic analysis of discretely coded morphological characters (Davesne et al. 2016). A number of molecular phylogenetic analyses do not resolve *Paracanthopterygii* as monophyletic (Wiley et al. 2000; Holcroft 2004; Sparks et al. 2005; Dettaï and Lecointre 2008; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Betancur-R et al. 2017; Near et al. 2013; Davis et al. 2016; Smith et al. 2016), but these studies are either on the basis of relatively small DNA sequence datasets or result in phylogenies with low support at nodes reflecting paracanthopterygian paraphyly.

Long classified in *Lampriformes* (Olney et al. 1993), *Stylephorus chordatus* is consistently resolved in molecular phylogenies as nested within *Paracanthopterygii* as the sister lineage of all other *Gadiformes* (Miya et al. 2007; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Malmstrøm et al. 2016, 2017; Alfaro et al. 2018; T. Grande et al. 2018; Hughes et al. 2018; Musilova et al. 2019; Roth et al. 2020; Ghezelayagh et al. 2022; J.-F. Wang et al. 2023). Within *Paracanthopterygii*, the results of phylogenetic analyses differ, with molecular and morphological studies resolving *Polymixia* and *Percopsiformes* as sister lineages (W.-J. Chen et al. 2003; Miya et al. 2005, 2007; W. L. Smith and Wheeler 2006; Dillman et al. 2011; Alvarado-Ortega and Than-Marchese 2012; Murray and Wilson 2014; Malmstrøm et al. 2016; Alfaro et al. 2018; Musilova et al. 2019; Roth et al. 2020; Cantalice et al. 2021; Ghezelayagh et al. 2022; J.-F. Wang et al. 2023), but other molecular studies resolving *Polymixia* as the sister lineage of all other paracanthopterygians (T. Grande et al. 2013; W.-J. Chen, Santini, et al. 2014; Hughes et al. 2018; Roa-Varón et al. 2021). Bayesian concordance factors estimated using UCE data find the hypothesis that *Polymixia* and *Percopsiformes* are sister lineages is supported by the greatest proportion of sampled loci, and the phylogeny that depicts *Polymixia* as the sister lineage of all other *Paracanthopterygii* is identified as less optimal (Ghezelayagh et al. 2022). Phylogenetic analyses of morphological datasets provide resolution for several fossil lineages of *Paracanthopterygii* (Murray and Wilson 1999; Tyler and Santini 2005; Alvarado-Ortega and Than-Marchese 2012; Murray and Wilson 2014; Davesne et al. 2016, 2017; Cantalice et al. 2021; Schrøder et al. 2022).

Composition. *Paracanthopterygii* currently includes 681 species (Fricke et al. 2023), classified in *Gadiformes*, *Percopsiformes*, *Polymixia*, and *Zeiformes*. Fossil lineages include the pan-polymixiid †*Polyspinatus* (Schrøder et al. 2022), the pan-percopsiforms †*Sphenocephalidae* and †*Omosomopsis* (Patterson 1964; M. Gaudant 1978a; Murray and Wilson 1999; Newbrey et al. 2013; Davesne et al. 2016; Cantalice et al. 2021), and the pan-zeiforms †*Archaeozeus*, †*Bajaichthys*, and †*Protozeus* (Tyler and Santini 2005; Davesne et al. 2017). Details of the ages and locations for the fossil taxa are given in Appendix 1. Over the past 10 years, 35 new species of *Paracanthopterygii* have been described (Fricke et al. 2023), comprising 5.1% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Paracanthopterygii* include (1) presence of a full-length spine on dorsal surface of preural centrum 2 (Borden et al. 2013; T. Grande et al. 2013), (2) insertion sites of interradials on principal caudal and other rays (Borden et al. 2013), (3) first dorsal pterygiophore inserts posterior to neural spine 4 (Davesne et al. 2016; Cantalice et al. 2021), (4) no contact of pelvic girdle posterior to pectoral girdle (Davesne et al. 2016; Cantalice et al. 2021), and (5) base of pelvic fin spine asymmetrical (Cantalice et al. 2021).

Synonyms. *Paracanthomorphacea* (Betancur-R, Broughton, et al. 2013:12–13) is a partial synonym of *Paracanthopterygii*.

Comments. A consistent delimitation of *Paracanthopterygii* that includes *Gadiformes*, *Percopsiformes*, *Polymixia*, and *Zeiformes* in morphological and molecular studies is an important development in the resolution of phylogenetic relationships within *Acanthomorpha*. Remaining issues in the phylogenetics of *Paracanthopterygii* include the relationships of *Percopsiformes* and *Polymixia* and the resolution of the Cretaceous fossil lineages †*Berycopsis*, †*Berycopsia*, †*Dalmatichthys*, †*Homonotichthys*, and †*Omosoma* long classified with *Polymixia* in *Polymixiiformes* (Patterson 1964, 1993; Radovcic 1975; Bannikov and Bacchia 2005; Murray and Cumbaa 2013; Newbrey et al. 2013; Friedman et al. 2016).

The earliest fossils of *Paracanthopterygii* all date to the Cenomanian (100.5–93.9 Ma), including the species of †*Sphenocephalidae*, †*Xenyllion zonensis* from Canada, and the pan-percopsiform †*Omosomopsis simum* from Morocco (Otero and Gayet 1995; M. V. H. Wilson and Murray 1996; Newbrey et al. 2013; Murray and Wilson 2014; Davesne et al. 2016; Cantalice et al. 2021). Bayesian relaxed molecular clock analyses of *Paracanthopterygii* result in an average posterior crown age estimate of 120.7 million years ago, with the credible interval ranging between 101.9 and 135.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Gadiformes
Percopsiformes
*Polymixiidae**
Zeiformes
†*Archaeozeus*
†*Bajaichthys*
†*Omosomopsis*
†*Polyspinatus*
†*Protozeus*
†*Sphenocephalidae*

Percopsiformes L. S. Berg 1937:1279
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Percopsis omiscomaycus* (Walbaum 1792), *Aphredoderus sayanus* (Gilliams 1824), and *Chologaster cornuta* Agassiz 1853. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek πέρκη (pˈɜːke͡ɪ) meaning perch, specifically the freshwater European Perch, *Perca fluviatilis* or the marine Painted Comber, *Serranus scriba* (D. W. Thompson 1947:194–197), and ὄψις (ˈɑːpsɪs) meaning a vision or apparition. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 934.

Reference phylogeny. A phylogeny inferred using DNA sequences from one mtDNA gene and nine nuclear genes (Niemiller et al. 2013, fig. 1). Phylogenetic relationships of the living and fossil lineages of *Percopsiformes* are presented in Figure 13. The placements of fossil taxa in the phylogeny are on the basis of several phylogenetic studies (Murray and Wilson 1999; Borden et al. 2013; T. Grande et al. 2013; Guinot and Cavin 2018; Murray et al. 2020).

Phylogenetics. The delimitation of *Percopsiformes* presented here is consistent with several pre-Hennigian phylogenetic studies based on morphology (Rosen 1962; Gosline 1963a; Greenwood et al. 1966; McAllister 1968; Rosen and Patterson 1969). Phylogenetic analyses of morphological characters are incongruent, with some studies not supporting the monophyly of *Percopsiformes* (Rosen 1985; Patterson and Rosen 1989; Murray and Wilson 1999; Murray et al. 2020), but other analyses resolving *Percopsiformes* as a clade (Springer and Orrell 2004; Davesne et al. 2016; Cantalice et al. 2021). In contrast to the lack of agreement among morphological studies, molecular phylogenetic analyses consistently resolve *Percopsiformes* as monophyletic with *Percopsis* (troutperches) as the sister lineage of a clade containing *Amblyopsidae* (cavefishes) and *Aphredoderus sayanus*

(Pirate Perch) (W. L. Smith and Wheeler 2006; Dillman et al. 2011; Near, Eytan, et al. 2012; T. Grande et al. 2013; Near et al. 2013; Davis et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; T. Grande et al. 2018; Ghezelayagh et al. 2022). The presumed monophyly of *Percopsiformes* was the basis for the selection of *Percopsis* and *Aphredoderus sayanus* as the sole outgroups in morphological and molecular phylogenetic analyses of *Amblyopsidae* (Niemiller et al. 2013; Armbruster et al. 2016; Hart et al. 2020).

<u>Composition.</u> There are currently 13 living species of *Percopsiformes* that include *Aphredoderus sayanus* and species classified in *Percopsis* and *Amblyopsidae* (Poly 2004a, 2004b; Poly and Proudlove 2004; Fricke et al. 2023). Fossil taxa of *Percopsiformes* include †*Lindoeichthys albertensis* from the Maastrichtian Scollard Formation, Canada (Murray et al. 2020), †*Mcconichthys longipinnis* from the Danian Tullock Member, USA (L. Grande 1988), †*Amphiplaga brachyptera* and †*Erismatopterus levatus* from the Ypresian Green River Formation, USA (Cope 1871c, 1877a; L. Grande 1984), †*Libotonius blakeburnensis* from the Ypresian Blakeburn Mine, Canada (M. V. H. Wilson 1977), †*Lateopisciculus turrifumosus* and †*Massamorichthys wilsoni* from the Selandian–Thanetian Paskapoo Formation, Canada (Murray 1996; Murray and Wilson 1996), and †*Tricophanes foliarum* from the Priabonian Florissant, USA (Cope 1878; Meyer 2003:179). Details of the ages and locations for the fossil taxa are given in Appendix 1. In the last 10 years, a single new living species of *Percopsiformes* has been described (Chakrabarty et al. 2014; Fricke et al. 2023), comprising 8.3% of the living species diversity in the clade. Analyses of morphology and genomic data indicate that there are three additional species of *Aphredoderus* awaiting formal taxonomic description (Muller 2023).

<u>Diagnostic apomorphies.</u> Morphological apomorphies for *Percopsiformes* include (1) absence of postmaxillary process on premaxilla (Patterson and Rosen 1989; Murray and Wilson 1999; Davesne et al. 2016; Cantalice et al. 2021), (2) six branchiostegal rays (Murray and Wilson 1999), (3) presence of opercular dorsal projection that is anteriorly truncated or excavated (Murray and Wilson 1999), (4) transverses dorsales and obliqui dorsalis are combined and have a trapezoidal shape in dorsal view (Springer and Johnson 2004; Wiley and Johnson 2010), (5) obliquus dorsalis 4 extends posteriorly to insert on levator process of epibranchial 4 (Springer and Johnson 2004; Wiley and Johnson 2010), (6) two hypural plates do not contact any ural centra (Borden et al. 2013), (7) presence of a two-headed cranio-hyomandibular articulation (Davesne et al. 2016; Cantalice et al. 2021), (8) posterior and anterior ceratohyals sutured (Davesne et al. 2016; Cantalice et al. 2021), (9) metapterygoid contacts quadrate (Cantalice et al. 2021), and (10) condylar articulation between the anterior ceratohyal and ventral hypohyal (Cantalice et al. 2021).

<u>Synonyms.</u> *Percopsacea* (Wiley and Johnson 2010:147) and *Percopsaria* (Betancur-R et al. 2017:20) are ambiguous synonyms of *Percopsiformes*. *Salmopercae* (Goodrich 1909:425–426; Regan 1909a:79, 84–85, 1911b:294, 1929:305, 318) is a partial synonym of *Percopsiformes*.

<u>Comments.</u> *Percopsiformes* is the group name consistently applied to the clade as defined here (Rosen and Patterson 1969; Wiley and Johnson 2010; Davis et al. 2016; J. S. Nelson et al. 2016:287–289; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Percopsiformes* is †*Lindoeichthys albertensis* from Canada (Murray et al. 2020). Bayesian relaxed molecular clock analyses of *Percopsiformes* result in an average posterior crown age estimate of 53.5 million years ago, with the credible interval ranging between 40.1 and 72.4 million years ago (Ghezelayagh et al. 2022).

<u>Constituent lineages.</u> Redundant group names are marked with an asterisk.

Amblyopsidae
*Aphredoderidae**
*Percopsidae**
†*Amphiplaga*
†*Erismatopterus*
†*Lateopisciculus*
†*Libotonius*
†*Lindoeichthys*
†*Massamorichthys*
†*Mcconichthys*
†*Tricophanes*

Zeiformes L. S. Berg 1937:1279
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Zeus faber* Linnaeus 1758, *Cyttus australis* (Richardson 1843), *Cyttopsis rosea* (Lowe 1843), and *Macrurocyttus acanthopodus* (Fowler 1934). This is a minimum-crown-clade definition.

Etymology. Zeus is the god of thunder and the sky in ancient Greek religion. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 940.

Reference phylogeny. A phylogeny inferred from DNA sequences of three mtDNA regions and five nuclear genes (T. Grande et al. 2018, fig. 3). Phylogenetic relationships of the living lineages and fossil taxa of *Zeiformes* are presented in Figure 13. Placements of the fossil taxa in the phylogeny are on the basis of analyses of morphological characters (Tyler and Santini 2005; Davesne et al. 2017).

Phylogenetics. Prior to molecular phylogenetic analyses, *Zeiformes* was classified as a lineage of *Acanthopterygii* (Greenwood et al. 1966; Rosen 1984; G. D. Johnson and Patterson 1993). Molecular analyses consistently resolve *Zeiformes* and *Gadiformes* as sister lineages (Wiley et al. 2000; W.-J. Chen et al. 2003; Miya et al. 2003, 2005, 2007; Sparks et al. 2005; W. L. Smith and Wheeler 2006; Dettaï and Lecointre 2008; B. Li et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; Malmstrøm et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Roth et al. 2020; Roa-Varón et al. 2021; Ghezelayagh et al. 2022; Mu et al. 2022).

There are two sets of phylogenetic analyses of *Zeiformes* based on morphological characters that result in very different phylogenetic trees. A group of two morphological phylogenies work from the premise that *Zeiformes* are acanthopterygians and consequently use species of *Beryciformes*, *Trachichthyiformes*, *Antigonia*, *Tetraodontoidei*, *Moronidae*, and *Capros aper* as outgroups (Tyler et al. 2003; Tyler and Santini 2005). The other morphological phylogeny follows the inferences stemming from molecular phylogenetic analyses and uses species of *Polymixia*, *Percopsiformes*, and *Gadiformes* as outgroup taxa (T. Grande et al. 2018). Both sets of phylogenetic analyses resolve most of the major lineages (e.g., *Cyttus* [lookdown dories], *Oreosomatidae* [oreos], *Parazenidae* [smooth dories], *Zeidae* [dories], and *Zeniontidae* [armoreye dories]) of *Zeiformes* as monophyletic (Tyler et al. 2003; Tyler and Santini 2005; T. Grande et al. 2018), but the resolution of *Macrurocyttus acanthopodus* (Dwarf Dory) renders *Grammicolepididae* (tinselfishes) as paraphyletic in one of the studies (T. Grande et al. 2018). The two morphological phylogenies are completely incongruent with regard to the relationships among the major lineages of *Zeiformes* (Tyler et al. 2003; Tyler and Santini 2005; T. Grande et al. 2018), perhaps a result of using acanthopterygian rather than paracanthopterygian outgroups (T. Grande et al. 2018).

Relationships within *Zeiformes* inferred from a molecular phylogenetic analysis are not congruent with either of the morphological inferred phylogenies, but are more similar to the trees resulting from analyses using *Paracanthopterygii* as outgroups (T. Grande et al. 2018). In the molecular phylogeny, *Zeidae* is the sister lineage of all other *Zeiformes*, *Zeniontidae* is paraphyletic because *Capromimus* is resolved as the sister lineage of *Oreosomatidae*, and *Grammicolepididae*, *Parazenidae*, and *Zenion* are resolved as monophyletic. Relationships among the lineages of *Zeiformes* resolved in the molecular phylogeny are not strongly supported and are reasonably interpreted as a polytomy near the inferred common ancestor of the clade, which is indicative of a period of rapid lineage diversification early in the evolutionary history of *Zeiformes* (T. Grande et al. 2018). The enigmatic and infrequently encountered *Macrurocyttus* is not sampled in any molecular phylogeny, and analyses of combined molecular and morphological datasets resolve this lineage as a deeply branching sister lineage of all other *Zeiformes* (T. Grande et al. 2018).

Composition. There are currently 33 living species of *Zeiformes* classified in *Cyttus*, *Grammicolepididae*, *Oreosomatidae*, *Parazenidae*, *Zeidae*, and *Zeniontidae* (Fricke et al. 2023). Fossil taxa of *Zeiformes* include the pan-parazenid †*Cretazeus* and several species from the Oligocene and Miocene classified as *Zeus* and *Zenopsis* (Tyler et al. 2000, 2003; Tyler and Santini 2005; Santini et al. 2006). Details of the ages and locations for the fossil taxa are given in Appendix 1. In the last 10 years, a single new living species of *Zeiformes* has been described (Kai and Tashiro 2019; Fricke et al. 2023), comprising 3.0% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Zeiformes* include (1) distal portions of proximal-middle dorsal fin radials laterally expanded (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (2) distal radials of spinous portion of dorsal fin absent or reduced to minuscule cartilaginous or incompletely ossified elements (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (3) palatine has a mobile articulation with ectopterygoid that is dorsally truncated (G. D. Johnson and Patterson 1993; Tyler et al. 2003; Wiley and Johnson 2010; T. Grande et al. 2018), (4) reduced metapterygoid (G. D. Johnson and Patterson 1993; Tyler et al. 2003; Wiley and Johnson 2010; T. Grande et al. 2013, 2018), (5) flexible articulations on anterior vertebral centra; if ribs are present they are never anterior to fourth vertebra (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (6) pharyngobranchials 2 and 3 with upright columnar processes (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (7) absence of pharyngobranchial 4 and upper pharyngeal tooth plate (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010; T. Grande et al. 2018), (8) area below frontals from ethmoid cartilage to parasphenoid with a continuous medial cartilage (G. D. Johnson and Patterson 1993; Tyler et al. 2003; Wiley and Johnson 2010), (9) second pleural centrum with full neural spine (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (10) proximally truncated parhypural (G. D. Johnson and Patterson 1993; Tyler et al. 2003; Wiley and Johnson 2010), (11) presence of 3.5 gills and seven hemibranchs (Tyler et al. 2003), (12) dorsal-, anal-, and pectoral-fin rays unbranched (Tyler et al. 2003; Wiley and Johnson 2010), (13) absence of uncinate process on epibranchial 1 (Tyler et al. 2003; T. Grande et al. 2018), (14) absence of open gill slit between branchial arches 4 and 5 (Tyler et al. 2003; T. Grande et al. 2018), (15) fusion of hypurals 1–2 and 3–4; both elements fused to centrum (Tyler et al. 2003; Wiley and Johnson 2010; T. Grande et al. 2018), (16) first proximal radial of dorsal fin and first neural arch and spine in contact (T. Grande et al. 2013), (17) principal caudal-fin rays the only insertion site of caudal fin interradialis muscle (Borden et al. 2013), presence of single procurrent caudal-fin ray (T. Grande et al. 2018), and (18) 12 principal caudal-fin rays (T. Grande et al. 2018).

Synonyms. *Zeoidei* (Regan 1909a:80; Jordan 1923:171), *Zeomorphi* (Regan 1910a:481–482; Rosen 1984:44; Zehren 1987, fig. 1), *Zeacea* (Wiley and Johnson 2010:150), and *Zeiariae* (Betancur-R et al. 2017:20) are ambiguous synonyms of *Zeiformes*.

Comments. Since the mid-20th century *Zeiformes* was consistently applied as the group name for the clade defined above and was selected as the clade name over its synonyms because it is the name most frequently applied to a taxon approximating the named clade (e.g., Greenwood et al. 1966; Wiley et al. 2000; Borden et al. 2013; T. Grande et al. 2013; Davis et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022).

The earliest fossil *Zeiformes* is †*Cretazeus rinaldii* from the Campanian-Maastrichtian of Italy (Appendix 1; Tyler et al. 2000). Bayesian relaxed molecular clock analyses of *Zeiformes* result in an average posterior crown age estimate of 50.0 million years ago, with the credible interval ranging between 37.3 and 72.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Cyttidae**
Grammicolepididae
Oreosomatidae
Parazenidae
Zeidae
Zeniontidae
†*Cretazeus*

Gadiformes P. Bleeker 1859:xxvi

Definition. The least inclusive crown clade that contains *Stylephorus chordatus* Shaw 1791 and *Gadus morhua* Linnaeus 1758. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek γάδος (ɡˈɑːdo͡ʊz), which was a name applied to the European Hake, *Merluccius merluccius* (D. W. Thompson 1947:38). The suffix is from the Latin *forma* meaning form, figure, or appearance.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S1). Phylogenetic relationships of the major lineages of *Gadiformes* are presented in Figure 13.

Phylogenetics. Historically, *Stylephorus chordatus* was classified in *Lampriformes* (Regan 1908; Olney et al. 1993; J. S. Nelson 2006:228–229) and *Gadoidei* was hypothesized to be closely related to *Batrachoididae* and *Lophioidei* (Patterson and Rosen 1989). A more recent phylogenetic analysis of *Acanthomorpha* based on morphological characters resolves *Gadoidei* as the sister lineage to a clade containing *Stylephorus* and *Zeiformes* (Davesne et al. 2016). On the other hand, molecular phylogenetic analyses consistently resolve *Stylephorus* and *Gadoidei* as a monophyletic group (Miya et al. 2007; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Davis et al. 2016; Smith et al. 2016; Alfaro et al. 2018; T. Grande et al. 2018; Hughes et al. 2018; Roth et al. 2020; Ghezelayagh et al. 2022; Mu et al. 2022; J.-F. Wang et al. 2023).

Composition. There are currently 625 living species of *Gadiformes* (Fricke et al. 2023) that include *Stylephorus chordatus* and species classified in *Gadoidei*. Over the past 10 years, 32 new species of *Gadiformes* have been described (Cohen et al. 1990; Fricke et al. 2023), comprising 5.1% of the species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gadiformes* include (1) levator arcus palatini lies lateral to section A_2 of adductor mandibulae (T. Grande et al. 2013), (2) interradialis located only between caudal-fin rays (Borden et al. 2013), (3) hypochondral longtudinalis absent (Borden et al. 2013), and (4) most ural centra and pleural centra 2–4 exposed after removal of body musculature (Borden et al. 2013).

Synonyms. *Gadariae* (Betancur-R et al. 2017:20) is an ambiguous synonym of *Gadiformes*.

Comments. Since the first phylogenetic analysis that resolved *Stylephorus* and *Gadoidei* as a monophyletic group (Miya et al. 2007), the substantial molecular evidence is supported by the discovery of morphological apomorphies providing confidence to the resolution of a more inclusive *Gadiformes* that includes *Stylephorus* (Borden et al. 2013). Bayesian relaxed molecular clock analyses of *Gadiformes* result in an average posterior crown age estimate of 88.4 million years ago, with the credible interval ranging between 72.9 and 105.4 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Gadoidei

*Stylephoridae**

Gadoidei L. J. F. J. Fitzinger 1832:331

Definition. The least inclusive crown clade that contains *Bregmaceros cantori* Milliken and Houde 1984, *Gadus morhua* Linnaeus 1758, and *Macruronus novaezelandiae* (Hector 1871). This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek γάδος (ɡˈɑːdo͡ʊz), which was a name applied to the European Hake, *Merluccius merluccius* (D. W. Thompson 1947:38).

Reference phylogeny. A phylogeny inferred from DNA sequences of 14,208 exons (Roa-Varón et al. 2021, fig. 4). Phylogenetic relationships of the major lineages of *Gadoidei* are presented in Figure 13.

Phylogenetics. Precladistic studies of relationships within *Gadoidei* concluded that

Melanonus (pelagic cods) (Marshall 1965, 1966; Marshall and Cohen 1973) or *Muraenolepididae* (eel cods) (Rosen and Patterson 1969; Cohen 1984) represented the lineage with the least derived morphology in the clade. A theme in the study of gadoid morphology is that lineages are characterized by combinations of ancestral and derived character states (Rosen and Patterson 1969; Cohen 1984; Okamura 1989; Endo 2002). The heterogeneous nature of gadoid morphology is reflected in the dramatically minimal congruence among the more than 10 morphological phylogenies that examined a wide range of osteological, myological, and otolith characters (J. R. Dunn 1989; Howes 1989, 1991a, 1993; Iwamoto 1989; Markle 1989; Nolf and Steurbaut 1989; Okamura 1989; Howes 1990; Siebert 1990; Endo 2002; Teletchea et al. 2006; Grand et al. 2014). Heterochronic evolution has been invoked to explain the characteristic mosaic of ancestral and derived morphology in *Gadoidei* (Endo 2002), highlighting the potential challenges of using morphological characters to resolve phylogenetic relationships within the clade.

The first set of molecular phylogenetic studies of *Gadoidei* utilized data from Sanger-sequenced mitochondrial and nuclear genes and resulted in phylogenies with relatively poor node support (Møller et al. 2002; Bakke and Johansen 2005; Teletchea et al. 2006; von der Heyden and Matthee 2008; Roa-Varón and Ortí 2009; Betancur-R et al. 2017), limiting the ability of these analyses to resolve the deepest nodes in the gadoid phylogeny. Despite the challenge of limited resolution, the first group of gadoid molecular phylogenies demonstrated that previous delimitations of *Merlucciidae* (merluccid hakes) (Inada 1989; Cohen et al. 1990; Lloris et al. 2005) are not monophyletic, motivating the recognition of the monogeneric taxonomic families *Macruronidae* (southern grenadiers), *Lyconidae* (Atlantic hakes), and *Steindachneriidae* (*Steindachneria argentea*, Luminous Hake) (von der Heyden and Matthee 2008; Roa-Varón and Ortí 2009).

Next-generation phylogenomic analyses vary in the level of resolution and node support, but all result in phylogenies in which *Bregmaceros* (codlets) is placed as the sister lineage of all other *Gadoidei* (Malmstrøm et al. 2016; Hughes et al. 2018; Han et al. 2021; Roa-Varón et al. 2021; Ghezelayagh et al. 2022). The phylogenetic resolution of *Bregmaceros* is consistent with the observation that this lineage is “fundamentally different myologically and osteologically from other gadoids” (Rosen and Patterson 1969:427). The phylogenomic analyses agree with several earlier molecular studies in resolving *Gadidae* (cods), *Lotidae* (burbots), and *Phycidae* (hakes), all previously classified as *Gadidae*, as a monophyletic group (von der Heyden and Matthee 2008; Roa-Varón and Ortí 2009; Betancur-R et al. 2017). There is appreciable congruence among the trees generated from phylogenomic analyses but there is disagreement regarding the relationships of *Muraenolepididae*, *Trachyrincidae* (armored grenadiers), *Melanonus*, and *Merlucciidae* (Malmstrøm et al. 2016; Hughes et al. 2018; Han et al. 2021; Roa-Varón et al. 2021; Ghezelayagh et al. 2022).

<u>Composition.</u> There are currently 624 living species of *Gadoidei* that include *Raniceps raninus* (Tadpole Fish), *Steindachneria argentea*, and species classified in *Bathygadidae* (rattails), *Bregmaceros*, *Euclichthys* (eucla cods), *Gadidae*, *Gaidropsaridae* (rocklings), *Lotidae*, *Lyconus*, *Macrouridae* (grenadiers), *Macruronus* (blue grenadiers), *Melanonus*, *Merlucciidae*, *Moridae* (morid cods), *Muraenolepididae*, *Phycidae*, and *Trachyrincidae* (Cohen et al. 1990; Lloris et al. 2005; Roa-Varón et al. 2021; Fricke et al. 2023). Over the past 10 years, 32 new species of *Gadoidei* have been described (Fricke et al. 2023), comprising 5.1% of the living species diversity in the clade.

<u>Diagnostic apomorphies.</u> Morphological apomorphies for *Gadoidei* include (1) presence of X and Y bones in caudal skeleton (Cohen 1984; Fahay and Markle 1984; Markle 1989; Patterson and Rosen 1989), (2) first neural spine joined to occipital crest (Cohen 1984; Patterson and Rosen 1989), (3) larvae with anus that exits through the finfold (Fahay and Markle 1984; Markle 1989), (4) absence of ribs or epipleurals on vertebrae 1 and 2 (Markle 1989; Patterson and Rosen 1989; Howes 1993), (5) scapular foramen located between scapula and coracoid (Markle 1989; Patterson and

Rosen 1989; Howes 1993; Endo 2002; Wiley and Johnson 2010), (6) notch in the front of the prootic is exit point for trigeminal and facial nerves from braincase, with absence of lateral commissure or trigeminofacial chamber (Patterson and Rosen 1989), (7) anal and dorsal fins with three fin rays per segment (Patterson and Rosen 1989), (8) head canals with 33 neuromasts (Patterson and Rosen 1989), (9) presence of three struts on pharyngobranchial 3 (Markle 1989), (10) otolith with pince-nez-shaped sulcus and lateral collicular (Nolf and Steurbaut 1989; Endo 2002; Wiley and Johnson 2010), (11) absence of jugular foramen (Howes 1991a, 1993), (12) attrition of anterior border of lateral face of hyomandibular, exposing pathway of the hyoid branch of the facial nerve (Howes 1993), (13) dorsal hyomandibular with a single condyle (Endo 2002; Wiley and Johnson 2010), (14) basihyal absent (Endo 2002; Wiley and Johnson 2010; T. Grande et al. 2013), (15) flexor dorsalis and flexor ventralis separate with some bundles serving a single ray compounded (Borden et al. 2013), (16) flexor dorsalis and flexor dorsalis superior are a single muscle mass (Borden et al. 2013), and (17) flexor ventralis and flexor ventralis inferior are a single muscle mass (Borden et al. 2013).

Synonyms. *Gadiformes* (e.g., Cohen 1984; Patterson and Rosen 1989:13–19; Cohen et al. 1990, fig. 1; A. C. Gill and Mooi 2002, tbl. 2.3; Wiley and Johnson 2010:148–149; J. S. Nelson et al. 2016:293–302; Betancur-R et al. 2017:20) is an ambiguous synonym of *Gadoidei*.

Comments. The application of phylogenetic systematics has contributed to a flux in the classification of lineages that comprise *Gadoidei* since the mid-1980s (Cohen 1984; Markle 1989; Endo 2002; Roa-Varón and Ortí 2009; Roa-Varón et al. 2021). A more recent Linnaean classification of gadoids has an abundance of redundant group names as it recognizes 17 families of which seven comprise a single genus and five suborders of which three contain a single family (Roa-Varón et al. 2021).

The early fossil record of *Gadoidei* is dominated by otoliths (Kriwet and Hecht 2008). The earliest otolith fossils of *Gadoidei* include †*Rhinocephalus cretaceus* and †*Archaemacruroides vanknippenbergi* from the Maastrichtian (72.2–66.0 Ma) of Belgium and Netherlands (Schwarzhans and Jagt 2021), and †*Dakotaichthys hogansoni*, †*Palaeogadus weltoni*, and †*Archaemacruroides bratishkoi* from the Maastrichtian of Texas, USA (Schwarzhans and Stringer 2020). Bayesian relaxed molecular clock analyses of *Gadoidei* result in an average posterior crown age estimate of 77.0 million years ago, with the credible interval ranging between 61.5 and 98.2 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Bathygadidae
*Bregmacerotidae**
*Euclichthyidae**
Gadidae
Gaidropsaridae
Lotidae
*Lyconidae**
Macrouridae
*Macruronidae**
*Melanonidae**
Merlucciidae
Moridae
Muraenolepididae
Phycidae
*Ranicipitidae**
*Steindachneriidae**
Trachyrincidae

Acanthopterygii P. Artedi 1738:26

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Diretmus argenteus* Johnson 1864 (*Trachichthyiformes*), *Beryx decadactylus* Cuvier 1829 in Cuvier and Valenciennes (1829b) (*Beryciformes*), *Holocentrus rufus* (Walbaum 1792) (*Beryciformes*), *Carapus bermudensis* (Jones 1874) (*Ophidiiformes*), and *Micropterus salmoides* (Lacépède 1802) (*Centrarchiformes*), but not *Percopsis omiscomaycus* (Walbaum 1792) (*Percopsiformes*) nor *Gadus morhua* Linnaeus 1758 (*Gadiformes*). This is a minimum-crown-clade definition with external specifiers.

Etymology. From the ancient Greek ἄκανθα (ækˈænθə) meaning thorn or spine and πτερόν (tˈɛɹɑːn) meaning feather, wing, or any winged animal.

Registration number. 943.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S2–S25). Phylogenetic relationships of the major lineages of *Acanthopterygii* are presented in Figures 2 and 14. The placements of the pan-trachichthyiforms †*Judeoberyx* and †*Lissoberyx*, and the pan-percomorph †*Pepemkay* in the phylogeny are on the basis of inferences from morphological studies (Moore 1993a, 1993b; Patterson 1993; Friedman 2009; Cantalice et al. 2021).

Phylogenetics. Morphological and molecular phylogenetic analyses consistently support the monophyly of *Acanthopterygii* (Miya et al. 2003, 2005; W. L. Smith and Wheeler 2006; Alfaro, Santini, et al. 2009; Santini et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davesne et al. 2016; Davis et al. 2016; Malmstrøm et al. 2016, 2017; Smith et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Musilova et al. 2019; Roth et al. 2020; Cantalice et al. 2021; Ghezelayagh et al. 2022; Mu et al. 2022; J.-F. Wang et al. 2023). However, earlier morphological studies nested the paracanthopterygian *Zeiformes* in *Acanthopterygii* (Stiassny and Moore 1992; G. D. Johnson and Patterson 1993).

Phylogenetic analyses of *Acanthopterygii* differ on the relationships among *Trachichthyiformes*, *Beryciformes*, and *Percomorpha*. Morphological phylogenetic studies led to delimitations of *Trachichthyiformes* and *Beryciformes* that differ from current classifications and deviate from one another primarily in the relationships of *Holocentridae* and *Berycidae* (Rosen 1973; Stiassny and Moore 1992; G. D. Johnson and Patterson 1993; Moore 1993b). Molecular studies result in four sets of phylogenies of *Acanthopterygii*: a clade containing *Beryciformes* and *Trachichthyiformes* that is the sister lineage of *Percomorpha* (W. L. Smith and Wheeler 2006; Alfaro, Santini, et al. 2009; Santini et al. 2009; Near, Eytan, et al. 2012; T. Grande et al. 2013; Near et al. 2013; Malmstrøm et al. 2017; Mu et al. 2022), *Beryciformes* (excluding *Holocentridae*) and *Trachichthyiformes* as a monophyletic group that is the sister lineage of *Holocentridae* (Near et al. 2013; Rabosky et al. 2018; J.-F. Wang et al. 2023), *Beryciformes* (excluding *Holocentridae*) and *Trachichthyiformes* as a monophyletic group that is the sister lineage of a clade containing *Holocentridae* and *Percomorpha* (Betancur-R, Broughton, et al. 2013; Smith et al. 2016; Betancur-R et al. 2017), and *Trachichthyiformes* as the sister lineage of a clade containing *Beryciformes* and *Percomorpha* (Figures 2 and 14; Miya et al. 2003, 2005; Thacker 2009; W.-J. Chen, Santini, et al. 2014; Malmstrøm et al. 2016; Dornburg et al. 2017; Hughes et al. 2018, fig. S2; Musilova et al. 2019; Roth et al. 2020; Ghezelayagh et al. 2022).

Morphological studies aimed at resolving the relationships of several Cretaceous acanthomorph fossil lineages place *Hoplostethus* (*Trachichthyiformes*) as the sister lineage of a clade containing *Sargocentron* (*Beryciformes*) and *Percomorpha*, but these studies are limited in taxon sampling and do not test the monophyly of *Trachichthyiformes* or *Beryciformes* (Davesne et al. 2016; Cantalice et al. 2021). Bayesian concordance factors estimated in a phylogenomic analysis of UCE loci find the hypothesis that *Beryciformes* and *Percomorpha* are sister lineages is supported by the greatest proportion of sampled loci, and phylogenies that depict either *Holocentridae* or a clade containing *Beryciformes* and *Trachichthyiformes* as the sister lineage of *Percomorpha* are less optimal (Ghezelayagh et al. 2022).

Composition. There are currently more than 19,185 living species of *Acanthopterygii* classified in *Trachichthyiformes*, *Beryciformes*, and *Percomorpha*. Fossil lineages include the pan-trachichthyiforms †*Judeoberyx* and †*Lissoberyx* (Patterson 1967; Gayet 1980b), and the pan-percomorph †*Pepemkay* (Alvarado-Ortega and Than-Marchese 2013). Details of the ages and locations of fossil taxa are presented in Appendix 1. Over the past 10 years, 1,641 new living species of *Acanthopterygii* have been described (Fricke et al. 2023), comprising 8.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Acanthopterygii* include (1) retractor dorsalis muscle inserts primarily on pharyngobranchial 3 (Rosen 1973), (2) reduction of surface of epibranchial 4 and enlargement of epibranchials 2 and 3, which form the

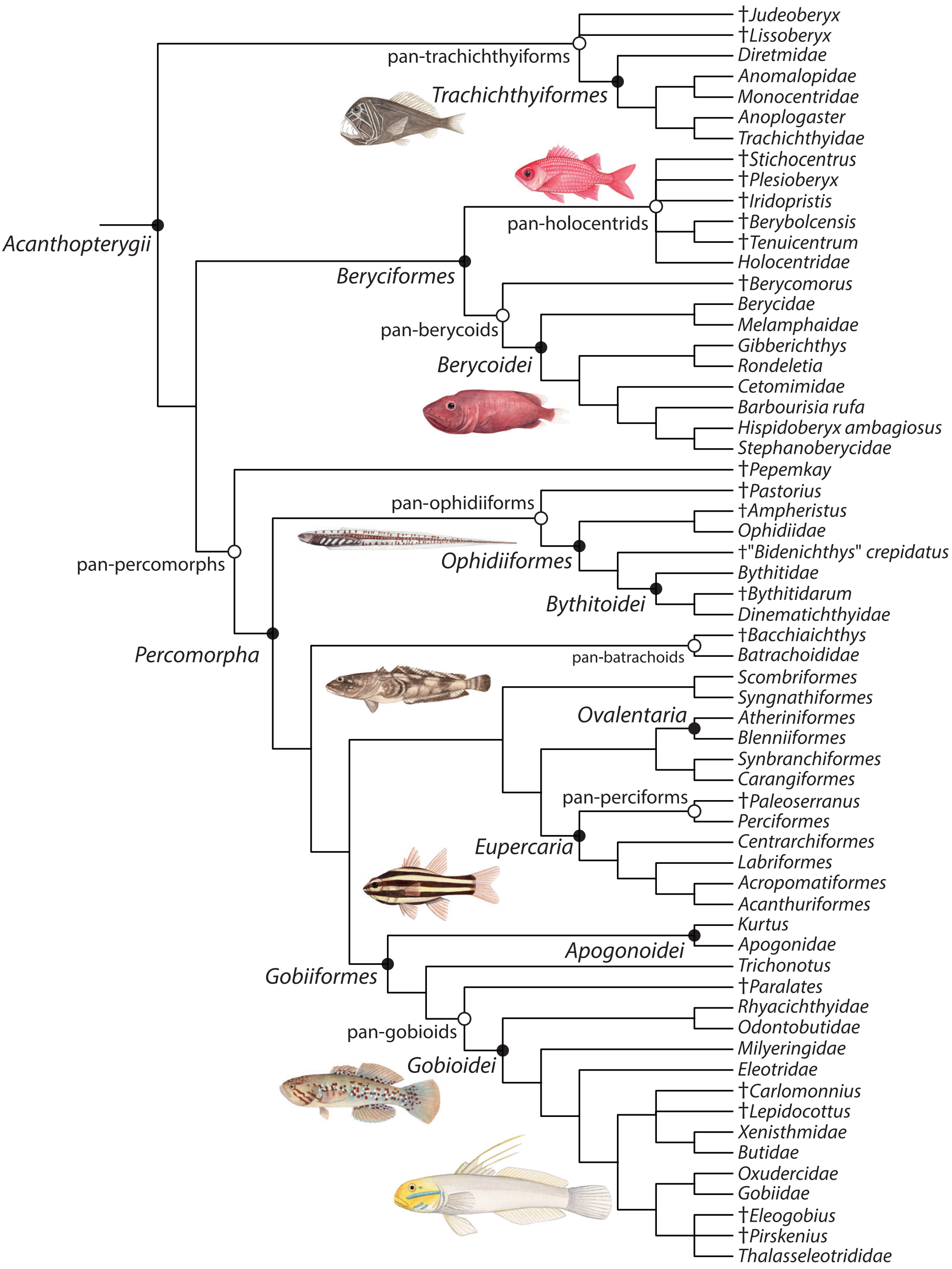

FIGURE 14. Phylogenetic relationships of the major living lineages and fossil taxa of *Acanthopterygii*, *Trachichthyiformes*, *Beryciformes*, *Berycoidei*, *Percomorpha*, *Ophidiiformes*, *Bythitoidei*, *Gobiiformes*, *Apogonoidei*, *Gobioidei*, *Ovalentaria*, and *Eupercaria*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

primary support for the upper pharyngeal jaw dentition (Rosen 1973), (3) presence of two hyomandibular articulation facets (Davesne et al. 2016), (4) proximal insertion of Baudelot's ligament onto the basioccipital (Davesne et al. 2016), and (5) presence of an antero-median pelvic process (Davesne et al. 2016).

Synonyms. *Euacanthomorphacea* (Betancur-R, Broughton, et al. 2013, app. 2) is an ambiguous synonym of *Acanthopterygii*. *Euacanthopterygii* (G. D. Johnson and Patterson 1993:607) is an approximate synonym of *Acanthopterygii*.

Comments. Classifications of *Acanthomorpha* differ in the application of the group name *Acanthopterygii*: (1) to the paraphyletic group that includes *Zeiformes*, *Lampriformes*, *Trachichthyiformes*, *Beryciformes*, and *Percomorpha* (Greenwood et al. 1966); (2) the likely paraphyletic group containing *Lampriformes*, *Trachichthyiformes*, *Beryciformes*, and *Percomorpha* (Davis et al. 2016); and (3) the clade containing *Trachichthyiformes*, *Beryciformes*, and *Percomorpha* as defined here (J. S. Nelson et al. 2016:302–303; Betancur-R et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022). The name *Acanthopterygii* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The morphological characterization of *Acanthopterygii* was hampered by previous phylogenetic studies and resulting classifications that placed the acanthopterygian lineages *Ophidiiformes*, *Batrachoididae*, and *Lophioidei* into *Paracanthopterygii* and treated the paracanthopterygian *Zeiformes* as an acanthopterygian (Lauder and Liem 1983; J. S. Nelson 1984, 1994, 2006; Rosen 1984; Patterson and Rosen 1989; Stiassny and Moore 1992; G. D. Johnson and Patterson 1993). The concept of *Acanthopterygii* as limited to *Trachichthyiformes*, *Beryciformes*, and *Percomorpha* originated from many molecular phylogenetic analyses (e.g., Miya et al. 2003; Alfaro, Santini, et al. 2009; Near, Eytan, et al. 2012; W.-J. Chen, Santini, et al. 2014; Malmstrøm et al. 2016; Ghezelayagh et al. 2022) and is validated in phylogenetic analyses of morphological characters (Davesne et al. 2016; Cantalice et al. 2021).

The earliest acanthopterygian fossils date to the Cenomanian (100.5–93.9 Ma) (Patterson 1993; Friedman 2009, 2010; Murray 2016). Bayesian relaxed molecular clock analyses of *Actinopterygii* result in an average posterior age estimate of 137.4 million years ago, with the credible interval ranging between 129.1 and 147.3 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.
Beryciformes
Percomorpha
Trachichthyiformes
†*Judeoberyx*
†*Lissoberyx*
†*Pepemkay*

Trachichthyiformes M. L. J. Stiassny and J. A. Moore 1992:212, figs. 14, 15, and 16
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Trachichthys australis* Shaw 1799 in Shaw and Nodder (1799), *Diretmus argenteus* J. Y. Johnson 1864, and *Aulotrachichthys prosthemius* (Jordan and Fowler 1902), but not *Beryx decadactylus* Cuvier in Cuvier and Valenciennes (1829b) nor *Holocentrus rufus* (Walbaum 1792). This is a minimum-crown-clade definition with external specifiers.

Etymology. From the ancient Greek τρᾱχὐς (tɹˈeɪ͡kəs) meaning rough and ἰχθὐς (ˈɪkθuːs) meaning fish. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 944.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S2). Although *Trachichthys australis* is not included in the reference phylogeny, it resolves in a clade with other species of *Trachichthyidae* in a phylogenetic analysis of morphological characters (Zehren 1979, figs. 4, 5). Phylogenetic relationships of the major lineages of *Trachichthyiformes* are presented in Figure 14.

Phylogenetics. Morphological analyses resolved the prephylogenetic delimitation of *Beryciformes* as paraphyletic relative to *Zeiformes* and *Percomorpha* (Stiassny and Moore

1992; G. D. Johnson and Patterson 1993). The relationships of these lineages differed among morphological phylogenetic analyses. One set of studies introduced *Trachichthyiformes* as a clade that includes *Anomalopidae* (flashlight fishes), *Anoplogaster* (fangtooths), *Diretmidae* (spinyfins), *Monocentridae* (pinecone fishes), *Trachichthyidae* (roughies), and all lineages delimited here as *Beryciformes* except for *Berycidae* (alfonsinos) and *Holocentridae* (squirrelfishes) (Stiassny and Moore 1992; Moore 1993b). In a different analysis of morphological characters, a clade *Stephanoberyciformes* was resolved that includes all lineages delimited here as *Beryciformes* to the exclusion of *Berycidae* and *Holocentridae* and a definition of *Beryciformes* that included what is delimited here as *Trachichthyiformes* with the addition of *Berycidae* and *Holocentridae* (G. D. Johnson and Patterson 1993).

The monophyly of *Trachichthyiformes* is supported in morphological (Zehren 1979; Moore 1993b; Baldwin and Johnson 1995; Konishi and Okiyama 1997) and molecular phylogenetic studies (Miya et al. 2003, 2005; T. Grande et al. 2013; Near et al. 2013; Davis et al. 2016; Betancur-R et al. 2017; Dornburg et al. 2017; Malmstrøm et al. 2017; Musilova et al. 2019; Ghedotti et al. 2021; Ghezelayagh et al. 2022; Mu et al. 2022). Phylogenetic relationships among lineages of *Trachichthyiformes* inferred from morphological and molecular data differ substantially. Morphological inferences resolve *Anoplogaster* and *Diretmidae* as a clade that is the sister lineage of all other *Trachichthyiformes* (Moore 1993b; Konishi and Okiyama 1997). Molecular phylogenies and analyses of combined molecular and morphological datasets consistently place *Diretmidae* as the sister lineage of all other *Trachichthyiformes* (Miya et al. 2003, 2005; Near et al. 2013; Betancur-R et al. 2017; Musilova et al. 2019; Ghedotti et al. 2021; Ghezelayagh et al. 2022).

Composition. There are currently 71 living species of *Trachichthyiformes* (Fricke et al. 2023) classified in *Anomalopidae*, *Anoplogaster*, *Diretmidae*, *Monocentridae*, and *Trachichthyidae*. Over the past 10 years, four new living species of *Trachichthyiformes* have been described (Su et al. 2022a, 2022b; Fricke et al. 2023), comprising 5.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Trachichthyiformes* include (1) presence of X pattern on the frontal (Zehren 1979; Moore 1993b; Ghedotti et al. 2021), (2) ethmoid very small and confined to area between upper portions of lateral ethmoids (Zehren 1979; Moore 1993b; Ghedotti et al. 2021), (3) presence of bony arches over infraorbitals (Moore 1993b), (4) presence of tack-like scales on larvae (Baldwin and Johnson 1995; Konishi and Okiyama 1997), (5) presence of ornamentation on lateral face of opercle in larvae (Baldwin and Johnson 1995), and (6) presence of spicules on rays of dorsal, anal, caudal, and pectoral fins of larvae (Konishi and Okiyama 1997; Ghedotti et al. 2021).

Synonyms. *Trachichthyoidei* (Moore 1993b:115) is an ambiguous synonym of *Trachichthyiformes.*

Comments. The group name *Trachichthyiformes* was initially applied to the paraphyletic group that included all species of *Trachichthyiformes* and *Beryciformes* to the exclusion of *Berycidae* (Stiassny and Moore 1992; Moore 1993b). *Trachichthyiformes* was used as the group name for the clade defined here in classifications resulting from molecular phylogenetic analyses (Betancur-R et al. 2017; Ghezelayagh et al. 2022) and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Trachichthyiformes* is the trachichthyid †*Gephyroberyx robustus* from the Rupelian (33.9–27.82 Ma) of the Caucasus area of Russia (Danil'chenko 1960). Bayesian relaxed molecular clock analyses of *Trachichthyiformes* result in an average posterior crown age estimate of 46.6 million years ago, with the credible interval ranging between 24.7 and 75.5 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Anomalopidae
*Anoplogastridae**
Diretmidae
Monocentridae
Trachichthyidae

Beryciformes A. C. L. G. Günther 1880:419

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Beryx decadactylus* Cuvier in Cuvier and Valenciennes (1829b) and *Holocentrus rufus* (Walbaum 1792), but not *Diretmus argenteus* J. Y. Johnson 1864 nor *Aulotrachichthys prosthemius* (Jordan and Fowler 1902). This is a minimum-crown-clade definition with external specifiers.

Etymology. From the ancient Greek βῆρυς (bˈe͡ɪɹuːz) meaning fish. The word is known primarily from the lexicon of the fifth- or sixth-century CE grammarian Hesychius of Alexandria (D. W. Thompson 1947:32). The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 945.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S2). Phylogenetic relationships of the major living and fossil lineages of *Beryciformes* are presented in Figure 14. The phylogenetic placements of the pan-holocentrids †*Berybolcensis*, †*Iridopristis*, †*Plesioberyx*, †*Stichocentrus*, and †*Tenuicentrum*, and the pan-berycoid †*Berycomorus* are on the basis of inferences from morphology (Friedman 2009; Andrews et al. 2023).

Phylogenetics. No phylogenetic analysis of morphological characters has resolved *Beryciformes* as a monophyletic group (Stiassny and Moore 1992; G. D. Johnson and Patterson 1993; Moore 1993b). Molecular phylogenetic analyses differ on the monophyly of *Beryciformes*, but the incongruence is limited to the identity of the sister lineage of *Holocentridae* (squirrelfishes). One set of molecular analyses resolves *Beryciformes* as paraphyletic, with *Holocentridae* and *Percomorpha* as sister lineages (Betancur-R, Broughton, et al. 2013; Smith et al. 2016; Betancur-R et al. 2017). Alternatively, another group of analyses results in phylogenies in which a monophyletic *Beryciformes* is placed as the sister group of *Percomorpha* (Figures 2 and 14; Miya et al. 2003; Thacker 2009; W.-J. Chen, Santini, et al. 2014; Malmstrøm et al. 2016; Dornburg et al. 2017; Hughes et al. 2018, fig. S2; Musilova et al. 2019; Ghezelayagh et al. 2022). Within *Beryciformes*, *Berycoidei* and *Holocentridae* are resolved as sister lineages (Figure 14; Miya et al. 2003, 2005; Thacker 2009; Near, Eytan, et al. 2012; W.-J. Chen, Santini, et al. 2014; Malmstrøm et al. 2016; Dornburg et al. 2017; Hughes et al. 2018, fig. S2; Musilova et al. 2019; Roth et al. 2020; Ghedotti et al. 2021; Ghezelayagh et al. 2022).

Composition. There are 213 living species of *Beryciformes* (Fricke et al. 2023) classified in *Berycoidei* and *Holocentridae*. Fossil lineages include the pan-holocentrids †*Berybolcensis*, †*Iridopristis*, †*Plesioberyx*, †*Stichocentrus*, and †*Tenuicentrum* (Patterson 1967; Gayet 1980a; Andrews et al. 2023), and the pan-berycoid †*Berycomorus* (Arambourg 1966). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 20 new living species of *Beryciformes* have been described (Fricke et al. 2023), comprising 9.4% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Beryciformes* (Moore 1993b; Ghedotti et al. 2021).

Synonyms. *Berycimorphaceae* (Betancur-R et al. 2017:21) is a partial synonym of *Beryciformes*.

Comments. Since the introduction of *Beryciformes* as a taxonomic group (Günther 1880), its composition has included *Polymixia*, *Caristiidae* (*Scombriformes*), *Ostracoberyx* (*Acropomatiformes*), and lineages now classified as *Trachichthyiformes* (Starks 1904; Regan 1911c; Berg 1940:467–468; Patterson 1964:432–434; McAllister 1968; Gosline 1971:147–148; Rosen 1973; J. S. Nelson 1984:232–240; G. D. Johnson and Patterson 1993; Near, Eytan, et al. 2012). A more restricted composition of *Beryciformes* came after the mid-20th century in a series of morphological phylogenetic studies (Zehren 1979; Stiassny and Moore 1992; Moore 1993b). Molecular phylogenetic analyses consistently support the monophyly of *Beryciformes* (e.g., Hughes et al. 2018, fig. S2; Ghezelayagh et al. 2022), highlighting the need for morphological studies to continue testing this hypothesis with the aim of discovering morphological apomorphies for the clade. The name *Beryciformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossils of *Beryciformes* include the Cenomanian (100.5–93.9 Ma) pan-holocentrids †*Stichocentrus liratus*, †*S. elegans*, †*S. spinulosus*, †*Plesioberyx maximus*, and †*P. discoides* from Lebanon (Patterson 1967; M. Gaudant 1969; Gayet 1980a; Forey et al. 2003). Bayesian relaxed molecular clock analyses of *Beryciformes* result in an average posterior crown age estimate of 95.8 million years ago, with the credible interval ranging between 71.6 and 117.6 million years ago (Andrews et al. 2023).

Constituent lineages.
Berycoidei
Holocentridae
†*Berybolcensis*
†*Berycomorus*
†*Iridopristis*
†*Plesioberyx*
†*Stichocentrus*
†*Tenuicentrum*

Berycoidei P. Bleeker 1874:15
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Beryx decadactylus* Cuvier in Cuvier and Valenciennes (1829b) and *Cetostoma regani* Zugmayer 1914. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek word βῆρυς (bˈeɪ͡ɹuːz) meaning fish. The word is known primarily from the lexicon of the fifth- or sixth-century CE grammarian Hesychius of Alexandria (D. W. Thompson 1947:32).

Registration number. 946.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S2). Phylogenetic relationships of the major lineages of *Berycoidei* are presented in Figure 14. The relationships of *Gibberichthys* follow Kobyliansky et al. (2020) and *Hispidoberyx* follow Moore (1993b) and Ghedotti et al. (2021).

Phylogenetics. No phylogenetic analysis of morphological characters has resolved *Berycoidei* as monophyletic (Stiassny and Moore 1992; G. D. Johnson and Patterson 1993; Moore 1993b); however, the resolution of *Stephanoberycoidei* in a morphological phylogeny differs from the composition of *Berycoidei* in the exclusion of *Berycidae* (alfonsinos) (Moore 1993b). With a notable exception (Colgan et al. 2000), molecular phylogenetic analyses consistently resolve *Berycoidei* as a clade (Miya et al. 2003, 2005; W. L. Smith and Wheeler 2006; Dettaï and Lecointre 2008; Thacker 2009; Near, Eytan, et al. 2012; T. Grande et al. 2013; Near et al. 2013; Davis et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Ghedotti et al. 2021; Ghezelayagh et al. 2022). Within *Berycoidei*, *Berycidae* and *Melamphaidae* (ridgeheads) comprise a clade that is the sister lineage to all other berycoids (e.g., Miya et al. 2003; Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022). Molecular phylogenies differ on the relationships of *Barbourisia rufa* (Velvet Whalefish), *Cetomimidae* (flabby whalefishes), and *Stephanoberycidae* (pricklefishes). Phylogenies inferred from mtDNA or combinations of mtDNA and nuclear genes resolve *Barbourisia* and *Cetomimidae* as sister lineages (Near et al. 2013; Rabosky et al. 2018; Kobyliansky et al. 2020; Ghedotti et al. 2021), consistent with inferences from morphology (Moore 1993b). However, phylogenetic analyses of a supermatrix of Sanger-sequenced genes and a dataset comprising more than 980 UCE loci resolve *Barbourisia* and *Stephanoberycidae* as a clade (Betancur-R et al. 2017; Ghezelayagh et al. 2022).

Morphological phylogenies resolve *Gibberichthys* (gibberfishes) as the sister lineage of a clade containing *Hispidoberyx ambagiosus* (Bristlyskin) and *Stephanoberycidae*, and resolve the deepsea whalefishes as a monophyletic group comprising *Barbourisia*, *Cetomimidae*, and *Rondeletia* (red mouth whalefishes) (Moore 1993b). However, the presence of Tominaga's organ, a large globular mass of tissue below the nasal rosette with a potential secretory function, was presented as morphological evidence that *Gibberichthys* and *Rondeletia* are sister lineages (Paxton et al. 2001), a result supported in a phylogenetic analysis of mtDNA gene sequences (Kobyliansky et al. 2020). The previously recognized lineages *Mirapinnidae* (tapetails) and *Megalomycteridae* (bignose fishes) are larvae and males, respectively, of species of *Cetomimidae* (G. D. Johnson et al. 2009).

Composition. There are currently 123 living species of *Berycoidei* that include *Barbourisia rufa*, *Hispidoberyx ambagiosus*, and species classified in *Berycidae*, *Cetomimidae*, *Gibberichthys*, *Melamphaidae*, *Rondeletia*, and *Stephanoberycidae*. Over the past 10 years, 13 new living species of *Berycoidei* have been described (Fricke et al. 2023), comprising 10.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Berycoidei* are found in all lineages except *Berycidae* and include (1) ocular sclera absent (Moore 1993b; Ghedotti et al. 2021), (2) orbitosphenoid absent (Moore 1993b; Ghedotti et al. 2021), (3) cranium with thinly ossified bones consisting mostly of cartilage and connective tissue (Moore 1993b; Ghedotti et al. 2021), and (4) lower branchial tooth patches absent (Moore 1993b; Ghedotti et al. 2021).

Synonyms. *Stephanoberycoidei* (Moore 1993b, fig. 5; J. S. Nelson et al. 2016:308–309; Betancur-R et al. 2017:21; Afonso et al. 2021) is a partial synonym of *Berycoidei*.

Comments. The group name *Berycoidei* has been applied to several para- and polyphyletic groups, including: (1) *Trachichthyidae* and *Holocentridae* (Patterson 1964); (2) *Berycidae*, *Trachichthyidae*, *Diretmidae*, *Anoplogaster*, *Anomalopidae*, and *Holocentridae* (Greenwood et al. 1966); (3) *Berycidae* and *Melamphaidae* (J. S. Nelson et al. 2016:313–314; Betancur-R et al. 2017); or (4) limited to *Berycidae* (Nelson 1994:288, 2006:302–303). The composition of *Berycoidei* as defined here follows the results of several molecular phylogenetic analyses (e.g., Davis et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Ghedotti et al. 2021; Ghezelayagh et al. 2022) and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

Bayesian relaxed molecular clock analyses of *Berycoidei* result in an average posterior crown age estimate of 85.8 million years ago, with the credible interval ranging between 65.8 and 101.9 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Barbourisiidae**
Berycidae
Cetomimidae
*Gibberichthyidae**
*Hispidoberycidae**
Melamphaidae
*Rondeletiidae**
Stephanoberycidae

Percomorpha O. P. Hay 1903:693
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade that contains *Carapus bermudensis* (Jones 1874) (*Ophidiiformes*), *Perca fluviatilis* Linnaeus 1758 (*Perciformes*), and *Micropterus salmoides* (Lacépède 1802) (*Centrarchiformes*), but not *Diretmoides pauciradiatus* (Woods 1973) in Woods and Sonoda (1973) (*Trachichthyiformes*) nor *Beryx decadactylus* Cuvier 1829 in Cuvier and Valenciennes (1829b) (*Beryciformes*). This is a minimum-crown-clade definition with external specifiers.

Etymology. From the ancient Greek πέρκη (pˈɜːke͡ɪ), a name applied to many species of fishes by ancient authors (D. W. Thompson 1947:195–197) and μορφή (mˈɔːɹ͡fiː) meaning form or shape.

Registration number. 947.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, figs. S3–S25). Phylogenetic relationships of *Percomorpha* are shown in Figures 2 and 14. In the phylogeny, the placement of the fossil pan-ophidiiform †*Pastorius* is the more conservative of two hypotheses presented by Carnevale and Johnson (2015) and resolution of the pan-batrachoid †*Bacchiaichthys* follows Carnevale and Collette (2014).

Phylogenetics. *Percomorpha* was first delimited as a result of comparative morphological studies and included all lineages currently classified in *Acanthopterygii* except *Atheriniformes* (=*Atherinomorpha*), *Batrachoididae*, *Lophioidei* (=*Lophiiformes*), and *Ophidiiformes* (Rosen and Patterson 1969). Over the next two decades, *Percomorpha* and *Atheriniformes* were presented as sister lineages in several phylogenetic trees (Hinegardner and Rosen 1972; Rosen 1973, 1982; C. L. Smith 1975; Rosen and Parenti 1981; Lauder 1983; Lauder and Liem 1983). During this period, *Percomorpha* was identified as a clade that was inadequately diagnosed with morphological characters and contained many lineages with unresolved relationships (Rosen 1982; Lauder and Liem 1983). Subsequent morphological phylogenetic studies indicated that Rosen and Patterson's (1969) concept of *Percomorpha* was paraphyletic due to the resolution of *Mugilidae* as the sister lineage to *Atheriniformes* (Stiassny 1990, 1993). A subsequent review and investigation of acanthomorph phylogeny based on 34 morphological characters led to a redefinition of *Percomorpha* to include *Atheriniformes* and exclude *Trachichthyiformes* and *Beryciformes* (G. D. Johnson and Patterson 1993).

Phylogenies resulting from analyses of molecular data offer a refined delimitation of *Percomorpha* that not only includes *Atheriniformes*, but also the lineages *Batrachoididae*, *Lophioidei*, and *Ophidiiformes* that were previously classified in *Paracanthopterygii* (W.-J. Chen et al. 2003; Miya et al. 2003, 2005). Subsequent molecular phylogenetic analyses consistently support the monophyly of this revised delimitation of *Percomorpha* (W. L. Smith and Wheeler 2006; Davis 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; Malmstrøm et al. 2016, 2017; Smith et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Roth et al. 2020; Ghezelayagh et al. 2022; Mu et al. 2022; J.-F. Wang et al. 2023). Molecular studies with inclusive taxon sampling resolve 13 major clades within *Percomorpha*, with *Ophidiiformes* and *Batrachoididae* as the first of two successive branching lineages in the clade; *Scombriformes* and *Syngnathiformes* as sister lineages; a clade containing *Ovalentaria*, *Synbranchiformes*, and *Carangiformes*; and *Eupercaria* as a clade containing *Perciformes*, *Centrarchiformes*, *Labriformes*, *Acropomatiformes*, and *Acanthuriformes* (Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022). Phylogenetic analyses of morphological characters support the monophyly of *Percomorpha* (Davesne et al. 2016; Cantalice et al. 2021), but these studies limit taxon sampling to four species, one representing each of *Acanthuriformes*, *Batrachoididae*, *Carangiformes*, and *Ophidiiformes*.

Composition. *Percomorpha* currently includes more than 18,900 living species (Fricke et al. 2023), classified in the subclades *Ophidiiformes*, *Batrachoididae*, *Syngnathiformes*, *Scombriformes*, *Ovalentaria*, *Gobiiformes*, *Synbranchiformes*, *Carangiformes*, and *Eupercaria*. Fossil lineages include the pan-ophidiiform †*Pastorius* (Carnevale and Johnson 2015) and the pan-batrachoid †*Bacchiaichthys* (Bannikov and Sorbini 2000; Carnevale and Collette 2014). Details of the ages and locations for the fossil taxa are given in Appendix 1. Over the past 10 years, 1,090 new living species of *Percomorpha* have been described (Fricke et al. 2023), comprising 5.8% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Percomorpha* include (1) external dorsal pelvic wing equal in size to external ventral wing (Stiassny and Moore 1992; Davesne et al. 2016), (2) first epibranchial and second pharyngobranchial with rodlike interarcual cartilage present between separated uncinate processes (G. D. Johnson and Patterson 1993; W. L. Smith 2005; Wiley and Johnson 2010), (3) absence of second ural centrum (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (4) five or fewer hypurals (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (5) fewer than six rays in pelvic fin (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010; Davesne et al. 2016), (6) absence of free pelvic radials (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010; Davesne et al. 2016),

(7) all but the first two epineurals have a point of origin that is displaced ventrally with distal parts of all epineurals displaced ventrally into the horizontal septum (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), (8) 17 principal caudal rays arranged as I,8,7,I (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010; Davesne et al. 2016; Cantalice et al. 2021), (9) absence of anterior supramaxilla (Davesne et al. 2016; Cantalice et al. 2021), (10) absence of orbitosphenoid (Davesne et al. 2016; Cantalice et al. 2021), (11) anterior and posterior ceratohyals sutured (Davesne et al. 2016), and (12) the first dorsal pterygiophore inserts between neural spines 2 and 4 (Davesne et al. 2016).

Synonyms. *Percomorphacea* (Wiley and Johnson 2010:127, 151–152; Betancur-R et al. 2017:22) is an ambiguous synonym of *Percomorpha*.

Comments. *Percomorpha* was famously referred to the "bush at the top of the tree" in reference to the limited phylogenetic resolution among the more than 18,900 species and at least 288 taxonomic families in the clade (G. J. Nelson 1989:328). This was later restated as the "percomorph problem" in reference to the lack of morphological apomorphies diagnosing the group and the fact that *Percomorpha* represented the largest polytomy in the phylogeny of living vertebrates, a consequence of too many lineages and too few morphological characters to resolve relationships (G. D. Johnson and Patterson 1993; Chakrabarty 2010). Despite impressive efforts that involve careful and elegant studies of comparative morphology (G. D. Johnson and Patterson 1993; Patterson and Johnson 1995; Datovo et al. 2014; Pastana et al. 2022), the status of efforts using morphology to resolve the phylogeny of *Percomorpha* is summarized as "any tree can be justified by special pleading, by insisting that certain characters are uniquely derived but others are more labile or plastic" as "very few of the characters found among percomorphs and their relatives are uniquely derived" (G. D. Johnson and Patterson 1993:555). Molecular phylogenetics has not only led to a dramatic increase in the resolution of relationships within *Percomorpha*, but has also provided a mechanism for the development of exciting and surprising hypotheses of relationships that were undiscovered and wholly unanticipated from the study of morphology (Dornburg and Near 2021). The future of phylogenetic studies of *Percomorpha* likely involves a full integration of molecular phylogenetics and comparative morphology as evidenced by studies that lead to reinterpretations of morphological traits in the context of phylogenies resulting from analysis of molecular data (e.g., Chanet et al. 2013; Ghedotti et al. 2018; M. G. Girard et al. 2020).

Since the turn of the 21st century, *Percomorpha* is consistently delimited as including *Ophidiiformes* and *Batrachoididae* and excluding *Beryciformes* and *Trachichthyiformes* (Miya et al. 2003, 2005; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; J. S. Nelson et al. 2016:314–315; Smith et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Dornburg and Near 2021; Ghezelayagh et al. 2022; Mu et al. 2022; J.-F. Wang et al. 2023). The name *Percomorpha* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossils of *Percomorpha* all date to the Campanian and Maastrichtian (83.6–72.1, 72.1–66.0 Ma) of the Late Cretaceous and include the pan-ophidiiform †*Pastorius* (Carnevale and Johnson 2015), the pan-batrachoid †*Bacchiaichthys* (Bannikov and Sorbini 2000), and the pan-centriscoid †*Gasterorhamphosus* (Sorbini 1981). Bayesian relaxed molecular clock analyses of *Percomorpha* result in an average posterior crown age estimate of 126.8 million years ago, with the credible interval ranging between 116.9 and 135.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Batrachoididae
Carangiformes
Eupercaria
Gobiiformes
Ophidiiformes
Ovalentaria
Scombriformes
Synbranchiformes
Syngnathiformes
†*Bacchiaichthys*
†*Pastorius*

Ophidiiformes P. Bleeker 1859:xxv
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Ophidion barbatum* Linnaeus 1758, *Dinematichthys iluocoeteoides* Bleeker 1855, *Aphyonus gelatinosus* Günther 1878a, *Brotula barbata* (Bloch and Schneider 1801), *Carapus acus* (Brünnich 1768), and *Dicrolene introniger* Goode and Bean 1883. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek όφίς (ˈo͡ʊfɪs) meaning snake. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 948.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S3). Although *Ophidion barbatum* is not included in the reference phylogeny, it resolves in a clade with other species of *Ophidion* in a phylogenomic analysis of Sanger-sequenced mitochondrial and nuclear genes (Betancur-R et al. 2017, fig. S6; Rabosky et al. 2018). Phylogenetic relationships of the major living lineages and fossil taxa of *Ophidiiformes* are presented in Figure 14. Placements of the fossil taxa in the phylogeny are on the basis of inferences from morphology (Patterson and Rosen 1989; Schwarzhans 2003, 2010; Møller et al. 2016; Schwarzhans and Stringer 2020).

Phylogenetics. *Ophidiiformes* was previously classified in *Paracanthopterygii* on the basis of studies of morphology (e.g., Greenwood et al. 1966; Rosen and Patterson 1969; Patterson and Rosen 1989; J. S. Nelson 2006:243–248), but they are distantly related to paracanthopterygians and are resolved as the sister group of all other *Percomorpha* in molecular phylogenetic analyses (Miya et al. 2003, 2005; W. L. Smith and Wheeler 2006; Davis 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; Malmstrøm et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Roth et al. 2020; Ghezelayagh et al. 2022; Mu et al. 2022). Despite being resolved as monophyletic in analyses of molecular data (Miya et al. 2003; Near et al. 2013; Møller et al. 2016; Betancur-R et al. 2017; Campbell, Nielsen, et al. 2017; Ghezelayagh et al. 2022), there is little evidence from morphology for the monophyly of *Ophidiiformes* (Rosen 1985; Patterson and Rosen 1989; Howes 1992; Nielsen et al. 1999).

The mode of reproduction is an important trait in classifying *Ophidiiformes* into the oviparous *Ophidiidae* (cusk eels) and viviparous *Bythitoidei* (Cohen and Nielsen 1978; Nielsen et al. 1999; J. S. Nelson et al. 2016). Phylogenies inferred from molecular data result in paraphyly of the traditional delimitation of *Ophidiidae* because of the resolution of *Carapidae* (pearlfishes) (Miya et al. 2003, 2005; Near et al. 2013; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022; M. G. Girard et al. 2023), prompting the delineation of a more inclusive *Ophidiidae* to include species previously classified in *Carapidae* (Betancur-R et al. 2017). Molecular phylogenetic analyses resolve both the more inclusive *Ophidiidae* and *Bythitoidei* as monophyletic groups (Near et al. 2013; Møller et al. 2016; Betancur-R et al. 2017; Campbell, Nielsen, et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022).

Composition. There are currently 569 living species of *Ophidiiformes* (Nielsen et al. 1999; Fricke et al. 2023) classified in *Ophidiidae* and *Bythitoidei*. Fossil lineages of *Ophidiiformes* include the pan-bythitoid †"*Bidenichthys*" *crepidatus* and the pan-ophiid †*Ampheristus americanus* (Schwarzhans 2003, 2010; Schwarzhans and Stringer 2020). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, there have been 43 new living species of *Ophidiiformes* described (Fricke et al. 2023), comprising 7.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Ophidiiformes* include (1) supraoccipital excluded from posterior cranial margin by posterodorsal extension of exoccipitals (Howes 1992; Carnevale and Johnson 2015), (2) presence of angled bursa-like cavity between exoccipitals and basioccipital, and (3) posterior portion of first infraorbital covered by second infraorbital (Ohashi 2018).

Synonyms. *Ophidiicae* (Hubbs 1952:51, fig. 1), *Ophidiimorpharia* (Betancur-R, Broughton, et al. 2013:13), *Ophidiida* (J. S. Nelson et al. 2016:315), and *Ophidiaria* (Sanciangco et al. 2016, fig. 1; Betancur-R et al. 2017:22) are ambiguous synonyms of *Ophidiiformes*.

Comments. *Ophidiiformes* is a diverse clade with more than 560 species classified among 121 genera (Fricke et al. 2023), but very little of this rich diversity has been integrated into phylogenetic studies (Møller et al. 2016; Rabosky et al. 2018). The migration of *Ophidiiformes*, *Batrachoididae*, and *Lophioidei* from *Paracanthopterygii* to *Percomorpha* speaks to the effect of molecular data on inferring the phylogeny of ray-finned fishes and is “akin to placing a morphologically established lineage of marsupials as the sister lineage of rodents or vipers as the sister lineage of *Anolis*” (Dornburg and Near 2021:441).

The earliest fossil *Ophidiiformes* are the pan-bythitoid †“*Bidenichthys*” *crepidatus* and the pan-ophiid †*Ampheristus americanus* from the Maastrichtian (72.2–66.0 Ma) in the Cretaceous (Appendix 2; Voigt 1926; Schwarzhans 2010; Schwarzhans and Stringer 2020). Bayesian relaxed molecular clock analyses of *Ophidiiformes* result in an average posterior crown age estimate of 84.5 million years ago, with the credible interval ranging between 59.3 and 111.3 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Bythitoidei
Ophidiidae
†*Ampheristus*
†“*Bidenichthys*” *crepidatus*

Bythitoidei D. M. Cohen and J. G. Nielsen 1978:42

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Bythites fuscus* Reinhardt 1837, *Dinematichthys iluocoeteoides* Bleeker 1855, and *Aphyonus gelatinosus* Günther 1878a. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek βῠθὸς (bˈuːθo͡ʊz) meaning the depths of the sea.

Registration number. 949.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S3). Although *Bythites fuscus* is not included in the reference phylogeny, morphological studies indicate that *B. fuscus*, species of *Grammonus*, and species of *Cataetyx* share common ancestry (Cohen and Nielsen 1978). Phylogenetic relationships of the major living lineages and fossil taxa of *Bythitoidei* are presented in Figure 14. Placements of the fossil taxa in the phylogeny are on the basis of inferences from morphology (Schwarzhans 2003, 2010; Møller et al. 2016; Schwarzhans and Stringer 2020).

Phylogenetics. *Bythitoidei* was delimited to include *Bythitidae* (livebearing brotulas) and *Aphyonidae* (aphyonids) based on the presence of an intromittent organ in males and the placement of the anterior nostril well above the upper lip (Cohen and Nielsen 1978). From the late 1960s through the 1990s, *Parabrotulidae* (false brotulas) was classified in *Zoarcoidei* on the basis of the presence of a one-to-one ratio of vertebrae to fin pterygiophores, an eel-shaped body, ventral fins, lack of fin spines, and a confluent dorsal and anal fin (Nielsen 1968; Cohen and Nielsen 1978; Nielsen et al. 1990; Miya and Nielsen 1991). It was argued that the presence of paired nostrils, a bilobed ovary, and a well-developed intromittent organ in *Parabrotulidae* is evidence for their shared ancestry with *Ophidiiformes*, specifically *Bythitoidei*, and not *Zoarcoidei* (Anderson 1994; Nelson 1994:227). A detailed analysis of the osteology of *Parabrotula plagiophthalmus* highlighted the morphology of the intromittent organ and the presence of six caudal rays as consistent with shared common ancestry of *Parabrotulidae* and *Bythitidae* (Hilton et al. 2021).

Molecular phylogenetic analyses consistently resolve *Bythitoidei* as monophyletic (Near et al. 2013; Møller et al. 2016; Betancur-R et al. 2017; Campbell, Nielsen, et al. 2017; Evseenko et al. 2018; Arroyave et al. 2022; Ghezelayagh et al. 2022). *Parabrotulidae* and the abyssal

Aphyonidae are phylogenetically nested in *Bythitidae*, while *Bythitidae* and *Dinematichthyidae* (viviparous brotulas) are resolved as sister lineages making up the more inclusive clade *Bythitoidei* (Møller et al. 2016; Betancur-R et al. 2017; Campbell, Nielsen, et al. 2017; Ghezelayagh et al. 2022). The results from molecular phylogenetic analyses were the basis for the reclassification of *Aphyonidae* and *Parabrotulidae* within *Bythitidae* and the elevation of *Dinematichthyidae* from lineages formerly classified in *Dinematichthyini* (Møller et al. 2016).

Composition. There are currently 246 living species of *Bythitoidei* (Møller et al. 2016; Fricke et al. 2023) classified in *Bythitidae* and *Dinematichthyidae*. Fossil lineages of *Bythitoidei* include †*Bythitidarum rasmussenae* from the Danian (66.0–61.7 Ma) of Denmark (Appendix 1; Schwarzhans 2003; Møller et al. 2016). Over the past 10 years, there have been 13 new living species of *Bythitoidei* described (Fricke et al. 2023), comprising 5.3% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Bythitoidei* include (1) presence of a male intromittent organ (Cohen and Nielsen 1978; Patterson and Rosen 1989; Wiley and Johnson 2010), (2) anterior nostril positioned low on snout and close to upper lip (Cohen and Nielsen 1978; Patterson and Rosen 1989), and (3) reduction of pelvic fin to a single ray or entirely absent (Møller et al. 2016).

Synonyms. There are no synonyms of *Bythitoidei*.

Comments. The earliest fossil taxon of *Bythitoidei* is the otolith species †*Bythitidarum rasmussenae* from the Danian (66.0–61.7 Ma) of Denmark (Schwarzhans 2003; Møller et al. 2016). Bayesian relaxed molecular clock analyses of *Bythitoidei* result in an average posterior crown age estimate of 46.0 million years ago, with the credible interval ranging between 28.1 and 69.3 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Bythitidae
Dinematichthyidae
†*Bythitidarum*

Batrachoididae D. S. Jordan 1896:231
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Opsanus tau* (Linnaeus 1766), *Batrachoides pacifici* (Günther 1861), and *Halobatrachus didactylus* (Bloch and Schneider 1801). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek word βάτρᾰχος (bætɹˈækoʊ͡z) meaning frog.

Registration number. 950.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S3). The phylogenetic resolution of *Batrachoididae* relative to other lineages of *Percomorpha* is presented in Figures 2 and 14.

Phylogenetics. *Batrachoididae* (toadfishes) was previously classified in *Paracanthopterygii* (e.g., Greenwood et al. 1966; Rosen and Patterson 1969; Patterson and Rosen 1989; J. S. Nelson 2006:243–248), and viewed as closely related to *Lophioidei* (Regan 1912c; Patterson and Rosen 1989; Datovo et al. 2014). Molecular phylogenetic analyses resolve *Batrachoididae* as nested within *Percomorpha*, and most studies place batrachoids as the sister lineage of an inclusive clade that contains all other percomorphs except for *Ophidiiformes* (Miya et al. 2005; W. L. Smith and Wheeler 2006; Davis 2010; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; T. Grande et al. 2013; Near et al. 2013; W.-J. Chen, Santini, et al. 2014; Davis et al. 2016; Malmstrøm et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Roth et al. 2020; Ghezelayagh et al. 2022; Mu et al. 2022).

The monophyly of *Batrachoididae* is supported in several molecular and morphological phylogenetic analyses (W. L. Smith and Wheeler 2006; Near et al. 2013; Betancur-R et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Vaz 2020; Ghezelayagh et al. 2022). Morphological and molecular phylogenetic studies infer relationships within *Batrachoididae* that are congruent, with *Halophryninae* resolved as the sister group of a clade containing *Batrachoidinae*, *Porichthyinae*, and *Thalassophryninae* (Greenfield et al. 2008; Rice and Bass 2009; Rabosky et al. 2018). A detailed description of the caudal skeleton identified potential apomorphies for *Batrachoididae* and several subclades (Vaz and Hilton 2020). A phylogenetic analysis of 191 morphological characters with extensive taxon sampling resolves lineages of *Batrachoididae* in a polytomy containing *Triathalassothia*, a clade of lineages traditionally classified in *Halophryninae* (*Barchatus*, *Batrichthys*, *Bifax*, *Chatrabus*, *Colletteichthys*, *Halobatrachus*, *Perulibatrachus*, and *Riekertia*), and a clade containing *Halophryninae* (*Allenbatrachus*, *Batrachomoeus*, and *Halophryne*), *Thalassophryninae* (*Daector* and *Thalassophryne*), *Porichthyinae* (*Aphos* and *Porichthys*), and *Batrachoidinae* (*Amphichthys*, *Batrachoides*, *Opsanus*, *Sanopus*, and *Vladichthys*) (Vaz 2020).

Composition. There are currently 84 living species of *Batrachoididae* (Fricke et al. 2023) that include *Bifax lacinia*, *Halobatrachus didactylus*, *Riekertia ellisi*, and species classified in *Batrachoidinae*, *Halophryninae*, *Porichthyinae*, *Thalassophryninae*, and *Triathalassothia* (Greenfield et al. 2008; Vaz 2020; Fricke et al. 2023). Over the past 10 years, one new living species of *Batrachoididae* was described (Fricke et al. 2023), comprising 1.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Batrachoididae* include (1) large yolk sac with a ventral adhesive disc present in larvae (Wiley and Johnson 2010), (2) tightly packed configuration in the dorsal spine and pterygiophore complex (Wiley and Johnson 2010), (3) robust and hypertrophied epineural bound to medial surface of cleithrum (Wiley and Johnson 2010; Vaz 2020), (4) supracleithrum articulates with ankylosed posttemporal (Wiley and Johnson 2010; Vaz 2020), (5) parietals absent (Wiley and Johnson 2010), (6) mesethmoid unossified (Wiley and Johnson 2010; Vaz 2020), (7) swimbladder heart shaped with anterior portion separated in two lobes with bands of musculature along the lateral surface of each lobe (Wiley and Johnson 2010), (8) dorsal edge of metapterygoid with a trapezoidal shape (Vaz 2020), (9) subopercle with one, two, or three spines (Vaz 2020), (10) urohyal with lateral projections giving a T-shape (Vaz 2020), (11) uncinate process longer than the anterior half of epibranchial process (Vaz 2020), (12) fifth ceratobranchial is one-half the length of fourth ceratobranchial (Vaz 2020), (13) origin of first epineural bone articulates with the neural spine of the first vertebra (Vaz 2020), (14) the origin of third epineural at the level of neural arch of third vertebra (Vaz 2020), (15) ventral limb of posttemporal reduced to a knob (Vaz 2020), (16) presence of anterodorsal process of the supracleithrum, (17) propterygium hypertrophied as long pectoral radials (Vaz 2020; Vaz and Hilton 2023), (18) propterygium rod shaped (Vaz 2020), and (19) presence of a filamentous cushion organ on the pelvic spine and lateralmost soft ray (Vaz 2020).

Synonyms. *Haplodoci* (Cope 1871a:458), *Batrachoidiformes* (Berg 1937:1279; Greenwood et al. 1966:396; Lauder and Liem 1983, fig. 37; Patterson and Rosen 1989:23–24; Wiley and Johnson 2010:159–160; J. S. Nelson et al. 2016:320–321; Betancur-R et al. 2017:22), *Batrachoidimorpharia* (Betancur-R et al. 2013a:13), *Batrachoidida* (J. S. Nelson et al. 2016:320), and *Batrachoidaria* (Betancur-R et al. 2017:22) are ambiguous synonyms of *Batrachoididae*.

Comments. *Batrachoididae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:64), has long been applied as the group name for the clade presented in the definition (Jordan 1923:238; McAllister 1968:164; J. S. Nelson et al. 2016:321–323), and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil taxon of *Batrachoididae* is the otolith-based species †*Batrachoididarum trapezoidalis* from the Ypresian (56.0–48.1 Ma) of France (Nolf 1988; Carnevale and Collette 2014), and the earliest skeletal fossil is †*Louckaichthys novosadi* from the Rupelian (33.9–27.3 Ma) of the Czech Republic (Přikryl and Carnevale 2017). Bayesian relaxed molecular clock analyses of *Batrachoididae* result in an average posterior crown age estimate of 49.1 million years ago, with the credible interval ranging between 25.3 and 76.3 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.
Batrachoidinae
Bifax
Halobatrachus
Halophryninae
Porichthyinae
Riekertia
Thalassophryninae
Triathalassothia

Gobiiformes P. Bleeker 1859:xxv

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Gobius niger* Linnaeus 1758, *Lythrypnus dalli* (Gilbert 1890), *Trichonotus filamentosus* (Steindachner 1867), *Ostorhinchus doederleini* (Jordan and Snyder 1901), and *Kurtus indicus* Bloch 1786. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κωβιός (kˈo͡ʊbɪˌo͡ʊz) meaning small insignificant fish. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 951.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, figs. S3, S4). Although *Gobius niger* is not included in the reference phylogeny, it resolves in a clade with other species of *Gobiidae* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (Tornabene et al. 2013, fig. 2; McCraney et al. 2020, fig. 6). Phylogenetic relationships among the major lineages of *Gobiiformes* are presented in Figure 14. Placement of the fossil pan-gobioid †*Paralates* in the phylogeny is on the basis of an analysis of morphological characters (Gierl et al. 2022).

Phylogenetics. One of the most remarkable results from molecular phylogenetic analyses of *Percomorpha* is the discovery that *Apogonidae*, *Gobioidei*, *Kurtus*, and *Trichonotus* resolve in a strongly supported clade, delimited here as *Gobiiformes*, that is the sister lineage of a clade containing all other lineages of *Percomorpha* exclusive of *Ophidiiformes* and *Batrachoididae* (Thacker and Hardman 2005; W. L. Smith and Wheeler 2006; W. L. Smith and Craig 2007; Thacker 2009; Thacker and Roje 2009; Chakrabarty et al. 2012; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Thacker et al. 2015; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Kuang et al. 2018; McCraney et al. 2020; Ghezelayagh et al. 2022; Satoh and Katayama 2022). Within *Gobiiformes*, a clade containing *Gobioidei* and *Trichonotus* is the sister lineage of *Apogonoidei*, including *Apogonidae* and *Kurtus* (Near et al. 2013; Thacker et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018; McCraney et al. 2020; Ghezelayagh et al. 2022). Alternative phylogenetic relationships among *Gobiiformes* resulting from molecular phylogenetic analyses include the resolution of *Kurtus* as the sister lineage of all other *Gobiiformes* (Thacker 2009; Chakrabarty et al. 2012; Alfaro et al. 2018; Kuang et al. 2018) and a clade containing *Apogonidae*, *Kurtus*, and *Trichonotus* as the sister lineage of *Gobioidei* (Satoh and Katayama 2022).

Composition. There are currently 2,740 living species of *Gobiiformes* (Fricke et al. 2023) classified in *Apogonoidei*, *Gobioidei*, and *Trichonotus*. Fossil lineages include the pan-gobioid †*Paralates* (Gierl and Reichenbacher 2017; Gierl et al. 2022). Over the past 10 years, 368 new living species of *Gobiiformes* have been described (Fricke et al. 2023), comprising 13.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gobiiformes* include (1) presence of large gap between symplectic and preopercle in *Gobioidei* and *Trichonotus* (J. S. Nelson 1986; Winterbottom 1993b), (2) presence of sensory papillae rows on the head and body in *Gobioidei*, *Kurtus*, and *Apogonidae* (G. D. Johnson 1993; Thacker 2009), but see Sato (2022), and (3) presence of eggs with adhesive filaments around the micropyle in *Gobioidei*, *Kurtus*, and *Apogonidae* (G. D. Johnson 1993; Thacker et al. 2015). All *Gobiiformes* engage in egg guarding or brooding by the male, either in a benthic nest (*Gobioidei*), in the mouth (*Apogonidae*), on the forehead (*Kurtus*), or in the gill chamber (*Trichonotus*) (Clark and Pohle 1996; Berra and Humphrey 2002; Östlund-Nilsson and Nilsson 2004; Thacker et al. 2015).

Synonyms. *Gobiomorpharia* (Betancur-R, Broughton, et al. 2013, fig. 1) and *Gobiaria* (Betancur-R et al. 2017:23) are ambiguous synonyms of *Gobiiformes*. *Gobiida* (J. S. Nelson et al. 2016:323) is a partial synonym of *Gobiiformes*.

Comments. *Gobiiformes* has been applied as a group name for (1) a group that included *Apogonidae*, *Gobioidei*, *Kurtus*, and *Pempheridae* (Thacker 2009); (2) a clade containing *Trichonotus* and *Gobioidei* (Betancur-R et al. 2017); and (3) a clade containing *Apogonoidei*, *Gobioidei*, and *Trichonotus* as presented here in the definition (Thacker et al. 2015; Davis et al. 2016; Dornburg and Near 2021; Ghezelayagh et al. 2022). The name *Gobiiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The resolution of a monophyletic *Gobiiformes* is one of many unexpected results stemming from molecular phylogenetic analyses of *Percomorpha*. Morphological studies exploring the phylogenetic affinities of *Apogonidae*, *Gobioidei*, *Kurtus*, and *Trichonotus* all predate the resolution of these lineages as a clade in molecular studies (G. D. Johnson 1993; Winterbottom 1993b; D. G. Smith and Johnson 2007). A potentially fruitful area of future research is the exploration of comparative morphological and anatomical studies among the seemingly disparate lineages that comprise *Gobiiformes*, with the goal of understanding their history of phenotypic trait diversification and the discovery of additional morphological apomorphies.

The earliest fossils of *Gobiiformes* are the otolith-based species of †*Apogonidarum* classified as *Apogonidae* from the Maastrichtian (72.2–66.0 Ma) in the Cretaceous of India and North Dakota, USA (Khajuria and Prasad 1998; Hoganson et al. 2019). The earliest skeletal fossils of *Gobiiformes* include the gobioid †*Carlomonnius* and the apogonids †*Apogoniscus*, †*Bolcapogon*, †*Eoapogon*, †*Eosphaeramia*, and †*Leptolumamia* all from the Ypresian (56.0–48.1 Ma) of Monte Bolca, Italy (Bannikov and Carnevale 2016; Bannikov and Fraser 2016). Bayesian relaxed molecular clock analyses of *Gobiiformes* result in an average posterior crown age estimate of 109.6 million years ago, with the credible interval ranging between 98.9 and 119.9 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.
Apogonoidei
Gobioidei
*Trichonotidae**
†*Paralates*

Gobioidei Bleeker 1849:4
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Gobius niger* Linnaeus 1758, *Lythrypnus dalli* (Gilbert 1890), *Periophthalmus barbarus* (Linnaeus 1766), *Eleotris pisonis* (Gmelin 1789), *Milyeringa veritas* Whitley 1945, and *Rhyacichthys aspro* (Valenciennes in Cuvier and Valenciennes 1837). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κωβιός (kˈo͡ʊbɪˌo͡ʊz) meaning small insignificant fish.

Registration number. 952.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S4). Although *Gobius niger* is not included in the reference phylogeny, it resolves in a clade with other species of *Gobiidae* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (Tornabene et al. 2013, fig. 2; McCraney et al. 2020, fig. 6). Phylogenetic relationships among the living and fossil lineages of *Gobioidei* are presented in Figure 14. Placements of the fossil pan-butids †*Carlomonnius* and †*Lepidocottus* and the pan-thalasseleotrids †*Eleogobius* and †*Pirskenius* follow Gierl et al. (2022).

Phylogenetics. Prior to the application of molecular data to the study of fish phylogeny, the relationships of *Gobioidei* among

Percomorpha were unresolved (P. J. Miller 1973, 1986; Springer 1983; Hoese 1984). In a study of osteological characters, Winterbottom (1993b) concluded that *Hoplichthys*, *Gobiesocidae*, *Callionymidae*, and various "trachinoids" that included *Creediidae*, *Hemerocoetidae*, and *Trichonotus* were the lineages with the greatest number of character states shared with *Gobioidei*. Despite many morphological apomorphies diagnosing *Gobioidei* (Springer 1983; Hoese 1984; P. J. Miller 1992; G. D. Johnson and Brothers 1993; Winterbottom 1993b), comparative morphological studies did not provide a strong hypothesis for the phylogenetic affinities of gobioids among percomorphs. Morphology of the dorsal gill arches was cited as evidence of shared common ancestry for *Apogonidae* and *Kurtus* (G. D. Johnson 1993).

Gobioidei is consistently resolved as monophyletic in molecular phylogenetic studies (W. L. Smith and Wheeler 2006; Thacker 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Thacker et al. 2015, 2023; Betancur-R et al. 2017; Hughes et al. 2018; Kuang et al. 2018; McCraney et al. 2020; Ghezelayagh et al. 2022). Within *Gobioidei*, molecular phylogenies resolve a clade containing *Rhyacichthyidae* (loach gobies) and *Odontobutidae* (freshwater sleepers) as the sister lineage of all other gobioids, with *Milyeringidae* (blind cave gobies), *Eleotridae* (spinycheek sleepers), *Butidae* (butid sleepers), and *Thalasseleotrididae* (ocean sleepers) as successive branching lineages leading to a clade containing *Gobiidae* (gobies) and *Oxudercidae* (mudskippers and relatives) (Thacker et al. 2015; McCraney et al. 2020; Ghezelayagh et al. 2022; Goatley and Tornabene 2022). A phylogenomic analysis of *Gobioidei* using UCE loci resolves *Xenisthmus* and *Butidae* as sister lineages, prompting the elevation of *Xenisthmidae* (collared wrigglers) out of synonymy with *Eleotridae* (Thacker 2003; McCraney 2019).

Phylogenies inferred from morphological characters are fairly congruent with relationships inferred from molecular data (Hoese and Gill 1993), specifically in resolving *Rhyacichthyidae* and *Odontobutidae* as the sister lineage of all other gobioids and supporting *Thalasseleotrididae* as the sister lineage of a clade containing *Gobiidae* and *Oxudercidae* (A. C. Gill and Mooi 2012; Reichenbacher et al. 2020; Gierl et al. 2022). The presence of five branchiostegal rays is consistent with the monophyly of a clade containing the gobioid lineages *Thalasseleotrididae*, *Oxudercidae*, and *Gobiidae* (Hoese 1984; Hoese and Gill 1993; A. C. Gill and Mooi 2012; Reichenbacher et al. 2020); the remaining lineages *Rhyacichthyidae*, *Odontobutidae*, *Milyeringidae*, *Xenisthmidae*, *Eleotridae*, and *Butidae* all have six branchiostegal rays. Molecular phylogenetic studies focusing on specific gobioid lineages have attempted to resolve relationships within *Rhyacichthys* (Haÿ et al. 2022), *Odontobutidae* (H. Li et al. 2018), *Butidae*, and *Eleotridae* (Thacker and Hardman 2005; Thacker 2017; Thacker, Shelley, McCraney, Adams, et al. 2022; Thacker, Shelley, McCraney, Unmack, et al. 2022), *Oxudercidae* (Yamada et al. 2009; Thacker 2013; Thacker et al. 2019; McMahan et al. 2021), and *Gobiidae* (Rüber et al. 2003; Herler et al. 2009; Neilson and Stepien 2009; Thacker and Roje 2011; Tornabene et al. 2013, 2023).

Composition. There are currently 2,347 living species of *Gobioidei* (Fricke et al. 2023) classified in *Rhyacichthyidae*, *Odontobutidae*, *Milyeringidae*, *Xenisthmidae*, *Butidae*, *Eleotridae*, *Thalasseleotrididae*, *Oxudercidae*, and *Gobiidae*. Fossil *Gobioidei* include the pan-butids †*Carlomonnius* and †*Lepidocottus* and the pan-thalasseleotrids †*Eleogobius* and †*Pirskenius* (Gierl et al. 2013, 2022; Přikryl 2014; Gierl and Reichenbacher 2015; Bannikov and Carnevale 2016; Reichenbacher et al. 2020). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 349 new living species of *Gobioidei* have been described (Fricke et al. 2023), comprising 14.9% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gobioidei* include (1) parietals absent (Springer 1983; G. D. Johnson and Brothers 1993; Winterbottom 1993b), (2) basisphenoid absent (Springer 1983; G. D. Johnson and Brothers 1993; Winterbottom 1993b), (3) two or fewer (usually zero) infraorbitals (Springer 1983; G. D. Johnson and Brothers

1993), (4) interhyal attached to preopercle by a ligament, not articulating at junction of symplectic and hyomandibular, resulting in gap between symplectic and preopercle (Springer 1983; G. D. Johnson and Brothers 1993; Winterbottom 1993b), (5) basibranchial 1 cartilaginous (Springer 1983; Winterbottom 1993b), (6) pelvic intercleithral cartilage present (Springer 1983; Winterbottom 1993b), (7) ventral intercleithral cartilage present (Springer 1983; Winterbottom 1993b), (8) sagittae and lapilli with elongate primordia (Brothers 1984; G. D. Johnson and Brothers 1993; Winterbottom 1993b), (9) accessory sperm-duct glands present in males (P. J. Miller 1992; G. D. Johnson and Brothers 1993), (10) supraneurals absent (Springer 1983; G. D. Johnson and Brothers 1993), (11) neural and haemal arches and spines developing as membrane bones with little to no cartilaginous precursors (G. D. Johnson and Brothers 1993), (12) first neural arch fused to first centrum at earliest appearance in ontogeny (G. D. Johnson and Brothers 1993), (13) dorsalmost pectoral ray articulating with posterior margin of dorsalmost actinost or radial cartilage rather than with scapula, medial part of ray lacking enlarged articular base and in early ontogeny not embracing ovoid cartilage lying at posterodorsal corner of scapulocoracoid cartilage (G. D. Johnson and Brothers 1993), and (14) hypurals 1+2 and 3+4 fused to one another and to the urostyle (G. D. Johnson and Brothers 1993; Winterbottom 1993b).

Synonyms. *Gobiiformes* (Betancur-R, Broughton, et al. 2013, fig. 3; J. S. Nelson et al. 2016:326) is an ambiguous synonym of *Gobioidei*.

Comments. *Gobioidei* has long been applied as the group name for the clade presented in the definition and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade (McAllister 1968:146–147; P. J. Miller 1973; Nelson 1994:412–418; Thacker 2009; McCraney et al. 2020).

Time-calibrated phylogenies of acanthopterygians have repeatedly identified *Gobioidei* as containing clades with significantly elevated rates of lineage diversification (Near et al. 2013; Rabosky et al. 2013, 2018; Ghezelayagh et al. 2022). Comparative studies have deployed phylogenies of *Gobioidei* to investigate the history of phenotypic diversification (Thacker 2014, 2017; Thacker and Gkenas 2019; Huie et al. 2020) and the biogeography of near-shore marine habitats (Thacker 2015, 2017; Tornabene et al. 2016).

The earliest *Gobioidei* fossil is the pan-butid †*Carlomonnius* from the Ypresian (56.0–47.8 Ma) of Monte Bolca, Italy (Bannikov and Carnevale 2016). Bayesian relaxed molecular clock analyses of *Gobioidei* result in an average posterior crown age estimate of 93.6 million years ago, with the credible interval ranging between 82.1 and 104.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Butidae
Eleotridae
Gobiidae
Milyeringidae
Odontobutidae
Oxudercidae
Rhyacichthyidae
Thalasseleotrididae
Xenisthmidae
†*Carlomonnius*
†*Eleogobius*
†*Lepidocottus*
†*Pirskenius*

Apogonoidei C. E. Thacker 2009:100
[C. E. Thacker and T. J. Near],
converted clade name.

Definition. The least inclusive crown clade that contains *Kurtus indicus* Bloch 1786, *Pseudamia gelatinosa* J. B. L. Smith 1955a, *Apogon imberbis* (Linnaeus 1758), and *Cheilodipterus quinquelineatus* Cuvier 1828 in Cuvier and Valenciennes (1828). This is a minimum-crown-clade definition.

Etymology. From the Greek prefix α- (a-) meaning without, and the ancient Greek πώγων (pˈo͜ʊgɑːn) meaning beard.

Registration number. 953.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S3). Although *Apogon imberbis* is not included in the reference phylogeny, it resolves in a clade with other species of *Apogonidae* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (Mabuchi et al. 2014, figs. 2–6). The phylogenetic relationships of *Apogonoidei* are presented in Figure 14.

Phylogenetics. The monophyly of *Apogonoidei* is supported in molecular phylogenetic analyses (W. L. Smith and Craig 2007; Near et al. 2013; Thacker et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018; McCraney et al. 2020; Ghezelayagh et al. 2022) and is consistent with suggestions of a close relationship between *Apogonidae* (cardinalfishes) and *Kurtus* (nurseryfishes) based on morphological characters of the gill arches, axial skeleton, and fine structures of the egg micropyle and filaments (G. D. Johnson 1993; Prokofiev 2006b).

Composition. There are currently 383 living species of *Apogonoidei* (Fricke et al. 2023) classified in *Apogonidae* and *Kurtus*. Over the past 10 years, 19 new living species of *Apogonoidei* have been described (Fricke et al. 2023), comprising 5.0% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Apogonoidei* include (1) second epibranchial articulates with third rather than second pharyngobranchial (G. D. Johnson 1993), (2) head of third pharyngobranchial expanded and much larger than fourth (G. D. Johnson 1993), (3) fourth pharyngobranchial cartilage absent (G. D. Johnson 1993), and (4) radial ridges of simple or bifid filaments around the micropyle of the eggs (G. D. Johnson 1993).

Synonyms. *Kurtiformes* (Betancur-R, Broughton, et al. 2013, fig. 3; J. S. Nelson et al. 2016:324; Betancur-R et al. 2017:23) is an ambiguous synonym of *Apogonoidei*.

Comments. The group name *Apogonoidei* has been applied to (1) a group containing *Apogonidae* and *Pempheridae* (Thacker 2009; Thacker and Roje 2009), (2) limited to *Apogonidae* (Betancur-R, Broughton, et al. 2013; Betancur-R et al. 2017; McCraney et al. 2020), and (3) a clade containing *Apogonidae* and *Kurtus* as presented here in the definition (Thacker et al. 2015; Ghezelayagh et al. 2022). The name *Apogonoidei* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

Apogonidae and *Kurtus* each have highly derived egg brooding behaviors in which the eggs bear filaments that allow them to adhere into a ball that is guarded in the mouth of male *Apogonidae* or on a forehead hook extending from the supraoccipital in *Kurtus* (Berra and Humphrey 2002; Berra 2003; Östlund-Nilsson and Nilsson 2004; Mabuchi et al. 2014). Several lineages of *Apogonidae*, including *Jaydia*, *Rhabdamia*, *Siphamia*, and *Taeniamia*, contain species with bioluminescent organs elaborated from the gut, which may host symbiotic luminescent bacteria or generate light endogenously; this luminescence has evolved multiple times within *Apogonidae* (Thacker 2009; Fraser 2013).

The earliest fossils of *Apogonoidei* are the otolith-based species of †*Apogonidarum* that are listed as *Apogonidae* from the Maastrichtian (72.2–66.0 Ma) in the Cretaceous of India and North Dakota, USA (Khajuria and Prasad 1998; Hoganson et al. 2019). The earliest skeletal fossils of *Apogonoidei* include the apogonids †*Apogoniscus*, †*Bolcapogon*, †*Eoapogon*, †*Eosphaeramia*, and †*Leptolumamia*, all from the Ypresian (56.0–48.1 Ma) of Monte Bolca, Italy (Bannikov and Fraser 2016). Bayesian relaxed molecular clock analyses of *Apogonoidei* result in an average posterior crown age estimate of 81.9 million years ago, with the credible interval ranging between 46.6 and 110.4 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Apogonidae *Kurtidae**

Scombriformes A. S. Woodward 1901:418
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Arripis trutta* (Bloch and Schneider 1801), *Icosteus aenigmaticus* Lockington 1880, *Scomber scombrus* Linnaeus 1758, *Brama japonica* Hilgendorf 1878, and *Trichiurus lepturus* Linnaeus 1758. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek σκόμβρος (skˈɑːmbɹoʊ͡z), which was the name for the Atlantic Mackerel, *Scomber scombrus* (D. W. Thompson 1947:243). The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 954.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, figs. S5, S6). See Figures 2 and 14 for the phylogenetic resolution of *Scombriformes* within *Percomorpha* and Figure 15 for a phylogeny of the living lineages and fossil taxa comprising *Scombriformes*. The placements of the fossil pan-trichiurid †*Anenchelum*, the pan trichiuroid †*Argestichthys*, the pan-chiasmodontid †*Bannikovichthys*, the pan-pomatomid †*Carangopsis*, and the pan-stromateid †*Pinichthys* are on the basis of inferences from morphology (Bannikov 1987, 1988, 2014b; Prokofiev 2002b; Carnevale 2007; Carnevale et al. 2014; Beckett et al. 2018b; Friedman et al. 2019; Collar et al. 2022).

Phylogenetics. Molecular phylogenetic analyses led to the discovery of the clade delimited here as *Scombriformes* (W.-J. Chen et al. 2003; W. L. Smith and Craig 2007; Dettaï and Lecointre 2008; B. Li et al. 2009; Yagishita et al. 2009; Wainwright et al. 2012; Betancur-R, Broughton, et al. 2013; Miya et al. 2013; Near et al. 2013; Davis et al. 2016; Sanciangco et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Campbell et al. 2018; Hughes et al. 2018; Friedman et al. 2019; Arcila et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022), consisting of lineages that were never grouped together in classifications based on morphology (Greenwood et al. 1966; Wiley and Johnson 2010). *Scombriformes* includes lineages previously classified in *Scombroidei* (*Scombridae* [mackerels and tunas], *Scombrolabrax heterolepis* [Longfin Escolar], *Gempylidae* [snake mackerels], and *Trichiuridae* [cutlassfishes]) and *Stromateoidei* (*Amarsipus carlsbergi* [Amparsipas], *Ariomma* [ariommatids], *Centrolophidae* [medusafishes], *Nomeidae* [driftfishes], *Stromateidae* [butterfishes], and *Tetragonuridae* [squaretails]) (Greenwood et al. 1966; Haedrich 1967; Collette, Potthoff, et al. 1984; Horn 1984; G. D. Johnson 1986). The billfishes, *Istiophoridae* (marlins) and *Xiphias gladius* (Swordfish), have been classified in *Scombroidei* since the earliest 20th century (Regan 1909b), but are distantly related to *Scombriformes* in molecular phylogenies (e.g., Orrell et al. 2006; Little et al. 2010; Hughes et al. 2018; Ghezelayagh et al. 2022).

Relationships among major lineages of *Scombriformes* resulting from phylogenomic analyses are characterized by a lack of resolution among the earliest nodes in the phylogeny that is likely the result of gene tree discordance and short branch lengths (e.g., Friedman et al. 2019; Arcila et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022). Despite the limited resolution, phylogenomic analyses resolve several clades in *Scombriformes* that include: a clade containing *Stromateidae* (butterfishes), *Ariomma*, and *Nomeidae* (driftfishes); a lineage that includes *Amarsipus carlsbergi* (Amarsipa) as the sister lineage of a clade containing *Tetragonurus* (squaretails) and *Chiasmodontidae* (swallowers); a clade that includes *Scombrolabrax heterolepis* (Longfin Escolar), *Lepidocybium flavobrunneum* (Escolar), a paraphyletic *Gempylidae* (snake mackerels), and *Trichiuridae* (cutlassfishes); and a lineage containing *Caristiidae* (manefishes) and *Bramidae* (pomfrets) (Friedman et al. 2019; Arcila et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022). The relationships of *Scombridae* (mackerels and tunas), *Icosteus aenigmaticus* (Ragfish), *Pomatomus saltatrix* (Bluefish), and *Arripis* (Australian Salmon) are not well resolved within *Scombriformes*; however, molecular analyses consistently resolve the lineages traditionally classified in *Stromateoidei* (e.g., Haedrich 1967; Horn 1984) as paraphyletic (Friedman et al. 2019; Arcila et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022).

The monophyly of *Scombriformes* is not supported in a morphological analysis of 207 characters that resolves the lineages traditionally classified in *Stromateoidei* as a monophyletic group (Pastana et al. 2022). The paraphyly of *Stromateoidei* consistently resolved in molecular phylogenetic analyses (e.g., Betancur-R, Broughton, et al. 2013; Near et al. 2013; Arcila

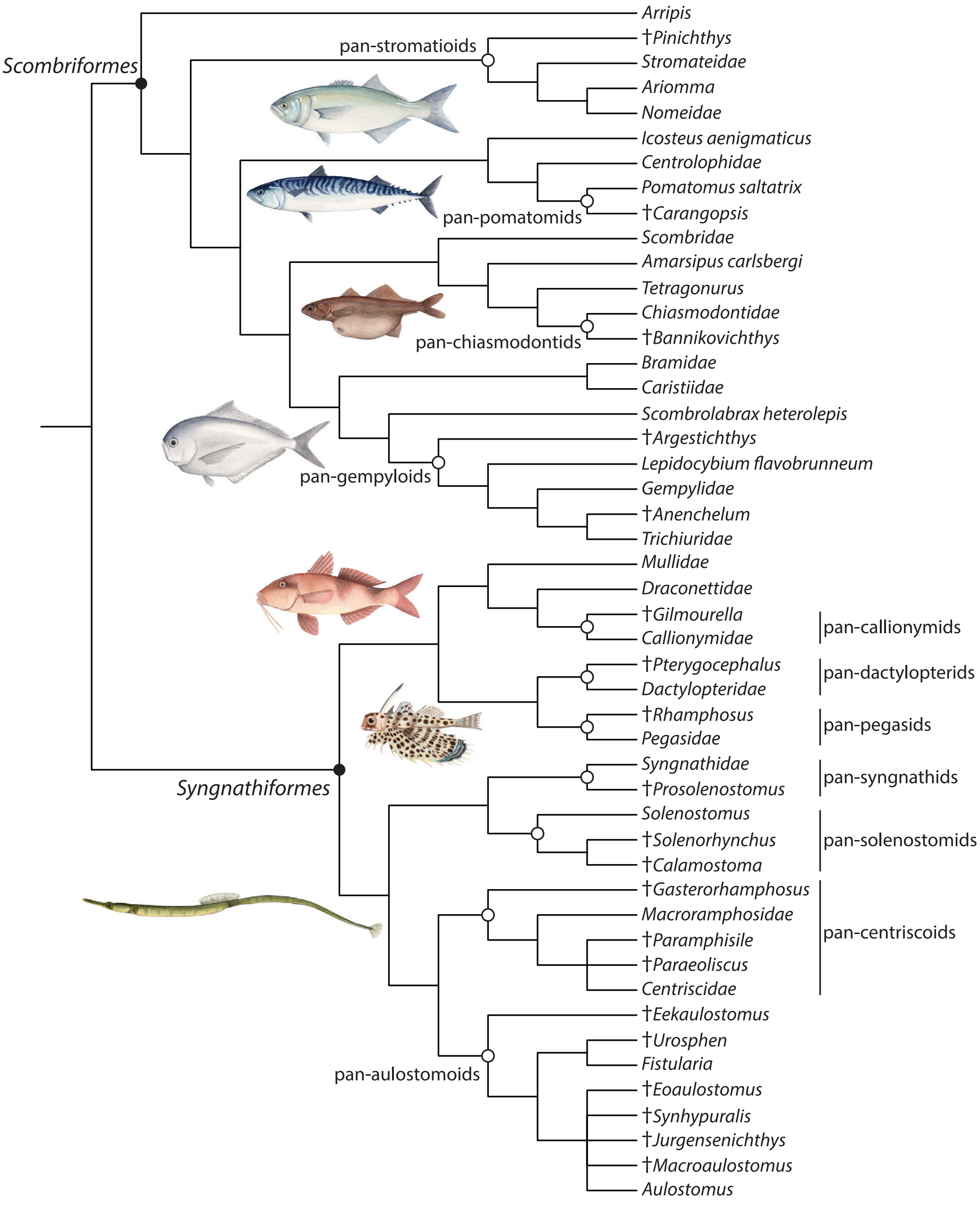

Figure 15. Phylogenetic relationships of the major living lineages and fossil taxa of *Scombriformes* and *Syngnathiformes*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022) is dismissed on the basis of the subjective assessment that morphological characters supporting stromateoid monophyly are "unparalleled and highly complex anatomical features unlikely to have evolved multiple times independently" (Pastana et al. 2022:957). There is a degree of uncertainty in the phylogenetic relationships among the major lineages of *Scombriformes* inferred from molecular data, including phylogenomic datasets (Arcila et al. 2021; Harrington et al. 2021); however, there is no analysis of character evolution for the traits offered as evidence for stromateoid monophyly that accommodates different models of trait evolution and uncertainty in the phylogenetic relationships of scombriforms and stromateoids.

Other morphological phylogenetic analyses have focused on lineages within *Scombriformes* that included the previous delimitations of *Scombroidei* and *Stromateoidei* (Collette, Potthoff, et al. 1984; Horn 1984; G. D. Johnson 1986; Doiuchi et al. 2004), *Gempylidae* and *Trichiuridae* (Gago 1997, 1998; Beckett et al. 2018b), and *Chiasmodontidae* (Melo 2009). A phylogenetic analysis of 29 morphological characters focused on *Scombroidei* resolves *Lepidocybium flavobrunneum*, long classified in *Gempylidae*, as the sister lineage of a clade containing all other *Gempylidae* and *Trichiuridae* (G. D. Johnson 1986), a result that is congruent with several molecular phylogenetic analyses (Friedman et al. 2019; Arcila et al. 2021; Harrington et al. 2021; Ghezelayagh et al. 2022). Phylogenetic analyses of DNA sequences from 13 mtDNA protein coding regions seems to resolve *Gempylidae* as monophyletic (Mthethwa et al. 2023a, 2023b), but this result is likely an artifact of limiting the outgroups to two species of *Trichiuridae*. There is no available family-group name to classify *Lepidocybium flavobrunneum*.

Composition. There are currently 287 living species of *Scombriformes* (Collette and Nauen 1983; Fricke et al. 2023) that include *Amarsipus carlsbergi*, *Icosteus aenigmaticus*, *Lepidocybium flavobrunneum*, *Pomatomus saltatrix*, *Scombrolabrax heterolepis*, and species classified in *Ariomma*, *Arripis*, *Bramidae*, *Caristiidae*, *Centrolophidae*, *Chiasmodontidae*, *Gempylidae*, *Nomeidae*, *Scombridae*, *Stromateidae*, *Tetragonurus*, and *Trichiuridae*. Fossil lineages of *Scombriformes* include the pan-stromateid †*Pinichthys pulcher* (Bannikov 1988), the pan-chiasmodontid †*Bannikovichthys paelignus* (Carnevale 2007), the pan-pomatomid †*Carangopsis maximus* (Agassiz 1835:42), the pan-trichiuroid †*Argestichthys vysotzkyi* (Prokofiev 2002b), and the pan-trichiurid †*Anenchelum eocaenicum* (Danilit'chenko 1962; Monsch and Bannikov 2011). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, six new living species of *Scombriformes* have been described, comprising 2.1% of the living species diversity in the clade (Fricke et al. 2023).

Diagnostic apomorphies. There are no known morphological apomorphies for *Scombriformes*.

Synonyms. *Stromateoidei* (B. Li et al. 2009, tbl. 4), *Pelagia* (Miya et al. 2013:2; Campbell et al. 2018:172), and *Pelagiaria* (Betancur-R et al. 2017:22; Campbell et al. 2018:173; Friedman et al. 2019:1) are ambiguous synonyms of *Scombriformes*.

Comments. The name *Scombriformes* was applied to (1) the paraphyletic group containing *Carangidae*, *Scombridae*, *Stromateidae*, and *Xiphias* (Woodward 1901:418), (2) expanded to include *Trichiuridae*, *Coryphaena*, and *Luvarus* (Goodrich 1909:462–468), (3) limited to *Scombridae* (Regan 1909b), and (4) the monophyletic group as presented here in the definition (Betancur-R, Broughton, et al. 2013; Davis et al. 2016; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Scombriformes* is the scombrid †*Landanichthys* from the Danian (66.0–61.7 Ma) of Angola (Friedman et al. 2019). Bayesian relaxed molecular clock analyses of *Scombriformes* result in an average posterior crown age estimate of 72.8 million years ago, with the credible interval ranging between 66.4 and 81.7 million years ago (Friedman et al. 2019).

Constituent lineages. Redundant group names are marked with an asterisk.

*Amarsipidae**
*Ariommatidae**
*Arripidae**
Bramidae
Caristiidae
Centrolophidae
Chiasmodontidae
Gempylidae
*Icosteidae**
Lepidocybium
Nomeidae
*Pomatomidae**
Scombridae
*Scombrolabracidae**
Stromateidae
*Tetragonuridae**
Trichiuridae
†*Anenchelum*
†*Argestichthys*
†*Bannikovichthys*
†*Carangopsis*
†*Pinichthys*

Syngnathiformes P. Bleeker 1859:xv
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Pegasus volitans* Linnaeus 1758, *Mullus auratus* Jordan and Gilbert 1882b, *Callionymus curvicornis* Valenciennes 1837 in Cuvier and Valenciennes (1837), *Centriscus scutatus* Linnaeus 1758, and *Syngnathus acus* Linnaeus 1758. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek σύμφῠσις (sˈɪmfuːsiz) meaning grown together or fused, especially in reference to bones, and γνάθος (nˈæθo͡ʊz) meaning jaw. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 955.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, figs. S7–S9). See Figures 2 and 14 for the phylogenetic resolution of *Syngnathiformes* within *Percomorpha* and Figure 15 for a phylogeny of the living lineages and fossil taxa comprising *Syngnathiformes*. The phylogenetic placement of the fossil pan-pegasid †*Rhamphosus* follows Pietsch (1978), Bannikov (2014b), Carnevale et al. (2014), and Calzoni et al. (2023); the pan-aulostomoid †*Eekaulostomus* follows Cantalice and Alvarado-Ortega (2016); the pan-aulostomids †*Eoaulostomus*, †*Jurgensenichthys*, †*Macroaulostomus*, and †*Synhypuralis* follows Blot (1980) and Orr (1995); the pan-fistularid †*Urosphen* follows Orr (1995); the pan centriscoid †*Gasterorhamphosus* follows Orr (1995) and Friedman (2009); the pan-centriscids †*Paraeoliscus* and †*Paramphisile* follows Blot (1980), Friedman (2009), and Brownstein (2023); the pan-solenostomids †*Calamostoma* and †*Solenorhynchus* follows Bannikov and Carnevale (2017) and Brownstein (2023); the pan-syngnathid †*Prosolenostomus* follows Orr (1995), A. B. Wilson and Orr (2011), and Brownstein (2023); the pan-callionymid †*Gilmourella* follows Carnevale and Bannikov (2019); and the pan-dactylopterid †*Pterygocephalus* follows Bannikov (2014b) and Carnevale et al. (2014). The phylogenetic placements of †*Eekaulostomus* and †*Prosolenostomus* differ from those presented in other phylogenetic analyses (Murray 2022).

Phylogenetics. Reflecting earlier classifications (e.g., Goodrich 1909:410–416), Greenwood et al. (1966) placed many lineages of *Syngnathiformes*, including pipefishes and seahorses, in *Gasterosteiformes* along with sticklebacks (e.g., *Gasterosteidae*) and *Indostomus* (armored sticklebacks). This delimitation of *Gasterosteiformes* was corroborated with several putative morphological synapomorphies (Pietsch 1978; G. D. Johnson and Patterson 1993; Orr 1995; Britz and Johnson 2002; Wiley and Johnson 2010).

The first set of molecular phylogenetic analyses aimed at relationships with *Percomorpha* resolved lineages traditionally classified in *Gasterosteiformes* into three disparately related clades (W.-J. Chen et al. 2003; Miya et al. 2003; W. L. Smith and Wheeler 2004, 2006; Dettaï and Lecointre 2005; W. L. Smith and Craig 2007; Kawahara et al. 2008; B. Li et al. 2009). Subsequent molecular phylogenetic studies with a broad taxon sampling of percomorph lineages consistently resolved *Syngnathiformes* as a clade containing a paraphyletic *Syngnathoidei* (e.g., *Pegasidae*, *Syngnathidae*, and *Centriscidae*), *Callionymidae* (dragonets), *Draconettidae* (slope dragonets), *Mullidae* (goatfishes), and *Dactylopteridae* (flying gurnards) (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Song et al. 2014; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Roth et al. 2020; Ghezelayagh et al. 2022). Molecular phylogenetic analyses of *Syngnathiformes* consistently resolve two lineages: a clade of benthic lineages that contains *Pegasidae* (seamoths), *Dactylopteridae*, *Draconettidae*, *Callionymidae*, and *Mullidae*, and a clade of the long-snouted lineages *Syngnathidae* (seahorses and pipefishes), *Solenostomus* (ghost pipefishes), *Centriscidae* (shrimpfishes), *Macrorhamphosus* (snipefishes), *Aulostomus* (trumpetfishes), and *Fistularia* (cornetfishes) (Longo et al. 2017; Santaquiteria et al. 2021; Ghezelayagh et al. 2022). Several molecular phylogenetic studies have focused on resolving relationships within

Syngnathidae (Hamilton et al. 2017; Longo et al. 2017; Santaquiteria et al. 2021; Stiller et al. 2022).

Composition. There are currently 690 living species of *Syngnathiformes* (Fricke et al. 2023) classified in *Aulostomus*, *Callionymidae*, *Centriscidae*, *Dactylopteridae*, *Draconettidae*, *Fistularia*, *Macroramphosidae*, *Mullidae*, *Pegasidae*, *Solenostomus*, and *Syngnathidae*. Fossil lineages of *Syngnathiformes* include the pan-pegasid †*Rhamphosus rastrum* (Volta 1796); the pan-aulostomoid †*Eekaulostomus cuevasae* (Cantalice and Alvarado-Ortega 2016); the pan-aulostomids †*Eoaulostomus bolcensis*, †*Jurgensenichthys elongatus*, †*Macroaulostomus veronensis*, and †*Synhypuralis banister* (Blot 1980); the pan-fistularid †*Urosphen dubius* (Blainville 1818); the pan-centriscid †*Gasterorhamphosus zuppichinii* (Sorbini 1981); the pan-centriscids †*Paraeoliscus robinetae* and †*Paramphisile weileri* (Blot 1980); the pan-solenostomids †*Calamostoma breviculum* and †*Solenorhynchus elegans* (Blainville 1818; Heckel 1853); the pan-syngnathid †*Prosolenostomus lessinii* (Blot 1980); the pan-callionymid †*Gilmourella minuta* (Carnevale and Bannikov 2019); and the pan-dactylopterid †*Pterygocephalus paradoxus* (Agassiz 1835). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 51 new living species of *Syngnathiformes* have been described, comprising 7.4% of the living species diversity in the clade (Fricke et al. 2023).

Diagnostic apomorphies. There are no known morphological apomorphies for *Syngnathiformes*.

Synonyms. *Syngnatharia* (Betancur-R et al. 2017:22) is an ambiguous synonym of *Syngnathiformes*. *Gasterosteiformes* (Goodrich 1909:410–416; Greenwood et al. 1966:398; G. D. Johnson and Patterson 1993:580; J. S. Nelson 2006:308–316; Wiley and Johnson 2010:154) and *Gobiesociformes* (Wiley and Johnson 2010:162–163) are partial synonyms of *Syngnathiformes*.

Comments. *Syngnathiformes* was the name applied to the clade containing *Aulostomus*, *Centriscidae*, *Fistularia*, *Macroramphosidae*, *Solenostomus*, and *Syngnathidae* (McAllister 1968:111–114; J. S. Nelson 1984:249–253). In recent classifications of percomorphs, the name *Syngnathiformes* was applied for a more inclusive clade presented here in the definition (Davis et al. 2016; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022). The name *Syngnathiformes* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Syngnathiformes* is the pan-centriscoid †*Gasterorhamphosus zuppichinii* from the Campanian and Maastrichtian (83.6–66.0 Ma) of Italy. Bayesian relaxed molecular clock analyses of *Syngnathiformes* result in an average posterior crown age estimate of 104.6 million years ago, with the credible interval ranging between 95.0 and 114.8 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Aulostomidae**
Callionymidae
Centriscidae
Dactylopteridae
Draconettidae
*Fistulariidae**
Macroramphosidae
Mullidae
Pegasidae
*Solenostomidae**
Syngnathidae
†*Calamostoma*
†*Eekaulostomus*
†*Eoaulostomus*
†*Gasterorhamphosus*
†*Gilmourella*
†*Jurgensenichthys*
†*Macroaulostomus*
†*Paraeoliscus*
†*Paramphisile*
†*Prosolenostomus*
†*Pterygocephalus*
†*Rhamphosus*
†*Solenorhynchus*
†*Synhypuralis*
†*Urosphen*

Ovalentaria W. L. Smith and T. J. Near in Wainwright et al. 2012

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Ambassis urotaenia* Bleeker 1852, *Mugil cephalus* Linnaeus 1758, *Embiotoca lateralis* Agassiz 1854, *Pseudochromis fridmani* Klausewitz 1968, *Gobiesox maeandricus* (C. Girard 1858a), *Gillellus semicinctus* Gilbert 1890, *Polycentrus schomburgkii* Müller and Troschel 1848, *Pholidichthys leucotaenia*

Bleeker 1856, *Cichla temensis* Humboldt in Humboldt and Valenciennes 1821, *Labidesthes sicculus* (Cope 1865), *Gambusia affinis* (Baird and Girard 1853), and *Oryzias latipes* (Temminck and Schlegel 1846). This is a minimum-crown-clade definition.

Etymology. From the Latin *ovum* meaning egg and *lentae* meaning sticky or tenacious.

Registration number. 998.

Reference phylogeny. A phylogeny inferred from DNA sequences of 10 concatenated Sanger-sequenced nuclear genes (Wainwright et al. 2012, fig. 2). The phylogenetic resolution of *Ovalentaria* within *Percomorpha* is presented in Figure 2, and the phylogenetic relationships of the major lineages of *Ovalentaria* are presented in Figures 14 and 16.

Phylogenetics. Monophyly of *Ovalentaria* was discovered in early molecular analyses aimed at resolving relationships within *Percomorpha* (W.-J. Chen et al. 2003; Dettaï and Lecointre 2005; Miya et al. 2005; W. L. Smith and Wheeler 2006; Mabuchi et al. 2007; W. L. Smith and Craig 2007; Kawahara et al. 2008; Setiamarga et al. 2008). A phylogenetic analysis of DNA sequences from four nuclear genes resolved a clade comprising *Mugilidae* (mullets), *Plesiopidae* (roundheads), *Blennioidei* (blennies), *Atheriniformes* (silversides, needlefishes, and killifishes), *Cichlidae* (cichlids), *Gobiesocidae* (clingfishes), and *Pomacentridae* (damselfishes) (B. Li et al. 2009). A subsequent analysis of 10 exons expanded the clade to include *Polycentridae* (leaffishes), *Pholidichthys* (engineer blennies), *Embiotocidae* (surfperches), *Congrogadidae* (eel blennies), *Pseudochromidae* (dottybacks), *Gramma* and *Lipogramma* (basslets), and *Opistognathidae* (jawfishes) (Wainwright et al. 2012). Subsequent molecular analyses consistently support the monophyly of *Ovalentaria* (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Collins et al. 2015; Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Ghezelayagh et al. 2022; Mu et al. 2022). Initially, the monophyly of *Ovalentaria* was discussed in the context of the presence of demersal eggs with adhesive filaments that characterizes many of the lineages in the clade (Breder and Rosen 1966; Semple 1985; Mooi 1990; Wirtz 1993; Britz 1997; Breining and Britz 2000).

A morphological phylogenetic analysis of *Ovalentaria* based on 38 characters scored from the caudal skeleton did not include other percomorph lineages and therefore did not test monophyly of the clade (Thieme et al. 2022). Relationships within *Ovalentaria* differed from molecular phylogenetic analyses in that *Gramma* and *Lipogramma* were resolved as a clade, *Pholidichthys* and *Cichlidae* were not resolved as sister lineages, *Gobiesocidae* and *Blennioidei* did not form a monophyletic group, and both *Blennioidei* and *Atheriniformes* were resolved as paraphyletic (Thieme et al. 2022).

Composition. There are currently 5,940 living species of *Ovalentaria* (Fricke et al. 2023) classified in *Atheriniformes* and *Blenniiformes*. Over the past 10 years, 527 new living species of *Ovalentaria* have been described (Fricke et al. 2023), comprising approximately 8.9% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Ovalentaria* are currently limited to features of the caudal skeleton and include (1) fusion of two ural centra to form the compound centrum during development (Thieme et al. 2022), and (2) second uroneural present (Thieme et al. 2022).

Synonyms. *Blenniiformes* (Dornburg and Near 2021; Ghezelayagh et al. 2022) and *Ovalentariae* (Betancur-R, Broughton, et al. 2013:13) are ambiguous synonyms of *Ovalentaria*. *Stiassnyiformes* (B. Li et al. 2009, tbl. 4) is a partial synonym of *Ovalentaria*.

Comments. *Ovalentaria* is one of the most species-rich named clades of *Percomorpha* and similarly to nearly every percomorph clade was discovered primarily through molecular phylogenetic analyses (e.g., Wainwright et al. 2012). A study examining the morphology of the caudal skeleton in *Ovalentaria* illustrates the potential of applying molecular inferred phylogenies with novel results to understanding phenotypic evolution in large inclusive

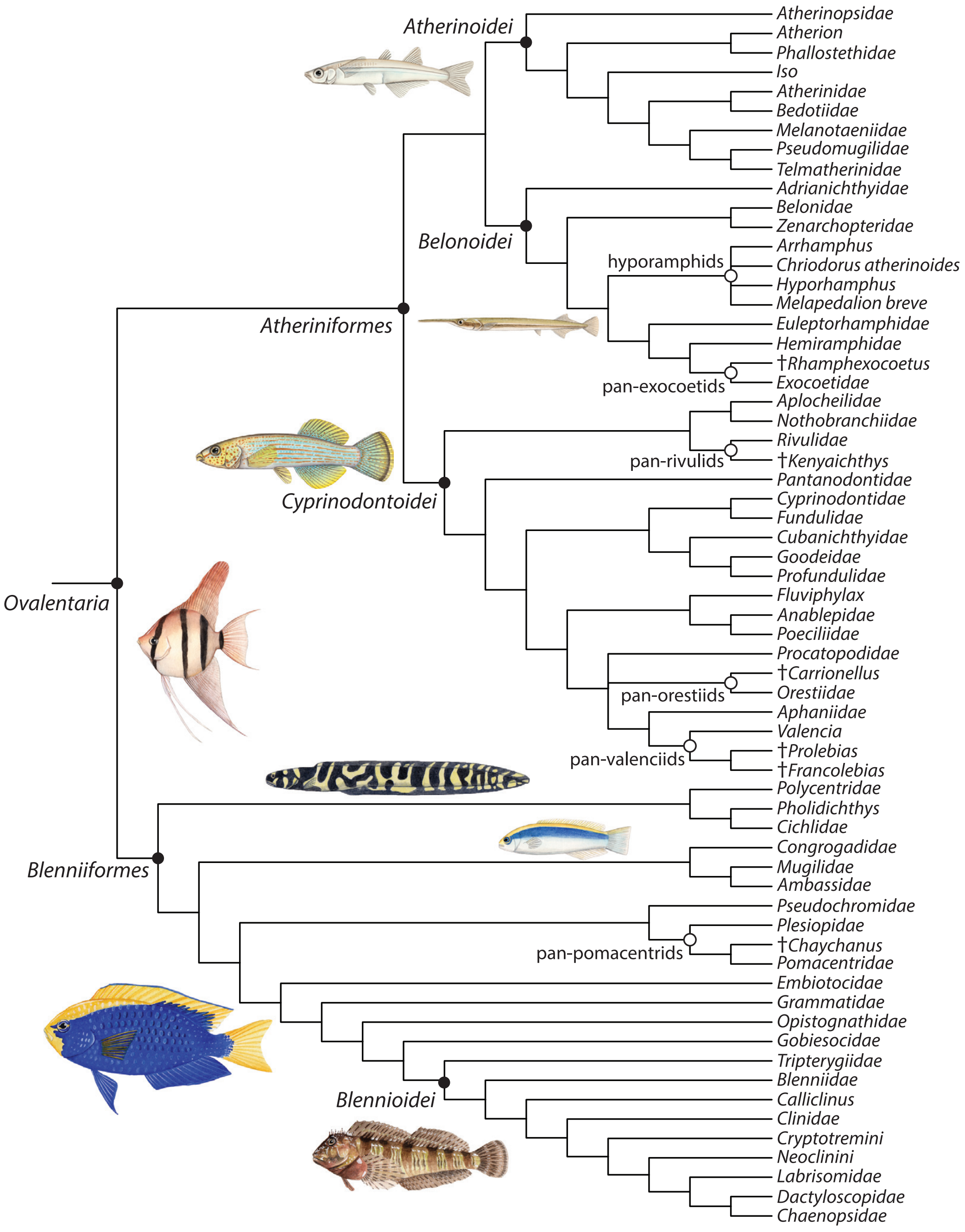

FIGURE 16. Phylogenetic relationships of the major living lineages and fossil taxa of *Ovalentaria*, *Atheriniformes*, *Atherinoidei*, *Belonoidei*, *Cyprinodontoidei*, *Blenniiformes*, and *Blennioidei*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

clades of *Percomorpha* (Thieme et al. 2022). The name *Ovalentaria* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

Bayesian relaxed molecular clock analyses of *Ovalentaria* result in an average posterior crown age estimate of 96.2 million years ago, with the credible interval ranging between 86.2 and 106.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Atheriniformes *Blenniiformes*

Atheriniformes J. Ferrer Aledo 1930:245

Definition. The least inclusive crown clade that contains *Oryzias latipes* (Temminck and Schlegel 1846), *Atherina hepsetus* Linnaeus 1758, and *Cyprinodon variegatus* Lacépède 1803. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek ἀθερίνη (æθɚɹˈiːnə), which is the name used by ancient authors (e.g., Aristotle and Oppian) in reference to the Mediterranean Sand Smelt, *Atherina hepsetus* Linnaeus (D. W. Thompson 1947:3–4).

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S10). Although *Atherina hepsetus* is not included in the reference phylogeny, it resolves in a clade with other species of *Atherina* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (Sparks and Smith 2004b, fig. 2; Astolfi et al. 2005, fig. 2; Francisco et al. 2008, fig. 2, 2011, fig. 2; Heras and Roldán 2011, fig. 2; Campanella et al. 2015, fig. 2B). See Figure 16 for a phylogeny of the lineages comprising *Atheriniformes*.

Phylogenetics. The delimitation of *Atheriniformes* that includes *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei* was first proposed in a pre-Hennigian study of osteology, musculature, and reproductive characters that aimed toward the identification of “a phylogenetically natural group” (Rosen 1964:260). Since this work, the monophyly of *Atheriniformes* has not been challenged. Analysis of the gill arch skeleton and hyoid apparatus led to the reclassification of *Adrianichthyidae* (ricefishes) from *Cyprinodontoidei* to *Belonoidei*, the discovery that *Atherinoidei* was not diagnosed by morphological synapomorphies, and the resolution of *Belonoidei* and *Cyprinodontoidei* as sister lineages (Rosen and Parenti 1981). Subsequent phylogenetic analyses using morphological characters consistently supported the monophyly of *Atheriniformes* and the sister lineage relationship between *Belonoidei* and *Cyprinodontoidei* (White 1985; Stiassny 1990; L. R. Parenti 1993, 2005; Saeed et al. 1994; Dyer and Chernoff 1996; Dyer H 2006).

Several of the earliest molecular phylogenies of *Percomorpha* resolved *Atheriniformes* as paraphyletic as a result of the placement of other lineages of *Ovalentaria* (W.-J. Chen et al. 2003; Dettaï and Lecointre 2005; Miya et al. 2005), but subsequent molecular phylogenetic studies support atheriniform monophyly (Mabuchi et al. 2007; Kawahara et al. 2008; Setiamarga et al. 2008; B. Li et al. 2009; Near, Eytan, et al. 2012; Wainwright et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Eytan et al. 2015; Davis et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Ghezelayagh et al. 2022). Within *Atheriniformes*, molecular phylogenies have resolved all three possible relationships among *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei*: *Belonoidei* and *Cyprinodontoidei* as sister lineages (Miya et al. 2005; Mabuchi et al. 2007; Kawahara et al. 2008; Setiamarga et al. 2008; Wainwright et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Smith et al. 2016; Hughes et al. 2018; Rabosky et al. 2018), *Atherinoidei* and *Belonoidei* as sister lineages (B. Li et al. 2009; Eytan et al. 2015; Ghezelayagh et al. 2022), and *Atherinoidei* and *Cyprinodontoidei* as sister lineages (Davis et al. 2016; Betancur-R et al. 2017). Node support for these relationships is typically low, and changes in taxon sampling for similar sets of sampled genes seem to affect the resolution of relationships within *Atheriniformes* (e.g., Betancur-R, Broughton, et al. 2013; Betancur-R et al. 2017). While there is strong support from both morphological and molecular data for monophyly of *Atheriniformes*, there remains uncertainty in the relationships among *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei*.

Composition. There are currently 2,126 living species of *Atheriniformes* (Fricke et al. 2023) classified in *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei*. Over the past 10 years, 259 new living species of *Atheriniformes* have been described (Fricke et al. 2023), comprising approximately 12.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Atheriniformes* include (1) separation of afferent and efferent circulation during development (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (2) a restricted lobular type of testis, in which the spermatogonia are present at the lobule ends only rather than throughout the entire length of the lobule (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; L. R. Parenti and Grier 2004; Wiley and Johnson 2010; Uribe et al. 2014), (3) protrusible upper jaw mechanism with palatomaxillary ligaments crossed and with maxillary ligament to the cranium (Rosen and Parenti 1981), (4) dermal and endochondral disclike ethmoid ossifications (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (5) medial hooklike projection and ventral flange on fifth ceratobranchial (Stiassny 1990; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (6) supraneurals absent (Stiassny 1990; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (7) infraorbital series consisting of lacrimal, dermosphenotic, and two or fewer anterior infraorbital bones (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (8) dorsal portion of gill arch with large fourth epibranchial as the supporting bone (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (9) fourth pharyngobranchial absent in dorsal gill arch (Rosen and Parenti 1981; L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (10) saccus vasculosus absent (Tsuneki 1992; L. R. Parenti 2005; Wiley and Johnson 2010), (11) coupling during mating (L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (12) distal end of pleural rib and lateral process of pelvic bone in close association and sometimes attached with a ligament (L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (13) supracleithrum reduced or absent (L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (14) superficial (A_1) division of adductor mandibulae with two tendons, one inserting on maxilla, second inserting on lacrimal (L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (15) olfactory sensory epithelium arranged in sensory islets (L. R. Parenti 1993, 2005; Wiley and Johnson 2010), (16) fluid (rather than granular) egg yolk (L. R. Parenti and Grier 2004; L. R. Parenti 2005; Wiley and Johnson 2010), (17) caudal fin supported by three preural centra (Thieme et al. 2022), (18) lower hypural plate fused with compound centrum (Thieme et al. 2022), (19) uroneural fused with compound centrum (Thieme et al. 2022), (20) haemal arch of preural centrum 2 fused with its centrum (Thieme et al. 2022), and (21) absence of interhaemal spine cartilage 2 (Thieme et al. 2022).

Synonyms. *Atherinomorpha* (Greenwood et al. 1966:397; Rosen 1973:510, fig. 129; Rosen and Parenti 1981:23; J. S. Nelson et al. 2016:353–354) and *Atherinomorphae* (Wiley and Johnson 2010:154; Betancur-R, Broughton, et al. 2013, fig. 8; Betancur-R et al. 2017:25) are ambiguous synonyms of *Atheriniformes*.

Comments. *Atheriniformes* was applied as the name of a taxonomic group that included species classified in *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei* (Rosen 1964; Greenwood et al. 1966:397–398).

The earliest fossils of *Atheriniformes* are all from the Ypresian (56.0–48.1 Ma) of Italy and include the pan-exocoetid †*Rhamphexocoetus* (Appendix 1; Bannikov et al. 1985) and the atherinoid †*Latellagnathus* (Bannikov et al. 1985; Bannikov 2008, 2014b; Carnevale et al. 2014). Bayesian relaxed molecular clock analyses of *Atheriniformes* result in an average posterior crown age estimate of 87.5 million years ago, with the credible interval ranging between 76.8 and 97.2 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Atherinoidei
Belonoidei
Cyprinodontoidei

Atherinoidei P. Bleeker 1859:xxiv

Definition. The least inclusive crown clade that contains *Atherinella panamensis* Steindachner 1875, *Atherinopsis californiensis* C. Girard 1854, *Atherina hepsetus* Linnaeus 1758, and *Atherion elymus* Jordan and Starks 1901. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek ἀθερίνη (ˈæθɚɹˌɪniː), which is the name for the Mediterranean Sand Smelt, *Atherina hepsetus* Linnaeus, used by Aristotle and Oppian (D. W. Thompson 1947:3–4).

Reference phylogeny. A phylogeny inferred from a dataset comprising eight Sanger-sequenced mtDNA and nuclear genes (Campanella et al. 2015, fig. 2). Although *Atherina hepsetus* is not included in the reference phylogeny, it resolves in a clade with other species of *Atherina* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (e.g., Campanella et al. 2015, fig. 2B). Phylogenetic relationships of the major lineages of *Atherinoidei* are presented in Figure 16.

Phylogenetics. Subsequent to the delimitation of *Atherinoidei* (Rosen 1964), several morphological studies did not support the monophyly of the group (Rosen and Parenti 1981; L. R. Parenti 1984, 1989, 1993; Ivantsoff et al. 1987; Saeed et al. 1994); however, studies based on adult and larval morphology provided evidence for the monophyly of the lineage (White et al. 1984; Dyer and Chernoff 1996; Aarn and Ivantsoff 1997). Molecular phylogenetic studies consistently resolve *Atherinoidei* as monophyletic (Setiamarga et al. 2008; Bloom et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Campanella et al. 2015; Betancur-R et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Ghezelayagh et al. 2022).

Morphological and molecular phylogenetic analyses are congruent in resolving *Atherinopsidae* (New World silversides) as the sister lineage of all other *Atherinoidei* (Aarn and Ivantsoff 1997; Bloom et al. 2012; Near et al. 2013; Campanella et al. 2015; Betancur-R et al. 2017; Ghezelayagh et al. 2022). One area of incongruence among phylogenetic analyses is the support for *Notocheirus hubbsi* (Surf Silverside) and species of *Iso* (surf sardines) as sister lineages in a morphological study (Dyer and Chernoff 1996); however, *Notocheirus* is nested well within *Atherinopsidae* and *Iso* is resolved as the sister lineage of a clade containing *Atherinidae* (silversides), *Bedotiidae* (Madagascar rainbowfishes), *Melanotaeniidae* (rainbowfishes), *Telmatherinidae* (Celebes rainbowfishes), and *Pseudomugilidae* (blue eyes) in molecular phylogenies (Bloom et al. 2012, 2013; Campanella et al. 2015; Rabosky et al. 2018; Ghezelayagh et al. 2022).

Phylogenetic analyses of Sanger-sequenced mtDNA and nuclear genes result in the paraphyly of *Melanotaeniidae* because *Cairnsichthys* is resolved as the sister lineage all other sampled species of *Telmatherinidae* and *Pseudomugilidae* (Bloom et al. 2012; Campanella et al. 2015; Rabosky et al. 2018); however, *Melanotaeniidae* is monophyletic in morphological and phylogenomic analyses (Aarn and Ivantsoff 1997; Aarn et al. 1998; Ghezelayagh et al. 2022). Following conclusions from a morphological phylogenetic analysis (Dyer and Chernoff 1996), Nelson et al. (2016:358–360) treat *Bedotiidae*, *Pseudomugilidae*, and *Telmatherinidae* as lineages of *Melanotaeniidae*.

A molecular phylogeny resolves *Atherion* (pricklenose silversides) and *Phallostethidae* (priapiumfishes) as sister lineages (Campanella et al. 2015). To date, there are no molecular data available for *Dentatherina merceri* (Mercer's Tusked Silverside), but several morphological studies place it as the sister lineage of *Phallostethidae* (L. R. Parenti 1984; Dyer and Chernoff 1996; Aarn and Ivantsoff 1997). This has prompted the classification of *D. merceri* in *Phallostethidae* (Dyer and Chernoff 1996; Aarn and Ivantsoff 1997; J. S. Nelson 2006:273); however, the group name *Dentatherinidae*, including only *D. merceri*, is endorsed by others (Ivantsoff et al. 1987; J. S. Nelson et al. 2016:360–361). Because *D. merceri* is convincingly resolved as the sister lineage of a clade containing all other priapiumfishes, we include it in *Phallostethidae* as an optimal reflection of phylogenetic relationships and an effort to reduce redundant group names in the classification of ray-finned fishes.

<u>Composition.</u> There are currently 385 living species of *Atherinoidei* (Fricke et al. 2023) classified in *Atherinidae*, *Atherinopsidae*, *Atherion*, *Bedotiidae*, *Iso*, *Melanotaeniidae*, *Phallostethidae*, *Pseudomugilidae*, and *Telmatherinidae*. Over the past 10 years, there have been 38 new species of *Atherinoidei* described (Fricke et al. 2023), comprising 9.9% of the species diversity in the clade.

<u>Diagnostic apomorphies.</u> Morphological apomorphies for *Atherinoidei* include (1) preanal length of flexion larvae short, approximately 33% of body length (White et al. 1984; Wiley and Johnson 2010), (2) single row of melanophores on dorsal midline of larvae (White et al. 1984; L. R. Parenti 2005; Wiley and Johnson 2010), (3) ventral face of vomer concave (Dyer and Chernoff 1996; Wiley and Johnson 2010), (4) adductor mandibulae A_1 with long tendon to lacrimal (Dyer and Chernoff 1996; Wiley and Johnson 2010), (5) two anterior infraorbital bones (Dyer and Chernoff 1996; L. R. Parenti 2005; Wiley and Johnson 2010), (6) presence of pelvic rib ligament (Dyer and Chernoff 1996; Wiley and Johnson 2010), (7) pelvic plate does not extend to anterior tip of longitudinal shaft (Dyer and Chernoff 1996; Wiley and Johnson 2010), and (8) presence of a flexible second dorsal fin (Dyer and Chernoff 1996; Wiley and Johnson 2010).

<u>Synonyms.</u> *Atherinidae* (Jordan and Hubbs 1919:12–19; Schultz 1948:2–3) and *Atheriniformes* (Saeed et al. 1994:47–48; Dyer and Chernoff 1996, tbl. 1; Wiley and Johnson 2010:155; Betancur-R, Broughton, et al. 2013, fig. 3; J. S. Nelson et al. 2016:354–355; Betancur-R et al. 2017:25) are ambiguous synonyms of *Atherinoidei*.

<u>Comments.</u> In the mid-20th century, *Atherinoidei* was applied as the name of a group containing *Atherinidae*, *Bedotiidae*, *Isonidae*, *Melanotaeniidae*, *Phallostethidae*, and *Pseudomugilidae* (Rosen 1964; Greenwood et al. 1966).

The earliest fossil taxa of *Atherinoidei* are all from the Ypresian (56.0–48.1 Ma) and include the otolith taxon †'*Atherinidarum*' from France and India (Nolf 1988; Nolf et al. 2006) and the skeletal fossils †*Rhamphognathus*, †*Latellagnathus*, and †*Mesogaster* from Italy (Bannikov 2008, 2014b; Carnevale et al. 2014). Bayesian relaxed molecular clock analyses of *Atherinoidei* result in an average posterior crown age estimate of 71.0 million years ago, with the credible interval ranging between 56.5 and 84.4 million years ago (Ghezelayagh et al. 2022).

<u>Constituent lineages.</u> Redundant group names are marked with an asterisk.

Atherinidae
Atherinopsidae
*Atherionidae**
Bedotiidae
*Isonidae**
Melanotaeniidae
Phallostethidae
Pseudomugilidae
Telmatherinidae

Belonoidei E. Postel 1959:150

<u>Definition.</u> The least inclusive crown clade that contains *Adrianichthys oophorus* (Kottelat 1990), *Xenentodon cancila* (Hamilton 1822), *Hemiramphus far* (Fabricius in Niebuhr 1775), and *Belone belone* (Linnaeus 1761). This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

<u>Etymology.</u> From the ancient Greek βελόνη (bɨlˈɑːne͡ɪ) meaning needle, but also the name applied to the Greater Pipefish (*Syngnathus acus*) and the Garfish (*Belone belone*) in the biological writings of Aristotle (D. W. Thompson 1947:29–32).

<u>Reference phylogeny.</u> A phylogeny of 123 species of *Belonoidei* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). Phylogenetic relationships among the major lineages of *Belonoidei* are presented in Figure 16. The placement of †*Rhamphexocoetus* in the phylogeny is on the basis of inferences from morphology (Bannikov et al. 1985; Benton et al. 2015).

<u>Phylogenetics.</u> *Hemiramphidae* (halfbeaks), *Exocoetidae* (flyingfishes), *Belonidae* (needlefishes), and *Scomberesocidae* (sauries) were grouped together in early 20th-century classifications (Schlesinger 1909; Regan 1911f). Phylogenetic analysis of morphology led to a

delimitation of *Belonoidei* that includes those lineages plus *Adrianichthyidae* (ricefishes) (Rosen and Parenti 1981). Subsequent morphological and molecular studies provided additional support for the monophyly of *Belonoidei* and for the resolution of *Adrianichthyidae* as the sister lineage to all other belonoids (Collette, McGowen, et al. 1984; L. R. Parenti 1987, 1993, 2008; Miya et al. 2003, 2005; Kawahara et al. 2008; Setiamarga et al. 2008; Near, Eytan, et al. 2012; Wainwright et al. 2012; Near et al. 2013; Davis et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022; Ding et al. 2023).

Phylogenetic analyses of morphological and molecular data motivated changes to the traditional classification of *Belonoidei* (Lovejoy et al. 2004; Aschliman et al. 2005), but current classifications continue to include paraphyletic groups (J. S. Nelson et al. 2016:363–370; Betancur-R et al. 2017). For example, *Belonidae* as traditionally delimited is paraphyletic because species classified in *Scomberesocidae* (sauries), *Cololabis*, and *Scomberesox* are nested within *Belonidae* as the sister lineage of *Belone* (Lovejoy 2000; Lovejoy et al. 2004; Daane et al. 2021). *Cololabis* and *Scomberesox* are now placed in *Belonidae* (Betancur-R et al. 2017). *Hemiramphidae* is resolved as paraphyletic in both morphological (Tibbetts 1991; Aschliman et al. 2005) and molecular phylogenetic analyses (Lovejoy 2000; Lovejoy et al. 2004; Betancur-R et al. 2017; Daane et al. 2021; Ghezelayagh et al. 2022; Ding et al. 2023). The paraphyly of *Hemiramphidae* led to the recognition of *Zenarchopteridae* (viviparous halfbeaks) as a separate Linnean-ranked taxonomic family (Lovejoy et al. 2004); however, the remaining lineages of *Hemiramphidae* are paraphyletic relative to *Exocoetidae*. Three lineages comprise the current delimitation of *Hemiramphidae* (Lovejoy 2000; Lovejoy et al. 2004; Daane et al. 2021): a clade we refer to with the informal name hyporhamphids that contains *Arrhamphus*, *Chriodorus atherinoides*, *Hyporhamphus*, and *Melapedalion breve* for which there is no available family-group name (Van der Laan et al. 2014:77); *Euleptorhamphus* and *Rhynchorhamphus* that we delimit as *Euleptorhamphidae*, an elevation of *Euleptorhamphinae* (Fowler 1934:323); and *Hemiramphidae* that is limited here to species of *Hemiramphus* and *Oxyporhamphus*. The more exclusive *Hemiramphidae* and *Exocoetidae* are consistently resolved as sister lineages in molecular phylogenetic analyses (Lovejoy 2000; Lovejoy et al. 2004; Betancur-R et al. 2017; Daane et al. 2021; Ghezelayagh et al. 2022). Morphological phylogenetic analyses result in the resolution of most lineages traditionally classified in *Hemiramphidae* in a large polytomy with a clade containing *Oxyporhamphus* and *Exocoetidae* (Tibbetts1991; Aschliman et al. 2005).

Composition. There are currently 292 living species of *Belonoidei* (Collette 2003, 2004a, 2004b; Bemis and Collette 2019; Collette and Bemis 2019a, 2019b, 2019c; Parin et al. 2019; Fricke et al. 2023) that include *Arrhamphus sclerolepis*, *Chriodorus atherinoides*, *Melapedalion breve*, and species classified in *Adrianichthyidae*, *Belonidae*, *Euleptorhamphidae*, *Exocoetidae*, *Hemiramphidae*, *Hyporhamphus*, and *Zenarchopteridae*. Fossil *Belonoidei* include the pan-exocoetid †*Rhamphexocoetus volans* (Appendix 2; Bannikov et al. 1985). Over the past 10 years, 25 new species of *Belonoidei* have been described (Fricke et al. 2023), comprising 8.6% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Belonoidei* include (1) interarcual cartilage absent (Rosen and Parenti 1981; L. R. Parenti 2005, 2008; Wiley and Johnson 2010), (2) relatively small second and third epibranchials (Rosen and Parenti 1981; L. R. Parenti 2005, 2008; Wiley and Johnson 2010), (3) vertically reoriented second pharyngobranchial (Rosen and Parenti 1981; L. R. Parenti 2005, 2008; Wiley and Johnson 2010), (4) dorsal hypohyal absent (Rosen and Parenti 1981; L. R. Parenti 2005, 2008; Wiley and Johnson 2010), (5) interhyal absent (Rosen and Parenti 1981; L. R. Parenti 1987, 2005, 2008; Wiley and Johnson 2010), (6) upper lobe of caudal fin with fewer principal fin rays than lower lobe (Rosen and Parenti 1981; L. R. Parenti 2005, 2008; Wiley and Johnson 2010), and (7) parietals extremely small or absent (L. R. Parenti 2008; Wiley and Johnson 2010).

Synonyms. *Beloniformes* (Rosen and Parenti 1981:23; Wiley and Johnson 2010:156;

Betancur-R, Broughton, et al. 2013, fig. 8; J. S. Nelson et al. 2016:363–370; Betancur-R et al. 2017:25) is an ambiguous synonym of *Belonoidei*. *Synentognathi* (Regan 1911f:331–335) and *Exocoetoidei* (Greenwood et al. 1966:397) are partial synonyms of *Belonoidei*.

Comments. In earlier classifications, *Belonoidei* is used as a group name for all belonoids to the exclusion of *Adrianichthyidae* (Nelson 1994:266; Betancur-R et al. 2017). The earliest fossil taxa of *Belonoidei* are all from the Ypresian (56.0–48.1 Ma) of Italy and include the pan-exocoetid †*Rhamphexocoetus* and the taxa †"*Engraulis*" *evolans* and †"*Hemiramphus*" *edwardsi* of uncertain phylogenetic resolution within the clade (Bannikov et al. 1985; Bannikov 2014b; Carnevale et al. 2014). Bayesian relaxed molecular clock analyses result in an average posterior crown age estimate of the *Belonoidei* crown of 68.0 million years ago, with the credible interval ranging between 56.8 and 81.2 million years ago (Ghezelayagh et al. 2022). *Euleptorhamphidae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:77).

Constituent lineages.

Adrianichthyidae
Arrhamphus
Belonidae
Chriodorus
Euleptorhamphidae
Exocoetidae
Hemiramphidae
Hyporhamphus
Melapedalion
Zenarchopteridae
†*Rhamphexocoetus*

Cyprinodontoidei P. Bleeker 1859:xxix

Definition. The least inclusive crown clade that contains *Cyprinodon variegatus* Lacépède 1803, *Poecilia velifera* (Regan 1914a), *Pantanodon stuhlmanni* (Ahl 1924), *Austrolebias nigripinnis* (Regan 1912f), and *Aplocheilus lineatus* (Valenciennes in Cuvier and Valenciennes 1846). This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek κυπρῖνος (kuːpɹˈiːno͡ʊz), frequently applied to the Eurasian Carp, *Cyprinus carpio* (D. W. Thompson 1947:135–136), and ὀδών (ˈo͡ʊdɑːn) meaning tooth.

Reference phylogeny. A phylogeny inferred from DNA sequences of 295 genes captured using anchored hybrid enrichment (Piller et al. 2022, figs. 3–7). Although *Cyprinodon variegatus* is not included in the reference phylogeny, it resolves in a clade with other species of *Cyprinodon* in phylogenetic analyses of mtDNA (Echelle et al. 2005, 2006; Martin and Wainwright 2011). Phylogenetic relationships of the major living and fossil lineages of *Cyprinodontoidei* are presented in Figure 16. The phylogenetic resolutions of the pan-rivulid †*Kenyaichthys*, the pan-orestiid †*Carrionellus*, and the pan-valenciids †*Francolebias* and †*Prolebias* are on the basis of inferences from morphology (Costa 2011, 2012b; Altner and Reichenbacher 2015).

Phylogenetics. The lineages that comprise *Cyprinodontoidei* were grouped together in many pre-Hennigian classifications of teleost fishes (e.g., Garman 1895), but were thought to be related to such disparate lineages as *Esocidae* and *Amblyopsidae* (T. N. Gill 1872; Boulenger 1904a; Goodrich 1909:400–401; Regan 1909a, 1911g; Hubbs 1924; Gosline 1963a). Subsequent studies identified *Atheriniformes* as a clade containing *Cyprinodontoidei*, *Atherinoidei*, and *Belonoidei* (Rosen 1964; Greenwood et al. 1966; Rosen and Parenti 1981). Morphological and molecular phylogenetic analyses of relationships within *Cyprinodontoidei* are broadly congruent in supporting monophyly of the lineage and the resolution of two clades: the aplocheiloids and cyprinodontoids (L. R. Parenti 1981; Costa 1998, 2012a, 2012b; Hertwig 2008; Pohl et al. 2015; Helmstetter et al. 2016; Costa et al. 2017; Reznick et al. 2017; Amorim and Costa 2018; Bragança et al. 2018; Ghezelayagh et al. 2022; Piller et al. 2022).

Relationships among the aplocheiloids, including *Aplocheilidae* (Asian rivulines), *Nothobranchiidae* (African rivulines), and *Rivulidae* (New World rivulines), vary among different phylogenetic analyses. Studies using mtDNA and morphology resolve the traditional delimitation of *Aplocheilidae* (e.g., L. R. Parenti 1981) as paraphyletic (Murphy and Collier 1997; Costa 2004, 2012a, 2012b), with African lineages and the South American *Rivulidae* forming a clade that is the sister lineage of the Asian-Malagasy *Aplocheilidae* (*sensu* *stricto*). Because of the apparent paraphyly of *Aplocheilidae*, the African aplocheiloid lineages are now classified in *Nothobranchiidae* (Costa 2004, 2016). Subsequent phylogenetic analyses of morphology (Hertwig 2008), Sanger-sequenced mtDNA and nuclear genes (Pohl et al. 2015; Costa et al. 2017; Reznick et al. 2017; Amorim and Costa 2018; Bragança et al. 2018), and phylogenomic datasets (Ghezelayagh et al. 2022; Piller et al. 2022) resolve *Rivulidae* as the sister lineage of a clade containing *Aplocheilidae* and *Nothobranchiidae*.

Molecular phylogenies resolve *Pantanodon* (spine killifishes) as the sister lineage of all other cyprinodontoids (Pohl et al. 2015; Bragança et al. 2018; Piller et al. 2022). The remaining cyprinodontoid lineages resolve into three clades (Amorim and Costa 2018; Bragança and Costa 2019; Ghezelayagh et al. 2022; Piller et al. 2022): (1) *Cubanichthyidae* (Caribbean killifishes), *Cyprinodontidae* (pupfishes), *Fundulidae* (topminnows), *Goodeidae* (goodeids), and *Profundulidae* (Middle American killifishes) (Webb et al. 2004; Reznick et al. 2017); (2) *Anablepidae* (four-eyed fishes), *Fluviphylax* (American lampeyes), and *Poeciliidae* (livebearers) (Reznick et al. 2017; Bragança and Costa 2018); and (3) *Aphaniidae* (Asian killifishes), *Procatopodidae* (African lampeyes), *Orestiidae* (Andean pupfishes), and *Valencia* (toothcarps) (A. Parker and Kornfield 1995; Pohl et al. 2015; Helmstetter et al. 2016; Reznick et al. 2017; Bragança and Costa 2019). The traditional delimitations of *Cyprinodontidae* and *Poeciliidae* (L. R. Parenti 1981; Ghedotti 2000) are paraphyletic. *Fluviphylax*, *Pantanodon*, and *Procatopodidae* do not share common ancestry with *Poeciliidae*; *Aphaniidae*, *Cubanichthyidae*, and *Orestiidae* are distantly related to *Cyprinodontidae* (Freyhof et al. 2017; Bragança and Costa 2019; Piller et al. 2022).

Composition. There are currently 1,449 living species of *Cyprinodontoidei* (Fricke et al. 2023) classified in *Aplocheilidae*, *Nothobranchiidae*, *Rivulidae*, *Anablepidae*, *Aphaniidae*, *Cubanichthyidae*, *Cyprinodontidae*, *Fluviphylax*, *Fundulidae*, *Goodeidae*, *Orestiidae*, *Pantanodontidae* (Meinema and Huber 2023), *Poeciliidae*, *Profundulidae*, *Procatopodidae*, and *Valencia*. Fossil taxa include the pan-rivulid †*Kenyaichthys kipkechi* (Altner and Reichenbacher 2015), the pan-orestiid †*Carrionellus diumortuus* (Costa 2011), and the pan-valenciids †*Francolebias aymardi* and †*Prolebias stenoura* (J. Gaudant 1988; Costa 2012b). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 196 new species of *Cyprinodontoidei* have been described (Fricke et al. 2023), comprising 13.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Cyprinodontoidei* include (1) caudal fin endoskeleton with one epural symmetrically opposing parhypural (L. R. Parenti 1981; Rosen and Parenti 1981; Costa 2012a), (2) caudal fin unlobed, truncate or rounded (L. R. Parenti 1981; Rosen and Parenti 1981; Costa 1998), (3) first rib attached to second rather than third vertebra (L. R. Parenti 1981; Costa 1998), (4) pectoral fin set low on body, with large scalelike postcleithrum (L. R. Parenti 1981; Rosen and Parenti 1981; Costa 1998), (5) elongate interarcual cartilage joining expanded base of first epibranchial with shaft of second pharyngobranchial (Rosen and Parenti 1981), (6) presence of anterior expansion on the alveolar arm of premaxilla (Costa 1998), (7) tendon of the A_1 division of adductor mandibulae attached to the lacrimal (Costa 1998; Hertwig 2008), (8) dorsal edge of mesopterygoid reduced (Costa 1998), (9) urohyal deep (Costa 1998), (10) ventral process of lateral portion of epibranchial 2 absent (Costa 1998), (11) mesethmoid slightly anterior to lateral ethmoid (Costa 1998), (12) anteromedial process of pelvic girdle absent (Costa 1998), (13) subdivision of A_1 adductor mandibulae into two heads (Hertwig 2008), (14) many muscle fibers arising from the tendon or aponeurosis of the A_2 /A_3 adductor mandibulae (Hertwig 2008), (15) the A_2 /A_3 adductor mandibulae subdivided into three distinct heads by the ramus mandibularis (Hertwig 2008), (16) a separate section of the adductor mandibulae (AωQ) originates with a single tendon from the medial face of the quadrate (Hertwig 2008), (17) adductor arcus palatini inserts medially on the mesopterygoid (Hertwig 2008), (18) epural with bladelike shape (Costa 2012a), (19) caudal fin rays continuously arranged between upper and lower hypural plates (Costa 2012a), (20) distal tip of well-developed preural vertebra 2 acting in support of caudal fin rays (Costa 2012a), (21) stegural minute (Costa 2012a), (22) neural spine of preural vertebra 2 wider than neural spines of preural vertebrae 4 and 5 (Costa 2012a), and (23) complete ankylosis of upper hypurals and compound caudal centrum (Costa 2012a).

Synonyms. *Cyprinodontiformes* (L. R. Parenti 1981:462–463, 1993, tbl. 2; Rosen and Parenti 1981:23; Wiley and Johnson 2010:157; Betancur-R, Broughton, et al. 2013, fig. 8; J. S. Nelson et al. 2016:369–380; Betancur-R et al. 2017:26) is an ambiguous synonym of *Cyprinodontoidei*. *Microcyprini* (Regan 1911g:321–322) is a partial synonym of *Cyprinodontoidei*.

Comments. In the mid-20th century, *Cyprinodontoidei* was applied as the name of a group containing *Adrianichthyidae*, *Anablepidae*, *Cyprinodontidae*, *Goodeidae*, and *Poeciliidae* (Rosen 1964; Greenwood et al. 1966).

Time-calibrated molecular phylogenies estimate divergence times for clades in *Cyprinodontoidei* that are too young for Gondwanan fragmentation to explain the disjunct geographic distribution of *Aplocheilidae* (Near et al. 2013; Amorim and Costa 2018; Hughes et al. 2018; Ghezelayagh et al. 2022; Piller et al. 2022). Initial phylogenetic analyses of mtDNA and morphological characters (Murphy and Collier 1997; Costa 2004, 2012a, 2012b) resolved *Nothobranchiidae* and *Rivulidae* as sister lineages to the exclusion of *Aplocheilidae*, a relationship consistent with vicariance-driven diversification resulting from Gondwanan fragmentation. However, both the consistent resolution of *Aplocheilidae* and *Nothobranchiidae* as sister lineages (e.g., Amorim and Costa 2018; Piller et al. 2022) and relaxed molecular clock age estimates that date the diversification of *Cyprinodontoidei* to the latest part of the Cretaceous (e.g., Amorim and Costa 2018; Ghezelayagh et al. 2022; Piller et al. 2022) contradict the Gondwanan vicariance scenario.

Bayesian relaxed molecular clock analyses of *Cyprinodontoidei* result in an average posterior crown age estimate of 76.2 million years ago, with the credible interval ranging between 65.0 and 88.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Anablepidae
Aphaniidae
Aplocheilidae
Cubanichthyidae
Cyprinodontidae
*Fluviphylacidae**
Fundulidae
Goodeidae
Nothobranchiidae
Orestiidae
Pantanodontidae
Poeciliidae
Procatopodidae
Profundulidae
Rivulidae
*Valenciidae**
†*Carrionellus*
†*Francolebias*
†*Kenyaichthys*
†*Prolebias*

Blenniiformes P. Bleeker 1859:xxv
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The most inclusive crown clade that contains *Lamprologus callipterus* Boulenger 1906, *Chromis chromis* (Linnaeus 1758), *Crenimugil crenilabis* (Forsskål in Niebuhr 1775), *Embiotoca jacksoni* Agassiz 1853, *Gobiesox maeandricus* (C. Girard 1858a), *Scartella cristata* (Linnaeus 1758), *Blennius ocellaris* Linnaeus 1758, and *Gibbonsia metzi* Hubbs 1927, but not *Atherina presbyter* Cuvier 1829. This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek βλέννος (blˈɛno͡ʊz) used in reference to blennies by ancient Mediterranean authors and also meaning slime or spittle (D. W. Thompson 1947:32–33). The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 956.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S11). Although *Blennius ocellaris* is not included in the reference phylogeny, it resolves in a clade with other species of *Blenniidae* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (Almada et al. 2005, fig. 1; Hundt et al. 2014, fig. 2; Hundt and Simons 2018, figs. 4–6; Vecchioni et al. 2019, fig. 1).

Phylogenetic relationships of the major lineages of *Blenniiformes* are presented in Figure 16. Placement of the fossil pan-pomacentrid †*Chaychanus* in the phylogeny is on the basis of analysis of morphological characters (Cantalice et al. 2022).

Phylogenetics. Monophyly of *Blenniiformes* was supported in early molecular analyses, but with limited taxon sampling (W. L. Smith and Wheeler 2006; Kawahara et al. 2008). The first resolution of blenniiform monophyly with strong support was a phylogenomic analysis of UCE loci (Ghezelayagh et al. 2022). Within *Blenniiformes* molecular analyses resolve a clade containing *Cichlidae*, *Pholidichthys*, and *Polycentridae* (Betancur-R et al. 2017; Ghezelayagh et al. 2022; Astudillo-Clavijo et al. 2023), with *Cichlidae* and *Pholidichthys* consistently resolved as sister lineages (Wainwright et al. 2012; Friedman, Keck, et al. 2013; Near et al. 2013; Collins et al. 2015; Eytan et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022; Astudillo-Clavijo et al. 2023). Previous morphological studies led to differing conclusions regarding the relationships of *Mugilidae* within *Percomorpha*: analysis of branchial musculature supported a hypothesis that *Mugilidae* and *Atheriniformes* are sister lineages (Stiassny 1990), but analysis of pelvic girdle morphology suggested a phylogenetic relationship of mullets with "higher" percomorphs (Stiassny 1993). Both of these analyses were conducted in the context of an *Acanthopterygii* that placed *Atheriniformes* outside of *Percomorpha* (Rosen 1973; Rosen and Parenti 1981; Lauder and Liem 1983), so these seemingly inconsistent conclusions from two different anatomical systems seem to be clarified in the context of a phylogeny in which *Atheriniformes* is nested within *Percomorpha* (G. D. Johnson and Patterson 1993; Miya et al. 2003). In some molecular phylogenies, *Mugilidae* is resolved as either the sister lineage of *Embiotocidae* or *Ambassidae* (Asiatic glassfishes) (Wainwright et al. 2012; Near et al. 2013; Collins et al. 2015; Betancur-R et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022). *Congrogadidae* is distantly related to *Pseudochromidae* in molecular phylogenies (Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022), despite being well nested in *Pseudochromidae* in phylogenetic analyses of egg morphology, osteology, and external morphological characters (Godkin and Winterbottom 1985; Mooi 1990; A. C. Gill 2013).

A notable result of molecular phylogenetic analyses of *Blenniiformes* is the consistent resolution of a clade containing *Gramma*, *Opistognathidae*, *Gobiesocidae*, and *Blennioidei*, but exclusive of *Lipogramma* (Wainwright et al. 2012; Near et al. 2013; Collins et al. 2015; Eytan et al. 2015; Betancur-R et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022). *Grammatidae* traditionally included *Gramma* and *Lipogramma* (G. D. Johnson 1984; J. S. Nelson 1984:281), and morphology of the adductor mandibulae muscles and a phylogenetic analysis of 38 caudal fin skeleton characters offers evidence for monophyly of *Grammatidae* (A. C. Gill and Mooi 1993; Thieme et al. 2022); however, *Lipogramma* and *Gramma* are not resolved as a monophyletic group in phylogenetic analyses of Sanger-sequenced mtDNA and nuclear genes (Betancur-R et al. 2017). *Gobiesocidae* and *Blennioidei* are resolved as sister lineages in many molecular phylogenetic studies (W.-J. Chen et al. 2003; Dettaï and Lecointre 2005; Miya et al. 2005; Mabuchi et al. 2007; Kawahara et al. 2008; Setiamarga et al. 2008; Wainwright et al. 2012; Lin and Hastings 2013; Near et al. 2013; Collins et al. 2015; Eytan et al. 2015; Smith et al. 2016; Betancur-R et al. 2017; Fricke et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022), supporting conclusions from morphological analyses of gill arch musculature and skeletal anatomy (Rosen and Patterson 1990; Springer and Johnson 2004; Springer and Orrell 2004).

Composition. There are currently 3,814 living species of *Blenniiformes* (Fricke et al. 2023) classified in *Ambassidae*, *Blennioidei*, *Cichlidae*, *Congrogadidae*, *Embiotocidae*, *Gobiesocidae*, *Gramma*, *Lipogramma*, *Mugilidae*, *Opistognathidae*, *Pholidichthys*, *Plesiopidae*, *Polycentridae*, *Pomacentridae*, and *Pseudochromidae*. Fossil blenniiforms include the pan-pomacentrid †*Chaychanus gonzalezorum* (Appendix 1; Cantalice et al. 2020). Over the past 10 years, 268 living species of *Blenniiformes* have been described (Fricke et al. 2023), comprising approximately 7.0% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Blenniiformes*.

Synonyms. There are no synonyms of *Blenniiformes*.

Comments. Alternative classifications apply the group name *Blenniiformes* to a less inclusive clade we define as *Blennioidei* (Lin and Hastings 2013; Betancur-R et al. 2017). The earliest fossil blenniiform is the pan-pomacentrid †*Chaychanus gonzalezorum* from the Danian (66.0–61.7 Ma) of Mexico (Cantalice et al. 2020). Bayesian relaxed molecular clock analyses of *Blenniiformes* result in an average posterior crown age estimate of 88.7 million years ago, with the credible interval ranging between 77.2 and 100.5 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Ambassidae
Blennioidei
Cichlidae
Congrogadidae
Embiotocidae
Gobiesocidae
Grammatidae
Mugilidae
Opistognathidae
*Pholidichthyidae**
Plesiopidae
Polycentridae
Pomacentridae
Pseudochromidae
†*Chaychanus*

Blennioidei P. Bleeker 1853a:114

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Lepidonectes corallicola* (Kendall and Radcliffe 1912), *Dactyloscopus lacteus* (Myers and Wade 1946), *Blennius ocellaris* Linnaeus 1758, and *Gibbonsia metzi* Hubbs 1927. This is a minimum-crown-clade definition.

Etymology. Derived from the ancient Greek βλέννος (blˈɛno͡ʊz) used in reference to blennies by ancient Mediterranean authors and also meaning slime or spittle (D. W. Thompson 1947:32–33).

Registration number. 957.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S11). Although *Blennius ocellaris* is not included in the reference phylogeny, it resolves in a clade with other species of *Blenniidae* in phylogenetic analyses of Sanger-sequenced mitochondrial and nuclear genes (e.g., Vecchioni et al. 2019, fig. 1). See Figure 16 for a phylogeny of the lineages comprising *Blennioidei*.

Phylogenetics. Prephylogenetic hypotheses of the relationships of *Blennioidei* include many disparately related lineages such as *Ammodytidae*, *Congrogadidae*, *Notothenioidei*, *Ophidiiformes*, *Uranoscopidae*, and *Zoarcoidei* (Regan 1912b; Jordan 1923:228–238; Gosline 1968). The delimitation of *Blennioidei* presented here was first proposed in studies investigating the systematics of *Pholidichthys* and *Clinidae* (Springer and Freihofer 1976; George and Springer 1980) and validated in a review of morphological evidence for blennioid monophyly (Springer 1993). Morphological apomorphies were presented for each of the lineages of *Blennioidei*, but there is no morphological evidence for the monophyly of *Labrisomidae* (labrosomid blennies) (Springer 1993). The shape of the cartilage of the third infrapharyngobranchials was presented as a possible synapomorphy for a clade within *Blennioidei* containing *Chaenopsidae* (true blennies), *Dactyloscopidae* (sand stargazers), *Labrisomidae*, and *Clinidae* (kelp blennies) (J. T. Williams 1990; Springer 1993).

Blennioidei is resolved as monophyletic in morphological (Springer and Orrell 2004) and molecular phylogenetic analyses (Lin and Hastings 2013; Near et al. 2013; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022). Phylogenetic relationships within *Blennioidei* resulting from morphological and molecular analyses are congruent. A phylogeny based on dorsal gill arch morphology resolved a paraphyletic *Tripterygiidae* (triplefin blennies) as successive branching lineages with *Lepidoblennius* as the sister lineage of all other blennioids and *Blenniidae* (combtooth blennies) as the sister lineage to a clade containing *Clinidae*, *Chaenopsidae*, *Dactyloscopidae*, and *Labrisomidae* (Springer and Orrell 2004). Molecular phylogenetic analyses resulted in a very similar phylogeny, except *Tripterygiidae* is monophyletic and relationships within the clade containing *Clinidae*, *Labrisomidae* (*sensu stricto*), *Calliclinus*, *Chaenopsidae* (*sensu stricto*), and *Dactylopteridae* are fully resolved (Lin and Hastings 2013; Near et al. 2013; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022).

Molecular phylogenetic analyses of *Blennioidei* with dense taxon sampling reveal that *Chaenopsidae* and *Labrisomidae* are paraphyletic (Lin and Hastings 2013; Rabosky et al. 2018). *Stathmonotus*, traditionally classified in *Chaenopsidae*, is phylogenetically nested in *Labrisomidae*. *Neoclinini*, containing *Neoclinus* and *Mccoskerichthys* and traditionally classified in *Chaenopsidae*, and *Cryptotremini*, traditionally classified in *Labrisomidae*, are resolved as successive branching sister lineages to a clade that contains *Labrisomidae* (*sensu stricto*), *Chaenopsidae* (*sensu stricto*), and *Dactyloscopidae*. *Calliclinus*, traditionally classified in *Cryptotremini* and *Labrisomidae*, is the sister lineage of the inclusive clade containing *Neoclinini*, *Cryptotremini*, *Labrisomidae* (*sensu stricto*), *Chaenopsidae* (*sensu stricto*), and *Dactyloscopidae* (Lin and Hastings 2013; Rabosky et al. 2018). There are available family group-names for *Calliclinus*, *Neoclinini*, and *Cryptotremini* (Van der Laan et al. 2014), but we leave the establishment of taxonomic families for these lineages to future research.

Composition. There are currently 948 living species of *Blennioidei* (Fricke et al. 2023) classified in *Blenniidae*, *Calliclinus*, *Chaenopsidae*, *Clinidae*, *Cryptotremini*, *Dactyloscopidae*, *Labrisomidae*, *Neoclinini*, and *Tripterygiidae*. Over the past 10 years, 24 new living species of *Blennioidei* have been described, comprising 2.5% of the living species diversity in the clade (Fricke et al. 2023).

Diagnostic apomorphies. Morphological apomorphies for *Blennioidei* include (1) first pharyngobranchial cartilaginous or absent (Springer 1993; Wiley and Johnson 2010), (2) second and fourth pharyngobranchials absent (Springer 1993; Wiley and Johnson 2010), (3) uncinate process or associated interarcual cartilage of first epibranchial absent (Springer 1993; Wiley and Johnson 2010), (4) unique pelvic girdle with bean-shaped pelvis (Springer 1993; Wiley and Johnson 2010), (5) unique, simplified caudal fin (Springer 1993; Wiley and Johnson 2010), (6) neural spines lacking on first vertebrae or several of the anteriormost vertebrae (G. D. Johnson 1993; Wiley and Johnson 2010), (7) first external levator and fourth transversus ventralis absent (Springer and Orrell 2004; Wiley and Johnson 2010), (8) proximal pectoral fin radials longer than wide (Lin and Hastings 2013), (9) unbranched pectoral fin rays (Lin and Hastings 2013), and (10) haemal arch of preural centrum 2 fused with its centrum (Thieme et al. 2022).

Synonyms. *Blenniicae* (Hubbs 1952:51, fig. 1) and *Blenniiformes* (Wiley and Johnson 2010:160; J. S. Nelson et al. 2016:346; Betancur-R et al. 2017:26) are ambiguous synonyms of *Blennioidei*. *Blenniiformes* (Betancur-R, Broughton, et al. 2013, fig. 8) is a partial synonym of *Blennioidei*.

Comments. The name *Blennioidei* has long been applied to a group that includes *Blenniidae*, *Chaenopsidae*, *Clinidae*, *Dactyloscopidae*, *Labrisomidae*, and *Tripterygiidae* (Springer and Freihofer 1976; George and Springer 1980; Springer 1993; Hastings and Springer 2009). Since the mid-20th century (Hubbs 1952; Springer and Freihofer 1976; George and Springer 1980), the monophyly of *Blennioidei* has never been seriously questioned; however, the close relationship between *Blennioidei*, *Opistognathidae*, *Grammatidae*, *Embiotocidae*, *Pomacentridae*, and *Pseudochromidae* is a novel phylogenetic resolution derived from analyses of molecular data (Wainwright et al. 2012; Ghezelayagh et al. 2022). The lineages not currently placed in Linnaean families are listed with generic and tribe names in the classification outlined in Appendix 2 and in the Constituent lineages section below.

The earliest fossil *Blennioidei* is the otolith species †*Exallias vectensis* from the Ypresian (56.0–48.1 Ma) of France (Nolf 1972; Nolf and Lapierre 1979). The earliest skeletal fossils of *Blennioidei* are from the Serravallian (13.82–11.63 Ma) of Azerbaijan, Bosnia, Croatia, and

Moldova (Anđelković 1989; Bannikov 1998). Bayesian relaxed molecular clock analyses of *Blennioidei* result in an average posterior crown age estimate of 48.5 million years ago, with the credible interval ranging between 38.6 and 60.2 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Blenniidae	*Dactyloscopidae*
Calliclinus	*Labrisomidae*
Chaenopsidae	*Neoclinini*
Clinidae	*Tripterygiidae*
Cryptotremini	

Carangiformes D. S. Jordan 1923:183
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Centropomus medius* Günther 1864b, *Polynemus melanochir* Valenciennes in Cuvier and Valenciennes (1831), *Psettodes erumei* (Bloch and Schneider 1801), *Pleuronichthys cornutus* (Temminck and Schlegel 1846), *Xiphias gladius* Linnaeus 1758, *Caranx melampygus* Cuvier in Cuvier and Valenciennes (1833), and *Caranx melampygus* (Linnaeus 1766). This is a minimum-crown-clade definition.

Etymology. From the French *carangue*, referring to a Caribbean flatfish. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 962.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S14–S15). Although *Caranx hippos* is not in the reference phylogeny, it resolves in a monophyletic *Carangidae* with other species of *Caranx* in phylogenies inferred from Sanger-sequenced genes and UCE loci (Reed et al. 2002, fig. 3; Damerau et al. 2018, fig. 1; Glass et al. 2023, fig. 2B). Phylogenetic relationships among the major lineages of *Carangiformes* are presented in Figure 17. The placement of the fossil panlatid †*Eolates* in the phylogeny of *Carangiformes* is on the basis of phylogenetic analysis of morphological characters (Otero 2004).

Phylogenetics. The resolution of *Carangiformes* as a monophyletic group is one of several surprising results in the phylogenetics of *Percomorpha* to emerge over the past two decades (Miya et al. 2003, 2005; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Musilova et al. 2019; Dornburg and Near 2021; Ghezelayagh et al. 2022). *Carangiformes* includes biologically and phenotypically disparate lineages, many of which have long evaded confident phylogenetic resolution. For example, *Pleuronectoidei* (flatfishes) are morphologically among the most atypical of all teleosts and prior to the application of molecular data had not been confidently placed among major lineages of percomorphs (Figure 1; Regan 1913b, 1929; Norman 1934; Chapleau 1993). On the other hand, the billfishes *Istiophoridae* (marlins) and *Xiphias gladius* (Swordfish) were classified with tunas in *Scombroidei* throughout the 20th century on the basis of presumably strong morphological evidence (Regan 1909b; Greenwood et al. 1966; Collette, Potthoff, et al. 1984; G. D. Johnson 1986; J. S. Nelson 2006:430–434), but are unvaryingly resolved within *Carangiformes* in molecular phylogenetic studies (e.g., Orrell et al. 2006; Little et al. 2010; Hughes et al. 2018; Ghezelayagh et al. 2022).

The lineages comprising *Carangiformes* were never grouped together in classifications based on morphology (Greenwood et al. 1966; Wiley and Johnson 2010); however, monophyly of the group is consistently supported in a wide range of molecular phylogenetic studies that include analyses of whole mtDNA genomes, Sanger-sequenced mtDNA and nuclear genes, and phylogenomic datasets (W.-J. Chen et al. 2003; Miya et al. 2003, 2005; Dettaï and Lecointre 2005, 2008; W. L. Smith and Wheeler 2006; W. L. Smith and Craig 2007; B. Li et al. 2009; C. H. Li et al. 2011; Betancur-R, Broughton, et al. 2013; Campbell, Chen, et al. 2013, 2014; Near et al. 2013; Davis et al. 2016; Harrington et al. 2016; Sanciangco et al. 2016; Smith et al. 2016; Betancur-R et al. 2017;Hughes et al. 2018; Ribeiro, Davis, et al. 2018; Shi et al. 2018; M. G. Girard et al. 2020; Ghezelayagh et al. 2022; M. G. Girard, Davis, Baldwin, et al. 2022; Mu et al. 2022). Phylogenetic analyses inferred from DNA sequences of more than 950 UCE loci and a combined dataset of 201 morphological

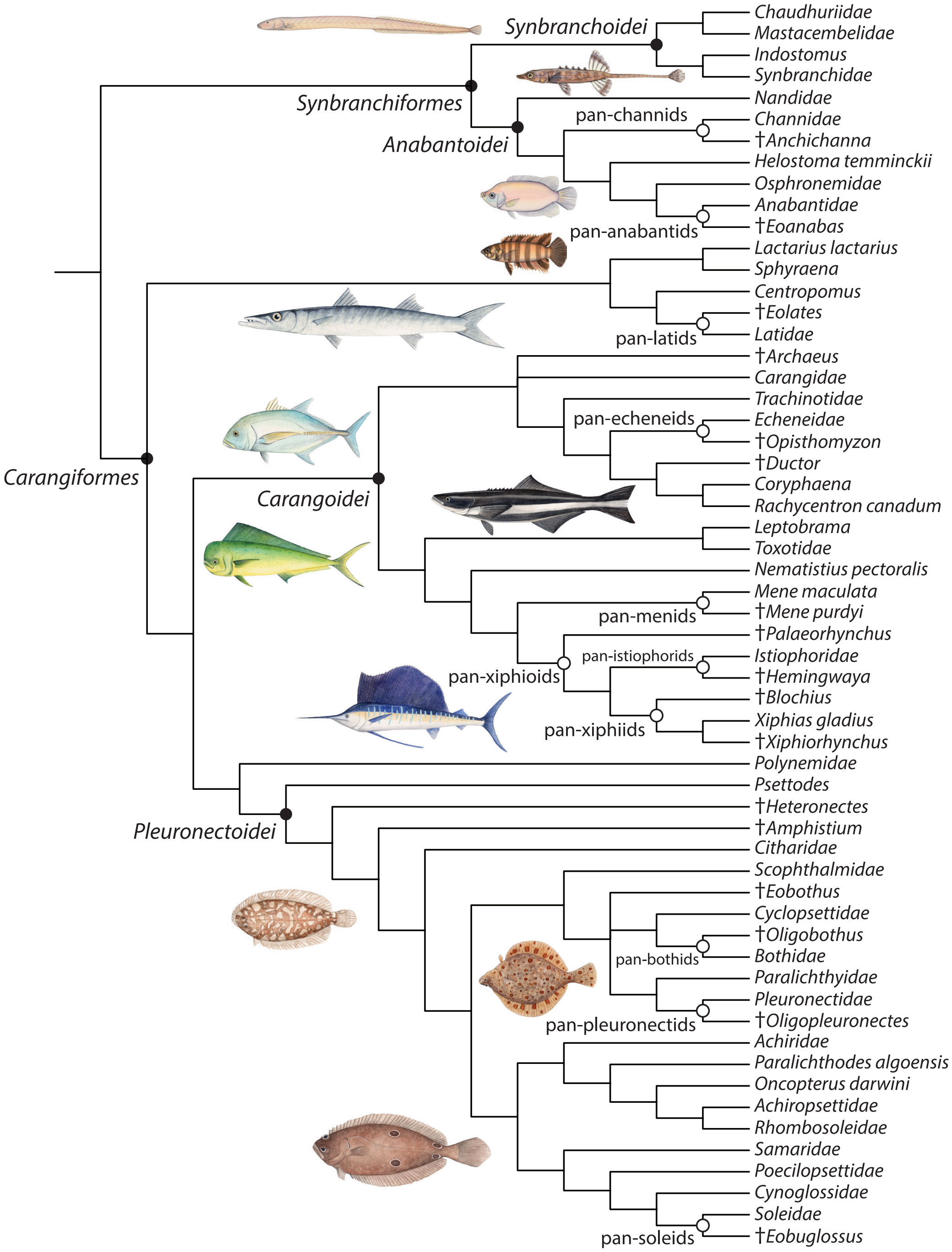

FIGURE 17. Phylogenetic relationships of the major living lineages and fossil taxa of *Synbranchiformes*, *Synbranchoidei*, *Anabantoidei*, *Carangiformes*, *Carangoidei*, and *Pleuronectoidei*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

characters and more than 450 UCE loci result in phylogenies that are strongly congruent and include three major clades within *Carangiformes* (M. G. Girard et al. 2020; Ghezelayagh et al. 2022): (1) *Centropomus* (snooks), *Latidae* (lates perches), *Lactarius lactarius* (False Trevally), and *Sphyraena* (barracudas); (2) *Polynemidae* (threadfins) and *Pleuronectoidei* (flatfishes); (3) and *Carangoidei*. The analysis of combined phenotypic and molecular characters results in the identification of morphological apomorphies for *Carangiformes* and several of the constituent lineages in the clade (M. G. Girard et al. 2020).

Composition. There are currently 1,107 living species of *Carangiformes* (Fricke et al. 2023) that include *Lactarius lactarius*, *Mene maculata*, *Nematistius pectoralis*, *Xiphias gladius*, and species classified in *Centropomus*, *Leptobrama*, *Sphyraena*, *Istiophoridae*, *Latidae*, *Polynemidae*, *Carangoidei*, and *Pleuronectoidei* (M. G. Girard et al. 2020; M. G. Girard, Davis, Tan, et al. 2022). Fossil lineages of *Carangiformes* include the pan-latid †*Eolates gracilis* (Sorbini 1970; Otero 2004) and several taxa in *Carangoidei* and *Pleuronectoidei*. Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 36 new living species of *Carangiformes* have been described (Fricke et al. 2023), comprising 3.3% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Carangiformes* include (1) presence of external process on the maxilla (M. G. Girard et al. 2020), (2) accessory gill rakers present on lateral aspect of branchial arches (M. G. Girard et al. 2020), (3) accessory gill rakers present on medial aspect of branchial arches (M. G. Girard et al. 2020), (4) presence of an epibranchial 2 toothplate that is serially associated with the second pharyngobranchial toothplate (M. G. Girard et al. 2020), (5) contact at metapterygoid-hyomandibular border ranging from a single pointed process inserting into evagination to a moderate amount of suturing between elements (M. G. Girard et al. 2020), (6) first hemal spine with a simple configuration, similar to more posterior hemal spines (M. G. Girard et al. 2020), and (7) pored lateral line scales absent from caudal fin (M. G. Girard et al. 2020).

Synonyms. *Carangaria* (Betancur-R et al. 2017:24), *Carangimorphariae* (Betancur-R, Broughton, et al. 2013, fig. 7; Betancur-R and Ortí 2014, fig. 1), and clade L (W.-J. Chen et al. 2003:279, tbl. 4; Dettaï and Lecointre 2005, fig. 3, tbl. 4, 2008, fig. 5, tbl. 4) are ambiguous synonyms of *Carangiformes*.

Comments. The resolution of the clade *Carangiformes* is not only one of several unexpected results in the molecular phylogenetics of *Percomorpha* (Dornburg and Near 2021), but also exemplifies the utility of molecular phylogenies in aiding with the discovery of morphological apomorphies for these newly delimited and inclusive lineages of teleost fishes (M. G. Girard et al. 2020). Over the past 10 years, the names *Carangimorphariae* (Betancur-R, Broughton, et al. 2013), *Carangiformes* (Davis et al. 2016, tbl. S3), and *Carangaria* (Betancur-R et al. 2017) have all been applied to this clade. We follow more recent efforts that use the name *Carangiformes* (Davis et al. 2016; M. G. Girard et al. 2020; Dornburg and Near 2021; Ghezelayagh et al. 2022).

Carangiformes includes a variety of large, usually laterally compressed and generally strong-swimming fishes, many of which exhibit a degree of phenotypic distinctiveness that motivated their classification in monotypic or monogeneric taxonomic families. Time-calibrated phylogenies indicate that *Carangiformes* originated in the Late Cretaceous and the major lineages diversified throughout the Paleogene (Santini and Carnevale 2015; Harrington et al. 2016; Ribeiro, Davis, et al. 2018; Ghezelayagh et al. 2022). Bayesian relaxed molecular clock analyses of *Carangiformes* result in an average posterior crown age estimate of 75.7 million years ago, with the credible interval ranging between 66.4 and 86.5 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Carangoidei
*Centropomidae**
*Lactariidae**
Latidae
Pleuronectoidei
Polynemidae
*Sphyraenidae**
†*Eolates*

Pleuronectoidei P. Bleeker 1849:6

Definition. The least inclusive crown clade that contains *Psettodes erumei* (Bloch and Schneider 1801), *Citharus linguatula* (Linnaeus 1758), *Pleuronichthys cornutus* (Temminck and Schlegel 1846), *Solea solea* (Linnaeus 1758), and *Pleuronectes platessa* Linnaeus 1758. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek πλευρόν (plˈɜːɹɑːn) meaning flank or side and νήκτος (nˈɛkto͡ʊz) meaning swimming.

Reference phylogeny. A phylogeny inferred from DNA sequences of mitochondrial and nuclear genes (Campbell et al. 2019, fig. 1). Although *Pleuronectes platessa* is not in the reference phylogeny, it resolves with other species of *Pleuronectidae* in molecular phylogenetic analyses (Kartavtsev et al. 2008, fig. 1; Ji et al. 2016, fig. 1; Vinnikov et al. 2018, fig. 1). Phylogenetic relationships of the major living lineages and fossil taxa of *Pleuronectoidei* are presented in Figure 17. The placements of fossil taxa in the phylogeny of *Pleuronectoidei* are on the basis of resolutions suggested in the literature for the pan-pleuronectoids †*Amphistium paradoxum* (Chanet et al. 2020), †*Eobothus minimus* (Chanet 1999; Friedman 2008; Campbell et al. 2019), †*Heteronectes chaneti* (Chanet et al. 2020), the pan-pleuronectid †*Oligopleuronectes germanicus* (Sakamoto et al. 2004; Harrington et al. 2016), the pan-bothid †*Oligobothus pristinus* (Baciu and Chanet 2002; Campbell et al. 2019), and the pan-soleid †*Eobuglossus eocenicus* (Chanet 1994; Campbell et al. 2019).

Phylogenetics. Classifications of teleosts from the late 19th through the 20th centuries grouped species of *Pleuronectoidei* into three separate lineages: *Psettodes* (spiny turbots), pleuronectoids (flounders), and soleioids (soles), often visualizing hypothesized relationships in prephylogenetic branching diagrams in which flounders and soles were depicted as closely related (Jordan and Evermann 1898:2602–2712; Regan 1910b:490; Norman 1934:43; Hubbs 1945, fig. 1; Amaoka 1969, fig. 131; Hensley and Ahlstrom 1984, fig. 358; Hensley 1997). The flounders and soles each contained two groups based on the orientation of the eyes: whether the eyes are placed on the right or left side of the head (Regan 1910b; Hubbs 1945).

A phylogenetic tree of *Pleuronectoidei* with 10 mapped morphological character state changes depicts *Psettodes* as the sister lineage of all other pleuronectoids and places the flounders as paraphyletic relative to the soles (Lauder and Liem 1983, fig. 63). The first explicit phylogenetic study of relationships within pleuronectoids was an analysis of 39 morphological characters and supported the monophyly of *Pleuronectoidei*, placed *Psettodes* as the sister lineage of all other pleuronectoids, and found that the traditional delimitation of *Pleuronectidae* (righteye flounders) is not monophyletic, prompting the removal of *Samaridae* (crested flounders), *Poecilopsettidae* (bigeye flounders), *Rhombosoleidae* (oblique flounders), and *Paralichthodes algoensis* (Peppered Flounder) (Chapleau 1993). Subsequent morphological phylogenetic analyses were aimed at resolving the relationships within *Pleuronectidae* (Cooper and Chapleau 1998a), the placement of *Paralichthodes* within *Pleuronectoidei* (Cooper and Chapleau 1998b), assessing the monophyly and relationships within *Citharidae* (largescale flounders) (Hoshino 2001), the relationships within *Scophthalmidae* (turbots) (Chanet 2003), and the phylogenetic resolution of pleuronectoid fossil lineages (Chanet 1999; Baciu and Chanet 2002; Friedman 2008).

The morphological dataset of Chapleau (1993) was modified by the rescoring of the recessus orbitalis, a fluid-filled sac behind the eyeballs that is used to elevate the eyes above the surface of the head (Bürgin 1989; Campbell et al. 2020), from present to absent in *Psettodes*; the addition of fossil taxa †*Heteronectes* and †*Amphistium* to the data matrix; and the inclusion of the carangiform lineages *Lates* and *Caranx* as outgroup taxa (Chanet et al. 2020). Analysis of 39 morphological characters resulted in 12 most parsimonious trees, among which six resolved *Psettodes* as the sister lineage of all other pleuronectoids and the other six resolved *Pleuronectoidei* as paraphyletic with *Psettodes* as the sister lineage of a clade containing *Caranx* and all other pleuronectoids (Chanet et al. 2020). In contrast to earlier studies that place †*Heteronectes* and †*Amphistium* as pan-pleuronectoids (Friedman 2008, 2012), phylogenetic analysis of the modified Chapleau (1993) morphological dataset resolves †*Heteronectes* as the sister lineage of a clade containing †*Amphistium* and all other pleuronectoids to the exclusion of *Psettodes* (Chanet et al. 2020).

The uncertainty regarding the monophyly of *Pleuronectoidei* in phylogenetic analyses of morphological characters is reflected in molecular studies. Most molecular phylogenetic studies resolve *Pleuronectoidei* as paraphyletic with *Psettodes* resolving as the sister lineage of any number of other lineages in *Carangiformes*, almost always with low node support and separated from other pleuronectoids by only one or a small number of nodes in the phylogeny (Dettaï and Lecointre 2005; W. L. Smith and Wheeler 2006; B. Li et al. 2009; C. H. Li et al. 2011; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Campbell, Chen, et al. 2013; Near et al. 2013; Shi et al. 2018; Lü et al. 2021). However, analysis of concatenated Sanger-sequenced mtDNA and nuclear genes and phylogenomic analyses of ultraconserved element loci resolves *Psettodes* as the sister lineage of all other pleuronectoids (Harrington et al. 2016; Sanciangco et al. 2016; Ghezelayagh et al. 2022), with substantial support in genome-wide concordance analysis (Harrington et al. 2016).

Other molecular studies had limited or no outgroup taxon sampling to test the monophyly of *Pleuronectoidei* (Berendzen and Dimmick 2002; Azevedo et al. 2008; Campbell et al. 2019; Atta et al. 2022), or obtained weak support for flatfish monophyly after ad hoc manipulation of DNA sequences through RY and AGY coding (Betancur-R, Li, et al. 2013). It is reasonable to consider that both random and systematic error through incomplete lineage sorting and unequal nucleotide base frequencies likely contribute to the monophyly of *Pleuronectoidei* as a challenging phylogenetic problem (Betancur-R, Li, et al. 2013; Betancur-R and Ortí 2014; Harrington et al. 2016). However, it is also important to consider the perspective of advocates of pleuronectoid paraphyly, who point out that higher support values in molecular phylogenies are not indicative of phylogenetic signal, the monophyly of *Pleuronectoidei* is not adequately demonstrated through phylogenetic analysis of morphological characters, and confidence in phylogenetic conclusions is weakened by selective reporting of results that match a researcher's expectations (Campbell et al. 2014).

Despite the uncertainty of pleuronectoid monophyly in molecular phylogenies, analyses with comprehensive taxon sampling resolve five major lineages of *Pleuronectoidei*: (1) *Psettodes*; (2) *Citharidae*; (3) *Scophthalmidae*, *Pleuronectidae*, *Paralichthyidae* (sand flounders), *Cyclopsettidae* (sand whiffs), and *Bothidae* (lefteye flounders) (Harrington et al. 2016; Byrne et al. 2018; Campbell et al. 2019; Ghezelayagh et al. 2022); (4) *Achiridae* (American soles), *Paralichthodes*, *Oncopterus darwini* (Remo Flounder), *Rhombosoleidae*, and *Achiropsettidae* (southern flounders) (Campbell et al. 2019); and (5) *Samaridae*, *Poecilopsettidae*, *Soleidae* (soles), and *Cynoglossidae* (tonguefishes) (Betancur-R, Li, et al. 2013; Harrington et al. 2016; Byrne et al. 2018; Campbell et al. 2019; Ghezelayagh et al. 2022). Phylogenetic analysis of molecular data demonstrated the paraphyly of *Paralichthyidae* and *Rhombosoleidae*, prompting the description of the taxonomic families *Cyclopsettidae* and *Oncopteridae* (Campbell et al. 2019).

Composition. There are currently 818 living species of *Pleuronectoidei* (Munroe 2015; Fricke et al. 2023) that include *Paralichthodes algoensis*, *Oncopterus darwini*, and species classified in *Achiridae*, *Achiropsettidae*, *Bothidae*, *Citharidae*, *Cyclopsettidae*, *Cynoglossidae*, *Paralichthyidae*, *Pleuronectidae*, *Poecilopsettidae*, *Psettodes*, *Rhombosoleidae*, *Samaridae*, *Scophthalmidae*, and *Soleidae*. Fossil lineages of *Pleuronectoidei* include the pan-pleuronectoids †*Amphistium paradoxum*, †*Eobothus minimus*, †*Heteronectes chaneti* (Chanet 1999; Friedman 2008, 2012), the pan-pleuronectid †*Oligopleuronectes germanicus* (Sakamoto et al. 2004), the pan-bothid †*Oligobothus pristinus* (Baciu and Chanet 2002), and the pan-soleid †*Eobuglossus eocenicus* (Chanet 1994). Details of the ages and locations of the fossil taxa are presented in

Appendix 1. Over the past 10 years, there have been 26 new living species of *Pleuronectoidei* described (Fricke et al. 2023), comprising approximately 3.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Pleuronectoidei* include (1) ontogeny characterized by migration of one eye across the dorsal midline (Chapleau 1993; Friedman 2008; Wiley and Johnson 2010; Chanet et al. 2020; M. G. Girard et al. 2020), (2) dorsal fin anteriorly placed, partially overlapping neurocranium (Chapleau 1993; Chanet 1995, 1997, 1999; Wiley and Johnson 2010; Chanet et al. 2020), (3) pseudomesial bar present (Harrington et al. 2016; M. G. Girard et al. 2020), (4) dorsalmost element of postcleithrum not expanded posteriorly through the margin (M. G. Girard et al. 2020), and (5) asymmetric pigmentation between eyed and blind sides (Harrington et al. 2016; M. G. Girard et al. 2020).

Synonyms. *Heterostomata* (Cope 1871a:458; Gill 1893:137; Jordan and Evermann 1898:2602; Regan 1910b:491), *Zeorhombiformes* (Goodrich 1909:465–474), *Pleuronectiformes* (Berg 1940:492–493; Greenwood et al. 1966:402; McAllister 1968:131–133; Gosline 1971:165–167; Wiley and Johnson 2010:167; J. S. Nelson et al. 2016:395–405; Betancur-R et al. 2017:25), and *Pleuronectoideo* (M. G. Girard et al. 2020:275) are ambiguous synonyms of *Pleuronectoidei*.

Comments. The phylogenetic relationships of *Pleuronectoidei*, particularly an inference of monophyly for the lineage, remains one of the most challenging problems in the phylogenetics of ray-finned fishes (Betancur-R, Li, et al. 2013; Betancur-R and Ortí 2014; Campbell et al. 2014; Harrington et al. 2016; Chanet et al. 2020). Molecular data applied to assessing pleuronectoid monophyly will likely continue to carry the burdens of random and systematic error, but recent efforts demonstrate the potential for additional discovery of morphological characters to aid in the phylogeny of *Pleuronectoidei* (Harrington et al. 2016; Chanet et al. 2020; M. G. Girard et al. 2020).

The earliest skeletal fossils of *Pleuronectoidei* are from the Ypresian (56.0–48.1 Ma) of Italy and include †*Amphistium*, †*Eobothus*, and †*Heteronectes* (Bannikov 2014b; Carnevale et al. 2014). Bayesian relaxed molecular clock analyses of *Pleuronectoidei* result in an average posterior crown age estimate of 67.6 million years ago, with the credible interval ranging between 59.0 and 77.5 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Achiridae
Achiropsettidae
Bothidae
Citharidae
Cyclopsettidae
Cynoglossidae
*Oncopteridae**
*Paralichthodidae**
Paralichthyidae
Pleuronectidae
Poecilopsettidae
*Psettodidae**
Rhombosoleidae
Samaridae
Scophthalmidae
Soleidae
†*Amphistium*
†*Eobothus*
†*Eobuglossus*
†*Heteronectes*
†*Oligobothus*
†*Oligopleuronectes*

Carangoidei P. Bleeker 1859:xxiii
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Leptobrama muelleri* Steindachner 1878, *Toxotes jaculatrix* (Pallas 1769), *Xiphias gladius* Linnaeus 1758, *Echeneis naucrates* Linnaeus 1758, *Caranx hippos* (Linnaeus 1766), and *Caranx melampygus* Cuvier in Cuvier and Valenciennes (1833). This is a minimum-crown-clade definition.

Etymology. From the French *carangue*, referring to a Caribbean flatfish.

Registration number. 964.

Reference phylogeny. A phylogeny inferred from sequences of 1,314 ultraconserved element loci (Glass et al. 2023, fig. 2). Phylogenetic relationships of the major living lineages and fossil taxa of *Carangoidei* are presented in Figure 17. The placements of fossil taxa in the phylogeny of *Carangoidei* are on the basis of resolutions suggested in the literature for the pan-menid †*Mene purdyi* (Friedman and Johnson 2005), the pan-coryphaenoid †*Ductor* (Friedman, Johanson, et al. 2013), the pan-echeneid †*Opisthomyzon* (Friedman, Johanson, et al. 2013), the pan-carangid †*Archaeus* (Santini and Carnevale 2015), the pan-xiphioid †*Palaeorhynchus* (Sytchevskaya and Prokofiev 2002; Monsch and Bannikov 2011), the pan-istiophorid †*Hemingwaya* (Monsch and Bannikov 2011), and the pan-xiphiids †*Blochius* and †*Xiphiorhynchus* (Monsch and Bannikov 2011).

Phylogenetics. *Carangoidei* was initially delimited to include *Carangidae* (jacks and pompanos), *Coryphaena* (dolphinfishes), *Echeneidae* (remoras), *Rachycentron canadum* (Cobia), and *Nematistius pectoralis* (Roosterfish) on the basis of two compelling morphological apomorphies (G. D. Johnson 1984; Smith-Vaniz 1984; G. D. Johnson 1993). Within *Carangoidei*, morphological and molecular phylogenetic analyses support the monophyly of the echeneoids including *Coryphaena*, *Echeneidae*, and *Rachycentron* and resolve a clade containing *Carangidae* and the echeneoids (G. D. Johnson 1984; Smith-Vaniz 1984; O'Toole 2002; Reed et al. 2002; Friedman, Johanson, et al. 2013; Near et al. 2013; Santini and Carnevale 2015; Harrington et al. 2016; Ribeiro, Davis, et al. 2018; M. G. Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023).

Where morphological and molecular phylogenies of *Carangoidei* differ is in the relationships of *Nematistius* and the monophyly of *Carangidae*. Molecular phylogenies suggest a more inclusive *Carangoidei* with *Nematistius* nested in a clade containing *Leptobrama* (beachsalmons), *Toxotidae* (archerfishes), *Mene maculata* (Moonfish), *Istiophoridae* (marlins), and *Xiphias gladius* (Swordfish) (M. G. Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023). The monophyly of *Carangidae* is supported by the morphology of the anal fin pterygiophores and the presence of a prominent gap between the second and third anal fin spines (G. D. Johnson 1984; Smith-Vaniz 1984; Gushiken 1988); however, phylogenetic analyses of molecular data and combined molecular and morphological datasets resolve the traditionally delimited *Carangidae* as paraphyletic with the lineages *Trachinotinae* and *Scomberoidinae* as a monophyletic group that is the sister lineage of the echeneoids (W. L. Smith and Wheeler 2006; Near, Eytan, et al. 2012; Santini and Carnevale 2015; Harrington et al. 2016; Mirande 2017; Rabosky et al. 2018; Ribeiro, Davis, et al. 2018; M. G. Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023). Consistent with a morphological phylogeny (Prokofiev 2002a), molecular phylogenies resolve *Trachinotinae* and *Scomberoidinae* as a monophyletic group, but both lineages are paraphyletic because *Lichia amia* (Leerfish, *Trachinotinae*) and *Parona signata* (Leatherjacket, *Scomberoidinae*) form a clade that is the sister lineage to a monophyletic group containing *Trachinotus*, *Oligoplites*, and *Scomberoides* (Rabosky et al. 2018; Glass et al. 2023). We classify species of *Lichia*, *Parona*, *Trachinotus*, *Oligoplites*, and *Scomberoides* in the clade *Trachinotidae*, which is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:98).

Composition. There are currently 193 living species (Fricke et al. 2023) of *Carangoidei* that include *Mene maculata*, *Nematistius pectoralis*, *Rachycentron canadum*, *Xiphias gladius*, and species classified in *Leptobrama*, *Toxotidae*, *Carangidae*, *Coryphaena*, *Echeneidae*, *Istiophoridae*, and *Trachinotidae*. Fossil lineages of *Carangoidei* include the pan-menid †*Mene purdyi* (Friedman and Johnson 2005), the pan-coryphaenoid †*Ductor vestenae* (Friedman, Johanson, et al. 2013), the pan-istiophorid †*Hemingwaya sarissa* (Sytchevskaya and Prokofiev 2002; Monsch and Bannikov 2011), the pan-carangid †*Archaeus oblongus* (Danil'chenko 1968; Sytchevskaya and Prokofiev 2002), the pan-xiphiids †*Blochius longirostris* and †*Xiphiorhynchus parvus* (Volta 1796; Casier 1966:314–315; Bannikov 2014b; Carnevale et al. 2014), the pan-xiphioid †*Palaeorhynchus senectus* (Danilit'chenko 1962), and the pan-echeneid †*Opisthomyzon glaronensis* (Wettstein 1886; Friedman, Johanson, et al. 2013). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, there have been 10 new living species of *Carangoidei* described (Fricke et al.

2023), comprising 5.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Carangoidei* include (1) dentition present on basihyal (M. G. Girard et al. 2020), (2) supracleithrum short (M. G. Girard et al. 2020), (3) neural spine of second preural centrum reduced, not extending posteriorly to bend in ural centrum (M. G. Girard et al. 2020), and (4) cycloid scales (M. G. Girard et al. 2020).

Synonyms. *Carangiformes* (Wiley and Johnson 2010:160; Betancur-R, Broughton, et al. 2013, fig. 7; J. S. Nelson et al. 2016:383; Betancur-R et al. 2017:24-25) is a partial synonym of *Carangoidei*.

Comments. *Carangoidei* was the name applied to a clade consisting of *Carangidae*, *Coryphaena*, *Echeneidae*, *Rachycentron canadum*, and *Nematistius pectoralis* (G. D. Johnson 1993). Molecular phylogenies result in a more inclusive *Carangoidei* because *Nematistius* is nested in a clade containing *Leptobrama*, *Toxotidae*, *Mene*, *Istiophoridae*, and *Xiphias* (M. G. Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023).

The earliest fossil *Carangoidei* is the panmenid †*Mene purdyi* from the Thanetian and Ypresian (59.2–56.0, 56.0–47.1 Ma) of Peru (Friedman and Johnson 2005). Bayesian relaxed molecular clock analyses of *Carangoidei* result in an average posterior crown age estimate of 69.0 million years ago, with the credible interval ranging between 61.6 and 77.9 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Carangidae
*Coryphaenidae**
Echeneidae
Istiophoridae
*Leptobramidae**
*Menidae**
*Nematistiidae**
*Rachycentridae**
Toxotidae
Trachinotidae
*Xiphiidae**
†*Archaeus*
†*Blochius*
†*Ductor*
†*Hemingwaya*
†*Mene purdyi*
†*Opisthomyzon*
†*Palaeorhynchus*
†*Xiphiorhynchus*

Synbranchiformes P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Myers 1966:398

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Indostomus paradoxus* Prashad and Mukerji 1929, *Synbranchus marmoratus* Bloch 1795, *Mastacembelus mastacembelus* (Banks and Solander in A. Russell 1794), *Channa argus* (Cantor 1842), *Badis badis* (Hamilton 1822), and *Anabas testudineus* (Bloch 1792b). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek σύν (sˈɪn) meaning together or with and βραγχίον (bɹˈæɡkiə͡n) which is Latinized as *branchium* meaning a fish gill. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 965.

Reference phylogeny. A phylogeny inferred from combined DNA sequence dataset consisting of 998 ultraconserved element loci and Sanger-sequenced mitochondrial and nuclear genes (Harrington et al. 2023, figs. 2, 3). Phylogenetic relationships among the major lineages of *Synbranchiformes* are presented in Figure 17.

Phylogenetics. The lineages that comprise *Synbranchiformes* were traditionally classified in groups delimited here as *Synbranchoidei* (sans *Indostomus*) and *Anabantoidei* (Greenwood et al. 1966; Wiley and Johnson 2010; J. S. Nelson et al. 2016:380–383, 390–395). There were suggestions based on morphology that synbranchoids and anabantoids shared common ancestry (Gosline 1971:161; Lauder and Liem 1983; Rosen and Patterson 1990; Roe 1991), but this hypothesis was dismissed in a phylogenetic study utilizing morphological characters (G. D. Johnson and Patterson 1993). Molecular phylogenetic analyses of *Percomorpha* consistently resolve *Synbranchiformes* as monophyletic (W.-J. Chen et al. 2003; B. Li et al. 2009; Near, Eytan, et al. 2012; Wainwright et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Davis et al. 2016; Smith et al. 2016; Betancur-R et al.

2017; Hughes et al. 2018; Ghezelayagh et al. 2022; Harrington et al. 2023).

Composition. There are currently 414 living species (Fricke et al. 2023) of *Synbranchiformes* classified in *Anabantoidei* and *Synbranchoidei*. Over the past 10 years, there have been 63 new living species of *Synbranchiformes* described (Fricke et al. 2023), comprising 15.2% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies have not been identified for *Synbranchiformes*; however, most species have an accessory respiratory organ (suprabranchial organ or suprabranchial pouches), which are highly vascularized chambers located above the gill chamber that allow the fishes to breathe air (Johansen 1966; Rosen and Greenwood 1976; Lauder and Liem 1983; Tate et al. 2017).

Synonyms. *Labyrinthici* (Rosen and Patterson 1990:3), *Anabantiformes* (B. Li et al. 2009, tbl. 4; Near et al. 2013, fig. S1), *Anabantomorphariae* (Betancur-R, Broughton, et al. 2013:13), and *Anabantaria* (Betancur-R et al. 2017:24) are ambiguous synonyms of *Synbranchiformes.*

Comments. The name *Synbranchiformes* is applied to the clade containing *Anabantoidei* and *Synbranchoidei* in several recent classifications of percomorphs (Davis et al. 2016; Dornburg and Near 2021; Ghezelayagh et al. 2022).

Several lineages of *Synbranchiformes* have distributions that are disjunct between Africa and South Asia, with phylogenetic patterns consistent with vicariance due to the breakup of Gondwana and rafting of African species to Asia via the Indian subcontinent (F. Wu et al. 2019; Britz et al. 2020). However, age estimates from relaxed molecular clock analyses for *Channidae* and *Mastacembelidae* are too young to be the result of vicariance due to Gondwanan breakup and infer an Asian origin for both lineages (X. Li et al. 2006; Adamson et al. 2010; Day et al. 2017; Rüber et al. 2020; Harrington et al. 2023). Paleontological data similarly do not support the African origin or Gondwanan vicariance hypothesis for *Channidae* (Capobianco and Friedman 2019). Bayesian relaxed molecular clock analyses of *Synbranchiformes* result in an average posterior crown age estimate of 79.2 million years ago, with the credible interval ranging between 70.8 and 88.5 million years ago (Harrington et al. 2023).

Constituent lineages.
Anabantoidei *Synbranchoidei*

Synbranchoidei P. Bleeker 1859:xxxii
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Indostomus paradoxus* Prashad and Mukerji 1929, *Synbranchus marmoratus* Bloch 1795, and *Mastacembelus mastacembelus* (Banks and Solander in A. Russell 1794). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek σύν (sˈɪn) meaning together or with and βραγχίον (bɹˈægki͡ən) which is Latinized as *branchium* meaning a fish gill.

Registration number. 966.

Reference phylogeny. A phylogeny inferred from combined DNA sequence dataset consisting of 998 ultraconserved element loci and Sanger-sequenced mitochondrial and nuclear genes (Harrington et al. 2023, fig. 2). The phylogenetic relationships among the major lineages of *Synbranchoidei* are presented in Figure 17.

Phylogenetics. Several morphological studies suggest that *Mastacembelidae*, *Chaudhuriidae*, and *Synbranchidae* share common ancestry (McAllister 1968:156–159; Gosline 1983; Travers 1984; G. D. Johnson and Patterson 1993; Britz 1996; Britz and Kottelat 2003). Early molecular phylogenetic studies did not sample *Chaudhuriidae* but confirmed the monophyly of a lineage containing *Mastacembelidae* and *Synbranchidae* (e.g., W.-J. Chen et al. 2003; Dettaï and Lecointre 2005, 2008). Species of *Indostomus* (armored sticklebacks) were traditionally classified with seahorses and sticklebacks in the polyphyletic *Gasterosteiformes* or *Gasterosteoidei* on the basis of the presence of dermal plates along the side of the body, a reduced cranial skeleton, and small mouth size

(Greenwood et al. 1966; Britz and Johnson 2002; J. S. Nelson et al. 2016). Molecular phylogenetic analyses of *Percomorpha* consistently resolve *Indostomus* in *Synbranchoidei* (Miya et al. 2003, 2005; Kawahara et al. 2008; B. Li et al. 2009; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Pérez-Rodríguez et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022; Harrington et al. 2023). Morphological and molecular datasets are congruent in resolving *Chaudhuriidae* and *Mastacembelidae* as sister lineages (Travers 1984; Ghezelayagh et al. 2022).

Composition. There are currently 136 living species of *Synbranchoidei* (Britz and Kottelat 1999; Sabaj et al. 2022; Fricke et al. 2023) classified in *Chaudhuriidae*, *Indostomus*, *Mastacembelidae*, and *Synbranchidae*. Over the past 10 years, there have been 15 new living species of *Synbranchoidei* described, comprising 11% of the living species diversity in the clade.

Diagnostic apomorphies. *Synbranchoidei* is diagnosed by an arrangement of the upper jaw relative to the suspensorium that features a disconnect between the upper jaw elements (maxilla and premaxilla) and the palatine-ectopterygoid. The palatine is reduced or absent, the ectopterygoid is greatly enlarged, and neither element articulates with the premaxilla. The premaxilla lacks an ascending process and there is often no rostral cartilage. Instead, the premaxilla and maxilla are displaced anteriad, and the premaxilla articulates directly with the lower surface of the neurocranium (Gosline 1983; Britz and Johnson 2002; Britz and Kottelat 2003). Morphological apomorphies for *Synbranchoidei* that are not confirmed in *Indostomus* include (1) extension of dentary posteroventrally along ventral edge of anguloarticular (Travers 1984; Wiley and Johnson 2010), (2) palatine sutured along posterolateral face of vomerine shaft (Travers 1984; Wiley and Johnson 2010), (3) levator operculi inserting on dorsolateral face of opercle (Travers 1984; Wiley and Johnson 2010), (4) hyohyoidei adductores dorsolaterally expanded, sealing operculum to body wall and causing restricted opercular opening (Travers 1984; Wiley and Johnson 2010), (5) anterior surface of occipital joint of first vertebra convex, forming "pluglike" in *Synbranchidae* (Rosen and Greenwood 1976; Wiley and Johnson 52010) or "ball and socket" joint in *Mastacembelidae* and *Chaudhuriidae* (Travers 1984; G. D. Johnson and Patterson 1993; Wiley and Johnson 2010), and (6) anterior vertebrae with distinctive configuration (G. D. Johnson and Patterson 1993; Wiley and Johnson 2010).

Synonyms. *Synbranchiformes* is an ambiguous synonym (Gosline 1983:327; Travers 1984:141; Wiley and Johnson 2010:153; J. S. Nelson et al. 2016:380; Betancur-R et al. 2017:24) and partial synonym (Berg 1940:472) of *Synbranchoidei*.

Comments. The name *Synbranchoidei* is applied to this clade in several recent studies (Dornburg and Near 2021; Ghezelayagh et al. 2022; Harrington et al. 2023).

Bayesian relaxed molecular clock analyses of *Synbranchoidei* result in an average posterior crown age estimate of 69.7 million years ago, with the credible interval ranging between 58.1 and 79.7 million years ago (Harrington et al. 2023).

Constituent lineages. Redundant group names are marked with an asterisk.
Chaudhuriidae
*Indostomidae**
Mastacembelidae
Synbranchidae

Anabantoidei L. S. Berg 1940:485
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive clade that contains *Channa argus* (Cantor 1842), *Badis badis* (Hamilton 1822), and *Anabas testudineus* (Bloch 1792b). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek αναβαίνει (ˈænɐbˌeɪ͡niː) meaning goes up among.

Registration number. 967.

Reference phylogeny. A phylogeny inferred from combined DNA sequence dataset consisting of 998 ultraconserved element (UCE) loci and Sanger-sequenced mitochondrial and nuclear genes (Harrington et al. 2023, figs. 2, 3). Phylogenetic relationships of the major living and fossil lineages of *Anabantoidei* are presented in Figure 17. The placements of the fossil taxa †*Anchichanna* and †*Eoanabas* in the phylogeny are on the basis of inferences from morphology (Murray and Thewissen 2008; F. Wu et al. 2017, 2019).

Phylogenetics. *Anabantoidei* is consistently resolved as monophyletic in molecular phylogenetic analyses and consists of five major clades (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Collins et al. 2015; Betancur-R et al. 2017; F. Wu et al. 2019; Ghezelayagh et al. 2022; Harrington et al. 2023): (1) *Nandidae* (leaffishes and chameleonfishes), (2) *Channidae* (snakeheads), (3) *Helostoma temminckii* (Kissing Gourami), (4) *Anabantidae* (climbing gouramis), and (5) *Osphronemidae* (gouramies and fighting fishes).

We delimit *Nandidae* as containing species of *Nandus*, *Badis*, *Dario*, and *Pristolepis*. Alternatively, these four lineages are classified into three Linnaean-ranked taxonomic families, two of which contain a single genus (Rosen and Patterson 1990; Kullander and Britz 2002; Rüber et al. 2004; Britz et al. 2012; Collins et al. 2015; J. S. Nelson et al. 2016:394–395; Betancur-R et al. 2017; Kullander et al. 2019). Our delimitation of *Nandidae* is reflected in previous classifications (Jordan 1923:202; J. S. Nelson 2006:381–383), is consistently resolved in molecular phylogenetic analyses of Sanger-sequenced protein-coding loci and phylogenomic analysis of UCE loci (Near et al. 2013; Collins et al. 2015; Ghezelayagh et al. 2022; Harrington et al. 2023), and is supported with two distinct morphological apomorphies (Collins et al. 2015). Previous classifications involving anabantoids were complicated by the assumption that the South American and African *Polycentridae*, which includes *Monocirrhus polyacanthus*, *Polycentrus*, *Afronandus sheljuzhkoi*, and *Polycentropsis abbreviata* were related to lineages classified here as *Nandidae* (Regan 1913b; Greenwood et al. 1966:202; Liem 1970; Nelson 1994:371–373). However, molecular phylogenies resolve *Polycentridae* in *Blenniiformes* (Wainwright et al. 2012; Near et al. 2013; Collins et al. 2015; Ghezelayagh et al. 2022).

Morphological and molecular phylogenetic analyses are congruent in the resolution of a clade that contains lineages with a suprabranchial labyrinth organ: *Helostoma*, *Anabantidae*, and *Osphronemidae* (e.g., Lauder and Liem 1983; Britz 1994, 2001; Near et al. 2013; Ghezelayagh et al. 2022; Harrington et al. 2023). Most incongruence among previous phylogenetic hypotheses is because of the variable resolution of *Channidae* as either the sister group of the labyrinth organ clade (Springer and Johnson 2004; Near et al. 2013; Sanciangco et al. 2016; Hughes et al. 2018; F. Wu et al. 2019; Britz et al. 2020; Ghezelayagh et al. 2022; Harrington et al. 2023) or *Nandidae* (Betancur-R, Broughton, et al. 2013), and *Helostoma* as either the sister taxon of *Anabantidae* (Collins et al. 2015; Hughes et al. 2018; Britz et al. 2020), *Osphronemidae* (Rüber et al. 2006; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Sanciangco et al. 2016), or a clade containing *Anabantidae* and *Osphronemidae* (Collins et al. 2015; Ghezelayagh et al. 2022; Harrington et al. 2023).

Within *Channidae*, a phylogeny inferred from Sanger-sequenced mitochondrial and nuclear genes and a dataset of Sanger-sequenced genes and UCE loci resolves *Parachanna* as the sister taxon of a clade comprising *Aenigmachanna* and *Channa* (Britz et al. 2020, fig. S3; Harrington et al. 2023). In contrast, a phylogeny inferred from morphological characters places *Aenigmachanna* as sister lineage of a clade containing *Parachanna* and *Channa* (Britz et al. 2020, fig. 5). Several molecular analyses presented in Britz et al. (2020) were conducted using a topological constraint to reflect the results of the morphological phylogeny that prompted the description of the Linnaean-ranked family *Aenigmachannidae* (Britz et al. 2020). Even if *Aenigmachanna* was the sister taxon of a clade containing *Channa* and *Parachanna*, it would still be most effectively classified in *Channidae*. The description of a monogeneric *Aenigmachannidae* provides no information on phylogeny and only accomplishes the creation of a group name that is redundant with *Aenigmachanna*. We delimit *Channidae* as the species classified in *Aenigmachanna*, *Channa*, and *Parachanna*, which is supported with 10 morphological apomorphies (Britz et al. 2020, figs. S1, S2).

Composition. There are currently 278 living species of *Anabantoidei* (Fricke et al. 2023) that include *Helostoma temminckii* and species classified in *Anabantidae*, *Channidae*, *Nandidae*, and *Osphronemidae*. Fossil lineages of *Anabantoidei* include pan-anabantid †*Eoanabas thibetana* (F. Wu et al. 2017) and the pan-channid †*Anchichanna kuldanensis* (Murray and Thewissen 2008). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 48 new living species of *Anabantoidei* have been described (Fricke et al. 2023), comprising 17.3% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Anabantoidei* include (1) teeth on parasphenoid (Gosline 1968; Springer and Orrell 2004; Collins et al. 2015), and (2) presence of a cartilage-tipped uncinate process on epibranchial 1 (Springer and Orrell 2004; Collins et al. 2015).

Synonyms. *Anabantomorpha* (Springer and Johnson 2004) and *Anabantiformes* (Wiley and Johnson 2010:158; Betancur-R, Broughton, et al. 2013:18, fig. 6; J. S. Nelson et al. 2016:390–395; Betancur-R et al. 2017:24) are ambiguous synonyms of *Anabantoidei*. *Labyrinthici* (Müller 1845b:102, 130; Günther 1861:373–389), *Labyrinthiformes* (Müller 1845b:135), *Ophicephaliformes* (Berg 1940:470–471), *Luciocephaloidei* (Berg 1940:486), and *Anabantiformes* (Wiley and Johnson 2010:158–159) are partial synonyms of *Anabantoidei*.

Comments. The name *Anabantoidei* is applied to this clade in several recent studies (Dornburg and Near 2021; Ghezelayagh et al. 2022; Harrington et al. 2023).

The earliest fossil *Anabantoidei* are †*Eochanna chorlakkiensis* and †*Anchichanna kuldanensis* from the Lutetian (47.8–41.2 Ma) of Pakistan that may be conspecific (Roe 1991; Murray and Thewissen 2008). Bayesian relaxed molecular clock analyses of *Anabantoidei* result in an average posterior crown age estimate of 72.1 million years ago, with the credible interval ranging between 63.1 and 80.4 million years ago (Harrington et al. 2023).

Constituent lineages. Redundant group names are marked with an asterisk.

Anabantidae
Channidae
*Helostomatidae**
Nandidae
Osphronemidae
†*Anchichanna*
†*Eoanabas*

Eupercaria R. Betancur-R, E. O. Wiley, N. Bailly, M. Miya, G. Lecointre, and G. Ortí 2014:website
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown lineage that contains *Paracanthus hepatus* (Linnaeus 1766), *Gerres cinereus* (Walbaum 1792), *Acropoma japonicum* Günther 1859, *Labrus bergylta* Ascanius 1767, *Micropterus salmoides* (Lacépède 1802), and *Perca fluviatilis* (Linnaeus 1758). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek words εὖ (ˈiːuː) meaning well or good and πέρκη (pˈɜːke͡ɪ), a name applied to many species of fishes by ancient authors (D. W. Thompson 1947:195–197).

Registration number. 984.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S16–S25). The placement of the fossil panperciform †*Paleoserranus lakamhae* differs from a proposed resolution as the sister lineage of *Serranidae sensu lato* (Cantalice et al. 2022) and is motivated by the persistent paraphyly of *Serranidae* (e.g., W. L. Smith and Craig 2007; Lautredou et al. 2013; Ghezelayagh et al. 2022) and the resolution of *Acanthistius*, *Anthiadidae*, and *Epinephelidae* as early diverging lineages within *Perciformes* (Ghezelayagh et al. 2022). See Figures 2 and 14 for a phylogeny of the lineages comprising *Eupercaria*.

Phylogenetics. *Eupercaria* is a lineage resolved entirely as a result of molecular phylogenetic analyses (W.-J. Chen et al. 2003; Miya et al. 2003, 2005; Dettaï and Lecointre 2005; B. Li et al. 2009; Near, Eytan, et al. 2012; Near, Sandel, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013, 2015; Thacker et al. 2015; Davis et al. 2016; Sanciangco et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Alfaro et al. 2018; Ghedotti et al. 2018; Hughes et al. 2018; Rabosky et al. 2018; Ghezelayagh et al. 2022; W. L. Smith et al. 2022). Despite consistent resolution as a monophyletic group, relationships among the major lineages of *Eupercaria* initially proved difficult to resolve (e.g., Betancur-R et al. 2017; Alfaro et al. 2018; Hughes et al. 2018; Rabosky et al. 2018). Phylogenomic analysis of UCE loci resolves *Perciformes*, *Centrarchiformes*, and *Labriformes* as successively branching lineages to a clade containing *Acropomatiformes* and *Acanthuriformes* (Ghezelayagh et al. 2022).

Composition. There are more than 7,070 living species of *Eupercaria* (Fricke et al. 2023) classified in *Acanthuriformes*, *Acropomatiformes*, *Centrarchiformes*, *Labriformes*, and *Perciformes* (Dornburg and Near 2021; Ghezelayagh et al. 2022). Over the past 10 years, 522 new living species of *Eupercaria* have been described (Fricke et al. 2023), comprising 7.4% of the living species in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Eupercaria*.

Synonyms. *Percomorpharia* is an ambiguous synonym of *Eupercaria* (Betancur-R, Broughton, et al. 2013, fig. 9).

Comments. One of the triumphs of molecular phylogenetics is the resolution of relationships among the myriad lineages of *Percomorpha* (Dornburg and Near 2021). Toward the end of the 20th century, percomorphs were labeled as the "bush at the top" of the teleost phylogeny (G. J. Nelson 1989:328). After the first wave of molecular phylogenetic studies, the consistent resolution of *Eupercaria* as a monophyletic group with a limited support for relationships within the clade led to its appropriate identification as "the new bush at the top" (Betancur-R, Broughton, et al. 2013:22). However, phylogenomic studies provide support for the monophyly of *Eupercaria* and elimination of the last of the percomorph "bushes" through the resolution of relationships among the *Perciformes*, *Centrarchiformes*, *Labriformes*, *Acropomatiformes*, and *Acanthuriformes* (Ghezelayagh et al. 2022). The name *Eupercaria* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade.

The earliest fossil *Eupercaria* is the pan-perciform †*Paleoserranus lakamhae* dated to the Danian (66.0–61.7 Ma) in Mexico (Cantalice et al. 2022). Bayesian relaxed molecular clock analyses of *Eupercaria* result in an average posterior crown age estimate of 93.7 million years ago, with the credible interval ranging between 81.7 and 107.7 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.
Acanthuriformes
Acropomatiformes
Centrarchiformes
Labriformes
Perciformes
†*Paleoserranus*

Perciformes A. Günther 1880:374–397
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown lineage that contains *Trachypoma macracanthus* Günther 1859, *Cephalopholis cruentata* (Lacépède 1802), *Acanthistius cinctus* (Günther 1859), *Perca fluviatilis* Linnaeus 1758, *Cottus carolinae* (T. N. Gill 1861b), and *Sebastes norvegicus* (Ascanius 1772). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek πέρκη (pˈɜːke͡ɪ), a name applied to many species of fishes by ancient authors (D. W. Thompson 1947:195–197). The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 968.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S16–S19). Phylogenetic relationships of the major lineages of *Perciformes* are presented in Figure 18.

Phylogenetics. Throughout the 20th century, most species and lineages of *Percomorpha* were

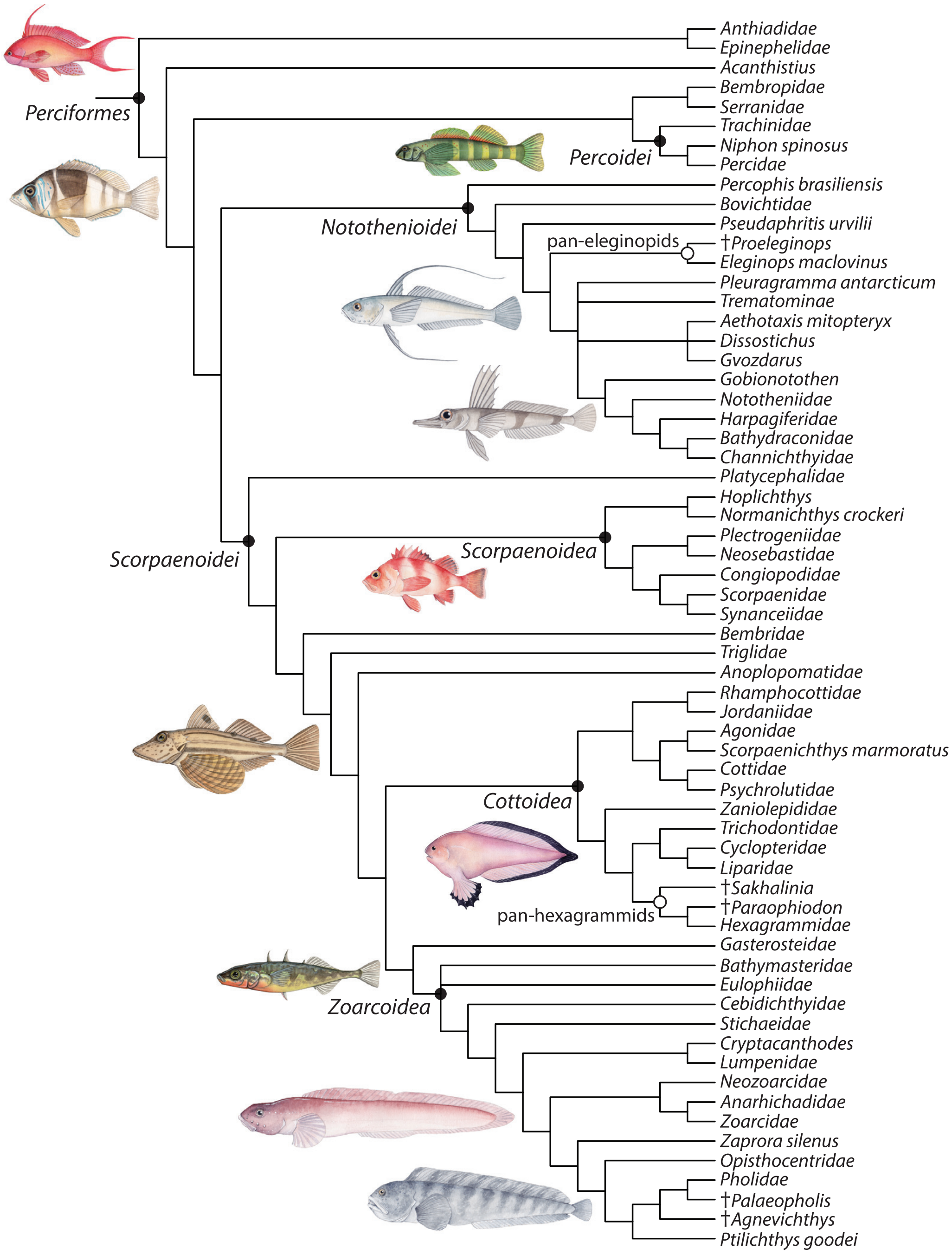

FIGURE 18. Phylogenetic relationships of the major living lineages and fossil taxa of *Perciformes*, *Percoidei*, *Notothenioidei*, *Scorpaenoidei*, *Scorpaenoidea*, *Cottoidea*, and *Zoarcoidea*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

classified in the catch-all taxon *Perciformes* (Goodrich 1909:472–490; Berg 1940; McAllister 1968:136–148; Gosline 1971:156–164; A. C. Gill and Mooi 2002; J. S. Nelson 2006:339–441). Any lineage of *Percomorpha* that was not as morphologically distinctive as flatfishes, pufferfishes, sticklebacks, or flying gurnards was relegated to *Perciformes*. At the turn of the century, more than half of all species of *Percomorpha* were classified in *Perciformes*, a grouping that was considered an assemblage of unrelated lineages (Figure 1; G. D. Johnson 1984, 1993; G. D. Johnson and Patterson 1993; J. S. Nelson 2006:340; J. S. Nelson et al. 2016:430). Molecular phylogenies revealed that lineages traditionally classified in *Perciformes* are distributed among 11 of the 13 major clades of *Percomorpha* (Figures 1 and 2). The two earliest branching lineages, *Ophidiiformes* and *Batrachoididae*, are the only clades of *Percomorpha* that do not include lineages previously classified in *Perciformes* (Figure 1; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The unraveling of the traditional composition of *Perciformes* began with the first molecular phylogenetic studies of *Percomorpha* (W.-J. Chen et al. 2003; Miya et al. 2003, 2005; Dettaï and Lecointre 2004; W. L. Smith and Wheeler 2004, 2006; Dettaï and Lecointre 2005, 2008; W. L. Smith and Craig 2007; B. Li et al. 2009; Malmstrøm et al. 2016, 2017). Phylogenetic studies that sampled most of the major lineages of *Percomorpha* resulted in the resolution of a clade delimited as *Perciformes* that included *Percidae* (perches, walleyes, darters) and all lineages previously classified as *Scorpaeniformes* (e.g., sculpins, rockfishes, scorpionfishes) (J. S. Nelson 2006:318–339); *Zoarcoidea* (e.g., eelpouts, ronquils, pricklebacks); all lineages of *Serranidae* (seabasses) except for *Hemilutjanus macrophthalmos* (Grape-eye Seabass) and *Caesioscorpis theagenes* (Blowhole Perch) (P. Parenti and Randall 2020; W. L. Smith et al. 2022); *Bembropidae* (duckbills); *Percophis brasiliensis* (Brazilian Flathead); *Trachinidae* (weeverfishes) traditionally classified in *Trachinoidei* or *Trachiniformes* (J. S. Nelson 2006:403–409; J. S. Nelson et al. 2016:421–427); the southern cold temperate and Antarctic marine *Notothenoidei* (e.g., icefishes, notothens, plunderfishes); and *Gasterosteidae* (sticklebacks) (Matschiner et al. 2011; Betancur-R, Broughton, et al. 2013; Lautredou et al. 2013; Near et al. 2013, 2015; Thacker et al. 2015; Betancur-R et al. 2017; Hughes et al. 2018; Ghezelayagh et al. 2022; T. Tang et al. 2023).

Serranidae is traditionally delimited to include more than 450 species classified among 73 genera (Fricke et al. 2023) and is consistently resolved as nonmonophyletic in *Perciformes* (Craig and Hastings 2007; W. L. Smith and Craig 2007; Lautredou et al. 2013; Near et al. 2013; Zhuang et al. 2013; Ma et al. 2016; Ghezelayagh et al. 2022). A phylogenomic analysis of UCE loci resolves lineages traditionally classified as *Serranidae* among *Epinephelidae* (groupers), *Anthiadidae* (basslets and anthians), *Serranidae* (*sensu stricto*), *Acanthistius* (wirrahs), and *Niphon spinosus* (Sawedged Perch) (W. L. Smith and Craig 2007; Near et al. 2015; Ghezelayagh et al. 2022).

There are seven major clades of *Perciformes*: (1) *Epinephelidae*, (2) *Anthiadidae*, (3) *Acanthistius*, (4) a clade containing *Bembropidae* and *Serranidae*, (5) *Percoidei*, (6) *Notothenioidei*, and (7) *Scorpaenoidei*. In phylogenomic analyses of UCE loci, *Epinephelidae*, *Anthiadidae*, and *Acanthistius* are resolved as successive early branching lineages of *Perciformes*, the clade containing *Serranidae* and *Bembropidae* is resolved as the sister lineage of *Percoidei*, and *Notothenioidei* and *Scorpaenoidei* are resolved as sister groups (Figure 18; Ghezelayagh et al. 2022).

Composition. There are currently 3,200 species of *Perciformes* (Fricke et al. 2023) classified in *Acanthistius*, *Anthiadidae*, *Bembropidae*, *Epinephelidae*, *Notothenioidei*, *Scorpaenoidei*, and *Serranidae*. Over the past 10 years, there have been 209 new living species of *Perciformes* described (Fricke et al. 2023), comprising 6.5% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Perciformes*; however, a backwardly directed opercle spine is a potential apomorphy as it is present in *Acanthistius*, *Anthiadidae*, *Bembrops* (*Bembropidae*), *Epinephelidae*, *Channichthyidae* (*Notothenioidei*), *Niphon* and *Trachinidae* (*Percoidei*), *Scorpaenoidei* sans the traditional cottoid lineages, and *Serranidae* (G. D. Johnson 1983; Iwami 1985; Imamura and Yabe 2002; W. L. Smith et al. 2018).

Synonyms. *Serraniformes* (B. Li et al. 2009, tbl. 4; Lautredou et al. 2013:140–141) and *Scorpaeniformes* (W. L. Smith and Busby 2014:333; Sparks et al. 2014, fig. 2; Davis et al. 2016, figs. 1, 4; W. L. Smith et al. 2016, sup. fig. 1, 2018, fig. 2B) are ambiguous synonyms of *Perciformes*.

Comments. The name *Perciformes* is applied to this clade in several studies and was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Betancur-R et al. 2017; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Perciformes* are two species of *Scorpaenoidei* dated to the Ypresian (56.0–48.1 Ma), the New Zealand platycephalid otolith taxon †*Platycephalus parapercoides* (Schwarzhans 2019) and †*Eosynanceja brabantica* from Belgium that is classified as a species of *Synanceiidae* (Casier 1946). Bayesian relaxed molecular clock analyses of *Perciformes* result in an average posterior crown age estimate of 66.9 million years ago, with the credible interval ranging between 55.2 and 78.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Acanthistiinae**
Anthiadidae
Bembropidae
Epinephelidae
Notothenioidei
Percoidei
Scorpaenoidei
Serranidae

Percoidei L. J. F. J. Fitzinger 1832:331
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade containing *Perca fluviatilis* (Linnaeus 1758), *Trachinus radiatus* Cuvier 1829, and *Niphon spinosus* Cuvier 1828 in Cuvier and Valenciennes (1828). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek πέρκη (pˈɜːke͡ɪ), a name applied to many species of fishes by ancient authors (D. W. Thompson 1947:195–197).

Registration number. 969.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S16). Phylogenetic relationships among the *Percoidei* are presented in Figure 18.

Phylogenetics. The first set of molecular phylogenetic studies that led to the unraveling of the traditional composition of *Perciformes* and *Serranidae* did not resolve the relationships of *Niphon spinosus* (Ara), *Percidae* (perches, walleyes, darters), or *Trachinidae* (weeverfishes) (W.-J. Chen et al. 2003; Dettaï and Lecointre 2004, 2005; W. L. Smith and Wheeler 2004; W. L. Smith and Wheeler 2006; W. L. Smith and Craig 2007; Dettaï and Lecointre 2008; B. Li et al. 2009). Two phylogenetic studies using Sanger-sequenced nuclear genes sampled two of the three lineages of *Percoidei*, one study resolving *Niphon* and *Percidae* as clade and the other resulting in *Trachinidae* and *Percidae* as a monophyletic group (Lautredou et al. 2013; Near et al. 2013). Subsequent molecular studies that sampled *Niphon*, *Percidae*, and *Trachinidae* resolved the lineages as a monophyletic group and placed *Trachinidae* as the sister lineage to a clade containing *Niphon* and *Percidae* (Figure 18; Near et al. 2015; Thacker et al. 2015; Ghezelayagh et al. 2022).

Composition. There are currently 254 living species of *Percoidei* (Fricke et al. 2023) that include *Niphon spinosus* and species classified in *Percidae* and *Trachinidae*. Over the past 10 years, there have been seven new living species of *Percoidei* described (Fricke et al. 2023), comprising 2.8% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Percoidei*.

Synonyms. There are no synonyms of *Percoidei*.

Comments. The name *Percoidei* is applied to this clade in several recent studies (Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Percoidei* is the otolith taxon †*Trachinus falcatus* from the Lutetian (48.1–41.0 Ma) of Germany (Schwarzhans 2007). Bayesian relaxed molecular clock analyses of *Percoidei* result in an average posterior crown age estimate of 52.7 million years ago, with the credible interval ranging between 38.7 and 65.4 million years ago (Ghezelayagh et al. 2022). *Niphonidae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Jordan 1923:191; Van der Laan et al. 2014:72).

<u>Constituent lineages.</u> Redundant group names are marked with an asterisk.

*Niphonidae**
Percidae
Trachinidae

Notothenioidei P. H. Greenwood, D. E. Rosen, S. H. Weitzman, and G. S. Myers 1966:401

[T. J. Near and C. E. Thacker],
converted clade name

<u>Definition.</u> The least inclusive clade containing *Percophis brasiliensis* Quoy and Gaimard 1825, *Bovichtus diacanthus* (Carmichael 1819), *Eleginops maclovinus* (Cuvier in Cuvier and Valenciennes 1830), and *Notothenia coriiceps* Richardson 1844. This is a minimum-crown-clade definition.

<u>Etymology.</u> From the ancient Greek νότος (nˈo͡ʊtˈo͡ʊz) meaning south and -θεν (ðˈɛn), a particle placed as a suffix to nouns indicating motion from a place.

<u>Registration number.</u> 970.

<u>Reference phylogeny.</u> A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S17). Phylogenetic relationships among the major lineages of *Notothenioidei* are presented in Figure 18. The placement of the pan-eleginopid †*Proeleginops grandeastmanorum* is on the basis of inferences from morphology (Balushkin 1994).

<u>Phylogenetics.</u> The traditional delimitation of *Notothenioidei* comprising *Bovichtidae* (thornfishes), *Pseudaphritis urvillii* (Congoli), *Eleginops maclovinus* (Patagonian Blennie), *Nototheniidae* (notothens), *Harpagiferidae* (plunderfishes), *Bathydraconidae* (Antarctic dragonfishes), and *Channichthyidae* (crocodile icefishes) was established in the first part of the 20th century (Dollo 1904; Regan 1913a, 1914b; Norman 1938a). Phylogenetic analyses of morphological and molecular characters resolve *Percophis brasiliensis* (Brazilian Flathead), *Bovichtidae*, and *Pseudaphritis* as successive branches from the lineage leading to a clade containing *Eleginops* and all species traditionally classified in *Nototheniidae*, *Harpagiferidae*, *Bathydraconidae*, and *Channichthyidae* (Balushkin 1992, 2000; Lecointre et al. 1997; Bargelloni et al. 2000; Dettaï and Lecointre 2004; Near, Pesavento, et al. 2004; Voskoboinikova 2004; Dettaï et al. 2012; Near, Dornburg, et al. 2012; Near et al. 2015, 2018; Ghezelayagh et al. 2022; Bista et al. 2023). *Harpagiferidae*, which includes species previously classified in *Artedidraconidae* (E. Parker and Near 2022), is the sister lineage of a clade containing *Bathydraconidae* and *Channichthyidae* (Iwami 1985; Hureau 1986; Balushkin 1992, 2000; Hastings 1993; Near et al. 2015, 2018; Ghezelayagh et al. 2022; Bista et al. 2023); however, in some morphological and molecular phylogenetic analyses *Bathydraconidae* is paraphyletic relative to *Channichthyidae* (Hastings 1993; Derome et al. 2002; Near, Dornburg, et al. 2012; Near et al. 2015; Ghezelayagh et al. 2022). The traditional delimitation of *Nototheniidae* is paraphyletic and comprises five disparately related lineages: *Pleuragramma antarcticum* (Antarctic Silverfish), a clade containing *Aethotaxis mitopteryx* (Longfin Icedevil) and *Dissostichus* (toothfishes), *Trematominae* (notoperches), *Gobionotothen* (goby rockcods), and a clade containing *Paranotothenia* and *Notothenia* (Dettaï et al. 2012; Near et al. 2015, 2018).

<u>Composition.</u> There are currently 102 species of *Notothenioidei* (Eastman and Eakin 2021; E. Parker et al. 2022) that include *Aethotaxis mitopteryx*, *Gvozdarus*, *Eleginops maclovinus*, *Percophis brasiliensis*, *Pseudaphritis urvillii*, and species classified in *Bovichtidae*, *Dissostichus*, *Trematominae*, *Gobionotothen*, *Nototheniidae*, *Harpagiferidae*, *Bathydraconidae*, and *Channichthyidae*. Fossil lineages of *Notothenioidei* include the pan-eleginopid †*Proeleginops grandeastmanorum* (Appendix 1; Balushkin 1994).

Over the past 10 years, there has been one new species of *Notothenioidei* described (Eastman and Eakin 2021), comprising 0.9% of the species diversity in the clade.

<u>Diagnostic apomorphies.</u> There are no known morphological apomorphies for *Notothenioidei* (Near et al. 2015).

<u>Synonyms.</u> *Nototheniiformes* (Regan 1913a:249–251; Jordan 1923:228; Norman 1938a:7–8) and *Notothenioidae* (Berg 1940:479; Gosline 1968:57–58, 1971:158) are approximate synonyms of *Notothenioidei*.

<u>Comments.</u> The traditional delimitation of *Notothenioidei* (Norman 1938a) was expanded to include *Percophis brasiliensis* (Near et al. 2015, 2018; Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Notothenioidei* is the pan-eleginopid †*Proeleginops grandeastmanorum* from the Ypresian (56.0–48.1 Ma) of Seymour Island, Antarctica (Balushkin 1994; Bieńkowska-Wasiluk et al. 2013). Bayesian relaxed molecular clock analyses of *Notothenioidei* result in an average posterior crown age estimate of 51.7 million years ago, with the credible interval ranging between 37.4 and 63.6 million years ago (Ghezelayagh et al. 2022).

<u>Constituent lineages.</u> Redundant group names are marked with an asterisk.

Aethotaxis
Bathydraconidae
Bovichtidae
Channichthyidae
Dissostichus
*Eleginopsidae**
Gobionotothen
Gvozdarus
Harpagiferidae
Nototheniidae
*Percophidae**
*Pleuragrammatinae**
*Pseudaphritidae**
Trematominae
†*Proeleginops*

Scorpaenoidei P. Bleeker 1859:xxi
[T. J. Near and C. E. Thacker],
converted clade name

<u>Definition.</u> The least inclusive clade containing *Platycephalus indicus* (Linnaeus 1758), *Normanichthys crockeri* Clark 1937, *Scorpaena porcus* Linnaeus 1758, *Sebastes norvegicus* (Ascanius 1772), *Cottus carolinae* (T. N. Gill 1861b), and *Zoarces elongatus* Kner 1868. This is a minimum-crown-clade definition.

<u>Etymology.</u> From the ancient Greek σκόρπαινα (skoːɹ͡pˈeɪ͡ni͡ə), which is the name used by ancient authors (e.g., Aristotle and Oppian) in reference to the Mediterranean species *Scorpaena porcus* Linnaeus (Black Scorpionfish) and *S. scrofa* Linnaeus (Red Scorpionfish) (D. W. Thompson 1947:245–246).

<u>Registration number.</u> 971.

<u>Reference phylogeny.</u> A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, figs. S17–S19). Although *Scorpaena porcus* is not included in the reference phylogeny, it resolves with other species of *Scorpaena* and *Scorpaenidae* in phylogenetic analyses of mtDNA sequences (Keskin and Atar 2013, fig. 2B; Yedier and Bostanci 2022, fig. 3). Phylogenetic relationships among the major lineages of *Scorpaenoidei* are presented in Figure 18.

<u>Phylogenetics.</u> *Scorpaeniformes* (*sensu* Greenwood et al. 1966), or mail-cheeked fishes, was a long-recognized taxonomic grouping of a range of lineages that included *Scorpaenidae* (scorpionfishes), *Platycephalidae* (flatheads), *Hexagrammidae* (greenlings), *Cottidae* (sculpins), *Cyclopteridae* (lumpfishes), *Liparidae* (snailfishes), *Dactylopteridae* (flying gurnards), and others (e.g., T. N. Gill 1889; Regan 1913c; Gregory 1933; Greenwood et al. 1966; Washington et al. 1984; Imamura and Shinohara 1998; J. S. Nelson 2006:318–339). Morphological and molecular studies confirm that the traditional delimitation of *Scorpaeniformes* is not monophyletic (Imamura and Yabe 2002; W.-J. Chen et al. 2003; Miya et al. 2003, 2005; W. L. Smith and Wheeler 2004, 2006; Imamura et al. 2005; W. L. Smith 2005; W. L. Smith and Craig 2007; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Lautredou et al. 2013; Near et al. 2013; Betancur-R et al. 2017). Specifically, *Trichodontidae* (sanddivers), traditionally classified in the polyphyletic *Trachinoidei* (e.g., Pietsch 1989; Pietsch and Zabetian 1990; J. S. Nelson et al. 2016:423), is closely related to the cottoids (Figure 18; Imamura et al. 2005;

W. L. Smith 2005; Ghezelayagh et al. 2022); *Dactylopteridae* is distantly related to lineages of *Scorpaenoidei* and is phylogenetically nested in *Syngnathiformes* (Figure 15; Imamura 2000; W. L. Smith and Wheeler 2004; W. L. Smith and Craig 2007; B. Li et al. 2009; Betancur-R, Broughton, et al. 2013; Lautredou et al. 2013; Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Santaquiteria et al. 2021; Ghezelayagh et al. 2022); and *Zoarcoidea* (eelpouts), *Gasterosteidae* (sticklebacks), and *Cottoidea* (sculpins, lumpsuckers, greenlings) resolve as a monophyletic group (Figure 18; Imamura and Yabe 2002; W.-J. Chen et al. 2003; Miya et al. 2003, 2005; W. L. Smith and Wheeler 2004; W. L. Smith and Craig 2007; B. Li et al. 2009; Lautredou et al. 2013; Near et al. 2013; Davis et al. 2016; Smith et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022; Maduna et al. 2022; L. Liu et al. 2023). An examination of myology and osteology led to the hypothesis that *Champsodon* (gapers) are related to *Scorpaenoidei* (Mooi and Johnson 1997); however, molecular analyses consistently resolve *Champsodon* as a lineage of *Acropomatiformes* that is distantly related to scorpaenoids (Figure 18; Near et al. 2013, 2015; Sanciangco et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022).

Platycephalidae was long classified in *Scorpaenoidei*, but classifications differ in placing the group as the sole lineage in a suprafamily-ranked taxon (Regan 1913c; Quast 1965; W. L. Smith 2005), with *Bembridae* (deepwater flatheads) and *Hoplichthys* (ghost flatheads) (Washington et al. 1984; Shinohara 1994), or with *Plectrogeniidae* (stinger flatheads), *Triglidae* (searobins), *Bembridae*, and *Hoplichthys* (W. L. Smith and Wheeler 2004). A morphological phylogeny and a phylogenetic analysis of combined morphological and molecular characters resolved *Platycephalidae* as the sister lineage of a clade containing *Triglidae* and *Hoplichthys* (Imamura 1996, 2004; W. L. Smith et al. 2018). Molecular phylogenies vary in the resolution of *Platycephalidae*: as the sister lineage of a clade containing *Congiopodidae* (horsefishes), *Bembridae*, and *Scorpaenoidea* (Lautredou et al. 2013); as the sister lineage of all other *Scorpaenoidei* except *Hoplichthys* (Near et al. 2013); nested in a clade that includes *Hoplichthys* and *Bembridae* that is the sister lineage of all other *Scorpaenoidei* (Betancur-R et al. 2017); or as the sister lineage of all other *Scorpaenoidei* (Figure 18; Ghezelayagh et al. 2022).

Triglidae was traditionally classified with other lineages of *Scorpaenoidea* (Regan 1913c; Quast 1965; Greenwood et al. 1966; W. L. Smith and Wheeler 2004). Many molecular phylogenies indicate *Triglidae* is more closely related to cottoids: as the sister lineage of a clade containing *Gasterosteidae*, *Zoarcoidea*, and *Cottoidea* (W. L. Smith and Craig 2007; B. Li et al. 2009; Lautredou et al. 2013) or as the sister lineage of a clade including *Anoplopomatidae*, *Gasterosteidae*, *Zoarcoidea*, and *Cottoidea* (Figure 18; Ghezelayagh et al. 2022). Other molecular phylogenies resolve *Triglidae* as the sister lineage of *Bembropidae* (duckbill flatheads) (Near et al. 2013; Betancur-R et al. 2017). Morphological phylogenies resolve *Triglidae* as paraphyletic relative to *Hoplichthys* (Imamura 1996, 2004), but a phylogeny inferred from a combined molecular and morphological dataset places *Triglidae* and *Hoplichthys* as sister lineages (W. L. Smith et al. 2018).

Anoplopomatidae (sablefishes) was placed with *Hexagrammidae* in several classifications (Regan 1913c; Quast 1965; Greenwood et al. 1966; Washington et al. 1984). A morphological phylogeny resolves *Anoplopomatidae* as the sister lineage of a clade containing all other sampled lineages of *Cottoidea* (Imamura et al. 2005). Molecular phylogenies resolve *Anoplopomatidae* as nested within *Cottoidea* as the sister lineage of *Zaniolepididae* (combfishes) (W. L. Smith and Craig 2007), as the sister lineage of all other *Cottoidea* (W. L. Smith and Wheeler 2004; Near et al. 2013), or as the sister lineage of a clade containing *Cottoidea*, *Gasterosteidae*, and *Zoarcoidea* (Figure 18; Betancur-R et al. 2017; Ghezelayagh et al. 2022; Maduna et al. 2022; L. Liu et al. 2023).

Composition. There are currently 2,208 living species of *Scorpaenoidei* (Fricke et al. 2023) classified in *Anoplopomatidae*, *Bembridae*, *Cottoidea*, *Gasterosteidae*, *Platycephalidae*, *Scorpaenoidea*, and *Triglidae*. Over the past 10 years, there have been 142 new living species of *Scorpaenoidei* described (Fricke et al. 2023), comprising 6.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Scorpaenoidei* include (1) third circumorbital modified as a suborbital stay with distal end broad and strongly attached to preopercle (Cuvier 1829:158; Boulenger 1904a, 1904b:692; Greenwood et al. 1966; Lauder and Liem 1983; Bowne 1994; Imamura and Yabe 2002; Imamura 2004; W. L. Smith et al. 2018), (2) presence of an extrinsic gas bladder muscle connected anteriorly to neurocranium and posteriorly to vertebrae (Imamura and Yabe 2002; Imamura 2004; W. L. Smith et al. 2018), (3) absence of supraneurals (W. L. Smith et al. 2018), and (4) hypurals 3 and 4 fused (W. L. Smith et al. 2018).

Synonyms. *Cottoidea* (T. N. Gill 1872:6), *Scleroparei* (Boulenger 1904a:184–185, 1904b:692–702, fig. 399; Regan 1913c), *Cataphracti* (Jordan 1923:208–215), *Cottoidei* (Berg 1940:487–490; McAllister 1968:148), and *Cottida* (Matsubara 1955:1040–1048) are partial synonyms of *Scorpaenoidei*. *Scorpaeniformes* is both a partial (Goodrich 1909:449–454; Greenwood et al. 1966:399; Gosline 1971:167–168; Washington et al. 1984:438) and an approximate (J. S. Nelson et al. 2016:467–495) synonym of *Scorpaenoidei*.

Comments. *Scorpaenoidei* was the name applied to a paraphyletic group that contained *Platycephalidae*, *Scorpaenoidea*, *Bembridae*, and *Triglidae*, but excluded *Anoplopomatidae*, *Cottoidea*, *Gasterosteidae*, *Normanichthys*, and *Zoarcoidea* (W. L. Smith et al. 2018).

The earliest fossil *Scorpaenoidei* is the pan-synanceiid †*Eosynanceja brabantica* from the Ypresian (56.0–48.1 Ma) of Belgium (Casier 1946). Bayesian relaxed molecular clock analyses of *Scorpaenoidei* result in an average posterior crown age estimate of 59.3 million years ago, with the credible interval ranging between 50.2 and 67.8 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Anoplopomatidae
Bembridae
Cottoidea
Gasterosteidae
Platycephalidae
Scorpaenoidea
Triglidae
Zoarcoidea

Scorpaenoidea T. N. Gill 1889:579
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade containing *Hoplichthys langsdorfii* Cuvier 1829 in Cuvier and Valenciennes (1829b), *Congiopodus leucopaecilus* (Richardson 1846), *Inimicus didactylus* (Pallas 1769), *Scorpaena porcus* Linnaeus 1758, and *Sebastes norvegicus* (Ascanius 1772), but not *Platycephalus indicus* (Linnaeus 1758). This is a minimum-crown-clade definition with an external specifier.

Etymology. From the ancient Greek σκόρπαινα (skoːɹ͡pˈeɪ͡ni͡ə), which is the name used by ancient authors (e.g., Aristotle and Oppian) in reference to the Mediterranean species *Scorpaena porcus* Linnaeus (Black Scorpionfish) and *S. scrofa* Linnaeus (Red Scorpionfish) (D. W. Thompson 1947:245–246).

Registration number. 972.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S17). Although *Scorpaena porcus* is not included in the reference phylogeny, it resolves with other species of *Scorpaena* and *Scorpaenidae* in phylogenetic analyses of mtDNA sequences (e.g., Yedier and Bostanci 2022, fig. 3). The phylogenetic relationships of the major lineages of *Scorpaenoidea* are presented in Figure 18. The placement of *Plectrogeniidae* (stinger flatheads) follows a phylogenetic analysis of a combined dataset of morphological and molecular characters (W. L. Smith et al. 2018).

Phylogenetics. The monophyly of *Scorpaenoidea* is supported in phylogenomic analyses of UCE loci (Ghezelayagh et al. 2022). Morphological studies result in phylogenies that do not resolve *Congiopodidae* (horsefishes), *Hoplichthys* (ghost flatheads), or *Normanichthys crockeri* (Mote Sculpin) within *Scorpaenoidea* (Ishida 1994; Imamura 2004) and place *Triglidae* (searobins), *Bembridae* (deepwater flatheads), and *Platycephalidae* (flatheads) as phylogenetically nested in *Scorpaenoidea* (Imamura 2004). Molecular phylogenies inferred from Sanger-sequenced mitochondrial and nuclear genes do not resolve *Scorpaenoidea* as monophyletic; specifically, *Bembridae*, *Percoidei*, *Triglidae*, *Cottoidea*, *Platycephalidae*, and *Serranidae* are nested within *Scorpaenoidea* (W. L. Smith and Craig 2007); *Bembridae* is nested within *Scorpaenoidea* and resolved as the sister lineage of *Synanceiidae* (stonefishes) (Lautredou et al. 2013), *Hoplichthys* is placed outside of *Scorpaenoidea* as the sister lineage of a clade containing *Bembridae* and *Platycephalidae* (Betancur-R et al. 2017), and *Hoplichthys* and *Congiopodidae* are placed outside of *Scorpaenoidea*, respectively as the sister lineages of *Triglidae* and *Cottoidea* (W. L. Smith et al. 2018).

The phylogenetic relationships of *Normanichthys crockeri* were unresolved from the time the species was described (Clark 1937) to the application of phylogenomic datasets to investigate relationships of *Acanthomorpha* (Ghezelayagh et al. 2022). On the basis of morphology, *Normanichthys* was hypothesized to be closely related to lineages of *Cottoidea* (Norman 1938b; Berg 1940:489; Fowler 1951; Greenwood et al. 1966) or a distinct lineage within *Scorpaenoidei* (Washington et al. 1984; Yabe and Uyeno 1996; J. S. Nelson et al. 2016:478). Larval morphology was the basis to suggest the phylogenetic placement of *Normanichthys* outside *Scorpaenoidei* (Velez et al. 2003). A maximum parsimony analysis of DNA sequences from mitochondrial and nuclear genes resolved *Normanichthys* as the sister lineage of an unlikely clade containing *Hoplichthys*, *Synanceiidae*, and the ovalentarians *Gramma*, *Menidia*, *Labrisomus*, and *Salarias* (W. L. Smith and Wheeler 2004). Phylogenomic analyses of UCE loci resolve *Normanichthys* and *Hoplichthys* as a clade that is the sister lineage of all other *Scorpaenoidea* (Figure 18; Ghezelayagh et al. 2022).

Composition. There are currently 579 species of *Scorpaenoidea* (Fricke et al. 2023) that include *Normanichthys crockeri* and species classified in *Congiopodidae*, *Hoplichthys*, *Neosebastidae* (gurnard perches), *Plectrogeniidae* (stinger flatheads), *Scorpaenidae* (scorpionfishes), and *Synanceiidae*. Over the past 10 years, there have been 44 new living species of *Scorpaenoidei* described (Fricke et al. 2023), comprising 7.6% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Scorpaenoidea*.

Synonyms. *Scorpaeniformes* (Bleeker 1859:xxi; Regan 1913c:170–171; W. L. Smith 2005:153), *Scorpaenoidae* (Berg 1940:488; Quast 1965:587–589), *Scorpaenicae* (Matsubara 1955:1040–1048), and *Scorpaenoidei* (Greenwood et al. 1966:399; Washington et al. 1984:439; J. S. Nelson et al. 2016:468–475) are all partial synonyms of *Scorpaenoidea*.

Comments. The group name *Scorpaenoidea* has been applied to several paraphyletic groups of species classified in *Scorpaenoidei*. The first use of *Scorpaenoidea* was for a group containing *Synanceiidae*, *Scorpaenidae*, *Hexagrammidae*, and *Anoplopomatidae* (T. N. Gill 1889). By the early 20th century, *Platycephalidae*, *Hoplichthys*, *Plectrogeniidae*, *Neosebastidae*, *Scorpaenidae*, *Synanceiidae*, *Bembridae*, and *Triglidae* were included in *Scorpaenoidea* (Imamura 2004).

The earliest fossil *Scorpaenoidea* is the pan-synanceiid †*Eosynanceja brabantica* from the Ypresian (56.0–48.1 Ma) of Belgium (Casier 1946). Bayesian relaxed molecular clock analyses of *Scorpaenoidea* result in an average posterior crown age estimate of 52.3 million years ago, with the credible interval ranging between 41.3 and 62.7 million years ago (Ghezelayagh et al. 2022). *Scorpaenoidea* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:83).

Constituent lineages. Redundant group names are marked with an asterisk.

Congiopodidae
*Hoplichthyidae**
Neosebastidae
*Normanichthyidae**
Plectrogeniidae
Scorpaenidae
Synanceiidae

Cottoidea T. N. Gill 1872:6
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade that contains *Cottus gobio* Linnaeus, *Cottus carolinae* (T. N. Gill 1861b), *Zaniolepis latipinnis* C. Girard 1858b, *Hexagrammos decagrammus*

(Pallas 1810), and *Eumicrotremus orbis* (Günther 1861). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κόττος (kˈɑːtˈʌs), which is the name used by ancient authors (e.g., Aristotle) in reference to *Cottus gobio* Linnaeus (European Bullhead) (D. W. Thompson 1947:128–129).

Registration number. 973.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S18). Although *Cottus gobio* is not in the reference phylogeny, several phylogenetic studies based on mtDNA, DNA sequences from nuclear genes, and morphology nest *C. gobio* in a clade with other species of *Cottus* (Kontula et al. 2003, fig. 2; Yokoyama and Goto 2005, fig. 1; Lautredou et al. 2013, fig. 3; W. L. Smith and Busby 2014, fig. 3). Phylogenetic relationships of the major living and fossil lineages of *Cottoidea* are presented in Figure 18. The placement of *Jordaniidae* (longfin sculpins) follows a phylogenetic analysis of a combined dataset of morphological and molecular characters (W. L. Smith and Busby 2014). The placement of the fossil pan-hexagrammids †*Sakhalinia* and †*Paraophiodon* are on the basis of inferences from morphology (Nazarkin 1997; Nazarkin et al. 2013).

Phylogenetics. The cottoids were traditionally delimited to include *Scorpaenichthys marmoratus* (Cabezon) and species now classified in *Rhamphocottidae* (grunt sculpins), *Agonidae* (poachers), *Cottidae* (sculpins), *Jordaniidae*, and *Psychrolutidae* (fathead sculpins) (Greenwood et al. 1966; Yabe 1985; Jackson 2003; W. L. Smith 2005; W. L. Smith and Busby 2014). Morphological and molecular analyses consistently resolve *Hexagrammidae* (greenlings), *Zaniolepididae* (combfishes), *Trichodontidae* (sandfishes), *Cyclopteridae* (lumpfishes), *Liparidae* (snailfishes), and *Anoplopomatidae* as closely related to the cottoids (Washington et al. 1984; Yabe 1985; Shinohara 1994; W. L. Smith and Wheeler 2004; Imamura et al. 2005; W. L. Smith and Craig 2007; B. Li et al. 2009; Lautredou et al. 2013; Near et al. 2013; W. L. Smith and Busby 2014; Betancur-R et al. 2017). However, phylogenetic analysis of whole mtDNA genomes and UCE loci resolves *Anoplopomatidae* as the sister lineage of a more inclusive clade containing *Cottoidea*, *Gasterosteidae* (sticklebacks), and *Zoarcoidea* (Figure 18; Ghezelayagh et al. 2022; Maduna et al. 2022; L. Liu et al. 2023). Within *Cottoidea*, *Zaniolepididae*, *Hexagrammidae*, and a clade containing *Trichodontidae*, *Cyclopteridae*, and *Liparidae* are successive branching lineages leading to a core cottoid clade containing *Rhamphocottidae*, *S. marmoratus*, *Agonidae*, *Cottidae*, and *Psychrolutidae* (Figure 18). Phylogenetic analysis of a combined morphological and molecular dataset resolves *Jordaniidae* as the sister lineage to all other core cottoids (W. L. Smith and Busby 2014).

Composition. There are currently 897 species of *Cottoidea* (Fricke et al. 2023) that include *Scorpaenichthys marmoratus* and species classified in *Agonidae*, *Cottidae*, *Cyclopteridae*, *Hexagrammidae*, *Jordaniidae*, *Liparidae*, *Psychrolutidae*, *Rhamphocottidae*, *Trichodontidae*, and *Zaniolepididae*. Fossil lineages of *Cottoidea* include the pan-hexagrammids †*Sakhalinia multispinata* and †*Paraophiodon nessovi* from the Serravallian (13.82–11.63 Ma) of Russia (Nazarkin 1997; Nazarkin et al. 2013). Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 61 new living species of *Scorpaenoidei* have been described (Fricke et al. 2023), comprising 6.8% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological and reproductive apomorphies for *Cottoidea* include (1) presence of a lachryopalatine articulation (Yabe 1985; Shinohara 1994; Imamura et al. 2005), (2) parhypural and lower hypural plate fused (Yabe 1985; Shinohara 1994; Imamura et al. 2005), (3) third and fourth hypurals fused (Shinohara 1994; Imamura et al. 2005), (4) spawn adhesive demersal eggs (Watson et al. 1984; Shinohara 1994; Imamura et al. 2005; Muñoz 2010), and (5) absence of a connection between preopercle and the temporal sensory canals (Imamura et al. 2005).

Synonyms. *Cottiformes* (Regan 1913c:171–172; Jordan 1923:211–215), *Cottoidae* (Berg 1940:489–490; Quast 1965:595–597), *Copticae* (Matsubara 1955:1040–1048), *Cottoidei* (Greenwood et al. 1966:399; Washington et al. 1984:444–445; Shinohara 1994:80; Imamura et al. 2005:274; W. L. Smith 2005:153; J. S. Nelson et al. 2016:485–494), and *Cottales* (Betancur-R et al. 2017:31) are all partial synonyms of *Cottoidea*.

Comments. The name *Cottoidea* was applied to a less inclusive group that included *Agonidae*, *Cottidae*, *Jordaniidae*, *Psychrolutidae*, *Rhamphocottidae*, and *Scorpaenichthys* (W. L. Smith and Busby 2014).

The earliest fossil *Cottoidea* is †*Cottus otiakensis*, an otolith taxon from the Late Oligocene (27.30–23.04 Ma) of New Zealand (Frost 1928; PBDB 2023). Bayesian relaxed molecular clock analyses of *Cottoidea* result in an average posterior crown age estimate of 40.5 million years ago, with the credible interval ranging between 33.8 and 49.0 million years ago (Ghezelayagh et al. 2022). *Cottoidea* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:87).

Constituent lineages. Redundant group names are marked with an asterisk.

Agonidae
Cottidae
Cyclopteridae
Hexagrammidae
Jordaniidae
Liparidae
Psychrolutidae
Rhamphocottidae
*Scorpaenichthyidae**
Trichodontidae
Zaniolepididae
†*Paraophiodon*
†*Sakhalinia*

Gasterosteidae C. L. Bonaparte 1831:156, 169
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown lineage that contains *Hypoptychus dybowskii* Steindachner 1880, *Aulichthys japonicus* Brevoort in T. N. Gill 1862, *Aulorhynchus flavidus* T. N. Gill 1861c, *Gasterosteus aculeatus* Linnaeus 1758, and *Apeltes quadracus* (Mitchill 1815). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek γαστήρ (gˈæstɚ) meaning belly and ὀστέον (ˈɑːstɪən) meaning bone.

Registration number. 974.

Reference phylogeny. A phylogeny of 10 species of *Gasterosteidae* inferred from a supermatrix of 27 nuclear and mitochondrial genes (Rabosky et al. 2018; J. Chang et al. 2019). The phylogeny is available on the Dryad data repository (Rabosky et al. 2019). The phylogenetic resolution of *Gasterosteidae* within *Perciformes* is shown in Figure 18.

Phylogenetics. The identification of a natural group containing species traditionally classified in *Gasterosteidae* (sticklebacks) and *Aulorhynchidae* (tubesnouts) is reflected in precladistic classifications from the second half of the 19th century (T. N. Gill 1862, 1872; Jordan and Evermann 1896:742–753). Long classified with species of *Ammodytidae* (sand lances) (Jordan 1923:230; Berg 1940:481; Gosline 1963b; Greenwood et al. 1966), a study citing osteology and reproductive traits proposed *Hypoptychus dybowskii* (Korean Sandlance) as most closely related to *Gasterosteidae* (Ida 1976). While not universally accepted initially (J. S. Nelson 1978, 1984:245), morphological and molecular phylogenetic analyses resolve a clade containing *Hypoptychus* and all other sampled species of *Gasterosteidae* (Pietsch 1978; Kawahara et al. 2008; Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022). A study of the osteology of the oral jaws concluded that the traditional delimitation of *Aulorhynchidae* is paraphyletic because *Aulichthys japonicus* (Tubenose) and *Hypoptychus* are more closely related relative to *Aulorhynchus flavidus* (Tubesnout) (G. D. Johnson and Patterson 1993), a result supported in molecular phylogenetic analyses of Sanger-sequenced mtDNA and nuclear genes (Betancur-R et al. 2017; Rabosky et al. 2018). However, phylogenetic analyses of Sanger-sequenced nuclear genes and a phylogenomic analysis of ultraconserved element loci do not resolve a clade containing *Hypoptychus* and *Aulichthys*, but rather place *Hypoptychus* as the sister lineage of all other *Gasterosteidae* (Near et al. 2013; Ghezelayagh et al. 2022). Two phylogenetic studies of *Gasterosteidae* did not test the monophyly of *Aulorhynchidae*: an analysis of morphological characters did not sample *Hypoptychus* but resolved *Aulichthys* and *Aulorhynchus* as sister lineages (Orr 1995), and analysis of Sanger-sequenced whole mtDNA genomes and nuclear genes did not test the monophyly of *Aulorhynchidae* because the inferred phylogenies were rooted with *Hypoptychus* (Kawahara et al. 2009).

Phylogenetic relationships inferred among the core gasterosteiids, *Apeltes quadracus* (Fourspine Stickleback), *Culaea inconstans* (Brook Stickleback), *Gasterosteus* (threespine sticklebacks), *Pungitius* (ninespined sticklebacks), and *Spinachia spinachia* (Sea Stickleback) vary among studies and types of data analyzed. Phylogenies inferred from morphology, behavior, and mtDNA gene trees resolve *Spinachia* as the sister lineage of all other core gasterosteiids (McLennan 1993; Bowne 1994; McLennan and Mattern 2001; Keivany and Nelson 2004; Mattern 2004, 2007; Mattern and McLennan 2004). However, molecular phylogenies inferred from combinations of mtDNA and nuclear genes resolve either *Gasterosteus* (Kawahara et al. 2009; Rabosky et al. 2018) or a clade containing *Gasterosteus* and *Pungitius* as the sister lineage of all other core gasterosteiids (Betancur-R et al. 2017). Regardless of the type of character data, most phylogenetic analyses are consistent in resolving *Culaea* and *Pungitius* as sister lineages (McLennan 1993; Bowne 1994; McLennan and Mattern 2001; Keivany and Nelson 2004; Mattern 2004; Mattern and McLennan 2004; Kawahara et al. 2009; Rabosky et al. 2018).

Composition. There are currently 23 species of *Gasterosteidae* (Fricke et al. 2023) that include *Apeltes quadracus*, *Aulichthys japonicus*, *Aulorhynchus flavidus*, *Culaea inconstans*, *Hypoptychus dybowskii*, *Spinachia spinachia*, and species classified in *Gasterosteus* and *Pungitius*. Over the past 10 years, there have been two new living species of *Gasterosteidae* described (Fricke et al. 2023), comprising 8.7% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Gasterosteidae* include (1) loss of both upper circumorbital bones (W. L. Smith 2005), (2) nasal and neurocranium fused (W. L. Smith 2005), (3) medial extrascapulars absent (W. L. Smith 2005), (4) articular and ascending process of premaxilla continuous (W. L. Smith 2005), (5) palatine teeth absent (W. L. Smith 2005), (6) endopterygoid absent (W. L. Smith 2005), (7) four branchiostegal rays (W. L. Smith 2005), (8) basihyal uniform in width rostrally (W. L. Smith 2005), (9) loss of gill rakers from second, third, and fourth epibranchials (W. L. Smith 2005), (10) absence of Baudelot's ligament, (11) four pelvic fin rays (W. L. Smith 2005), (12) absence of anterior pelvic fin ray processes (W. L. Smith 2005), (13) dorsal spines absent from first two dorsal pterygiophores (W. L. Smith 2005), (14) second preural centrum with elongate neural spines (W. L. Smith 2005), (15) caudal hypurapophysis absent (W. L. Smith 2005), and (16) fused upper and lower hypural plates (W. L. Smith 2005).

Synonyms. *Gasterosteoidei* is a partial (Bleeker 1859:xxiii; Goodrich 1909:411–412) and approximate synonym (Greenwood et al. 1966:398; J. S. Nelson et al. 2016:482–485) of *Gasterosteidae*. *Hemibranchii* (Jordan 1923:173–174) and *Gasterosteiformes* (Berg 1940:458–460) are approximate synonyms of *Gasterosteidae*. *Gasterosteales* is an ambiguous synonym of *Gasterosteidae* (Betancur-R et al. 2017:31).

Comments. The species *Aulichthys japonicus*, *Aulorhynchus flavidus*, and *Hypoptychus dybowskii* are classified in *Gasterosteidae*, in contrast to the traditional classification of these species in *Aulorhynchidae* and *Hypoptychidae* (e.g., J. S. Nelson et al. 2016:482–483). This is motivated by the consistent resolution of *Gasterosteidae* as a monophyletic group (Pietsch 1978; Kawahara et al. 2008; Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022). If *Aulichthys japonicus* is classified in *Aulorhynchidae* or *Hypoptychidae*, a rank-based classification would include two family group names for three species. Classifying all three of these species in *Gasterosteidae* reflects the most robust inferences of their phylogenetic relationships and reduces the number of redundant group names among ray-finned fishes. The name *Gasterosteidae* was selected as the clade name over its synonyms because it seems to be the name most frequently applied to a taxon approximating the named clade. *Gasterosteidae* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:64).

The earliest fossil *Gasterosteidae* is †*Gasterosteus* cf. *aculeatus* from the Serravallian (13.82–11.63 Ma) of California, USA (Bell et al. 2009). Bayesian relaxed molecular clock analyses of *Gasterosteidae* result in an average posterior crown age estimate of 30.9 million years ago, with the credible interval ranging between 23.1 and 39.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages.

Apeltes quadracus
Aulichthys japonicus
Aulorhynchus flavidus
Gasterosteus
Culaea inconstans
Hypoptychus dybowskii
Pungitius
Spinachia spinachia

Zoarcoidea O. A. Radchenko, I. A. Chereshnev, and A. V. Petrovskaya 2014:473

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade containing *Azygopterus corallinus* Andriashev and Makushok 1955, *Bathymaster signatus* Cope 1873, *Stichaeus punctatus* (Fabricus 1780), and *Zoarces viviparus* (Linnaeus 1758). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ζωαρκής (zˈoːɹ͡kəz) meaning life supporting.

Registration number. 975.

Reference phylogeny. A phylogeny inferred from sequences of DNA sequences of Sanger-sequenced mitochondrial and nuclear genes (Hotaling et al. 2021, fig. S1). Phylogenetic relationships of the major lineages of living and fossil lineages of *Zoarcoidea* are presented in Figure 18. The placements of the pan-pholids †*Agnevichthys gretchinae* and †*Palaeopholis laevis* in the phylogeny are on the basis of an analysis of morphological characters (Nazarkin 2002).

Phylogenetics. *Zoarcoidea* as delimited here was first presented in mid-20th century prephylogenetic morphological studies (Makushok 1958; Gosline 1968). The monophyly of *Zoarcoidea* is supported in several morphological (Anderson 1984, 1994; Kiernan 1990; Imamura and Yabe 2002; Kwun 2013; Clardy 2014) and molecular (Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022) phylogenetic studies. Two molecular phylogenetic analyses of *Zoarcoidea* provide dense taxon sampling but do not test monophyly of the clade because they each utilize a single outgroup taxon (Kwun and Kim 2013; Hotaling et al. 2021). Morphological phylogenies differ in resolving *Ulvaria subbifurcata* (Radiated Shanny) (Clardy 2014) or *Bathymasteridae* (ronquils) (Anderson 1984, 1994; Hilton et al. 2019) as the sister lineage of all other *Zoarcoidea*, and molecular studies differ in placing *Bathymasteridae* (Turanov et al. 2012; Radchenko, Chereshnev, Petrovskaya, et al. 2014; Radchenko 2015, 2016, 2017; Turanov et al. 2017; Hotaling et al. 2021) or *Eulophiidae* (spinous eelpouts) (Kwun 2013; Kwun and Kim 2013) as the earliest diverging lineages of *Zoarcoidea*.

Morphological (Clardy 2014) and molecular (Radchenko et al. 2010; Turanov et al. 2012; Chereshnev et al. 2013; Radchenko, Chereshnev, Petrovskaya, et al. 2014; Radchenko 2015, 2016, 2017; Betancur-R et al. 2017; Rutenko et al. 2019; Hotaling et al. 2021) phylogenetic analyses resolve the traditional delimitation of *Stichaeidae* (pricklebacks) (Makushok 1958; Mecklenburg and Sheiko 2004; Zemnukhov 2012; J. S. Nelson et al. 2016:480) as nonmonophyletic. Specifically, the enigmatic Graveldiver, *Scytalina cerdale*, long classified in the monotypic *Scytalinidae* (Mecklenburg 2003e; Hilton 2009), is nested in *Stichaeidae* as the sister lineage of a clade containing *Phytichthys chirus* (Ribbon Prickleback) and *Xiphister* in a phylogenomic analysis of ultraconserved element (UCE) loci (Ghezelayagh et al. 2022). Morphological studies resolve a clade containing *Scytalina* and *Xiphister* or place *Scytalina* as the sister lineage of a clade containing *Phytichthys*, *Xiphister*, *Ptilichthys goodei* (Quillfish), and *Pholidae* (gunnels) (Hilton 2009; Clardy 2014). At least five other lineages traditionally classified as *Stichaeidae* are more closely related to other lineages of *Zoarcoidea* in molecular and morphological phylogenetic analyses: *Opisthocentridae* (rearspined pricklebacks) is the sister lineage of a clade containing *Ptilichthys* and *Pholidae* (Figure 18; Radchenko et al. 2012; Chereshnev et al. 2013; Kwun 2013; Kwun and Kim 2013; Radchenko 2015, 2016; Rutenko et al. 2019; Hotaling et al. 2021; Ghezelayagh et al. 2022); *Lumpenidae* (eel pricklebacks) is the sister lineage of *Cryptacanthodes* (wrymouths) (Figure 18; Kwun and Kim 2013; Radchenko 2015, 2016; Hotaling et al. 2021; Ghezelayagh et al. 2022); *Cebidichthyidae* (monkeyfaces), including *Cebidichthys*, *Dictyosoma*, *Esselenia*, and *Esselenichthys*, was formerly classified in the stichaeid subclade *Xiphisterinae* but is now resolved as the sister lineage of all other *Zoarcoidea* to the exclusion of *Bathymasteridae* and possibly *Eulophiidae* (Figure 18; Radchenko et al. 2012; Turanov et al. 2012; Chereshnev et al. 2013; Radchenko, Chereshnev, Petrovskaya, et al. 2014; Radchenko 2015, 2016; Hotaling et al. 2021; Ghezelayagh et al. 2022); *Neozoarcidae* (kissing eelpouts) is resolved as sister to a clade containing *Anarhichadidae* (wolffishes) and *Zoarcidae* (eelpouts) (Figure 18; Radchenko 2015, 2016; Turanov et al. 2017; Hotaling et al. 2021; Ghezelayagh et al. 2022) or as the sister lineage of *Zoarcidae* (Clardy 2014); and *Kasatkia*, thought to be closely related to *Opisthocentridae* (Posner and Lavenberg 1999), is resolved as the sister lineage of *Ptilichthys* (Hotaling et al. 2021).

Composition. There are currently 431 species of *Zoarcoidea* (Mecklenburg 2003a, 2003b, 2003c, 2003d, 2003e, 2003f; Mecklenburg and Sheiko 2004; Fricke et al. 2023) that include *Ptilichthys goodei*, *Zaprora silenus* (Prowfish), and species classified in *Anarhichadidae*, *Bathymasteridae*, *Cebidichthyidae*, *Cryptacanthodes*, *Eulophiidae*, *Lumpenidae*, *Neozoarcidae*, *Opisthocentridae*, *Pholidae*, *Stichaeidae*, and *Zoarcidae*. Fossil taxa include the pan-pholids †*Agnevichthys gretchinae* and †*Palaeopholis*. Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, there have been 19 new living species of *Zoarcoidea* described (Fricke et al. 2023), comprising approximately 4.4% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Zoarcoidea* include (1) basisphenoid absent (Anderson 1984, 1994; Imamura and Yabe 2002; Wiley and Johnson 2010), (2) a single pair of nostrils present due to loss of the posterior nostrils (Anderson 1984, 1994; Imamura and Yabe 2002; Wiley and Johnson 2010), (3) mesial portion of $A_{2,3}$ section of adductor mandibulae extends posterior to levator arcus palatini (Anderson 1994), and (4) dorsal and anal fin stays absent (Imamura and Yabe 2002; Wiley and Johnson 2010).

Synonyms. *Zoarceoidea* (Gill 1893:136; Makushok 1958:34; Gosline 1971:158), *Zoarcicae* (Hubbs 1952:51, fig. 1), *Zoarcoidei* (Greenwood et al. 1966:397; Springer and Johnson 2004:209; Wiley and Johnson 2010:161; J. S. Nelson et al. 2016:478–482), and *Zoarcales* (Betancur-R et al. 2017:31) are ambiguous synonyms of *Zoarcoidea*.

Comments. Makushok (1958) is attributed as using the group name *Zoarcoidea* to delimit *Zoarcidae* and other closely related lineages (Radchenko, Chereshnev, and Petrovskaya 2014); however, Makushok (1958:34) used the name *Zoarceoidea*. The group name *Zoarcoidea* is used in reference to a taxonomic suborder without attribution (Fletcher et al. 1988). The application of molecular and morphological data to the phylogenetics of *Zoarcoidea* led to the discovery that the traditional delimitation of *Stichaeidae* was not monophyletic (e.g., Clardy 2014; Radchenko 2015; Betancur-R et al. 2017; Hotaling et al. 2021; Ghezelayagh et al. 2022), necessitating the addition of five families to *Zoarcoidea* in rank-based classifications (Fricke et al. 2023). The Graveldiver *Scytalina cerdale* is classified in *Stichaeidae* on the basis of the results of phylogenomic analyses of UCE loci (Ghezelayagh et al. 2022).

The earliest fossil *Zoarcoidea* include †*Zaprora koreana* from the Middle Miocene (16.0–11.6 Ma) of Korea (Nam and Nazarkin 2018) and the pan-pholids †*Agnevichthys gretchinae* and †*Palaeopholis laevis* from the Serravallian of Russia (Nazarkin 2002). Bayesian relaxed molecular clock analyses of *Zoarcoidea* result in an average posterior crown age estimate of 29.9 million years ago, with the credible interval ranging between 23.0 and 37.2 million years ago (Ghezelayagh et al. 2022). *Zoarcoidea* is a valid family-group name under the *International Code of Zoological Nomenclature* (Van der Laan et al. 2014:114).

Constituent lineages. Redundant group names are marked with an asterisk.

Anarhichadidae
Bathymasteridae
Cebidichthyidae
*Cryptacanthodidae**
Eulophiidae
Lumpenidae
Neozoarcidae
Opisthocentridae
Pholidae
*Ptilichthyidae**
Stichaeidae
*Zaproridae**
Zoarcidae
†*Agnevichthys*
†*Palaeopholis*

Centrarchiformes P. Bleeker 1859:xix
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive clade that contains *Centrarchus macropterus* (Lacépède 1801), *Micropterus salmoides* (Lacépède 1802), *Percalates colonorum* (Günther 1863b), and *Kuhlia marginata* (Valenciennes in Cuvier and Valenciennes 1829a). This is a minimum-crown-clade definition.

Etymology. From the ancient Greek κέντρον (kˈɛntɹɑːn), which can refer to any sharp point such as the tip of a spear, and άρχός (ˈɑːɹ͡ko͡ʊz) meaning anus. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 977.

Reference phylogeny. A phylogeny inferred from DNA sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S20). Although *Centrarchus macropterus* is not included in the reference phylogeny, the species resolves with other species of *Centrarchidae* in phylogenetic analyses of DNA sequences of Sanger-sequenced mitochondrial and nuclear genes (Near, Bolnick, et al. 2004, fig. 1; Near and Kim 2021, fig. 2A). Phylogenetic relationships among the major lineages of *Centrarchiformes* are presented in Figure 19. The phylogenetic placement of *Caesioscorpis theagenes* (Blowhole Perch) is on the basis of preliminary analyses of 10 Sanger-sequenced nuclear genes used in other studies of centrarchiform and acanthomorph phylogeny (e.g., Near et al. 2012c, 2013).

Phylogenetics. *Centrarchiformes* as delimited here was first resolved as a monophyletic group in phylogenetic analyses of Sanger-sequenced mtDNA and nuclear genes (Near et al. 2012c, 2013; Betancur-R, Broughton, et al. 2013; W.-J. Chen, Lavoué, et al. 2014; Sanciangco et al. 2016). Molecular phylogenetic analyses consistently resolve three major lineages within *Centrarchiformes*: (1) *Percalates* (estuary perches) as the sister lineage of all other *Centrarchiformes* (Figure 19; Near et al. 2012c; W.-J. Chen, Lavoué, et al. 2014; Lavoué, Nakayama, et al. 2014; Ghezelayagh et al. 2022); (2) *Terapontoidei* including *Girellidae* (nibblers), *Scorpididae* (halfmoons), *Parascorpis typus* (Jutjaw), *Dichistius* (galjoen fishes), *Microcanthidae* (stripeys), *Caesioscorpis theagenes* (Blowhole Perch), *Oplegnathus* (knifejaws), *Kyphosidae* (sea chubs), *Kuhlia* (flagtails), and *Terapontidae* (grunters) (Figure 19; Yagishita et al. 2002, 2009; Knudsen and Clements 2016; Sanciangco et al. 2016; Betancur-R et al. 2017; Knudsen et al. 2019; Ghezelayagh et al. 2022); and (3) *Centrarchoidei* including *Enoplosus armatus* (Oldwife), *Percichthyidae* (temperate perches), *Centrarchidae* (sunfishes, blackbasses, and pygmy sunfishes), *Sinipercidae* (Chinese perches), *Cirrhitidae* (hawkfishes), *Latridae* (trumpeters), *Chironemus* (kelpfishes), *Cheilodactylus* (fingerfins), and *Aplodactylus* (marblefishes) (Figure 19; C. H. Li, Ortí, et al. 2010; Near et al. 2012c, 2013; Sanciangco et al. 2016; Betancur-R et al. 2017; Song et al. 2017; Ghezelayagh et al. 2022).

The classification of *Centrarchiformes* is dynamic and unsettled, reflected in part by a high proportion of families in rank-based classifications that contain a single genus (Regan 1913b; J. B. L. Smith 1935; G. D. Johnson 1984; Gosline 1985; Betancur-R et al. 2017; Fricke et al. 2023). Molecular phylogenies consistently resolve two sets of traditionally delimited centrarchiform families as nonmonophyletic. First, the two species of *Percalates* were classified as *Percichthyidae* (G. D. Johnson 1984), but resolve as the sister lineage of all other centrarchiforms and there is no described rank-based

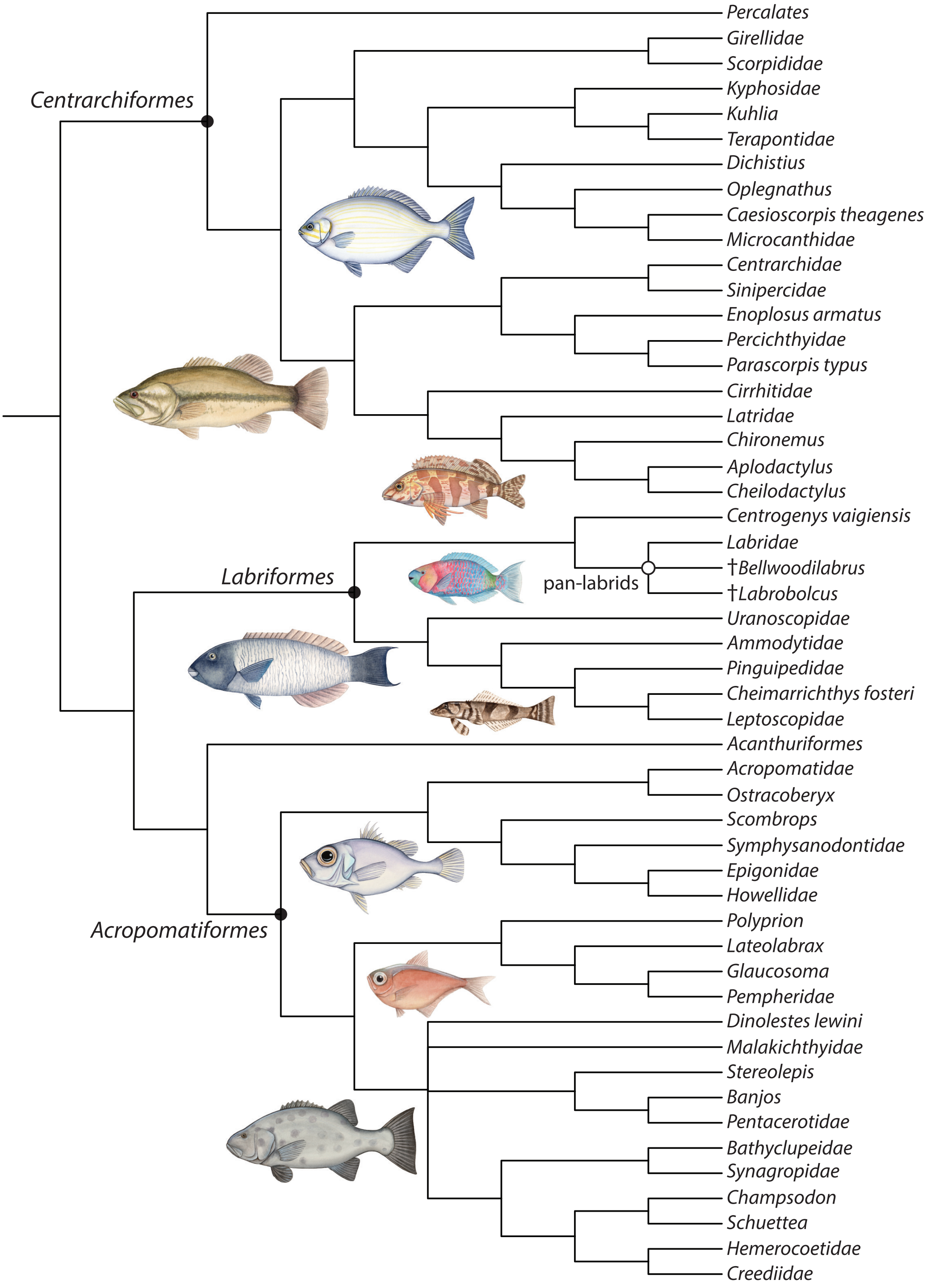

FIGURE 19. Phylogenetic relationships of the major living lineages and fossil taxa of *Centrarchiformes*, *Labriformes*, and *Acropomatiformes*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

taxonomic family to accommodate the classification of *Percalates* (Figure 19; Near et al. 2012c, 2013; Betancur-R, Broughton, et al. 2013; Sanciangco et al. 2016; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022). Second, the classification of families within cirrhitoids was dramatically realigned because of molecular phylogenetic analyses. Traditionally, *Cheilodactylidae* (morwongs) contained three to five genera and approximately 22 species (Greenwood 1995; J. S. Nelson 2006:386). Phylogenetic analyses of mtDNA gene sequences, morphology, and a phylogenomic UCE dataset resolved *Cheilodactylidae* as polyphyletic, with all but two of the species traditionally classified as cheilodactylids nested within a paraphyletic *Latridae* (Figure 19; Burridge and Smolenski 2004; Kimura et al. 2018; Ludt et al. 2019). The results of these phylogenetic analyses resulted in a transfer of these species to *Latridae* from *Cheilodactylidae*. Phylogenomic analyses of UCE loci differ in resolving *Cheilodactylus* and *Chironemus* rather than *Cheilodactylus* and *Aplodactylus* as sister lineages (Ludt et al. 2019; Ghezelayagh et al. 2022).

The two species of *Percilia* (southern basses) were traditionally classified in the monogeneric family *Perciliidae* (J. S. Nelson et al. 2016:433–434). They are classified here as species of *Percichthyidae*, reflecting the results of several molecular phylogenetic analyses (Near et al. 2013; W.-J. Chen, Lavoué, et al. 2014; Lavoué, Nakayama, et al. 2014; Betancur-R et al. 2017; Ghezelayagh et al. 2022).

The relationships of *Elassoma* (pygmy sunfishes) were a long-standing problem in the systematics and taxonomy of percomorph fishes (Boulenger 1895:34–35; Branson and Moore 1962; G. D. Johnson and Patterson 1993; Jones and Quattro 1999; Near et al. 2012c). The consistent resolution of *Elassoma* and all other centrarchids as sister lineages in molecular phylogenetic analyses (Near et al. 2012c; W.-J. Chen, Lavoué, et al. 2014; Ghezelayagh et al. 2022) motivated the classification of *Elassoma* as a lineage of *Centrarchidae* (Near et al. 2012c:391).

Composition. There are currently 304 species of *Centrarchiformes* (Fricke et al. 2023) that include *Enoplosus armatus*, *Parascorpis typus*, and species classified in *Aplodactylus*, *Caesioscorpis*, *Centrarchidae*, *Cheilodactylus*, *Chironemus*, *Cirrhitidae*, *Dichistius*, *Girellidae*, *Kuhlia*, *Kyphosidae*, *Latridae*, *Microcanthidae*, *Oplegnathus*, *Percalates*, *Percichthyidae*, *Scorpididae*, *Sinipercidae*, and *Terapontidae*. Over the past 10 years, there have been 11 new living species of *Centrarchiformes* described (Fricke et al. 2023), comprising 3.6% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Centrarchiformes*.

Synonyms. There are no synonyms of *Centrarchiformes*.

Comments. The name *Centrarchiformes* was applied to a clade containing *Girellidae*, *Oplegnathus*, *Kuhlia*, *Kyphosidae*, *Terapontidae*, *Percalates*, *Enoplosus*, *Percichthyidae*, *Cheilodactylus*, *Cirrhitidae*, *Sinipercidae*, and *Centrarchidae* resolved in phylogenetic analyses of Sanger-sequenced nuclear genes (Near et al. 2013, fig. S1).

The earliest *Centrarchiformes* fossils include a premaxilla attributed to an undetermined species of *Oplegnathidae* from the Ypresian (56.0–48.1 Ma) of Seymour Island, Antarctica (Cione et al. 1995), and the centrarchid †*Plioplarchus whitei* from the Priabonian (37.7–33.9 Ma) of North Dakota, USA (Cope 1883; Near and Kim 2021). Bayesian relaxed molecular clock analyses of *Centrarchiformes* result in an average posterior crown age estimate of 53.3 million years ago, with the credible interval ranging between 35.7 and 78.1 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

*Aplodactylidae**
*Caesioscorpididae**
Centrarchidae
*Cheilodactylidae**
*Chironemidae**
Cirrhitidae
*Dichistiidae**
*Enoplosidae**
Girellidae
*Kuhliidae**
Kyphosidae
Latridae
Microcanthidae
*Oplegnathidae**
*Parascorpididae**
Percalates
Percichthyidae
Scorpididae
Sinipercidae
Terapontidae

Labriformes P. Bleeker 1862:416
[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Labrus mixtus* Linnaeus 1758, *Labrus bergylta* Ascanius 1767, *Bodianus rufus* (Linnaeus 1758), *Parapercis hexophtalma* (Cuvier in Cuvier and Valenciennes 1829a), *Astroscopus y-graecum* (Cuvier in Cuvier and Valenciennes 1829a), and *Centrogenys vaigiensis* Quoy and Gaimard 1824. This is a minimum-crown-clade definition.

Etymology. Derived from the Latin *labrum* meaning lip. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 978.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S21). Although not included in the reference phylogeny, *Labrus mixtus* is nested in *Labridae* with other species of *Labrus* in a phylogeny resulting from analysis of Sanger-sequenced mitochondrial and nuclear genes (Aiello et al. 2017, fig. S2). Phylogenetic relationships among major lineages of *Labriformes* are presented in Figure 19. The placements of fossils in the phylogeny of *Labriformes* are on the basis of resolutions suggested from morphological inferences for the pan-labrids †*Bellwoodilabrus* (Bannikov and Carnevale 2010) and †*Labrobolcus* (Bannikov and Bellwood 2015).

Phylogenetics. Phylogenomic analysis of UCE loci and analysis of Sanger-sequenced mitochondrial and nuclear genes resolves *Labriformes* as a monophyletic group that contains two major lineages: (1) a clade containing *Uranoscopidae* (stargazers), *Ammodytidae* (sand lances), *Pinguipedidae* (sandperches), *Leptoscopidae* (southern sandfishes), and *Cheimarrichthys fosteri* (Torrentfish) (Figure 19; Betancur-R et al. 2017; Ghezelayagh et al. 2022); and (2) *Labridae* (wrasses and parrotfishes) and *Centrogenys* (false scorpionfishes) (Figure 19; Ghezelayagh et al. 2022; Hughes et al. 2023; Matsunuma and Johnson 2023). Molecular phylogenetic studies are the basis for considerable adjustments to the delimitation of *Labridae*, specifically the inclusion of species formerly classified as *Scaridae* (parrotfishes) and *Odacidae* (cales) (Westneat and Alfaro 2005; Alfaro, Brock, et al. 2009; Cowman et al. 2009; Baliga and Law 2016; Hughes et al. 2023).

Morphological studies place *Cheimarrichthys* as closely related to *Pinguipedidae* or as the sister lineage of all "trachinioids" including *Uranoscopidae*, *Ammodytidae*, *Pinguipedidae*, and *Leptoscopidae* (McDowall 1973; Pietsch 1989; Pietsch and Zabetian 1990). The hypothesis that *Cheimarrichthys* and *Pinguipedidae* share common ancestry was rejected through the discovery that *Cheimarrichthys* shares more derived character states with *Leptoscopidae* than any other "trachinioid" lineage (Imamura and Matsuura 2003). Reflective of the shared common ancestry inferred from morphology and molecular phylogenetic studies (Imamura and Matsuura 2003; Thacker et al. 2015; Ghezelayagh et al. 2022), *Cheimarrichthys* and *Leptoscopidae* have a similar geographic distribution: *Cheimarrichthys* is an anadromous species widely distributed among the rivers of New Zealand, and leptoscopids are distributed along the Pacific and Indian coasts of Australia and New Zealand (McDowall 2000; Last 2001).

Labridae and *Centrogenys vaigiensis* are resolved as sister lineages (Betancur-R et al. 2017; Ghezelayagh et al. 2022; Hughes et al. 2023). The species-rich *Labridae* and the blenniiform lineages *Cichlidae*, *Embiotocidae*, and *Pomacentridae* were hypothesized to be closely related in a clade based on the morphology of the modified "labroid" pharyngeal jaw apparatus (Liem and Greenwood 1981; Kaufman and Liem 1982; Stiassny and Jensen 1987; Springer and Orrell 2004). Previous molecular phylogenetic analyses using Sanger-sequenced nuclear genes demonstrated that the lineages with the modified "labroid" pharyngeal jaw apparatus do not resolve as closely related, but these early molecular studies resulted in an ambiguous and poorly supported resolution of the species-rich *Labridae* (Streelman and Karl 1997; W. L. Smith and Wheeler 2004, 2006; Sparks and Smith 2004a; Mabuchi et al. 2007; Wainwright et al. 2012; Near et al. 2013). The resolution of *Labridae* and *Centrogenys vaigiensis* as sister lineages is interesting as both lineages have all three components of the modified labroid pharyngeal jaw apparatus, a set of traits that has originated multiple times in *Percomorpha* (Wainwright et al. 2012).

Composition. There are currently 887 living species of *Labriformes* (Fricke et al. 2023; Matsunuma and Johnson 2023) that include *Centrogenys*, *Cheimarrichthys fosteri*, and species classified in *Ammodytidae*, *Labridae*, *Leptoscopidae*, *Pinguipedidae*, and *Uranoscopidae*. Fossil lineages of *Labriformes* include the pan-labrids †*Bellwoodilabrus landinii* and †*Labrobolcus giorgioi* from the Ypresian (56.0–48.1 Ma) of Italy (Appendix 2; Bannikov and Carnevale 2010; Bannikov and Bellwood 2015). Over the past 10 years, there have been 77 new living species of *Labriformes* described (Fricke et al. 2023), comprising 8.7% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known morphological apomorphies for *Labriformes*.

Synonyms. There are no synonyms of *Labriformes*.

Comments. *Labriformes* was applied as a name to a polyphyletic group containing *Labridae*, *Embiotocidae*, *Cichlidae*, and *Pomacentridae* (Wiley and Johnson 2010). In a recent classification of ray-finned fishes, *Labriformes* was limited to *Labridae* (Betancur-R et al. 2017). The delimitation of *Labriformes* presented here is consistent with relationships inferred in phylogenomic studies (Ghezelayagh et al. 2022; Hughes et al. 2023).

The earliest fossil *Labriformes* are species classified as *Labridae* or pan-labrids that include †*Bellwoodilabrus landinii* (Bannikov and Carnevale 2010), †*Labrobolcus giorgioi* (Bannikov and Bellwood 2015), †*Eocoris bloti* (Bannikov and Sorbini 1990), †*Phyllopharyngodon longipinnis* (Bellwood 1990), †*Zorzinilabrus furcatus* (Bannikov and Bellwood 2017), and †*Paralabrus rossiae* (Bannikov and Zorzin 2019) from the Ypresian (56.0–48.1 Ma) of Italy. Bayesian relaxed molecular clock analyses of *Labriformes* result in an average posterior crown age estimate of 76.1 million years ago, with the credible interval ranging between 66.2 and 87.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Ammodytidae
*Centrogenyidae**
*Cheimarrichthyidae**
Labridae
Leptoscopidae
Pinguipedidae
Uranoscopidae
†*Bellwoodilabrus*
†*Labrobolcus*

Acropomatiformes M. P. Davis, J. S. Sparks, and W. L. Smith 2016:fig. 1

[C. E. Thacker and T. J. Near],
converted clade name

Definition. The least inclusive crown clade that contains *Acropoma japonicum* Günther 1859, *Pempheris schomburgkii* Müller and Troschel in Schomburgk 1848, *Stereolepis gigas* Ayres 1859, and *Pteropsaron evolans* Jordan and Snyder 1902. This is a minimum-crown-clade definition.

Etymology. Derived from the ancient Greek ἄκρος (ˈækɹoʊ̑z) meaning at the end or at the top and πῶμα (pˈoʊ̑mə) meaning lid or cover. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 979.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S22). Phylogenetic relationships of the major lineages of *Acropomatiformes* are presented in Figure 19. The placements of *Dinolestes lewini*, *Malakichthyidae*, *Schuettea*, and *Synagropidae* in the phylogeny are on the basis of analysis of DNA sequences from nine Sanger-sequenced mtDNA and nuclear genes, and 457 UCE loci (W. L. Smith et al. 2022).

Phylogenetics. *Acropomatiformes* is a lineage resolved entirely as a result of molecular phylogenetic analyses (W. L. Smith and Craig 2007; B. Li et al. 2009; Betancur-R, Broughton, et al. 2013; Near et al. 2013, 2015; Thacker et al. 2015; Davis et al. 2016; Sanciangco et al. 2016; Betancur-R et al. 2017; Mirande 2017;

Ghedotti et al. 2018; Rabosky et al. 2018; Satoh 2018; Oh et al. 2021; Ghezelayagh et al. 2022; W. L. Smith et al. 2022). Phylogenomic studies delimit three major clades of *Acropomatiformes* (Figure 19): (1) *Ostracoberyx* (shellskin alfonsinos), *Acropomatidae* (lanternbellies), *Scombrops* (gnomefishes), *Symphysanodontidae* (slopefishes), *Epigonidae* (deepwater cardinalfishes), and *Howellidae* (oceanic basslets); (2) *Polyprion* (wreckfishes), *Lateolabrax* (Asian seabasses), *Glaucosoma* (pearl perches), and *Pempheridae* (sweepers); and (3) *Stereolepis* (giant seabasses), *Banjos* (banjofishes), *Pentacerotidae* (armorheads), *Dinolestes lewini* (Long-finned Pike), *Malakichthyidae* (temperate seabasses), *Bathyclupeidae* (deepsea herrings), *Synagropidae* (splitfin seabasses), *Champsodon* (gapers), *Schuettea* (moony pomfrets), *Creediidae* (sandburrowers), and *Hemerocoetidae* (signalfishes).

The lineages comprising *Acropomatiformes* were previously classified in the defunct *Trachinoidei* or the historic taxonomic wastebasket *Percoidei* (G. D. Johnson 1984; Imamura and Odani 2013; J. S. Nelson et al. 2016:431–463). Less inclusive groups were classified with distantly related species in Linnean-ranked taxonomic families: *Scombrops* was classified in *Pomatomidae* (Nelson 1994:350–351), *Lateolabrax* was placed in *Percichthyidae* (J. S. Nelson 2006:344), *Hemilutjanus macrophthalmos* was considered a species of *Serranidae* (J. S. Nelson et al. 2016:446–448), and *Schuettea* was long classified in *Monodactylidae* (Regan 1913b; Jordan 1923:205; J. S. Nelson et al. 2016:452–453) despite the recognition of appreciable morphological differences with *Monodactylus* (Tominaga 1968). The traditional delimitation of *Acropomatidae* (J. S. Nelson et al. 2016:434) is not monophyletic (W. L. Smith and Craig 2007; Betancur-R, Broughton, et al. 2013; Near et al. 2013, 2015; Thacker et al. 2015; Davis et al. 2016; Sanciangco et al. 2016; Mirande 2017; Ghedotti et al. 2018; Rabosky et al. 2018; Oh et al. 2021; Ghezelayagh et al. 2022; W. L. Smith et al. 2022), necessitating the elevation of *Malakichthyidae* to include *Hemilutjanus macrophthalmos*, *Malakichthys*, and *Verilus*; *Synagropidae* to include *Caraibops trispinosus*, *Kaperangus microlepis*, *Parascombrops*, and *Synagrops*; and limiting *Acropomatidae* to *Acropoma* and *Doederleinia berycoides* (W. L. Smith et al. 2022).

Composition. There are currently 306 living species of *Acropomatiformes* (Fricke et al. 2023) that include *Dinolestes lewini* and species classified in *Acropomatidae*, *Banjos*, *Bathyclupeidae*, *Champsodon*, *Creediidae, Epigonidae*, *Glaucosoma*, *Hemerocoetidae*, *Howellidae*, *Lateolabrax*, *Malakichthyidae*, *Ostracoberyx*, *Pempheridae*, *Pentacerotidae*, *Polyprion*, *Scombrops*, *Schuettea*, *Synagropidae*, and *Symphysanodontidae* (W. L. Smith et al. 2022). Over the past 10 years, there have been 84 new living species of *Acropomatiformes* described (Fricke et al. 2023), comprising 27.5% of the living species diversity in the clade. Most of these new taxa are species of *Pempheris* (e.g., J. E. Randall and Victor 2015).

Diagnostic apomorphies. There are no known morphological apomorphies for *Acropomatiformes*.

Synonyms. *Pempheriformes* is an ambiguous (Sanciangco et al. 2016, fig. 5; Betancur-R et al. 2017:29) and partial synonym (Betancur-R, Broughton, et al. 2013, app. 2) of *Acropomatiformes*. *Trachiniformes* (J. S. Nelson et al. 2016:421) and Clade R (B. Li et al. 2009:358) are partial synonyms of *Acropomatiformes*.

Comments. Smith et al. (2022:9) provide a discussion and justification for the use of the group name *Acropomatiformes* for this clade.

Relative to other lineages of *Percomorpha*, *Acropomatiformes* includes a large proportion of species that exhibit bioluminescence and occupy deepwater oceanic habitats, traits that seem to have multiple origins in the clade (Davis et al. 2016; Ghedotti et al. 2018; W. L. Smith et al. 2022).

The earliest fossil *Acropomatiformes* are otoliths identified as *Pempheridae* or †*Pempheris huddlestoni* from the Maastrichtian (72.2–66.0 Ma) in the Cretaceous of Maryland, USA (Huddleston and Savoie 1983; Stringer and Schwarzhans 2021), †*Acropoma* sp. from the Selandian (61.7–59.2 Ma) of Denmark (Schwarzhans 2003), and †*Epigonidarum tyassminensis* from the Selandian (61.7–59.2 Ma) to

Thanetian (59.2–56.0 Ma) of Ukraine (Schwarzhans and Bratishko 2011). Bayesian relaxed molecular clock analyses of *Acropomatiformes* result in an average posterior crown age estimate of 46.5 million years ago, with the credible interval ranging between 32.6 and 61.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Acropomatidae
*Banjosidae**
Bathyclupeidae
*Champsodontidae**
Creediidae
*Dinolestidae**
Epigonidae
*Glaucosomatidae**
Hemerocoetidae
Howellidae
*Lateolabracidae**
Malakichthyidae
*Ostracoberycidae**
Pempheridae
Pentacerotidae
*Polyprionidae**
Schuettea
*Scombropidae**
*Stereolepididae**
Symphysanodontidae
Synagropidae

Acanthuriformes D. S. Jordan 1923:207
[T. J. Near and C. E. Thacker],
converted clade name

Definition. The most inclusive crown clade that contains *Acanthurus lineatus* (Linnaeus 1758), but not *Perca fluviatilis* (Linnaeus 1758), *Centrarchus macropterus* (Lacépède 1801), *Labrus mixtus* Linnaeus 1758, and *Acropoma japonicum* Günther 1859. This is a maximum-crown-clade definition.

Etymology. From the ancient Greek ἄκανθα (ɐkˈænθə) meaning thorn or spine. The suffix is from the Latin *forma* meaning form, figure, or appearance.

Registration number. 980.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, figs. S22–S25). Although *Centrarchus macropterus* is not included in the reference phylogeny, the species resolves with other species of *Centrarchidae* in phylogenetic analyses of DNA sequences of Sanger-sequenced mitochondrial and nuclear genes (Near, Bolnick, et al. 2004, fig. 1; Near and Kim 2021, fig. 2A), and *Labrus mixtus* is nested in *Labridae* with other species of *Labrus* in a phylogeny resulting from analysis of Sanger-sequenced mitochondrial and nuclear genes (Aiello et al. 2017, fig. S2). The phylogenetic relationships of the major living lineages and fossil taxa of *Acanthuriformes* are presented in Figure 20. The placements of †*Eoscatophagus*, †*Oligoscatophagus*, †*Ruffoichthys*, †*Eosiganus*, †*Siganopygaeus*, †*Protosiganus*, and †*Caprosimilis* in the phylogeny are on the basis of analyses of morphological characters (Tyler and Bannikov 1997; Tyler and Sorbini 1999; Bannikov and Tyler 2001; Bieńkowska-Wasiluk and Bonde 2015; Siqueira et al. 2019).

Phylogenetics. *Acanthuriformes* as delimited here is resolved as a monophyletic group in phylogenomic analyses of UCE loci (Ghezelayagh et al. 2022). Other phylogenomic analyses and analyses of DNA sequences from Sanger-sequenced mtDNA and nuclear genes place *Gerreidae* (mojarras) outside of *Acanthuriformes* in variable resolutions that include: as the sister lineage of an inclusive clade that contains all sampled *Acanthuriformes* and *Labriformes* (W.-J. Chen et al. 2003), the sister lineage of *Labridae* (Wainwright et al. 2012; Mu et al. 2022); a deeply branching lineage among *Labriformes*, *Centrarchiformes*, *Perciformes*, and *Acanthuriformes* (Near et al. 2013; Betancur-R et al. 2017); the sister lineage of a clade containing *Centrogenys* and *Labridae* (Smith et al. 2016); or as the sister lineage of *Labriformes* with (Hughes et al. 2018, 2023) and without *Labridae* (Rabosky et al. 2018).

The discovery that *Acanthuriformes* is a monophyletic group including more than 2,365 species classified into 59 taxonomic families in rank-based classifications is an important advance in the systematics of percomorph fishes, adding clarity to the relationships of several lineages that long evaded phylogenetic resolution. *Moronidae* (temperate basses) were traditionally classified in the catchall "percoid" taxonomic wastebasket (e.g., G. D. Johnson 1984); however, molecular phylogenies resolved *Moronidae* as a deeply nested lineage within *Acanthuriformes* (Wainwright et al. 2012; Near et al. 2013; Smith et al. 2016; Hughes et al. 2018) or in a clade with

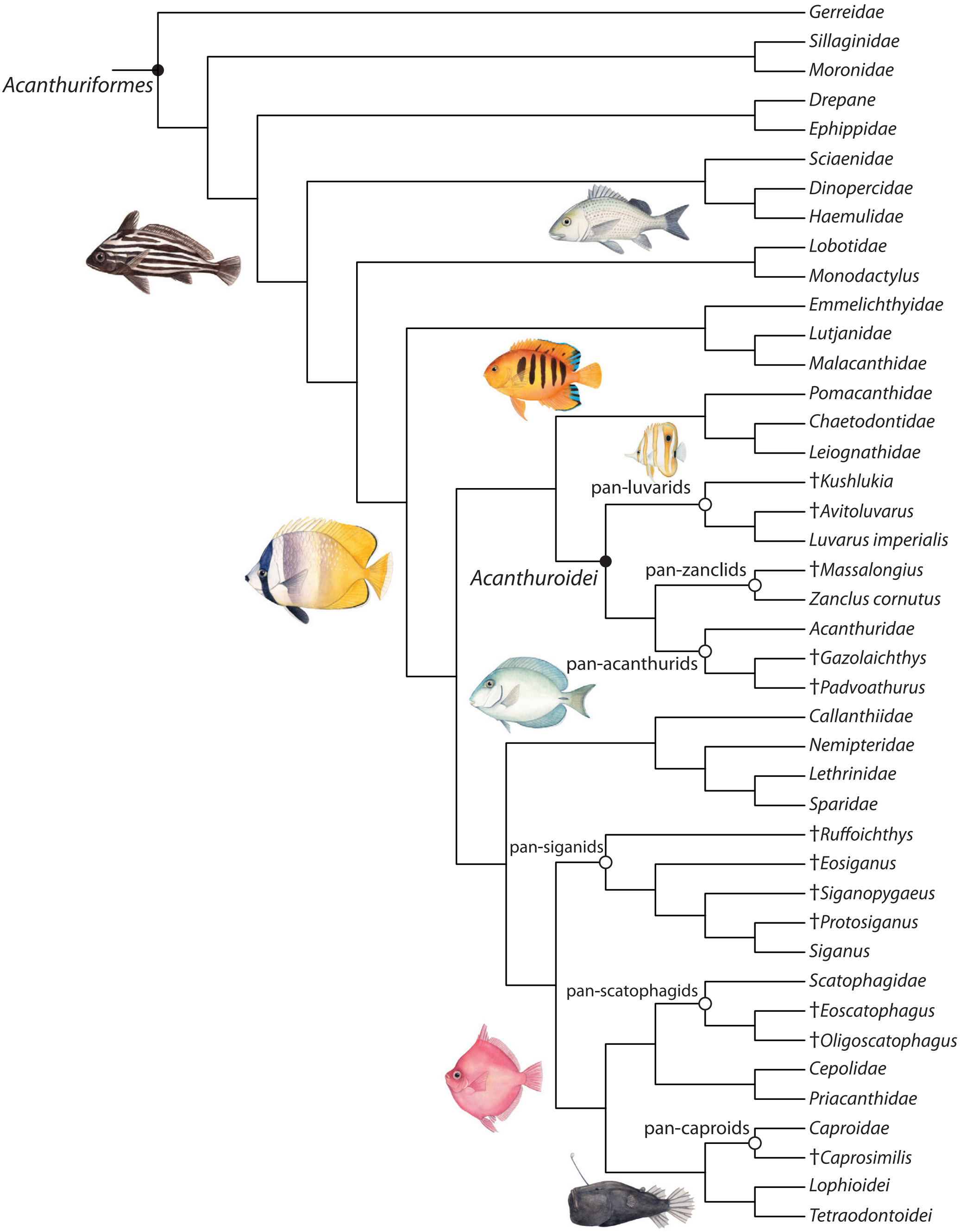

FIGURE 20. Phylogenetic relationships of the major living lineages and fossil taxa of *Acanthuriformes* and *Acanthuroidei*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

Sillaginidae (whitings) as the sister lineage of all other *Acanthuriformes* (Figure 20; Betancur-R et al. 2017; Ghezelayagh et al. 2022).

Lineages of *Acanthuriformes* were among those that comprised *Squamipinnes*, which are characterized by scales on the bases of the second dorsal and anal fins and are among the earliest proposed inclusive groups of percomorphs (Cuvier 1816; Matsubara 1955; Mok and Shen 1983). Hypotheses for the composition of *Squamipinnes* in the 20th century ranged from inclusion of lineages of *Carangiformes* (*Toxotidae*), *Acropomatiformes* (*Pentacerotidae*), and *Centrarchiformes* (*Scorpididae*) (Mok and Shen 1983) to a delimitation that included only lineages of *Acanthuriformes*: *Acanthuroidei*, *Caproidae* (boarfishes), *Chaetodontidae* (butterflyfishes), *Drepane* (sicklefishes), *Ephippidae* (spadefishes), *Pomacanthidae* (angelfishes), and *Scatophagidae* (scats) (Blum 1988; Tyler et al. 1989; Rosen and Patterson 1990). Morphological studies identified synapomorphies supporting the monophyly of a lineage containing *Acanthuroidei*, *Chaetodontidae*, *Ephippidae*, *Pomacanthidae*, *Scatophagidae*, and *Siganus* (rabbitfishes) (Tyler et al. 1989); however, molecular phylogenetic analyses of *Percomorpha* consistently fail to resolve lineages traditionally classified in *Squamipinnes* as a monophyletic group (Holcroft and Wiley 2008; Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022). A phylogeny inferred from morphology limited *Acanthuriformes* to *Acanthuroidei*, *Caproidae*, *Siganus*, *Scatophagidae*, *Leiognathidae* (ponyfishes), *Ephippidae*, *Chaetodontidae*, *Drepane*, *Pomacanthidae*, and *Lobotidae* (tripletails and barbled grunters: *Datnioides*, *Hapalogenys*, and *Lobotes*) (A. C. Gill and Leis 2019). A delimitation of *Acanthuriformes* that excludes *Lophioidei* and *Tetraodontoidei* is not resolved in molecular phylogenetic analyses (e.g., Miya et al. 2005; Holcroft and Wiley 2008; Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022; Mu et al. 2022).

Chaetodontidae and *Pomacanthidae* were long considered as closely related, which was reflected in classifications that treated pomacanthids as a subfamily of *Chaetodontidae* (Berg 1940:245–246; Greenwood et al. 1966; J. S. Nelson 1976). Other investigators noted differences between the two lineages, leading to their classification as two separate Linnaean-ranked taxonomic families (J. B. L. Smith 1955b; Burgess 1974; J. S. Nelson et al. 2016:454–456). Morphological phylogenetic analyses resolve *Chaetodontidae* and *Pomacanthidae* as sister lineages (Mok and Shen 1983; Blum 1988; Tyler et al. 1989); however, the two lineages do not resolve as a monophyletic group in molecular phylogenies (Bellwood et al. 2004; Fessler and Westneat 2007; Wainwright et al. 2012; Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022). Molecular phylogenetic analyses resolve *Chaetodontidae* and *Leiognathidae* as sister lineages (Wainwright et al. 2012; Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022). *Pomacanthidae* is resolved as a deeply nested lineage among *Acanthuriformes* with poor node support (Betancur-R, Broughton, et al. 2013; Near et al. 2013; Rabosky et al. 2018), as the sister lineage of the clade containing *Chaetodontidae* and *Leiognathidae* (Smith et al. 2016; Ghezelayagh et al. 2022), or as the sister lineage of *Scatophagidae* (Bellwood et al. 2004; Fessler and Westneat 2007).

Prephylogenetic systematic studies identified two "percoid" lineages (G. D. Johnson 1980), *Lutjanidae* (snappers) and *Caesionidae* (fusiliers), and the sparoids that includes *Sparidae* (porgies), *Nemipteridae* (threadfin breams), and *Lethrinidae* (emperors) that were each resolved as acanthuriform clades in molecular phylogenies (Near et al. 2013; Sanciangco et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022). *Callanthiidae* (splendid perches) is resolved as the sister lineage of the sparoids (Figure 20; Ghezelayagh et al. 2022). Phylogenies inferred from Sanger-sequenced mtDNA and nuclear genes resolve *Haemulidae* (grunts) as the sister lineage of a clade containing *Lutjanidae* and *Caesionidae* with low node support (Wainwright et al. 2012; Near et al. 2013; Betancur-R et al. 2017; Rabosky et al. 2018); however, this clade is not resolved in phylogenomic analyses (Hughes et al. 2018; Ghezelayagh et al. 2022). Phylogenomic analysis of UCE loci resolves *Haemulidae* and *Dinopercidae* (cavebasses) as sister lineages (Figure 20; Ghezelayagh et al. 2022). In contrast, a survey of morphological features associated with the skull and caudal skeleton identified the acropomatiform *Glaucosoma* and the perciform *Serranidae* (*sensu lato*) as the possible relatives of *Dinopercidae* (Heemstra and Hecht 1986). Molecular phylogenies support the monophyly of *Dinopercidae* (W. L. Smith and Craig 2007).

One of the most surprising findings from molecular studies of teleost phylogeny is the resolution of *Lophioidei* (anglerfishes, formerly *Lophiiformes*) and *Tetraodontoidei* (puffers and molas, formerly *Tetraodontiformes*) as sister lineages within *Acanthuriformes* (Miya et al. 2003, 2005; Yamanoue et al. 2007; Holcroft and Wiley 2008; Yagishita et al. 2009; Near, Eytan, et al. 2012; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Smith et al. 2016; Alfaro et al. 2018; Hughes et al. 2018; Ghezelayagh et al. 2022; Mu et al. 2022). In morphology-based classifications, the lophioids were placed in *Paracanthopterygii* (Patterson and Rosen 1989; J. S. Nelson 2006:250–260), phylogenetically distantly related to other lineages of *Percomorpha*. The migration of *Lophioidei* as paracanthopterygians into a derived clade of percomorphs is among the most significant changes in 21st-century vertebrate phylogenetics (Dornburg and Near 2021), akin to moving a morphologically placed lineage from within marsupials to the sister lineage of primates. While the discovery that *Lophioidei* and *Tetraodontoidei* are closely related is on the basis of phylogenetic analysis of molecular data, subsequent investigation of morphology identifies shared traits in the lateral line system (Nakae and Sasaki 2010), several soft tissue characters that are likely synapomorphies of a lophioid-tetraodontoid clade (Chanet et al. 2013), and unique morphology and pigmentation in larvae shared by lophioids and tetraodontoids (Baldwin 2013). Other traits thought to be unique to both lophioids and tetraodontoids may turn out to be morphological synapomorphies for this clade, including: absence of anal-fin spines (Pietsch 1981, 1984; Tyler and Sorbini 1996), absence of ribs (Pietsch 1981; Tyler and Sorbini 1996), reduced number of caudal-fin rays (Pietsch 1981, 1984; Tyler and Sorbini 1996), reduced number of vertebrae (Pietsch 1984; Tyler and Sorbini 1996), and a restricted opercular opening (Pietsch 1981; Tyler and Sorbini 1996).

Molecular phylogenetic analyses resolve an inclusive clade within *Acanthuriformes* that contains *Siganus*, *Scatophagidae*, *Priacanthidae* (bigeyes), *Cepolidae* (bandfishes), *Caproidae*, *Lophioidei*, and *Tetraodontoidei* (Near et al. 2013; Smith et al. 2016; Betancur-R et al. 2017; Ghezelayagh et al. 2022). A close relationship between *Caproidae* and *Tetraodontoidei* was proposed on the basis of analysis of morphology (Zehren 1987).

Composition. There are currently 2,376 living species of *Acanthuriformes* (Allen 1985; Carpenter 1988; Carpenter and Allen 1989; B. C. Russell 1990; McKay 1992, 1997; Fricke et al. 2023) classified in *Acanthuroidei*, *Callanthiidae*, *Caproidae*, *Cepolidae*, *Chaetodontidae*, *Dinopercidae*, *Drepane*, *Emmelichthyidae* (rovers), *Ephippidae*, *Gerreidae*, *Haemulidae*, *Leiognathidae*, *Lethrinidae*, *Lobotidae*, *Lophioidei*, *Lutjanidae*, *Malacanthidae* (tilefishes), *Monodactylus* (moonfishes), *Moronidae*, *Nemipteridae*, *Pomacanthidae*, *Priacanthidae*, *Scatophagidae*, *Sciaenidae* (drums), *Siganus*, *Sillaginidae*, *Sparidae*, and *Tetraodontoidei*. Fossil lineages of *Acanthuriformes* include the pan-scatophagids †*Eoscatophagus* and †*Oligoscatophagus* (Tyler and Sorbini 1999); the pan-siganids †*Ruffoichthys*, †*Eosiganus*, †*Siganopygaeus*, and †*Protosiganus* (Tyler and Bannikov 1997); the pan-caproid †*Caprosimilis* (Bieńkowska-Wasiluk and Bonde 2015); and several taxa in *Lophioidei* and *Tetraodontoidei*. Details of the ages and locations of the fossil taxa are presented in Appendix 1. Over the past 10 years, 141 new living species of *Acanthuriformes* have been described (Fricke et al. 2023), comprising 5.9% of the living species diversity in the clade.

Diagnostic apomorphies. There are no known synapomorphies for *Acanthuriformes*. The presence of posterolateral tooth replacement was hypothesized as a synapomorphy for a delimitation of *Acanthuriformes* limited to *Acanthuroidei*, *Caproidae*, *Siganus*, *Scatophagidae*, *Leiognathidae*, *Ephippidae*, *Chaetodontidae*, *Drepane*, *Pomacanthidae*, and *Lobotidae* (A. C. Gill and Leis 2019).

Synonyms. There are no synonyms of *Acanthuriformes*.

Comments. The first use of *Acanthuriformes* in post-Hennigian systematics was as the name for a group containing *Siganus*, *Luvarus*, *Zanclus*, and *Acanthuridae* (Wiley et al. 2000), which is a synonym of *Acanthuroidei* (Tyler et al. 1989). The delimitation of *Acanthuriformes* presented here follows on Davis et al. (2016), but we include *Gerreidae*.

The monophyly of the major lineages of *Percomorpha* delimited in this classification was discovered primarily as a result of molecular phylogenetic analyses (Dornburg and Near 2021). The earliest molecular phylogenetic studies of *Percomorpha* revealed the challenge of resolving relationships among *Perciformes*, *Centrarchiformes*, *Acropomatiformes*, and what Davis et al. (2016) first delimited as *Acanthuriformes* (Miya et al. 2005; Dettaï and Lecointre 2008; B. Li et al. 2009; Chanet et al. 2013; Near et al. 2013). The limits of the phylogenetic resolution offered in the first wave of molecular studies was particularly acute for the lineages classified as *Acanthuriformes*; however, the application of phylogenomic methods provide an important incremental step toward a strongly supported hypothesis and an inclusive classification. As the result of phylogenomic analyses, 10 of 11 lineages classified by Betancur-R et al. (2017) as *incertae sedis* in *Eupercaria* find resolution in *Acanthuriformes* (Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil *Acanthuriformes* include several lineages of pan-scatophagids and pan-siganids from the Ypresian (56.0–48.1 Ma). Details on the phylogenetic placement and location of these fossil species are given in Appendix 1. Bayesian relaxed molecular clock analyses of *Acanthuriformes* result in an average posterior crown age estimate of 78.5 million years ago, with the credible interval ranging between 72.0 and 86.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Acanthuroidei
Callanthiidae
Caproidae
Cepolidae
Chaetodontidae
Dinopercidae
*Drepaneidae**
Emmelichthyidae
Ephippidae
Gerreidae
Haemulidae
Leiognathidae
Lethrinidae
Lobotidae
Lophioidei
Lutjanidae
Malacanthidae
*Monodactylidae**
Moronidae
Nemipteridae
Pomacanthidae
Priacanthidae
Scatophagidae
Sciaenidae
*Siganidae**
Sillaginidae
Sparidae
Tetraodontoidei
†*Caprosimilis*
†*Eoscatophagus*
†*Eosiganus*
†*Oligoscatophagus*
†*Protosiganus*
†*Ruffoichthys*
†*Siganopygaeus*

Acanthuroidei P. Bleeker 1859:xxii

[T. J. Near and C. E. Thacker],
converted clade name

Definition. The least inclusive crown clade containing *Paracanthurus hepatus* (Linnaeus 1766), *Acanthurus lineatus* (Linnaeus 1758), *Zanclus cornutus* (Linnaeus 1758), and *Luvarus imperialis* Rafinesque 1810a. This is a minimum-crown-clade definition.

Etymology. From the ancient Greek ἄκανθα (ɐkˈænθə) meaning thorn or spine.

Registration number. 981.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element loci (Ghezelayagh et al. 2022, fig. S23). Phylogenetic relationships of the major living lineages and fossil taxa of *Acanthuroidei* are presented in Figure 20. The placements of pan-luvarids †*Avitoluvarus* and †*Kushlukia*, the pan-acanthurids †*Padovathurus* and †*Gazolaichthys*, and the pan-zanclid †*Massalongius* in the phylogeny are on the basis of inferences from morphological characters (Tyler 2005a, 2005b; Tyler and Bannikov 2005; Siqueira et al. 2019).

Phylogenetics. *Acanthuroidei* was traditionally delimited as including *Acanthuridae* (surgeonfishes), *Zanclus cornutus* (Moorish Idol), and *Siganus* (rabbitfishes) (Greenwood et al. 1966; Gosline 1968, 1971:158; Mok and Shen 1983). Morphological phylogenetic studies resulted in an expansion of *Acanthuroidei* to include *Luvarus imperialis* (Louvar), *Ephippidae* (spadefishes), and *Scatophagidae* (scats) (Tyler et al. 1989; Winterbottom 1993a; Winterbottom and McLennan 1993). Analysis of larval morphology grouped *Zanclus* and *Acanthuridae* as sister lineages (G. D. Johnson and Washington 1987), a relationship resolved in both morphological and molecular phylogenetic analyses (Tyler et al. 1989; Winterbottom 1993a; K. L. Tang et al. 1999; Holcroft and Wiley 2008; Near et al. 2013; Betancur-R et al. 2017; A. C. Gill and Leis 2019; Ghezelayagh et al. 2022). Molecular phylogenetic analyses are consistent with a delimitation of *Acanthuroidei* that includes *Luvarus*, *Zanclus*, and *Acanthuridae*; *Siganus*, *Ephippidae*, and *Scatophagidae* are more closely related to other lineages of *Acanthuriformes* (Figure 20; Holcroft and Wiley 2008; Near et al. 2013; Z. Liu et al. 2016; J. S. Nelson et al. 2016:499–500; Betancur-R et al. 2017; Ghezelayagh et al. 2022).

Composition. There are currently 87 living species of *Acanthuroidei* (Fricke et al. 2023) that include *Luvarus imperialis*, *Zanclus cornutus*, and species classified in *Acanthuridae*. Fossil taxa of *Acanthuroidei* include the pan-acanthurids †*Padovathurus* and †*Gazolaichthys* (Tyler 2005a, 2005b), and the pan-zanclid †*Massalongius* (Tyler and Bannikov 2005). Details of the phylogenetic placement and location of these fossil species are given in Appendix 1. Over the past 10 years, there has been one new living species of *Acanthuroidei* described (Fricke et al. 2023), comprising 1.1% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Acanthuroidei* include (1) presence of 9 precaudal vertebrae and 13 caudal vertebrae (Tyler et al. 1989; Winterbottom 1993a; Tyler and Sorbini 1999), (2) first dorsal pterygiophore fully inserts in the space of the first interneural and its tip extends into the dorsal area of the foramen magnum (Tyler et al. 1989; Winterbottom 1993a; Tyler and Sorbini 1999; Tyler and Bannikov 2005), (3) infraorbital series changes direction anteriorly below the lateral ethmoid, continuing along the side of the snout (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (4) palatine is forward of the lateral ethmoid and there is no articulation between the two bones (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (5) absence of the spinna occipitalis, specifically the epiotics contact along the posterior midline of the neurocranium, separating the supraoccipital from the exoccipitals and foramen magnum (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (6) presence of small spicules laterally along most or all of the length of the soft rays of the dorsal, anal, caudal, pectoral, and pelvic fins (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (7) scales of adults are circular to ovoid plates with upright spicules projecting from their surface (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (8) presence of a single postcleithrum in adults (Tyler et al. 1989; Winterbottom 1993a; Tyler and Bannikov 2005), (9) extremely compressed and kite-shaped body (Tyler et al. 1989; Winterbottom 1993a), (10) dome-shaped midbrain that is deeper than it is long, housed in an elongate cranial cavity (Tyler et al. 1989; Winterbottom 1993a), (11) early forming scales bear lamina that project upright from basal plane (Tyler et al. 1989; Winterbottom 1993a), (12) presence of spines on the ascending process of the premaxilla (Tyler et al. 1989; Winterbottom 1993a), (13) lateral surface of lachrymal with two or three serrate ridges (Tyler et al. 1989; Winterbottom 1993a), (14) dentary with two serrate longitudinal ridges (Tyler et al. 1989; Winterbottom 1993a), (15) presence of a locking mechanism for the elongate second or third dorsal spine (Tyler et al. 1989; Winterbottom 1993a), and (16) absence of insertion of abductor superficialis pelvicus on the pelvic spine (Winterbottom 1993a).

Synonyms. *Acanthuriformes* (Betancur-R et al. 2017:27) is an ambiguous synonym of *Acanthuroidei*.

Comments. *Acanthuroidei* is used as a group as delimited here in recent studies (Dornburg and Near 2021; Ghezelayagh et al. 2022).

The earliest fossil taxa of *Acanthuroidei* include several lineages from the Ypresian (56.0–48.1 Ma) that include the pan-luvarids †*Avitoluvarus* and †*Kushlukia* (Bannikov and Tyler 1995), the pan-acanthurids

†*Padovathurus* and †*Gazolaichthys* (Tyler 2005a, 2005b), and the pan-zanclid †*Massalongius* (Tyler and Bannikov 2005). Bayesian relaxed molecular clock analyses of *Acanthuroidei* result in an average posterior crown age estimate of 59.1 million years ago, with the credible interval ranging between 56.3 and 63.0 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Acanthuridae
*Luvaridae**
*Zanclidae**
†*Avitoluvarus*
†*Gazolaichthys*
†*Kushlukia*
†*Massalongius*
†*Padovathurus*

Lophioidei P. Bleeker 1859:xvi

Definition. The least inclusive crown clade that contains *Lophius piscatorius* Linnaeus 1758, *Lophius gastrophysus* Miranda Ribeiro 1915, *Ogcocephalus radiatus* (Mitchill 1818b), and *Cryptopsaras couesii* T. N. Gill 1883. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek λόφος (lˈo͡ʊfo͡ʊz) meaning the back of the neck or the crest of a helmet.

Reference phylogeny. A phylogeny inferred from sequences of 989 ultraconserved element (UCE) loci (Ghezelayagh et al. 2022, fig. S25). Although *Lophius piscatorius* is not in the reference phylogeny, the species resolves with other species of *Lophius* in phylogenetic analyses of morphology and mtDNA (Leslie and Grant 1994, fig. 4; Landi et al. 2014, fig. S1). Phylogenetic relationships of the major living lineages and fossil taxa of *Lophioidei* are presented in Figure 21. The placements of the fossil taxa †*Sharfia* and †*Tarkus* in the phylogeny are on the basis of inferences from morphological characters (Carnevale and Pietsch 2011, 2012).

Phylogenetics. The delimitation of *Lophioidei* presented here is similar or identical to several pre-Hennigian classifications (Jordan and Sindo 1902; Regan 1912c; Jordan 1923:242–243; Berg 1940:498–500; Greenwood et al. 1966; McAllister 1968; Gosline 1971:173–174). By the early 20th century, species of *Lophioidei* were classified into three main lineages (Regan 1912c): (1) *Lophiidae* (goosefishes); (2) the antennarioids that included *Antennariidae* (frogfishes), *Tetrabrachiidae* (four-armed frogfishes), *Brachionichthyidae* (handfishes), *Chaunacidae* (coffinfishes), *Ogcocephalidae* (batfishes), and *Lophichthys boschmai* (Boschma's Frogfish) (Boeseman 1964; Pietsch 1981, 1984); and (3) the ceratioids that included *Centrophryne spinulosa* (Horned Lanternfish), *Neoceratias spinifer* (Spiny Seadevil), *Caulophrynidae* (fanfins), *Ceratiidae* (warty seadevils), *Diceratiidae* (double anglers), *Gigantactinidae* (whipnose anglers), *Himantolophus* (footballfishes), *Linophrynidae* (leftvents), *Melanocetus* (black seadevils), *Oneirodidae* (dreamers), and *Thaumatichthyidae* (wolftrap anglers).

The first phylogenetic analyses of *Lophioidei* utilized morphological characters to test the monophyly of Regan's (1912c) delimitation of the antennarioids (Pietsch 1981, 1984). In the morphological phylogeny *Lophiidae* is resolved as the sister lineage of all other *Lophioidei*, which consists of two major clades: a modified antennarioid group that includes *Antennariidae*, *Tetrabrachiidae*, *Lophichthys*, and *Brachionichthyidae*, and a lineage comprising *Chaunacidae* that is the sister lineage of a clade containing *Ogcocephalidae* and the ceratioids (Pietsch 1984). Subsequent morphological phylogenetic analyses were aimed at resolving relationships among ceratioids and resulted in differing topologies and degrees of resolution resulting from the separate phylogenetic analyses of characters scored from metamorphosed females, metamorphosed males, and larvae (Pietsch and Orr 2007; Pietsch 2009, fig. 203), characters scored only from metamorphosed females (Pietsch 2009, fig. 202), and characters scored from metamorphosed females with the exclusion of characters that show reductive or simplified states (Miya et al. 2010). Congruence across these morphological phylogenetic analyses includes support for the monophyly of the ceratioids, the resolution of *Centrophryne* and *Ceratiidae* as a clade that is the sister lineage to all other ceratioids, and the resolution of *Neoceratias* and *Gigantactinidae* as sister lineages (Pietsch and Orr 2007; Pietsch 2009; Miya et al. 2010).

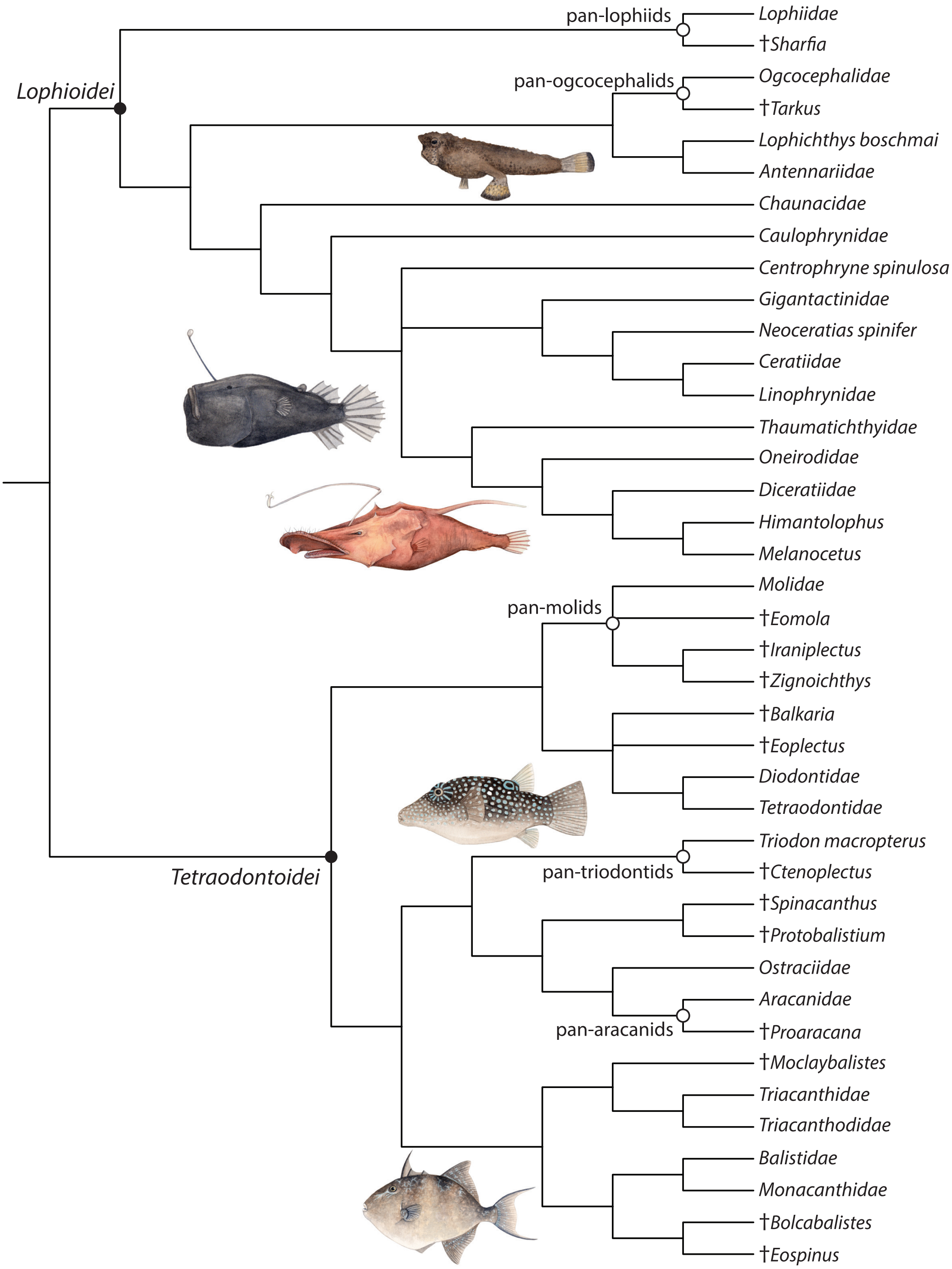

FIGURE 21. Phylogenetic relationships of the major living lineages and fossil taxa of *Lophioidei* and *Tetraodontoidei*. Filled circles identify the common ancestor of clades with formal names defined in the clade accounts. Open circles highlight clades with informal group names. Fossil lineages are indicated with a dagger (†). Details of the fossil taxa are presented in Appendix 1.

Molecular phylogenetic studies of *Lophioidei* include analyses of datasets of mtDNA (Shedlock et al. 2004; Miya et al. 2010; Poulsen 2019), nuclear genes (Near et al. 2013; Arnold 2014), combinations of mtDNA and nuclear genes (Lundsten et al. 2012; Arnold 2014; Derouen et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018), and phylogenomic datasets of UCE loci (Ghezelayagh et al. 2022; Hart et al. 2022). Consistent results across molecular studies include the placement of *Lophiidae* as the sister lineage of all other *Lophioidei* (Figure 21; Miya et al. 2010; Near et al. 2013; Arnold 2014; Derouen et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018; Poulsen 2019; Ghezelayagh et al. 2022; Hart et al. 2022), resolution of *Chaunacidae* and the ceratioids as sister lineages (Figure 21; Shedlock et al. 2004; Miya et al. 2010; Lundsten et al. 2012; Near et al. 2013; Arnold 2014; Derouen et al. 2015; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022; Hart et al. 2022), resolution of a clade containing *Ogcocephalidae*, *Antennariidae*, *Brachionichthyidae*, and *Tetrabrachiidae* (Lundsten et al. 2012; Arnold 2014; Ghezelayagh et al. 2022; Hart et al. 2022), *Caulophrynidae* placed as the sister lineage to all other ceratioids (Figure 21; Miya et al. 2010; Ghezelayagh et al. 2022), and the resolution of *Oneirodidae*, *Himantolophus*, *Diceratiidae*, and *Melanocetus* as a monophyletic group within the ceratioids (Figure 21; Shedlock et al. 2004; Miya et al. 2010; Lundsten et al. 2012; Arnold 2014; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022; Hart et al. 2022).

Within the ceratioids, phylogenomic analysis of UCE loci resolves *Neoceratias spinifer*, *Linophrynidae*, and *Ceratiidae* as a monophyletic group (Figure 21; Ghezelayagh et al. 2022). These three lineages all exhibit male obligate sexual parasitism and dramatically altered immunity through loss of the capacity for somatic diversification of antigen receptor genes (Regan 1925; Pietsch 2005; Swann et al. 2020). All previous morphological and molecular phylogenetic analyses of ceratioids result in nonmonophyly of the lineages exhibiting obligate male sexual parasitism, implying multiple origins of this reproductive mode (Pietsch and Orr 2007; Pietsch 2009; Miya et al. 2010; Lundsten et al. 2012; Arnold 2014; Swann et al. 2020; Hart et al. 2022). The phylogeny of *Lophioidei* shown in Figure 21 implies a single evolutionary origin of this unique trait.

Two molecular phylogenetic analyses with dense taxon sampling resolve *Tetrabrachiidae* and *Brachionichthyidae* nested within a paraphyletic *Antennariidae* (Arnold 2014; Hart et al. 2022). One proposed solution is to classify the lineages that comprise *Tetrabrachiidae* and *Brachionichthyidae* in *Antennariidae* (Arnold 2014:70–71). An alternative response to the paraphyly of *Antennariidae* is the description of three new Linnaean-ranked taxonomic families: *Histiophrynidae*, *Rhycheridae*, and *Tathicarpidae* (Hart et al. 2022).

Composition. There are currently 408 living species of *Lophioidei* (Fricke et al. 2023) that include *Centrophryne spinulosa*, *Lophichthys boschmai*, *Neoceratias spinifer*, and species classified in *Antennariidae*, *Caulophrynidae*, *Ceratiidae*, *Diceratiidae*, *Gigantactinidae*, *Himantolophus*, *Linophrynidae*, *Melanocetus*, *Oneirodidae*, and *Thaumatichthyidae*. Fossil lophioid taxa include the pan-lophiid †*Sharfia* (Pietsch and Carnevale 2011) and the pan-ogcocephalid †*Tarkus* (Carnevale and Pietsch 2011). Details of the phylogenetic placement and location of these fossil species are given in Appendix 1. Over the past 10 years, 43 new living species of *Lophioidei* have been described (Fricke et al. 2023), comprising 10.5% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies for *Lophioidei* include (1) eggs spawned in a double scroll-shaped sheath (Rasquin 1958; Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:269; Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:371), (2) a single hypural plate formed by fusion of the second ural centrum with first preural centra that emanates from a single half centrum (Rosen and Patterson 1969; Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:269; Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:371), (3) spinous dorsal fin modified as a luring apparatus (Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:268;

Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:369), (4) epiotics separated from parietals and meet on the midline posterior of the supraoccipital (Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:268; Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:369), (5) gill openings restricted to a small and elongate tubelike opening positioned near the base of the pectoral fin (Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:268–269; Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:371), (6) pectoral radials elongate and narrow, ventralmost radial expanded distally (Pietsch 1981, 1984, 2009:177; Pietsch and Grobecker 1987:269; Carnevale and Pietsch 2009, 2011; Wiley and Johnson 2010; Pietsch and Arnold 2020:371), (7) pterygiophores of the spinous dorsal fin develop from a single condensation of tissue that later divides into separate pterygiophores (Everly 2002), (8) the first pterygiophore supports both the first and second dorsal-fin spines (Everly 2002), and (9) urohyal absent, rectus communis muscle originating from the dorsal hypohyal (Datovo et al. 2014; Pietsch and Arnold 2020:371).

Synonyms. *Pediculati* (Günther 1861:178–205; T. N. Gill 1872:2; Boulenger 1904a:188–189, 1904b:717–720; Goodrich 1909:461–462; Jordan 1923:242–243; Regan 1929:326–327) and *Lophiiformes* (Regan 1926:3; Berg 1940:498–500; Greenwood et al. 1966:397; McAllister 1968:159–163; J. S. Nelson et al. 2016:508–518; Betancur-R et al. 2017:28) are ambiguous synonyms of *Lophioidei*.

Comments. More than 27% of the recognized taxonomic families in Linnaean-based classifications of *Percomorpha* contain only a single genus or a single species (J. S. Nelson et al. 2016; Fricke et al. 2023). The description of most of these monotypic and monogeneric lineages dates to a time before the introduction of phylogenetic systematics or the application of molecular data to the resolution of relationships among fishes (G. D. Johnson 1984, 1993). The description of the taxonomic families *Rhycheridae* and *Tathicarpidae* in 2022 to classify three species does not contribute to a classification of *Lophioidei* that reflects phylogeny but is anachronistic and only adds redundant group names. We follow the proposal presented by Arnold (2014) to classify the lineages traditionally placed in *Brachionichthyidae* (14 species) and *Tetrabrachiidae* (2 species) in *Antennariidae*, and treat *Histiophrynidae* (17 species), *Rhycheridae* (2 species), and *Tathicarpidae* (1 species) (Hart et al. 2022) as partial synonyms of *Antennariidae* (68 species).

The oldest lophioid fossils date to the Ypresian (56.0–48.1 Ma) of Italy and include the pan-lophiid †*Sharfia* (Pietsch and Carnevale 2011), the pan-ogcocephalid †*Tarkus* (Carnevale and Pietsch 2011), and the antennariids †*Eophryne*, †*Histionotophorus*, †*Orrichthys*, and †*Neilpeartia* (Carnevale and Pietsch 2009, 2010; Carnevale et al. 2020). Bayesian relaxed molecular clock analyses of *Lophioidei* result in an average posterior crown age estimate of 59.4 million years ago, with the credible interval ranging between 55.3 and 63.6 million years ago (Ghezelayagh et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Antennariidae
Caulophrynidae
*Centrophrynidae**
Ceratiidae
Chaunacidae
Diceratiidae
Gigantactinidae
*Himantolophidae**
Linophrynidae
*Lophichthyidae**
Lophiidae
*Melanocetidae**
*Neoceratiidae**
Ogcocephalidae
Oneirodidae
Thaumatichthyidae
†*Sharfia*
†*Tarkus*

Tetraodontoidei P. Bleeker 1866:19

Definition. The least inclusive crown clade that contains *Tetraodon lineatus* Linnaeus 1758, *Mola mola* (Linnaeus 1758), *Takifugu rubripes* (Temminck and Schlegel 1850), *Ostracion cubicus* Linnaeus 1758, and *Balistes vetula* Linnaeus 1758. This is a minimum-crown-clade definition, but the clade is not defined using the *PhyloCode*.

Etymology. From the ancient Greek τετρᾰ- (tˈɛtɹə) meaning four in compound words and ὀδούς (hˈo͡ʊduːz) meaning tooth.

Reference phylogeny. A phylogeny inferred from DNA sequences of 1,103 exons (Troyer et al. 2022, fig. S2). Although *Tetraodon lineatus* is not included in the reference phylogeny, the species resolves with other species of *Tetraodontidae* in phylogenetic analysis of Sanger-sequenced mitochondrial and nuclear genes (Santini, Nguyen, et al. 2013, fig. 1; Mar'ie and Allam 2019, figs. 1, 4). Phylogenetic relationships of the major lineages of *Tetraodontoidei* are presented in Figure 21. The placements of the fossil taxa †*Balkaria*, †*Bolcabalistes*, †*Ctenoplectus*, †*Eomola*, †*Eoplectus*, †*Eospinus*, †*Iraniplectus*, †*Moclaybalistes*, †*Proaracana*, †*Protobalistum*, †*Spinacanthus*, and †*Zignoichthys* in the phylogeny are on the basis of inferences from morphological characters (Santini and Tyler 2003, 2004; Tyler et al. 2006; Close et al. 2016; Arcila and Tyler 2017; Bannikov et al. 2017; Carnevale et al. 2021; Troyer et al. 2022).

Phylogenetics. Most of the lineages classified in *Tetraodontoidei* were grouped together in the early 19th century in one of the first comprehensive classifications of teleosts (Cuvier 1816). Essentially all post-Darwinian classifications of teleosts that predate Hennigan phylogenetic systematics recognize the tetraodontoids as a lineage sharing common ancestry (e.g., Cope 1871a; T. N. Gill 1872, 1884a; Regan 1903; Boulenger 1904a:189–190; Jordan 1923:239–241; Berg 1940:495–497; Greenwood et al. 1966).

Some of the earliest phylogenetic analyses of ray-finned fishes focused on relationships within *Tetraodontoidei*, and there are several phylogenetic analyses based on morphological and molecular datasets (Winterbottom 1974; Leis 1984; Rosen 1984; Santini and Tyler 2003, 2004; Holcroft 2005; Alfaro et al. 2007; Yamanoue et al. 2007; Betancur-R, Broughton, et al. 2013; Santini, Sorenson, et al. 2013; Arcila et al. 2015; Close et al. 2016; Arcila and Tyler 2017; Bannikov et al. 2017; Ghezelayagh et al. 2022; Troyer et al. 2022). While there are important differences among nearly all the hypothesized phylogenies of tetraodontoids, most analyses consistently resolve three to four sets of sister lineages that include *Triacanthodidae* (spikefishes) and *Triacanthidae* (triplespines); *Diodontidae* (porcupinefishes) and *Tetraodontidae* (puffers); *Balistidae* (triggerfishes) and *Monacanthidae* (filefishes); and *Aracanidae* (deepwater boxfishes) and *Ostraciidae* (boxfishes) (Winterbottom 1974; Santini and Tyler 2003; Alfaro et al. 2007; Betancur-R, Broughton, et al. 2013; Near et al. 2013; Santini, Sorenson, et al. 2013; Arcila et al. 2015; Matsuura 2015; Arcila and Tyler 2017; Bannikov et al. 2017; Ghezelayagh et al. 2022; Troyer et al. 2022).

Most phylogenetic analyses differ on how the four sets of sister lineages are related to one another and are also incongruent regarding the relationships of *Triodon macropterus* (Threetooth Puffer) and *Molidae* (molas and ocean sunfishes). Phylogenies inferred from morphology or combinations of morphological and molecular characters resolve *Triodon* as the sister lineage of a clade containing *Molidae*, *Diodontidae*, and *Tetraodontidae* (Winterbottom 1974; Santini and Tyler 2003; Arcila et al. 2015; Arcila and Tyler 2017). The monophyly of this group was inferred, in part, on the basis of the upper and lower jaws with beak-like teeth and a nonprotractile upper jaw (Santini and Tyler 2003). Early molecular studies are incongruent in the relationships of *Triodon* and *Molidae* (Holcroft 2005; Alfaro et al. 2007; Yamanoue et al. 2007; Santini, Sorenson, et al. 2013). Phylogenomic analyses are congruent with one another in resolving three major lineages of *Tetraodontoidei*: (1) *Aracanidae* and *Ostraciidae*; (2) *Triacanthodidae*, *Triacanthidae*, *Balistidae*, and *Monacanthidae*; and (3) *Molidae*, *Diodontidae*, and *Tetraodontidae* (Figure 21; Ghezelayagh et al. 2022; Troyer et al. 2022). *Triodon* resolves as the sister lineage of a clade containing *Aracanidae* and *Ostraciidae* (Figure 21; Ghezelayagh et al. 2022).

†*Plectocretacicoidei* is a lineage of four fossil tiny armored acanthomorph taxa from the Cretaceous of Italy (†*Cretatriacanthus*), Slovenia (†*Protriacanthus* and †*Slovenitriacanthus*), and Lebanon (†*Plectocretacius*), ranging in age from the Cenomanian (100.5–93.9 Ma) to the Campanian (83.2–72.2 Ma) and hypothesized to be the sister lineage of *Tetraodontoidei* (Tyler and Sorbini 1996; Santini and Tyler 2003, 2004; Tyler and Santini 2005; Tyler and Križnar 2013; Close et al. 2016; Arcila and Tyler 2017; Bannikov et al. 2017). When the hypothesis was

introduced by Tyler and Sorbini (1996), it was assumed the paracanthopterygian *Zeiformes* and *Tetraodontoidei* were sister lineages (Rosen 1984), limiting the sampling of outgroups and not ensuring a robust test of the monophyly in the morphological analyses (Santini and Tyler 2003; Arcila et al. 2015; Close et al. 2016; Arcila and Tyler 2017; Bannikov et al. 2017; Troyer et al. 2022). Regardless, phylogenetic analyses using the limited set of outgroups do not consistently resolve plectocretacicoids and tetraodontoids as sister lineages (Arcila and Tyler 2017). Many of the morphological features presented as synapomorphies in support of plectocretacicoid-tetraodontoid monophyly (e.g., absence of anal-fin spines, absence of ribs, reduced number of vertebrae, reduced number of caudal-fin rays, restricted opercular opening) are found in many or all species of *Lophioidei* (Regan 1912c; Pietsch 1981, 1984; Chanet et al. 2013), suggesting these features are synapomorphies for a more inclusive clade within acanthuriforms (Benton et al. 2015; A. C. Gill and Leis 2019). *Tetraodontoidei* and *Lophioidei* share several derived morphological traits not present in †*Plectocretacicoidei*, which include: absence of infraorbital bones (Pietsch 1981; Carnevale and Pietsch 2012); sutural relationship between the posttemporal and cranium (Pietsch 1981; Carnevale and Pietsch 2012); six or fewer branchiostegal rays, a trait shared with several other lineages of *Acanthuriformes* (McAllister 1968; Benton et al. 2015; A. C. Gill and Leis 2019); lateral line unenclosed by bony canals (Nakae and Sasaki 2010); and absence of procurrent caudal rays (Pietsch 1981, 1984).

Composition. There are currently 433 living species of *Tetraodontoidei* (Nyegaard et al. 2018; Fricke et al. 2023) that include *Triodon macropterus* and species classified in *Aracanidae*, *Balistidae*, *Diodontidae*, *Molidae*, *Monacanthidae*, *Ostraciidae*, *Tetraodontidae*, *Triacanthidae*, and *Triacanthodidae*. Fossil tetraodontoid taxa include †*Balkaria*, †*Bolcabalistes*, †*Ctenoplectus*, †*Eomola*, †*Eoplectus*, †*Eospinus*, †*Iraniplectus*, †*Moclaybalistes*, †*Proaracana*, †*Protobalistum*, †*Spinacanthus*, and †*Zignoichthys*. Details of the ages and locations of fossil taxa are given in Appendix 1. Over the past 10 years, 10 new living species of *Tetraodontoidei* have been described (Fricke et al. 2023), comprising 2.3% of the living species diversity in the clade.

Diagnostic apomorphies. Morphological apomorphies of *Tetraodontoidei* include (1) anal spines absent (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (2) caudal fin with 12 or fewer principal rays (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (3) infraorbitals absent (Rosen 1984; Tyler and Sorbini 1996), (4) parietals absent (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (5) a small gill opening slightly anterior to the pectoral fin base (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (6) posterior process of pelvic basipterygia fused or sutured medially (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (7) pelvic fin with no more than one spine and two rays (Rosen 1984; Tyler and Sorbini 1996; Wiley and Johnson 2010), (8) nasal bones absent (Tyler and Sorbini 1996; Wiley and Johnson 2010), and (9) sensory canal in dentary absent (Tyler and Sorbini 1996).

Synonyms. *Plectognathes* (Cuvier 1816:144–155), *Plectognathi* (Haeckel 1866:cxxviii; Günther 1870:207–320; Cope 1871a:456, 458; T. N. Gill 1872:1; Regan 1903:285–286, 1929:325–326; Boulenger 1904a:189–190, 1904b:721–727; Jordan 1923:239–241, *Gymnodontes* (Cuvier 1816:145), and *Tetraodontiformes* (Berg 1940:495–497; Greenwood et al. 1966:403; Gosline 1971:169–170) are ambiguous synonyms of *Tetraodontoidei*.

Comments. *Tetraodontoidei* has a rich fossil record with the earliest crown lineage taxa from the Ypresian (56.0–48.1 Ma) in localities that include Denmark, Italy, Russia, United Kingdom, and Turkmenistan (Figure 21; Appendix 2; e.g., Tyler and Bannikov 1992; Tyler and Santini 2002; Close et al. 2016; Bannikov et al. 2017). Phylogenetic analyses integrating morphological and molecular datasets to resolve relationships among extinct and living lineages of *Tetraodontoidei* advanced the practice of tip-dating, in which fossil taxa in phylogenies provide time calibration in relaxed clock analyses (Arcila et al. 2015), show the effect of changes in paleoclimate on extinction dynamics (Arcila and Tyler 2017), and reveal the relationship between changes in paleoclimate and the evolution of body size (Troyer et al. 2022). Bayesian relaxed molecular clock analyses of *Tetraodontoidei* result in an average posterior crown age estimate of 62.5 million years ago, with the credible interval ranging between 60.5 and 87.3 million years ago (Troyer et al. 2022).

Constituent lineages. Redundant group names are marked with an asterisk.

Aracanidae
Balistidae
Diodontidae
Molidae
Monacanthidae
Ostraciidae
Tetraodontidae
Triacanthidae
Triacanthodidae
*Triodontidae**
†*Balkaria*
†*Bolcabalistes*
†*Ctenoplectus*
†*Eomola*
†*Eoplectus*
†*Eospinus*
†*Iraniplectus*
†*Moclaybalistes*
†*Proaracana*
†*Protobalistum*
†*Spinacanthus*
†*Zignoichthys*

Acknowledgments

We thank Rosemary Volpe and Patrick Sweeney for outstanding editorial support throughout the production of this monograph. Julie Johnson of Life Science Studios, LLC, created the paintings of fish species used in the phylogeny figures. We are grateful for all of our colleagues who read and reviewed portions of this monograph: Gloria Arratia (*Albulidae*, *Elopiformes*, *Elopomorpha*, *Oseanacephala*, and *Teleostei*), Kevin Conway (*Cobitoidei* and *Cyprinoidei*), Jessica Glass (*Carangiformes*, *Carangoidei*, and *Pleuronectoidei*), Richard Harrington (*Anabantoidei*, *Carangiformes*, *Carangoidei*, *Pleuronectoidei*, and *Synbranchiformes*), Bruno Melo (*Characiformes*, *Citharimiformes*, *Gymnotiformes*, *Loricarioidei*, *Ostariophysi*, *Otophysi*, *Siluriformes*, and *Siluroidei*), Peter Rask Møller and Jørgen Nielsen (*Ophidiiformes* and *Bythitoidei*), Rene Martin (*Ctenosquamata* and *Myctophiformes*), Timo Moritz (*Argentiniformes*, *Euteleostei*, *Polypteridae*, and *Otophysi*), Theodore Pietsch (*Lophioidei*), Kyle Piller (*Atheriniformes*, *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei*), João Paulo C. B. da Silva (*Anguilliformes*, *Anguilloidei*, *Congroidei*, *Muraenoidei*, and *Synaphobranchoidei*), Melanie Stiassny (*Acanthomorpha*, *Acanthopterygii*, *Blenniiformes*, and *Percomorpha*), Peter Wainwright (*Blenniiformes*, *Labriformes*, and *Perciformes*), Mark Westneat (*Labriformes*), Mark Wilson (*Osteoglossomorpha*, *Osteoglossiformes*, *Osteoglossidae*, *Salmoniformes*, *Esocidae*, and *Percopsiformes*), and Diego Vaz (*Batrachoididae*). Prosanta Chakrabarty, Bruno Melo, Jon Moore, and Kevin de Queiroz provided peer reviews for the journal. Leo Smith and John Sullivan identified errors in preprint versions of the monograph. Alex Dornburg, Kevin de Queiroz, and Larry Page provided advice and encouragement through the course of our work on this monograph. The Bingham Oceanographic fund maintained by the Yale Peabody Museum, Yale University, provided support for this research. The resources and staff at the Yale University Library were fundamental to the completion of this project. Thacker thanks Bill Fink and Bill Gosline for their insights into actinopterygian phylogeny and evolution. Near thanks Allison Near, Alice Near, and Rebecca Near for their unwavering support and humor though the course of preparing this monograph.

Received 11 April 2023; revised and accepted 10 October 2023.

Appendix 1
Fossil Taxa Included in the Phylogenetic Trees

The age intervals of the stages follow the Geologic Time Scale 2020 (Gradstein and Ogg 2020). Fossil species are indicated with a dagger (†) and are listed in an approximate order according to their phylogenetic relationships.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Evenkia eunoptera*	*Actinopterygii*, †*Scanilepiformes*	Induan	251.9–249.9	Lower Tunguska River, Yenisey Basin, Russia	Figure 3
†*Boreosomus piveteaui*	*Actinopteri*, pan-acipenseriforms	Induan	251.9–249.9	Kap Stosch area, Fish-zone II, Greenland	Figure 3
†*Chondrosteus acipenseroides*	*Actinopteri*, pan-acipenseriforms	Hettangian and Sinemurian	201.4–192.9	Lower Lias of Lyme Regis, Dorset, Somerset, and Leicestershire, England, UK	Figure 3
†*Peipiaosteus pani*	*Actinopteri*, pan-acipenseriforms	Barremian and Aptian	126.5–113.2	Jiufotang Formation, Chaoyang, Liaoning, China	Figure 3
†*Brembodus ridens*	*Actinopteri*, pan-neopterygians, †*Pycnodontiformes*	Norian	227.3–205.7	Calcare di Zorzino Formation, Italy	Figure 3
†*Discoserra pectinodon*	*Actinopteri*, pan-neopterygians, †*Guildayichthyidae*	Serpukhovian	330.3–323.4	Bear Gulch Member (Heath Formation), Montana, USA	Figure 3
†*Ebenaqua ritchiei*	*Actinopteri*, pan-neopterygians, †*Bobasatraniidae*	Changhsingian	254.2–251.9	Rangal Coal Measures Formation, Queensland, Australia	Figure 3
†*Australosomus kochi*	*Actinopteri*, pan-neopterygians	Wuchiapingian	259.5–254.2	Wegener Halvo Formation, Greenland	Figure 3
†*Redfieldius gracilis*	*Actinopteri*, pan-neopterygians, †*Redfieldiidae*	Norian	227.3–205.7	Bull Run Formation (Chatham Group), Virginia, USA	Figure 3
†*Helmolepis cyphognathus*	*Actinopteri*, pan-neopterygians, †*Platysiagidae*	Olenekian	249.9–246.7	Vega-Phroso Siltstone Member (Sulphur Mountain Formation), British Columbia, Canada	Figure 3
†*Dipteronotus ornatus*	*Actinopteri,* pan-neopterygians	Anisian	246.7–241.5	Grenzbitumenzone Member (Besano Formation), Switzerland	Figure 3
†*Peltopleurus lissocephalus*	*Actinopteri*, pan-neopterygians, †*Peltopleuridae*	Anisian	246.7–241.5	Grenzbitumenzone Member (Besano Formation), Switzerland	Figure 3

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Thoracopterus wushaensis*	*Actinopteri*, pan-neopterygians, †*Thoracopteridae*	Ladinian	241.5–237.0	Zhuganpo Member (Falang Formation), Guizhou, China	Figure 3
†*Venusichthys comptus*	*Actinopteri*, pan-neopterygians	Anisian	246.7–241.5	*Nicoraella kockeli* conodont zone, Guanling Formation, Yunnan, China	Figure 3
†*Habroichthys minimus*	*Actinopteri*, pan-neopterygians	Anisian	246.7–241.5	Grenzbitumenzone Member (Besano Formation), Switzerland	Figure 3
†*Hulettia americana*	*Neopterygii*, pan-holosteans	Bathonian	168.2–165.3	Canyon Springs Sandstone Member (Sundance Formation), South Dakota, USA	Figure 3
†*Dapedium noricum*	*Neopterygii*, pan-holosteans, †*Dapediidae*	Norian	227.3–205.7	Zorzino Limestone Formation, Lombardy, Italy	Figure 3
†*Aspidorhynchus crassus*	*Neopterygii, Pan-Teleostei*, †*Aspidorhynchidae*	Bathonian	168.2–165.3	Stonesfield Slate, Oxford, England, UK	Figure 3
†*Pachycormus macropterus*	*Neopterygii*, *Pan-Teleostei*, †*Pachycormidae*	Toarcian	184.2–174.7	La Caine-Curcy, Argiles à Poissons, *Harpoceras falciferum* ammonoid zone, France	Figure 3
†*Prohalecites porroi*	*Neopterygii*, *Pan-Teleostei*	Ladinian	241.5–237.0	Calcare di Perledo-Varenna, Ca' del Frate, Italy	Figure 3
†*Atacamichthys greeni*	*Neopterygii*, *Pan-Teleostei*	Oxfordian	161.5–154.8	Sierra de Varas, Cordillera de Domeyko, Antofagasta Region, Chile	Figure 3
†*Pseudopholidoctenus germanicus*	*Neopterygii*, *Pan-Teleostei*, †*Pholidophoridae*	Anisian	246.7–241.5	Middle Muschelkalk of Rüdersdorf, Germany	Figure 3
†*Catervariolus hornemanni*	*Neopterygii*, *Pan-Teleostei*	Aalenian	174.7–170.9	Stanleyville Formation, Tshopo, Democratic Republic of the Congo	Figure 3
†*Ankylophorus similis*	*Neopterygii*, *Pan-Teleostei*, †*Ankylophoriformes*	Kimmeridgian	154.8–149.2	Cerin Quarry, France	Figure 3
†*Dorsetichthys bechei*	*Neopterygii*, *Pan-Teleostei*	Sinemurian	199.5–192.9	Lyme Regis, Lower Lias, England, UK	Figure 3
†*Ichthyokentema purbeckensis*	*Neopterygii*, *Pan-Teleostei*	Tithonian	149.2–143.1	Purbeck Limestone, ARC Broadcraft Quarry, Roach blocks, England, UK	Figure 3

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Leptolepis coryphaenoides*	*Neopterygii*, *Pan-Teleostei*	Toarcian	184.2–174.7	La Caine-Curcy, Argiles à Poissons, Harpoceras falciferum ammonoid zone, France	Figure 3
†*Ascalabos voithi*	*Neopterygii*, *Pan-Teleostei*	Tithonian	149.2–143.1	Solnhofen site, Solnhofen Plattenkalk, Germany	Figure 3
†*Tharsis dubius*	*Neopterygii*, *Pan-Teleostei*	Tithonian	149.2–143.1	Wegscheid Quarry in the community of Schernfeld, near Eichstätt, Bavaria, Germany	Figure 3
†*Varasichthys ariasi*	*Neopterygii*, *Pan-Teleostei*, †*Varasichthyidae*	Oxfordian	161.5–154.8	Quebrada El Profeta, Cordillera de Domeyko, Chile	Figure 3
†*Thrissops subovatus*	*Neopterygii*, *Pan-Teleostei*, †*Ichthyodectiformes*	Kimmeridgian	154.8–149.2	Beckeri ammonoid zone, Liegende Bankkalk Formation, Baden-Württemberg, Germany	Figure 3
†*Tselfatia formosa*	*Neopterygii, Teleostei*, pan-clupeocephalans, †*Tselfatiiformes*	Cenomanian	100.5–93.9	Scaglia Variegata Alpina Formation, Schievenin Valley (Quero), Belluno, Italy	Figure 3
†*Priscosturion longipinnis*	*Actinopteri, Acipenseriformes,* stem-acipenserids	Campanian	83.2–72.2	Fanny Hill, McClelland Ferry Member (Judith River Formation), Montana, USA	Figure 5A
†*Protopsephurus liui*	*Actinopteri*, *Acipenseriformes*, stem-polyodontids	Barremian	126.5–121.4	Songzhangzi, Yixian Formation (Jehol Group), Liaong, China	Figure 5A
†*Paleopsephurus wilsoni*	*Actinopteri*, *Acipenseriformes*, stem-polyodontids	Campanian	83.2–72.2	Hogback South, MNA Locality B, Fruitland Formation, New Mexico, USA	Figure 5A
†*Watsonulus eugnathoides*	*Neopterygii, Holostei,* pan-amiiform	Induan	251.9–249.9	Middle Sakamena Formation (Sakamena Group), Diana, Madagascar	Figure 5B
†*Panxianichthys imparilis*	*Neopterygii, Holostei,* pan-amiiform	Anisian	246.7–241.5	Guanling Formation, Guizhou, China	Figure 5B
†*Ionoscopus cyprinoides*	*Neopterygii, Holostei,* pan-amiiform	Kimmeridgian	154.8–149.2	Beckeri ammonoid zone, Liegende Bankkalk Formation, Baden-Württemberg, Germany	Figure 5B
†*Caturus furcatus*	*Neopterygii, Holostei,* pan-amiiform	Kimmeridgian	154.8–149.2	Beckeri ammonoid zone, Liegende Bankkalk Formation, Baden-Württemberg, Germany	Figure 5B

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Sinamia zdanskyi*	*Neopterygii, Holostei,* pan-amiiform	Berriasian	143.1–137.7	Mengyin Formation, Shandong, China	Figure 5B
†*Amiopsis lepidota*	*Neopterygii, Holostei,* pan-amiiform	Tithonian	149.2–143.1	Solnhofen site, Solnhofen Plattenkalk, Germany	Figure 5B
†*Solnhofenamia elongata*	*Neopterygii, Holostei,* pan-amiiform	Kimmeridgian	154.8–149.2	Beckeri ammonoid zone, Liegende Bankkalk Formation, Baden-Württemberg, Germany	Figure 5B
†*Vidalamia catalunica*	*Neopterygii, Holostei,* pan-amiiform	Barremian	126.5–121.4	La Huérguina Formation, Castilla-La Mancha, Spain	Figure 5B
†*Cyclurus kehreri*	*Neopterygii, Holostei,* pan-amiiform	Lutetian	48.1–41.0	Messel Formation, MP 11, Hessen, Germany	Figure 5B
†*Ticinolepis longaeva*	*Neopterygii, Holostei,* pan-lepisosteiform	Ladinian	241.5–237.0	Meride Formation, Switzerland	Figure 5B
†*Fuyuanichthys wangi*	*Neopterygii, Holostei,* pan-lepisosteiform	Ladinian	241.5–237.0	Zhuganpo Member (Falang Formation), Yunnan, China	Figure 5B
†*Semionotus elegans*	*Neopterygii, Holostei,* pan-lepisosteiform	Sinemurian	199.5–192.9	Boonton Fish Bed, Boonton Formation (Agawam Group), New Jersey, USA	Figure 5B
†*Macrosemius rostratus*	*Neopterygii, Holostei,* pan-lepisosteiform	Kimmeridgian	154.8–149.2	Kelheim, Bavaria, Germany	Figure 5B
†*Lepidotes semiserratus*	*Neopterygii, Holostei,* pan-lepisosteiform	Toarcian	184.2–174.7	Whitby (Enniskillen), England, UK	Figure 5B
†*Thaiichthys buddhabutrensis*	*Neopterygii, Holostei,* pan-lepisosteiform	Berriasian	143.1–137.7	Phu Nam Jun, Tambon LaoYai, Amphoe Kuchinarai, Kalasin Province, Thailand	Figure 5B
†*Araripelepidotes temnurus*	*Neopterygii, Holostei,* pan-lepisosteiform	Aptian	121.4–113.2	Romualdo Formation, Pernacumbo, Brazil	Figure 5B
†*Pliodetes nigeriensis*	*Neopterygii, Holostei,* pan-lepisosteiform	Aptian	121.4–113.2	Elrhaz Formation (Tegama Group), Agadez, Niger	Figure 5B
†*Obaichthys decoratus*	*Neopterygii, Holostei,* pan-lepisosteiform, †*Obaichtyidae*	Aptian	121.4–113.2	Romualdo Member (Santana Formation), Ceará, Brazil	Figure 5B
†*Nhanulepisosteus mexicanus*	*Neopterygii, Holostei,* pan-lepisosteiform	Kimmeridgian	154.8–149.2	Llano Yosobé deposits, Sabinal Formation, Oaxaca, Mexico	Figure 5B
†*Masillosteus janeae*	*Neopterygii, Holostei,* pan-lepisosteiform	Ypresian	56.0–48.1	Fossil Butte Member, Green River Formation, Wyoming, USA	Figure 5B

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Cuneatus wileyi*	*Neopterygii, Holostei,* pan-lepisosteiform	Ypresian	56.0–48.1	Lake Uinta, Green River Formation, Utah, USA	Figure 5B
†*Jiuquanichthys liui*	*Oseanacephala,* pan-osteoglossomorphs	Hauterivian	132.6–126.5	Chijinqiao Formation, Yumen, Gansu, China	Figure 6
†*Lycoptera davidi*	*Oseanacephala,* pan-osteoglossomorphs	Aptian	121.4–113.2	Yixinian Formation, Liaoning Province, China	Figure 6
†*Plesiolycoptera daqingensis*	*Oseanacephala, Osteoglossomorpha,* pan-hiodontid	Coniacian	89.4–85.7	Yaojia Formation, Daqing Oil Field, Heilongjiang, China	Figure 6
†*Yanbiania wangqingica*	*Oseanacephala, Osteoglossomorpha,* pan-hiodontid	Albian	113.2–100.5	Dalazi Formation, Luozigou Basin, Wangqing, Jilin, China	Figure 6
†*Paralycoptera wui*	*Oseanacephala, Osteoglossomorpha,* pan-osteoglossiform	Aptian	121.4–113.2	Guantou Formation, Yongkang, Zheijiang, China	Figure 6
†*Jinanichthys longicephalus*	*Oseanacephala, Osteoglossomorpha,* pan-osteoglossiform	Aptian	121.4–113.2	Jiufotang Formation, China	Figure 6
†*Huashia gracilis*	*Oseanacephala, Osteoglossomorpha,* pan-osteoglossiform	Aptian	121.4–113.2	Lishugou Formation, China	Figure 6
†*Kuntulunia longipterus*	*Oseanacephala, Osteoglossomorpha,* pan-osteoglossiform	Aptian	121.4–113.2	Madongshan Formation, Tongxin, Ningxia, China	Figure 6
†*Laeliichthys ancestralis*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes,* pan-notopterid	Barremian	126.5–121.4	Areado Formation, Brazil	Figure 6
†*Palaeonotopterus greenwoodi*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes,* pan-mormyroid	Cenomanian	100.5–93.9	Kem Kem Beds, Taouz, Morocco	Figure 6
†*Joffrichthys symmetropterus*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes, Osteoglossidae*	Selandian and Thanetian	61.7–56.0	Paskapoo Formation, Joffre Bridge roadcut, Alberta, Canada	Figure 6
†*Sinoglossus lushanensis*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes, Osteoglossidae*	Lutetian	48.1–41.0	Lushan Xian, North Sichuan, China	Figure 6
†*Phareodus testis*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes, Osteoglossidae*	Ypresian	56.0–48.1	Green River Formation, Fossil Butte, Wyoming, USA	Figure 6

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Cretophareodus alberticus*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes, Osteoglossidae*	Campanian	83.2–72.2	Oldman, Dinosaur Provincial Park, Alberta, Canada	Figure 6
†*Singida jacksonoides*	*Oseanacephala, Osteoglossomorpha, Osteoglossiformes, Osteoglossidae*	Lutetian	48.1–41.0	Mahenge, Tanzania	Figure 6
†*Anaethalion zapporum*	*Oseanacephala, Elopomorpha,* pan-elopiforms	Kimmeridgian	154.8–149.2	Stark Quarry, Schamhaupten, Germany	Figure 6
†*Daitingichthys tischlingeri*	*Oseanacephala, Elopomorpha,* pan-elopiforms	Tithonian	149.2–143.1	Daiting, Bavaria, Germany	Figure 6
†*Paraelops cearensis*	*Oseanacephala, Elopomorpha,* pan-elopiforms	Albian	113.2–100.5	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 6
†*Elopoides tomassoni*	*Oseanacephala, Elopiformes*, pan-megalopids	Albian	113.2–100.5	Aube, France	Figure 6
†*Elopsomolos frickhingeri*	*Oseanacephala, Elopiformes,* pan-elopids	Tithonian	149.2–143.1	Blumenberg, Germany	Figure 6
†*Ichthyemidion vidali*	*Oseanacephala, Elopiformes,* pan-elopids	Barremian	126.5–121.4	La Pedrera de Rúbies Formation, Spain	Figure 6
†*Bullichthys santanensis*	*Oseanacephala, Elopomorpha,* pan-albulids	Albian	113.2–100.5	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 6
†*Osmeroides lewesiensis*	*Oseanacephala, Elopomorpha,* pan-albulids	Albian	113.2–100.5	Gault Formation, Folkestone, Gault, England, UK	Figure 6
†*Farinichthys gigas*	*Oseanacephala, Elopomorpha,* pan-albulids	Thanetian	59.2–56.0	Poty Quarry locality, Pernambuco, Brazil	Figure 6
†*Brannerion latum*	*Oseanacephala, Elopomorpha,* pan-albulids	Aptian and Albian	121.4–100.5	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 6
†*Baugeichthys caeruleus*	*Oseanacephala, Elopomorpha,* pan-albulids	Hauterivian	132.6–126.5	Massif des Bauges, France	Figure 6
†*Lebonichthys namourensis*	*Oseanacephala, Elopomorpha,* pan-albulids	Cenomanian	100.5–93.9	Sannine Formation, Nammoura Quarry, Lebanon	Figure 6
†*Deltaichthys albuloides*	*Oseanacephala, Elopomorpha, Albulidae*	Cenomanian	100.5–93.9	Eagle Ford Group, Texas, USA	Figure 6
†*Macabi tojolabalensis*	*Oseanacephala, Elopomorpha, Albulidae*	Campanian and Maastrichtian	83.2–66.0	Tzimol Quarry, Chiapas, Mexico	Figure 6

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Hajulia multidens*	*Oseanacephala, Elopomorpha, Albulidae*	Cenomanian	100.5–93.9	Hadjoula, Lebanon	Figure 6
†*Istieus grandis*	*Oseanacephala, Elopomorpha, Albulidae*	Campanian	83.2–72.2	Ahlen Formation, Sendenhorst, Germany	Figure 6
†*Nunaneichthys mexicanus*	*Oseanacephala, Elopomorpha, Albulidae*	Albian and Cenomanian	113.2–93.9	La Negra Member (El Doctor Formation), Muhi Quarry, Hidalgo, Mexico	Figure 6
†*Echidnocephalus troscheli*	*Oseanacephala, Elopomorpha*, pan-halosaurid	Campanian	83.2–72.2	Westphalia, Germany	Figure 6
†*Anguillavus mazeni*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Cenomanian	100.5–93.9	Sannine Limestone, Hajula, Hakel, Namoura, Lebanon	Figure 6
†*Enchelurus anglicus*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Turonian	93.9–89.4	English Chalk Group, England, UK	Figure 6
†*Abisaadia hakelensis*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Cenomanian	100.5–93.9	Sannine Limestone, Hajula, Hakel, Namoura, Lebanon	Figure 6
†*Luenchelys minimus*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Cenomanian	100.5–93.9	Sannine Limestone, Hajula, Hakel, Namoura, Lebanon	Figure 6
†*Hayenchelys germanus*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Cenomanian	100.5–93.9	Sannine Limestone, Hajula, Hakel, Namoura, Lebanon	Figure 6
†*Urenchelys germanum*	*Oseanacephala, Elopomorpha*, pan-anguilliforms	Cenomanian	100.5–93.9	Sannine Limestone, Hajula, Hakel, Namoura, Lebanon	Figure 6
†*Santanasalmo elegans*	*Clupeocephala*, pan-euteleosts	Albian	113.2–100.5	Morro do Barro Formation, Almada Basin, Bahia, Brazil	Figure 7
†*Tchernovichthys exspectatum*	*Clupeocephala*, pan-euteleosts	Hauterivian	132.6–126.5	Wadi-el-Maloj, Israel	Figure 7
†*Scombroclupeoides scutata*	*Clupeocephala*, pan-euteleosts	Barremian	126.5–121.4	Morro do Barro Formation, Almada Basin, Bahia, Brazil	Figure 7
†*Wenzichthys congolensis*	*Clupeocephala*, pan-euteleosts	Aptian	121.4–113.2	Cocobeach Formation, Gabon	Figure 7
†*Helgolandichthys schmidi*	*Clupeocephala*, pan-euteleosts	Aptian	121.4–113.2	Tock Formation, Helgolang, Germany	Figure 7

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Beurlenichthys ouricuriensis*	*Clupeocephala*, pan-euteleosts	Albian	113.2–100.5	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 7
†*Erichalcis arcta*	*Clupeocephala*, pan-euteleosts	Albian	113.2–100.5	Northwest Territories, Canada	Figure 7
†*Gaudryella gaudryi*	*Clupeocephala*, pan-euteleosts	Cenomanian	100.5–93.9	Nammoura Quarry, Lebanon	Figure 7
†*Ghabouria libanica*	*Clupeocephala*, pan-euteleosts	Cenomanian	100.5–93.9	Aïn-el-Ghârboûr, Lebanon	Figure 7
†*Avitosmerus canadensis*	*Clupeocephala*, pan-euteleosts	Turonian	93.9–89.4	Great Bear Basin, Lac des Bois, Northwest Territories, Canada	Figure 7
†*Parawenzichthys minor*	*Clupeocephala*, pan-euteleosts	Turonian	93.9–89.4	Pelotas Basin, Atlantida Formation, Brazil	Figure 7
†*Ezkutuberezi carmeni*	*Otocephala*, pan-clupeiforms, †*Ellimmichthyiformes*	Berriasian and Valanginian	143.1–132.6	Villaro Member (Villaro Formation), Arratia Valley, Spain	Figure 8
†*Santanaclupea silvasantosi*	*Otocephala*, pan-clupeiforms	Aptian	121.4–113.2	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 8
†*Paleodenticeps tanganikae*	*Otocephala, Clupeiformes,* pan-denticipitid	Lutetian	48.1–41.0	Iramba Plateau, Singida, Tanzania	Figure 8
†*Cynoclupea nelsoni*	*Otocephala, Clupeiformes,* pan-clupeoids	Barremian	126.5–121.4	Cimpor Quarry, Morro do Chaves Formation, Alagoas State, Brazil	Figure 8
†*Pugliaclupea nolardi*	*Otocephala, Clupeiformes,* pan-alosid	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8
†*Eoalosa janvieri*	*Otocephala, Clupeiformes,* pan-alosid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 8
†*Italoclupea nolfi*	*Otocephala, Clupeiformes,* pan-clupeid	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8
†*Lecceclupea ehiravaensis*	*Otocephala, Clupeiformes,* pan-clupeid	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8
†*Nardoclupea grandei*	*Otocephala, Clupeiformes,* pan-dussumieriid	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8
†*Portoselvaggioclupea whiteheadi*	*Otocephala, Clupeiformes,* pan-dussumieriid	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Tischlingerichthys viohli*	*Otocephala*, pan-ostariophysan	Tithonian	149.2–143.1	Mulheim and Daiting, Germany	Figure 8
†*Notogoneus montanensis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Santonian	85.7–83.2	Two Medicine Formation, Montana, USA	Figure 8
†*Charitosomus formosus*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Campanian	83.2–72.2	Baumberge Formation, Westphalia, Germany	Figure 8
†*Charitopsis spinosus*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Cenomanian	100.5–93.9	Haqil, Lebanon	Figure 8
†*Hakeliosomus hakelensis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Cenomanian	100.5–93.9	Haqil, Lebanon	Figure 8
†*Judeichthys haasi*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Cenomanian	100.5–93.9	Bet Meir/Amminadav Formation, Ein Yabrud quarries, Palestinian Territory	Figure 8
†*Ramallichthys orientalis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-gonorynchid	Cenomanian	100.5–93.9	Bet Meir/Amminadav Formation, Ein Yabrud quarries, Palestinian Territory	Figure 8
†*Rubiesichthys gregalis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Berriasian and Valanginian	143.1–132.6	Montse, Lerida, Spain	Figure 8
†*Gordichthys conquensis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Barremian	126.5–121.4	La Huérguina Formation, Cuenca, Spain	Figure 8
†*Aethalionopsis robustus*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Barremian	126.5–121.4	Bernissart, Belgium	Figure 8
†*Tharrhias araripis*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Aptian	121.4–113.2	Romualdo Member, Santana Formation, Araipe Basin, Brazil	Figure 8
†*Dastilbe crandalli*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Aptian	121.4–113.2	Muribeca Formation of Riacho Doce, Brazil	Figure 8
†*Parachanos aethiopicus*	*Otocephala*, *Ostariophysi*, *Gonorynchiformes*, pan-chanid	Aptian	121.4–113.2	Rio San Benito, Equatorial Guinea	Figure 8
†*Lusitanichthys africanus*	*Otocephala*, *Ostariophysi*, pan-otophysan	Cenomanian	100.5–93.9	Kem Kem Group, Drâa-Tafilalet, Morocco	Figure 8

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Clupavus maroccanus*	*Otocephala, Ostariophysi,* pan-otophysan	Albian	113.2–100.5	La Cavere, Pietraroja, Italy	Figure 8
†*Nardonoides chardoni*	*Otocephala, Ostariophysi,* pan-otophysan	Campanian and Maastrichtian	83.2–66.0	Nardò, Italy	Figure 8
†*Chanoides macropoma*	*Otocephala, Ostariophysi,* pan-otophysan	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 8
†*Santanichthys diasii*	*Otocephala, Ostariophysi,* pan-otophysan	Aptian and Albian	121.4–100.5	Santana, Riachuelo, and Codo Formations, Romualdo Member, Brazil	Figure 8
†*Andinichthys bolivianensis*	*Otocephala, Ostariophysi, Otophysi, Pan-Siluriformes, †Andinichthyidae*	Maastrichtian	72.2–66.0	Tiupampa, El Molino, Bolivia	Figure 8
†*Eocitharinus macrognathus*	*Otocephala, Ostariophysi, Otophysi,* pan-citharliniform	Lutetian	48.0–41.0	Mahenge, Singida Plateau, Tanzania	Figure 8
†*Jianghanichthys hubeiensis*	*Otocephala, Ostariophysi, Otophysi, Cypriniformes*	early Eocene	56.0–47.8	Yangxi Formation, Hubei, China	Figure 9
†*Bachmannia chubutensis*	*Otocephala, Ostariophysi, Otophysi, Siluriformes*, pan-diplomystid	early Eocene	56.0–47.8	Tufolitas Laguna del Hunco, Chubut, Argentina	Figure 10
†*Hypsidoris farsonensis*	*Otocephala, Ostariophysi, Otophysi, Siluriformes*, pan-siluroid	early Middle Eocene	49.7–47.6	Laney Member deposits of the Green River Formation, Farson Beds, Wyoming	Figure 10
†*Surlykus longigracilis*	*Euteleostei,* pan-argentiniforms	Ypresian	56.0–48.1	Fur Formation, Denmark	Figure 7
†*Kermichthys daguini*	*Euteleostei,* pan-salmoniforms	Cenomanian	100.5–93.9	Jbel Tselfat, Moroco	Figure 7
†*Barcarenichthys joneti*	*Euteleostei,* pan-salmoniforms	Cenomanian	100.5–93.9	Barcarena, Portugal	Figure 7
†*Stompooria rogersmithi*	*Euteleostei,* pan-salmoniforms	Maastrichtian	72.2–66.0	Stompoor Crater, Marydale, Prieska District, Northern Cape Province, South Africa	Figure 7
†*Pyrenichthys jauzaci*	*Euteleostei,* pan-salmoniforms	Maastrichtian	72.2–66.0	Petites Pyrénées, Saint-Loup, Charente-Maritime, France	Figure 7
†*Oldmanesox canadensis*	*Euteleostei, Salmoniformes,* pan-esocids	Campanian	83.2–72.2	Oldman Formation, Alberta	Figure 7

Continued

Appendix 1 continued.

Species	**Clade**	**Stage**	**Age (Ma)**	**Location**	**Phylogeny**
†*Estesesox foxi*	*Euteleostei, Salmoniformes,* pan-esocids	Campanian and Maastrichtian	83.2–66.0	Milk River Formation, Alberta, Canada	Figure 7
†*Boltyshia brevicauda*	*Euteleostei, Salmoniformes, Esocidae,* pan-umbrid	Thanetian	59.2–56.0	Boltyshka Basin, Ukraine	Figure 7
†*Palaeoesox fritzschei*	*Euteleostei, Salmoniformes, Esocidae,* pan-umbrid	Lutetian	48.1–41.0	Geiseltal Valley, Germany	Figure 7
†*Proumbra irtyshensis*	*Euteleostei, Salmoniformes, Esocidae,* pan-umbrid	Aquitanian	23.04–20.45	Abrosimovka Formation, Siberia, Russia	Figure 7
†*Nybelinoides brevis*	Euteleostei, pan-stomiats	Barremian and Aptian	126.5–113.2	Bernissart, Belgium	Figure 7
†*Spaniodon latus*	*Euteleostei, Stomiati*, pan-osmeriform	Santonian	85.7–83.2	Sahel Alma, Lebanon	Figure 7
†*Speirsaenigma lindoei*	*Euteleostei, Stomiati, Osmeriformes,* pan-plecoglossid	Selandian and Thanetian	61.7–56.0	Paskapoo Formation, Joffre Bridge roadcut, Alberta, Canada	Figure 7
†*Paravinciguerria praecursor*	*Euteleostei, Stomiati,* pan-stomiiform	Cenomanian	100.5–93.9	Argille Varicolori, Sicily	Figure 7
†*Argillichthys toombsi*	*Aulopiformes*, pan-synodontid	Ypresian	56.0–48.1	London Clay, Isle of Sheppey, England, UK	Figure 12
†*Labrophagus esocinus*	*Aulopiformes*, pan-synodontid	Ypresian	56.0–48.1	London Clay, Isle of Sheppey, England, UK	Figure 12
†*Cimolichthys nepaholica*	*Aulopiformes,* pan-notosudid	Cenomanian	100.5–93.9	Hartland Shale Member, Greenhorn Limestone Formation, Colorado, USA	Figure 12
†*Holosteus esocinus*	*Aulopiformes*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 12
†*Pavlovichthys mariae*	*Aulopiformes*	Rupelian	33.9–27.3	Pshekha Formation, Maikop Group, North Caucasus, Russia	Figure 12
†*Enchodus zimapanensis*	*Aulopiformes, †Enchodontoidei*	Albian and Cenomanian	113.2–93.9	El Doctor Formation, Hidalgo, Mexico	Figure 12
†*Apateodus corneti*	*Aulopiformes,* pan-paralepidid	Maastrichtian	72.2–66.0	Maastricht Formation, Limburg, Netherlands	Figure 12
†*Sardinoides monasteri*	*Ctenosquamata,* pan-myctophiform	Campanian	83.2–72.2	Ahlen Formation, Germany	Figure 12

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Neocassandra mica*	*Ctenosquamata*, pan-myctophiform	Ypresian	56.0–48.1	Danata Formation, Uylya-Kushlyuk, Turkmenistan	Figure 12
†*Ctenothrissa signifer*	*Ctenosquamata*, pan-acanthomorphs, †*Ctenothrissiformes*	Cenomanian	100.5–93.9	Hajula, Lebanon	
†*Eomyctophum broncus*	*Myctophiformes*, pan-myctophid	Ypresian	56.0–48.1	Otaio Gorge Sandstone Formation, South Island, New Zealand	Figure 12
†*Beckerophotus gracilis*	*Myctophiformes*, pan-neoscopelid	Lutetian	48.1–41.0	Dabakhan Formation, Georgia	Figure 12
†*Choichix alvaradoi*	*Acanthomorpha*, pan-acanthopterygian	Cenomanian	100.5–93.9	El Chango Quarry, Cintalapa Formation, Sierra Madre Group, Chiapas, Mexico	Figure 12
†*Aipichthys minor*	*Acanthomorpha*, pan-lampriform	Cenomanian	100.5–93.9	Hakel, Lebanon	Figure 12
†*Zoqueichthys carolinae*	*Acanthomorpha*, pan-lampriform	Cenomanian	100.5–93.9	Cintalapa Formation, Sierra Madre Group, Chiapas, Mexico	Figure 12
†*Aipichthyoides galeatus*	*Acanthomorpha*, pan-lampriform	Cenomanian	100.5–93.9	Ein Yabrud quarries, Palestinian Territory	Figure 12
†*Nardovelifer altipinnis*	*Acanthomorpha*, pan-lampriform	Campanian and Maastrichtian	83.2–66.0	Nardò, "Calcari di Melissano," Porto Selvaggio, Apulia, Lecce, Italy	Figure 12
†*Megalampris keyesi*	*Acanthomorpha*, *Lampriformes*, pan-lamprid	Chattian	27.3–23.04	Kokoamu Greensand Formation, Otago, New Zealand	Figure 12
†*Turkmene finitimus*	*Acanthomorpha*, *Lampriformes*, pan-veliferid, †*Turkmenidae*	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 12
†*Palaeocentrotus boeggildi*	*Acanthomorpha*, *Lampriformes*, pan-veliferid, †*Palaeocentrotidae*	Ypresian	56.0–48.1	Fur Formation, Denmark	Figure 12
†*Eolophotes lenis*	*Acanthomorpha*, *Lampriformes*, pan-lophotid	Lutetian	48.1–41.0	Dabakhana Svita Formation, Tbilisi, Georgia	Figure 12
†*Oligolophotes fragosus*	*Acanthomorpha*, *Lampriformes*, pan-lophotid	Rupelian	33.9–27.3	Pshekha Horizon Formation, Georgia	Figure 12
†*Pycnosteroides levispinosus*	*Acanthomorpha*, pan-paracanthopterygian	Cenomanian	100.5–93.9	Hajula, Lebanon	Figure 12

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Polyspinatus fluere*	*Acanthomorpha*, *Paracanthopterygii*, pan-polymixiid	Ypresian	56.0–48.1	Fur Formation, Denmark	Figure 13
†*Omosomopsis simum*	*Acanthomorpha*, *Paracanthopterygii*, pan-percopsiform	Cenomanian	100.5–93.9	Jebel Telfat, Morocco	Figure 13
†*Xenyllion zonensis*	*Acanthomorpha*, *Paracanthopterygii*, pan-percopsiform, †*Sphenocephalidae*	Cenomanian	100.5–93.9	Fish Scale Zone, Shaftesbury Formation, Alberta, Canada	Figure 13
†*Mcconichthys longipinnis*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-aphreoderoid	Danian	66.0–61.7	Bonin Schoolhouse, Tullock Member (Fort Union Formation), McCone County, Montana, USA	Figure 13
†*Tricophanes foliarum*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-aphredoderoid	Priabonian	37.7–33.9	Florissant Fossil Beds, Colorado, USA	Figure 13
†*Lindoeichthys albertensis*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Maastrichtian	72.2–66.0	Scollard Formation, Pisces Point locality, Dry Island Buffalo Jump Provincial Park, Alberta, Canada	Figure 13
†*Libotonius blakeburnensis*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Ypresian	56.0–48.1	Blakeburn Mine L95, south of Coalmont, British Columbia, Canada	Figure 13
†*Amphiplaga brachyptera*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Ypresian	56.0–48.1	Fossil Lake Sample Site H-1 [Thompson Ranch Quarry; Locality H], Fossil Butte Member (Green River Formation), Lincoln Co., Wyoming, USA	Figure 13
†*Erismatopterus levatus*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Ypresian	56.0–48.1	Lake Gosiute and Lake Uinta deposits, Green River Formation	Figure 13
†*Lateopisciculus turrifumosus*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Selandian and Thanetian	61.7–56.0	Joffre Bridge road cut, Paskapoo Formation, Alberta, Canada	Figure 13
†*Massamorichthys wilsoni*	*Acanthomorpha*, *Paracanthopterygii*, *Percopsiformes*, pan-percopsid	Selandian and Thanetian	61.7–56.0	Joffre Bridge road cut, Paskapoo Formation, Alberta, Canada	Figure 13
†*Archaeozeus skamolensis*	*Acanthomorpha*, *Paracanthopterygii*, pan-zeiform	Ypresian	56.0–48.1	Fur Formation, Denmark	Figure 13

Continued

APPENDIX 1 CONTINUED.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Bajaichthys elegans*	*Acanthomorpha, Paracanthopterygii,* pan-zeiform	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 13
†*Protozeus kuehnei*	*Acanthomorpha, Paracanthopterygii,* pan-zeiform	Ypresian	56.0–48.1	Fur Formation, Denmark	Figure 13
†*Cretazeus rinaldii*	*Acanthomorpha, Paracanthopterygii, Zeiformes,* pan-parazenid	Campanian and Maastrichtian	83.2–66.0	Nardò, “Calcari di Melissano,” Porto Selvaggio, Apulia, Lecce, Italy	Figure 13
†*Judeoberyx princeps*	*Acanthomorpha, Acanthopterygii,* pan-trachichthyiform	Cenomanian	100.5–93.9	Ein Yabrud quarries, Palestinian Territory	Figure 14
†*Lissoberyx dayi*	*Acanthomorpha, Acanthopterygii,* pan-trachichthyiform	Cenomanian	100.5–93.9	Hakel, Lebanon	Figure 14
†*Stichocentrus liratus*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-holocentrid	Cenomanian	100.5–93.9	Hajula, Lebanon	Figure 14
†*Plesioberyx maximus*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-holocentrid	Cenomanian	100.5–93.9	Hakel, Lebanon	Figure 14
†*Iridopristis parrisi*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-holocentrid	Danian	66.0–61.7	Hornerstown Formation, New Jersey, USA	Figure 14
†*Berybolcensis leptacanthus*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-holocentrid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 14
†*Tenuicentrum lanceolatum*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-holocentrid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 14
†*Berycomorus firdoussii*	*Acanthomorpha, Acanthopterygii, Beryciformes,* pan-berycoid	Middle and Late Eocene	48.1–33.9	Pabdeh Formation, near Ilam, Zagros Basin, Iran	Figure 14
†*Pepemkay maya*	*Acanthomorpha, Acanthopterygii,* pan-percomorph	Cenomanian	100.5–93.9	El Chango Quarry, Cintalapa Formation, Sierra Madre Group, Chiapas, Mexico	Figure 14
†*Pastorius methenyi*	*Acanthomorpha, Acanthopterygii, Percomorpha,* pan-ophidiiform	Campanian and Maastrichtian	83.2–66.0	Trebiciano locality, Trieste Province, Italy	Figure 14

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Ampheristus americanus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Ophidiiformes,* pan-ophiid	Maastrichtian	72.2–66.0	Kemp Clay, Texas, USA	Figure 14
†*“Bidenichthys” crepidatus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Ophidiiformes,* pan-bythitoid	Maastrichtian	72.2–66.0	Gerhartsreiter Graben, Bavaria, Germany	Figure 14
†*Bythitidarum rasmussenae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Ophidiiformes,* pan-dinematichthyin	Danian	66.0–61.7	Faske, Denmark	Figure 14
†*Bacchiaichthys zucchiae*	*Acanthomorpha, Acanthopterygii, Percomorpha,* pan-batrachoid	Campanian and Maastrichtian	83.2–66.0	Trebiciano locality, Trieste Province, Italy	Figure 14
†*Paleoserranus lakamhae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Eupercaria,* pan-perciforms	Danian	66.0–61.7	Marine deposits of Belisario Domínguez, Chiapas, Mexico	Figure 14
†*Paralates chapelcorneri*	*Acanthomorpha, Acanthopterygii, Percomorpha, Gobiiformes,* pan-gobioid	Priabonian	37.7–33.9	Chapelcorner Fish Bed (Colenutt’s bed 3), Isle of Wight, UK	Figure 14
†*Carlomonnius quasigobius*	*Acanthomorpha, Acanthopterygii, Percomorpha, Gobiiformes,* pan-butid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 14
†*Lepidocottus aries*	*Acanthomorpha, Acanthopterygii, Percomorpha, Gobiiformes,* pan-butid	Chattian	27.3–23.04	Niveau du gypse d’Aix Formation, Bouches-du-Rhone, France	Figure 14
†*Eleogobius gaudanti*	*Acanthomorpha, Acanthopterygii, Percomorpha, Gobiiformes,* pan-thalasseleotrid	Burdigalian and Langhian	20.45–13.82	Illerkirchberg, Molasse Basin, Baden-Württemberg, Germany	Figure 14
†*Pirskenius radoni*	*Acanthomorpha, Acanthopterygii, Percomorpha, Gobiiformes,* pan-thalasseleotrid	Rupelian	33.9–27.3	České Středohoří Mountains, Czech Republic	Figure 14
†*Pinichthys pulcher*	*Acanthomorpha, Acanthopterygii, Percomorpha, Scombriformes,* pan-stromateid	Rupelian	33.9–27.3	Pshekha Horizon Formation, Georgia	Figure 15
†*Carangopsis maximus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Scombriformes,* pan-pomatomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Bannikovichthys paelignus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Scombriformes,* pan-chiasmodontid	Serravallian	13.82–11.63	Toricella Paligna, Italy	Figure 15

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Argestichthys vysotzkyi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Scombriformes,* pan-trichiuroid	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 15
†*Anenchelum eocaenicum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Scombriformes,* pan-trichiurid	Lutetian	48.1–41.0	Dabakhana Svita, Tbilisi, Georgia	Figure 15
†*Gilmourella minuta*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-callionymid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Pterygocephalus paradoxus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-dactylopterid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Rhamphosus rastrum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-pegasid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Prosolenostomus lessinii*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-syngnathid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Solenorhynchus elegans*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-solenostomid	Ypresian	56.0–48.1	Monte Bolca, Monte Postale, Italy	Figure 15
†*Calamostoma breviculum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-solenostomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Gasterorhamphosus zuppichinii*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-centriscoid	Campanian and Maastrichtian	83.2–66.0	Nardò, "Calcari di Melissano," Porto Selvaggio, Apulia, Lecce, Italy	
†*Paramphisile weileri*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-centriscid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Paraeoliscus robinetae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-centriscid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Eekaulostomus cuevasae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-aulostomoid	Danian	66.0–61.7	Marine deposits of Belisario Domínguez, Chiapas, Mexico	Figure 15
†*Urosphen dubius*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-fistularid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Eoaulostomus bolcensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-aulostomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Synhypuralis banister*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-aulostomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Jurgensenichthys elongatus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-aulostomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Macroaulostomus veronensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Syngnathiformes,* pan-aulostomid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 15
†*Rhamphexocoetus volans*	*Acanthomorpha, Acanthopterygii, Percomorpha, Atheriniformes, Belonoidei,* pan-exocoetid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 16
†*Kenyaichthys kipkechi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Atheriniformes, Cyprinodontoidei,* pan-rivulid	Messinian	7.25–5.33	Lukeino Formation, Tugen Hills, Kenya	Figure 16
†*Carrionellus diumortuus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Atheriniformes, Cyprinodontoidei,* pan-orestiid	Aquitanian and Burdigalian	23.04–15.99	Loja, Ecuador	Figure 16
†*Francolebias aymardi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Atheriniformes, Cyprinodontoidei,* pan-valenciid	Rupelian	33.9–27.3	Ronzon, Le Puy-en-Velay, France	Figure 16
†*Prolebias stenoura*	*Acanthomorpha, Acanthopterygii, Percomorpha, Atheriniformes, Cyprinodontoidei,* pan-valenciid	Rupelian	33.9–27.3	Corent, Puy-de-Dôme, France	Figure 16
†*Chaychanus gonzalezorum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Blenniiformes,* pan-pomacentrid	Danian	66.0–61.7	Marine deposits of Belisario Domínguez, Chiapas, Mexico	Figure 16
†*Anchichanna kuldanensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Synbranchiformes, Anabantoidei,* pan-channid	Lutetian	48.1–41.0	Kuldana Formation, Pakistan	Figure 17

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Eoanabas thibetana*	*Acanthomorpha, Acanthopterygii, Percomorpha, Synbranchiformes, Anabantoidei,* pan-anabantid	Chattian	27.3–23.04	Dingqing Formation, Jiangnongtangga, Lunpola Basin, Tibet	Figure 17
†*Eolates gracilis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes,* pan-latid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 17
†*Archaeus oblongus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-carangid	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 17
†*Opisthomyzon glaronensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-echeneid	Rupelian	33.9–27.3	Engi Slates, Matt Formation, Canton Glarus, Switzerland	Figure 17
†*Ductor vestenae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 17
†*Mene purdyi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-menid	Thanetian and Ypresian	59.2–48.1	Máncora Formation, Peru	Figure 17
†*Palaeorhynchus senectus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-xiphioid	Lutetian	48.1–41.0	Dabakhana Svita, Tbilisi, Georgia	Figure 17
†*Hemingwaya sarissa*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-istiophorid	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 17
†*Blochius longirostris*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-xiphiid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 17
†*Xiphiorhynchus parvus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Carangoidei,* pan-xiphiid	Ypresian	56.0–48.1	London Clay, Isle of Sheppey, England, UK	Figure 17
†*Heteronectes chaneti*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-pleuronectoid	Ypresian	56.0–48.1	Monte Bolca, Pesicara or Monte Postale, Italy	Figure 17
†*Amphistium paradoxum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-pleuronectoid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 17

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Eobothus minimus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-pleuronectoid	Ypresian	56.0–48.1	Monte Bolca, Pesicara or Monte Postale, Italy	Figure 17
†*Oligobothus pristinus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-bothid	Rupelian	33.9–27.3	Piatra Neamţ, Romania	Figure 17
†*Oligopleuronectes germanicus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-pleuronectid	Rupelian	33.9–27.3	Bott-Eder clay pit, Rauenberg, Baden-Württemberg, Germany	Figure 17
†*Eobuglossus eocenicus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Carangiformes, Pleuronectoidei,* pan-soleid	Lutetian	48.1–41.0	Mokkatam Formation, Gebel Turah, Egypt	Figure 17
†*Proeleginops grandeastmanorum*	*Acanthomorpha, Acanthopterygii, Percomorpha, Perciformes,* pan-eleginopid	Ypresian	56.0–48.1	La Meseta Formation, Tertiary Eocene La Maseta (Telm) 4, Seymour Island, Antarctica	Figure 18
†*Sakhalinia multispinata*	*Acanthomorpha, Acanthopterygii, Percomorpha, Perciformes,* pan-hexagrammid	Serravallian	13.82–11.63	Agnevo Formation, Sakhalin Island, Russia	Figure 18
†*Paraophiodon nessovi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Perciformes,* pan-hexagrammid	Serravallian	13.82–11.63	Agnevo Formation, Sakhalin Island, Russia	Figure 18
†*Agnevichthys gretchinae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Perciformes,* pan-pholid	Serravallian	13.82–11.63	Agnevo Formation, Sakhalin Island, Russia	Figure 18
†*Palaeopholis laevis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Perciformes,* pan-pholid	Serravallian	13.82–11.63	Agnevo Formation, Sakhalin Island, Russia	Figure 18
†*Bellwoodilabrus landinii*	*Acanthomorpha, Acanthopterygii, Percomorpha, Labriformes,* pan-labrids	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 19
†*Labrobolcus giorgioi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Labriformes,* pan-labrids	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 19
†*Eoscatophagus frontalis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-scatophagids	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 20

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Oligoscatophagus capellini*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-scatophagids	Rupelian	33.9–27.3	Chiavon, Italy	Figure 20
†*Ruffoichthys spinosus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-siganids	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 20
†*Eosiganus kumaensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-siganids	Bartonian	41.0–37.7	Kuma Horizon, Pshekha River, Russia	Figure 20
†*Siganopygaeus rarus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-siganids	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 20
†*Protosiganus glaronensis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-luvarids	Rupelian	33.9–27.3	Canton Glarus, Switzerland	Figure 20
†*Avitoluvarus dianae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-luvarids	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 20
†*Kushlukia permira*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-luvarids	Ypresian	56.0–48.1	Danata Formation, Turkmenistan	Figure 20
†*Caprosimilis carpathicus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes,* pan-caproids	Rupelian	33.9–27.3	Jamma Dolna 2 locality, Outer Carpathians, Poland	Figure 20
†*Padovathurus gaudryi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Acanthuroidei,* pan-acanthurid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 20
†*Gazolaichthys vestenanovae*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Acanthuroidei,* pan-acanthurid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 20
†*Massalongius gazolai*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Acanthuroidei,* pan-zanclid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 20
†*Sharfia mirabilis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Lophioidei,* pan-lophiid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21

Continued

Appendix 1 continued.

Species	Clade	Stage	Age (Ma)	Location	Phylogeny
†*Tarkus squirei*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Lophioidei*, pan-ogcocephalid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Balkaria histiopterygia*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Abazinka Formation, Kabardino-Balkarian, Russian Federation	Figure 21
†*Zignoichthys oblongus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*, pan-molid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Iraniplectus bakhtiari*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*, pan-molid	Chattian	27.29–23.04	Pabdeh Formation (zone NP 24), Babaheidar, Iran	Figure 21
†*Eomola bimaxillaria*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*, pan-molid	Rupelian	33.9–27.3	Pshekha Formation, Maikop Group, North Caucasus, Russia	Figure 21
†*Protobalistum imperialis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Spinacanthus cuneiformis*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Proaracana dubia*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*, pan-aracanid	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Ctenoplectus williamsi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*, pan-triodontid	Ypresian	56.0–48.1	London Clay Formation, Greenways landfill, England, UK	Figure 21
†*Moclaybalistes danekrus*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Mo-clay, Fur Formation, Denmark	Figure 21
†*Eoplectus bloti*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21
†*Eospinus daniltshenkoi*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Danata Formation, Uylya-Kushlyuk, Turkmenistan	Figure 21
†*Bolcabalistes varii*	*Acanthomorpha, Acanthopterygii, Percomorpha, Acanthuriformes, Tetraodontoidei*	Ypresian	56.0–48.1	Monte Bolca, Pesciara Cave, Italy	Figure 21

Appendix 2
Classification of Living Lineages of *Actinopterygii*

An asterisk (*) identifies family-group names that are monotypic or monogeneric.
A double dagger (‡) identifies taxa currently not classified in a taxonomic family.
Names in bold are formal names defined in the clade accounts.

- ***Actinopterygii***
  - ***Polypteridae***
  - ***Actinopteri***
    - ***Acipenseriformes***
      - _Acipenseridae_
      - _Polyodontidae_
    - ***Neopterygii***
      - ***Holostei***
        - _Amiidae*_
        - _Lepisosteidae_
      - ***Teleostei***
        - ***Oseanacephala***
          - ***Elopomorpha***
            - ***Albulidae***
            - ***Anguilliformes***
              - ***Anguilloidei***
                - _Anguillidae*_
                - _Cyematidae*_
                - _Eurypharyngidae*_
                - _Monognathidae*_
                - _Moringuidae_
                - _Nemichthyidae_
                - _Neocyematidae*_
                - _Saccopharyngidae*_
                - _Serrivomeridae_
              - _Chlopsidae_
              - ***Congroidei***
                - _Colocongridae*_
                - _Congridae_
                - _Derichthyidae_
                - _Muraenesocidae_
                - _Nettastomatidae_
                - _Ophichthidae_
              - ***Muraenoidei***
                - _Heterenchelyidae_
                - _Muraenidae_
                - _Myrocongridae*_
              - ***Synaphobranchoidei***
                - _Protanguillidae*_
                - _Synaphobranchidae_
            - ***Elopiformes***
              - _Elopidae*_
              - _Megalopidae*_
            - ***Notacanthiformes***

- *Halosauridae*
- *Notacanthidae*

Osteoglossomorpha
- *Hiodontidae**
- **_Osteoglossiformes_**
  - *Gymnarchidae**
  - *Mormyridae*
  - *Notopteridae*
  - **_Osteoglossidae_**
  - *Pantodontidae**

Clupeocephala
- **_Otocephala_**
  - **_Alepocephaliformes_**
    - *Alepocephalidae*
    - *Platytroctidae*
  - **_Clupeiformes_**
    - **_Clupeoidei_**
      - *Alosidae*
      - *Chirocentridae**
      - *Clupeidae*
      - *Dorosomatidae*
      - *Dussumieriidae*
      - *Ehiravidae*
      - *Engraulidae*
      - *Pristigasteridae*
      - *Spratelloididae*
    - *Denticipitidae**
  - **_Ostariophysi_**
    - **_Gonorynchiformes_**
      - *Chanidae**
      - *Gonorynchidae**
      - *Kneriidae*
    - **_Otophysi_**
      - **_Characiformes_**
        - *Acestrorhynchidae*
        - *Alestidae*
        - *Anostomidae*
        - *Bryconidae*
        - *Chalceidae**
        - *Characidae*
        - *Chilodontidae*
        - *Crenuchidae*
        - *Ctenoluciidae*
        - *Curimatidae*
        - *Cynodontidae*
        - *Erythrinidae*
        - *Gasteropelecidae*
        - *Hemiodontidae*
        - *Hepsetidae**
        - *Iguanodectidae*
        - *Lebiasinidae*

- *Parodontidae*
- *Prochilodontidae*
- *Serrasalmidae*
- *Triportheidae*

Characiniformes

Citharinformes

- *Citharinidae*
- *Distichodontidae*

Cypriniformes

- *Catostomidae*
- ***Cobitoidei***
  - *Balitoridae*
  - *Botiidae*
  - *Cobitidae*
  - *Ellopostomatidae**
  - *Nemacheilidae*
  - *Vaillantellidae**
- ***Cyprinoidei***
  - *Acheilognathidae*
  - *Cyprinidae*
  - *Danionidae*
  - *Gobionidae*
  - *Leptobarbidae**
  - *Leuciscidae*
  - *Paedocyprididae**
  - *Psilorhynchidae**
  - *Sundadanionidae*
  - *Tanichthyidae**
  - *Tincidae**
  - *Xenocyprididae*
- *Gyrinocheilidae**

Gymnotiformes

- *Apteronotidae*
- *Gymnotidae*
- *Hypopomidae*
- *Rhamphichthyidae*
- *Sternopygidae*

Siluriformes

- *Diplomystidae*
- ***Loricarioidei***
  - *Astroblepidae**
  - *Callichthyidae*
  - *Loricariidae*
  - *Nematogenyidae**
  - *Scoloplacidae**
  - *Trichomycteridae*
- ***Siluroidei***
  - *Ailiidae*
  - *Akysidae*
  - *Amblycipitidae*
  - *Amphiliidae*
  - *Anchariidae*

- *Ariidae*
- *Aspredinidae*
- *Auchenipteridae*
- *Auchenoglanididae*
- *Austroglanididae**
- *Bagridae*
- *Cetopsidae*
- *Chacidae**
- *Clariidae*
- *Claroteidae*
- *Conorhynchos‡*
- *Cranoglanididae**
- *Doradidae*
- *Heptapteridae*
- *Heteropneustidae**
- *Horabagridae*
- *Ictaluridae*
- *Kryptoglanidae**
- *Lacantuniidae**
- *Malapteruridae*
- *Mochokidae*
- *Pangasiidae*
- *Phreatobiidae**
- *Pimelodidae*
- *Plotosidae*
- *Pseudopimelodidae*
- *Ritidae**
- *Schilbeidae*
- *Siluridae*
- *Sisoridae*

- ***Euteleostei***
  - *Lepidogalaxiidae**
  - ***Argentiniformes***
    - *Argentinidae*
    - *Bathylagidae*
    - *Microstomatidae*
    - *Opisthoproctidae*
  - ***Salmoniformes***
    - ***Esocidae***
    - *Salmonidae*
  - ***Stomiatii***
    - ***Stomiiformes***
      - *Gonostomatidae*
      - *Ichthyococcus‡*
      - *Phosichthyidae*
      - *Pollichthys‡*
      - *Polymetme‡*
      - *Stomiidae*
      - *Sternoptychidae*
      - *Vinciguerria‡*
      - *Yarrella‡*

  - ***Osmeriformes***
    - *Osmeridae*
    - *Salangidae*
    - *Plecoglossidae**
    - *Retropinnidae*
- *Galaxiidae*
- ***Neoteleostei***
  - *Ateleopodidae*
  - ***Aulopiformes***
    - *Alepisauridae**
    - *Aulopidae*
    - *Bathysauridae**
    - *Bathysauroididae**
    - *Bathysauropsidae**
    - *Chlorophthalmidae*
    - *Evermannellidae*
    - *Giganturidae**
    - *Ipnopidae*
    - *Notosudidae*
    - *Paralepididae*
    - *Paraulopidae**
    - *Pseudotrichonotidae**
    - *Scopelarchidae*
    - *Sudidae**
    - *Synodontidae*
  - ***Ctenosquamata***
    - ***Myctophiformes***
      - *Myctophidae*
      - *Neoscopelidae*
    - ***Acanthomorpha***
      - ***Lampriformes***
        - *Lampridae**
        - *Lophotidae*
        - *Radiicephalidae**
        - *Regalecidae*
        - *Trachipteridae*
        - *Veliferidae*
      - ***Paracanthopterygii***
        - ***Percopsiformes***
          - *Amblyopsidae*
          - *Aphredoderidae**
          - *Percopsidae**
        - *Polymixiidae**
        - ***Zeiformes***
          - *Cyttidae**
          - *Grammicolepididae*
          - *Oreosomatidae*
          - *Parazenidae*
          - *Zeidae*
          - *Zeniontidae*
        - ***Gadiformes***

- ***Gadoidei***
  - *Bathygadidae*
  - *Bregmacerotidae**
  - *Euclichthyidae**
  - *Gadidae*
  - *Gaidropsaridae*
  - *Lotidae*
  - *Lyconidae**
  - *Macrouridae*
  - *Macruronidae**
  - *Melanonidae**
  - *Merlucciidae*
  - *Moridae*
  - *Muraenolepididae*
  - *Phycidae*
  - *Ranicipitidae**
  - *Steindachneriidae**
  - *Trachyrincidae*
- *Stylephoridae**

Acanthopterygii
- ***Trachichthyiformes***
  - *Anomalopidae*
  - *Anoplogastridae**
  - *Diretmidae*
  - *Monocentridae*
  - *Trachichthyidae*
- ***Beryciformes***
  - ***Berycoidei***
    - *Barbourisiidae**
    - *Berycidae*
    - *Cetomimidae*
    - *Gibberichthyidae**
    - *Hispidoberycidae**
    - *Melamphaidae*
    - *Rondeletiidae**
    - *Stephanoberycidae*
  - *Holocentridae*
- ***Percomorpha***
  - ***Ophidiiformes***
    - ***Bythitoidei***
      - *Bythitidae*
      - *Dinematichthyidae*
    - *Ophidiidae*
  - ***Batrachoididae***
  - ***Gobiiformes***
    - ***Apogonoidei***
      - *Apogonidae*
      - *Kurtidae**
    - ***Gobioidei***
      - *Butidae*
      - *Eleotridae*

- *Gobiidae*
- *Milyeringidae*
- *Odontobutidae*
- *Oxudercidae*
- *Rhyacichthyidae*
- *Thalasseleotrididae*
- *Xenisthmidae*

*Trichonotidae**

Scombriformes

- *Amarsipidae**
- *Ariommatidae**
- *Arripidae**
- *Bramidae*
- *Caristiidae*
- *Centrolophidae*
- *Chiasmodontidae*
- *Gempylidae*
- *Icosteidae**
- *Lepidocybium*‡
- *Nomeidae*
- *Pomatomidae**
- *Scombridae*
- *Scombrolabracidae**
- *Stromateidae*
- *Tetragonuridae**
- *Trichiuridae*

Syngnathiformes

- *Aulostomidae**
- *Callionymidae*
- *Centriscidae*
- *Dactylopteridae*
- *Draconettidae*
- *Fistulariidae**
- *Macroramphosidae*
- *Mullidae*
- *Pegasidae*
- *Solenostomidae**
- *Syngnathidae*

Ovalentaria

- ***Atheriniformes***
  - ***Atherinoidei***
    - *Atherinidae*
    - *Atherinopsidae*
    - *Atherionidae**
    - *Bedotiidae*
    - *Isonidae**
    - *Melanotaeniidae*
    - *Phallostethidae*
    - *Pseudomugilidae*
    - *Telmatherinidae*
  - ***Belonoidei***

    - *Adrianichthyidae*
    - *Arrhamphus‡*
    - *Belonidae*
    - *Chriodorus‡*
    - *Euleptorhamphidae*
    - *Exocoetidae*
    - *Hemiramphidae*
    - *Hyporhamphus‡*
    - *Melapedalion‡*
    - *Zenarchopteridae*
  - ***Cyprinodontoidei***
    - *Anablepidae*
    - *Aphaniidae*
    - *Aplocheilidae*
    - *Cubanichthyidae*
    - *Cyprinodontidae*
    - *Fluviphylacidae**
    - *Fundulidae*
    - *Goodeidae*
    - *Nothobranchiidae*
    - *Orestiidae*
    - *Pantanodontidae*
    - *Poeciliidae*
    - *Procatopodidae*
    - *Profundulidae*
    - *Rivulidae*
    - *Valenciidae**
- ***Blenniiformes***
  - *Ambassidae*
  - ***Blennioidei***
    - *Blenniidae*
    - *Calliclinus‡*
    - *Chaenopsidae*
    - *Clinidae*
    - *Cryptotremini‡*
    - *Dactyloscopidae*
    - *Labrisomidae*
    - *Neoclinini‡*
    - *Tripterygiidae*
  - *Cichlidae*
  - *Congrogadidae*
  - *Embiotocidae*
  - *Gobiesocidae*
  - *Grammatidae*
  - *Mugilidae*
  - *Opistognathidae*
  - *Pholidichthyidae**
  - *Plesiopidae*
  - *Polycentridae*
  - *Pomacentridae*
  - *Pseudochromidae*

- ***Carangiformes***
  - ***Carangoidei***
    - *Carangidae*
    - *Coryphaenidae**
    - *Echeneidae*
    - *Istiophoridae*
    - *Leptobramidae**
    - *Menidae**
    - *Nematistiidae**
    - *Rachycentridae**
    - *Toxotidae*
    - *Trachinotidae*
    - *Xiphiidae**
  - *Centropomidae**
  - *Lactariidae**
  - *Latidae*
  - ***Pleuronectoidei***
    - *Achiridae*
    - *Achiropsettidae*
    - *Bothidae*
    - *Citharidae*
    - *Cyclopsettidae*
    - *Cynoglossidae*
    - *Oncopteridae**
    - *Paralichthodidae**
    - *Paralichthyidae*
    - *Pleuronectidae*
    - *Poecilopsettidae*
    - *Psettodidae**
    - *Rhombosoleidae*
    - *Samaridae*
    - *Scophthalmidae*
    - *Soleidae*
  - *Polynemidae*
  - *Sphyraenidae**
- ***Synbranchiformes***
  - ***Anabantoidei***
    - *Anabantidae*
    - *Channidae*
    - *Helostomatidae**
    - *Nandidae*
    - *Osphronemidae*
  - ***Synbranchoidei***
    - *Chaudhuriidae*
    - *Indostomidae**
    - *Mastacembelidae*
    - *Synbranchidae*
- ***Eupercaria***
  - ***Perciformes***
    - *Acanthistiinae**
    - *Anthiadidae*

- *Bembropidae*
- *Epinephelidae*
- *Serranidae*
- ***Notothenioidei***
  - *Aethotaxis*‡
  - *Bathydraconidae*
  - *Bovichtidae*
  - *Channichthyidae*
  - *Dissostichus*‡
  - *Eleginopsidae**
  - *Gobionotothen*‡
  - *Gvozdarus*‡
  - *Harpagiferidae*
  - *Nototheniidae*
  - *Percophidae**
  - *Pleuragrammatinae**
  - *Pseudaphritidae**
  - *Trematominae*
- ***Percoidei***
  - *Niphonidae**
  - *Percidae*
  - *Trachinidae*
- ***Scorpaenoidei***
  - *Anoplopomatidae*
  - *Bembridae*
  - ***Gasterosteidae***
  - *Platycephalidae*
  - ***Cottoidea***
    - *Agonidae*
    - *Cottidae*
    - *Cyclopteridae*
    - *Hexagrammidae*
    - *Jordaniidae*
    - *Liparidae*
    - *Psychrolutidae*
    - *Rhamphocottidae*
    - *Scorpaenichthyidae**
    - *Trichodontidae*
    - *Zaniolepididae*
  - ***Scorpaenoidea***
    - *Congiopodidae*
    - *Hoplichthyidae**
    - *Neosebastidae*
    - *Normanichthyidae**
    - *Plectrogeniidae*
    - *Scorpaenidae*
    - *Synanceiidae*
  - *Triglidae*
  - ***Zoarcoidea***
    - *Anarhichadidae*
    - *Bathymasteridae*

        - *Cebidichthyidae*
        - *Cryptacanthodidae**
        - *Eulophiidae*
        - *Lumpenidae*
        - *Neozoarcidae*
        - *Opisthocentridae*
        - *Pholidae*
        - *Ptilichthyidae**
        - *Stichaeidae*
        - *Zaproridae**
        - *Zoarcidae*

Centrarchiformes
- *Aplodactylidae**
- *Caesioscorpididae**
- *Centrarchidae*
- *Cheilodactylidae**
- *Chironemidae**
- *Cirrhitidae*
- *Dichistiidae**
- *Enoplosidae**
- *Girellidae*
- *Kuhliidae**
- *Kyphosidae*
- *Latridae*
- *Microcanthidae*
- *Oplegnathidae**
- *Parascorpididae**
- *Percalates*‡
- *Percichthyidae*
- *Scorpididae*
- *Sinipercidae*
- *Terapontidae*

Labriformes
- *Ammodytidae*
- *Centrogenyidae**
- *Cheimarrichthyidae**
- *Labridae*
- *Leptoscopidae*
- *Pinguipedidae*
- *Uranoscopidae*

Acropomatiformes
- *Acropomatidae*
- *Banjosidae**
- *Bathyclupeidae*
- *Champsodontidae**
- *Creediidae*
- *Dinolestidae**
- *Epigonidae*
- *Glaucosomatidae**
- *Hemerocoetidae*
- *Howellidae*

- *Lateolabracidae**
- *Malakichthyidae*
- *Ostracoberycidae**
- *Pempheridae*
- *Pentacerotidae*
- *Polyprionidae**
- *Schuettea‡*
- *Scombropidae**
- *Stereolepididae**
- *Symphysanodontidae*
- *Synagropidae*

Acanthuriformes

- ***Acanthuroidei***
    - *Acanthuridae*
    - *Luvaridae**
    - *Zanclidae**
- *Callanthiidae*
- *Caproidae*
- *Cepolidae*
- *Chaetodontidae*
- *Dinopercidae*
- *Drepaneidae**
- *Emmelichthyidae*
- *Ephippidae*
- *Gerreidae*
- *Haemulidae*
- *Leiognathidae*
- *Lethrinidae*
- *Lobotidae*
- ***Lophioidei***
    - *Antennariidae*
    - *Caulophrynidae*
    - *Centrophrynidae**
    - *Ceratiidae*
    - *Chaunacidae*
    - *Diceratiidae*
    - *Gigantactinidae*
    - *Himantolophidae**
    - *Linophrynidae*
    - *Lophichthyidae**
    - *Lophiidae*
    - *Melanocetidae**
    - *Neoceratiidae**
    - *Ogcocephalidae*
    - *Oneirodidae*
    - *Thaumatichthyidae*
- *Lutjanidae*
- *Malacanthidae*
- *Monodactylidae*
- *Moronidae*
- *Nemipteridae*

- *Pomacanthidae*
- *Priacanthidae*
- *Scatophagidae*
- *Sciaenidae*
- *Siganidae**
- *Sillaginidae*
- *Sparidae*
- ***Tetraodontoidei***
  - *Aracanidae*
  - *Balistidae*
  - *Diodontidae*
  - *Molidae*
  - *Monacanthidae*
  - *Ostraciidae*
  - *Tetraodontidae*
  - *Triacanthidae*
  - *Triacanthodidae*
  - *Triodontidae**

Appendix 3
Taxonomic Index

Fossil taxa are indicated with a dagger (†).
Numbers in bold italic are page ranges for clade accounts.

Literature Cited

Aarn, and W. Ivantsoff. 1997. Descriptive anatomy of *Cairnsichthys rhombosomoides* and *Iriatherina werneri* (Teleostei: Atheriniformes), and a phylogenetic analysis of Melanotaeniidae. Ichthyological Exploration of Freshwaters 8(2):107–150.

Aarn, W. Ivantsoff, and M. Kottelat. 1998. Phylogenetic analysis of Telmatherinidae (Teleostei: Atherinomorpha), with description of *Marosatherina*, a new genus from Sulawesi. Ichthyological Exploration of Freshwaters 9(3):311–323.

Adamson, E. A. S., D. A. Hurwood, and P. B. Mather. 2010. A reappraisal of the evolution of Asian snakehead fishes (Pisces, Channidae) using molecular data from multiple genes and fossil calibration. Molecular Phylogenetics and Evolution 56(2):707–717.

Afonso, G. V. F., F. Di Dario, L. N. Eduardo, F. Lucena-Frédou, A. Bertrand, and M. M. Mincarone. 2021. Taxonomy and distribution of deep-sea bigscales and whalefishes (Teleostei: Stephanoberycoidei) collected off northeastern Brazil, including seamounts and oceanic islands. Ichthyology and Herpetology 109(2):467–488.

Afsari, S., M. Yazdi, A. Bahrami, and G. Carnevale. 2014. A new deep-sea hatchetfish (Teleostei: Stomiiformes: Sternoptychidae) from the Eocene of Ilam, Zagros Basin, Iran. Bollettino della Società Paleontologica Italiana 53(1):27–37.

Agassiz, L. 1835. Recherches sur les Poissons Fossiles. Tome 4. Neuchatel, Switzerland: Petitpierre. 318 pp.

—1853. Extraordinary fishes from California, constituting a new family, described by L. Agassiz. American Journal of Science and Arts, Series 2, 16:380–390.

—1854. Appendix–Additional notes on the *Holconoti*. American Journal of Science and Arts, Series 2, 17:365–369.

Ahl, E. 1924. Neue afrikanische Zahnkarpfen aus dem Zoologischen Museum Berlin. Zoologischer Anzeiger 61:135–145.

Ahlstrom, E. H., H. G. Moser, and D. M. Cohen. 1984. Argentinoidei: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 155–169. (Special Publication 1.)

Aiello, B. R., M. W. Westneat, and M. E. Hale. 2017. Mechanosensation is evolutionarily tuned to locomotor mechanics. Proceedings of the National Academy of Sciences 114(17):4459–4464.

Albert, J. S. 2001. Species Diversity and Phylogenetic Systematics of American Knifefishes (Gymnotiformes, Teleostei). Ann Arbor: University of Michigan Museum of Zoology. 127 pp. (Miscellaneous Publications 190.)

Albert, J. S., and W. G. R. Crampton. 2005. Diversity and phylogeny of Neotropical electric fishes (Gymnotiformes). In: T. H. Bullock, C. D. Hopkins, A. N. Popper, and R. R. Fay, eds. Electroreception. Berlin: Springer. pp. 360–409.

Albert, J. S., and W. L. Fink. 2007. Phylogenetic relationships of fossil Neotropical electric fishes (Osteichthyes: Gymnotiformes) from the Upper Miocene of Bolivia. Journal of Vertebrate Paleontology 27(1):17–25.

Albert, J. S., M. J. Lannoo, and T. Yuri. 1998. Testing hypotheses of neural evolution in gymnotiform electric fishes using phylogenetic character data. Evolution 52(6):1760–1780.

Alcock, A. 1890. Natural history notes from H. M. Indian marine survey steamer ‘Investigator,’ Commander R. F. Hoskyn, R. N., commanding.—No. 18. On the bathybial fishes of the Arabian Sea, obtained during the season 1889–90. Annals and Magazine of Natural History, Series 6, 6(34):295–311.

Alda, F., V. A. Tagliacollo, M. J. Bernt, B. T. Waltz, W. B. Ludt, B. C. Faircloth, M. E. Alfaro, J. S. Albert, and P. Chakrabarty. 2019. Resolving deep nodes in an ancient radiation of Neotropical fishes in the presence of conflicting signals from incomplete lineage sorting. Systematic Biology 68(4):573–593.

Alfaro, M. E., C. D. Brock, B. L. Banbury, and P. C. Wainwright. 2009. Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? BMC Evolutionary Biology 9:255. https://doi.org/10.1186/1471-2148-9-255

Alfaro, M. E., B. C. Faircloth, R. C. Harrington, L. Sorenson, M. Friedman, C. E. Thacker, C. H. Oliveros, D. Černý, and T. J. Near. 2018. Explosive diversification of marine fishes at the Cretaceous–Palaeogene boundary. Nature Ecology and Evolution 2:688–696. https://doi.org/10.1038/s41559-018-0494-6

Alfaro, M. E., F. Santini, and C. D. Brock. 2007. Do reefs drive diversification in marine teleosts? Evidence from the pufferfishes and their allies (order Tetraodontiformes). Evolution 61(9):2104–2126.

Alfaro, M. E., F. Santini, C. Brock, H. Alamillo, A. Dornburg, D. L. Rabosky, G. Carnevale, and L. J. Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. Proceedings of the National Academy of Sciences of the United States of America 106(32):13410–13414.

Allen, G. R. 1985. Snappers of the World. Vol. 6 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 208 pp. (FAO Fisheries Synopsis 125.)

Almada, F., V. C. Almada, T. Guillemaud, and P. Wirtz. 2005. Phylogenetic relationships of the north-eastern Atlantic and Mediterranean blenniids. Biological Journal of the Linnean Society 86(3):283–295.

Altner, M., and B. Reichenbacher. 2015. †*Kenyaichthyidae* fam. nov. and †*Kenyaichthys* gen. nov.—first record of a fossil aplocheiloid killifish (Teleostei, Cyprinodontiformes). PLOS ONE 10(4):e0123056. https://doi.org/10.1371/journal.pone.0123056

Alvarado-Ortega, J., E. Ovalles-Damián, and G. Arratia. 2008. A review of the interrelationships of the order Ellimmichthyiformes (Teleostei: Clupeomorpha). In: G. Arratia, H. P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 4: Homology and Phylogeny. Munich: Verlag Dr. Friedrich Pfeil. pp. 257–278.

Alvarado-Ortega, J., and B. A. Than-Marchese. 2012. A Cenomanian aipichthyoid fish (Teleostei, Acanthomorpha) from America, *Zoqueichthys carolinae* gen. and sp. nov. from El Chango quarry (Cintalapa Member, Sierra Madre Formation), Chiapas, Mexico. Revista Mexicana de Ciencias Geológicas 29(3):735–748.

—2013. The first record of a North American Cenomanian Trachichthyidae fish (Acanthomorpha, Acanthopterygii), *Pepemkay maya*, gen. et sp. nov., from El Chango quarry (Sierra Madre Formation), Chiapas, Mexico. Journal of Vertebrate Paleontology 33(1):48–57.

Alvarado-Ortega, J., B. A. Than-Marchese, and M. P. Melgarejo-Damián. 2020. On the Albian occurrence of *Armigatus* (Teleostei, Clupeomorpha) in America, a new species from the Tlayúa Lagerstätte, Mexico. Palaeontologia Electronica 23(3):a52. https://doi.org/10.26879/1107

Alves, Y. M., J. Alvarado-Ortega, and P. M. Brito. 2020. †*Epaelops martinezi* gen. and sp. nov. from the Albian limestone deposits of the Tlayúa quarry, Mexico—a new late Mesozoic record of Elopiformes of the western Tethys. Cretaceous Research 110:104260. https://doi.org/10.1016/j.cretres.2019.104260

Alves-Gomes, J. A., G. Ortí, M. Haygood, W. Heiligenberg, and A. Meyer. 1995. Phylogenetic analysis of the South American electric fishes (order Gymnotiformes) and the evolution of their electrogenic system: a synthesis based on morphology, electrophysiology, and mitochondrial sequence data. Molecular Biology and Evolution 12(2):298–318.

Amaoka, K. 1969. Studies on the sinistral flounders found in the waters around Japan: taxonomy, anatomy and phylogeny. Journal of the Shimonoseki University of Fisheries 18:65–340.

Amaral, C. R. L., J. Avarado-Ortega, and P. Brito. 2013. *Sapperichthys* gen. nov., a new gonorynchid from the Cenomanian of Chiapas, Mexico. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Friedrich Pfeil. pp. 305–323.

Amaral, C. R. L., and P. M. Brito. 2012. A new Chanidae (Ostariophysii: Gonorynchiformes) from the Cretaceous of Brazil with affinities to Laurasian gonorynchiforms from Spain. PLOS ONE 7(5):e37247. https://doi.org/10.1371/journal.pone.0037247

Amorim, P. F., and W. J. E. M. Costa. 2018. Multigene phylogeny supports diversification of four-eyed fishes and one-sided livebearers (Cyprinodontiformes: Anablepidae) related to major South American geological events. PLOS ONE 13(6):e0199201. https://doi.org/10.1371/journal.pone.0199201

Anđelković, J. S. 1989. Tertiary Fishes of Yugoslavia: A Stratigraphic–Paleontologic–Paleoecological Study = Tercijarne Ribe Jugoslavije: Stratigrafsko–Paleontološko–Paleoekološka Studija. Zagreb: Jugoslavenska akademija znanosti i umjetnosti. 121 pp. (Palaeontologia Jugoslavica 38.)

Anderson, M. E. 1984. On the anatomy and phylogeny of Zoarcidae (Teleostei: Perciformes) [dissertation]. College of William and Mary. 254. pp. Dissertations, Theses, and Masters Projects, Paper 1539616550. https://scholarworks.wm.edu/etd/1539616550/

—1994. Systematics and Osteology of the Zoarcidae (Teleostei: Perciformes). Grahamstown, South Africa: Rhodes University. 120 pp. (Ichthyological Bulletin of the J. L. B. Smith Institute of Ichthyology 60.)

—1998. A late Cretaceous (Maastrichtian) Galaxiid Fish from South Africa. Grahamstown, South Africa: Rhodes University. 12 pp. (Special Publication of the J. L. B. Smith Institue of Ichthyology 60.)

Andrews, A. C. 1955. Greek and Latin terms for salmon and trout. Transactions and Proceedings of the American Philological Association 86(1955):308–318.

Andrews, J. V., J. P. Schein, and M. Friedman. 2023. An earliest Paleocene squirrelfish (Teleostei: Beryciformes: Holocentroidea) and its bearing on the timescale of holocentroid evolution. Journal of Systematic Palaeontology 21(1):2168571. https://doi.org/10.1080/14772019.2023.2168571

Andriashev, A. P., and V. M. Makushok. 1955. *Azygopterus corallinus* (Pisces, Blennioidei): a new fish without paired fins. Voprosy Ikhtiologii 3:50–53. [In Russian.]

Arambourg, C. 1966. Résultats scientifiques de la mission C. Arambourg en Syrie et en Iran (1938–1939). II. Les poissons oligocènes de l'Iran. Paris: Muséum national d'histoire naturelle. 210 pp. (Notes et Mémoires sur le Moyen-Orient 8.)

Arbour, V. M., M. E. Burns, and R. L. Sissons. 2009. A redescription of the ankylosaurid dinosaur *Dyoplosaurus acutosquameus* Parks, 1924 (Ornithischia: Ankylosauria) and a revision of the genus. Journal of Vertebrate Paleontology 29(4):1117–1135.

Arcila, D., L. C. Hughes, B. Melendez-Vazquez, C. C. Baldwin, W. T. White, K. E. Carpenter, J. T. Williams, M. D. Santos, J. J. Pogonoski, M. Miya, G. Ortí, and R. Betancur-R. 2021. Testing the utility of alternative metrics of branch support to address the ancient evolutionary radiation of tunas, stromateoids, and allies (Teleostei: Pelagiaria). Systematic Biology 70(6):1123–1144.

Arcila, D., G. Ortí, R. Vari, J. W. Armbruster, M. L. J. Stiassny, K. D. Ko, M. H. Sabaj, J. Lundberg, L. J. Revell, and R. Betancur-R. 2017. Genome-wide interrogation advances resolution of recalcitrant groups in the tree of life. Nature Ecology and Evolution 1:0020. https://doi.org/10.1038/s41559-016-0020

Arcila, D., P. Petry, and G. Ortí. 2018. Phylogenetic relationships of the family Tarumaniidae (Characiformes) based on nuclear and mitochondrial data. Neotropical Ichthyology 16(3):e180016. https://doi.org/10.1590/1982-0224-20180016

Arcila, D., R. A. Pyron, J. C. Tyler, G. Ortí, and R. Betancur-R. 2015. An evaluation of fossil tip-dating versus node-age calibrations in tetraodontiform fishes (Teleostei: Percomorphaceae). Molecular Phylogenetics and Evolution 82(Part A):131–145.

Arcila, D., and J. C. Tyler. 2017. Mass extinction in tetraodontiform fishes linked to the Palaeocene–Eocene thermal maximum. Proceedings of the Royal Society B, Biological Sciences 284(1866):20171771.

Argyriou, T., S. Giles, and M. Friedman. 2022. A Permian fish reveals widespread distribution of neopterygian-like jaw suspension. eLife 11:e58433. https://doi.org/10.7554/eLife.58433

Argyriou, T., S. Giles, M. Friedman, C. Romano, I. Kogan, and M. R. Sánchez-Villagra. 2018. Internal cranial anatomy of Early Triassic species of †*Saurichthys* (Actinopterygii: †Saurichthyiformes): implications for the phylogenetic placement of †saurichthyiforms. BMC Evolutionary Biology 18:161. https://doi.org/10.1186/s12862-018-1264-4

Armbruster, J. W., M. L. Niemiller, and P. B. Hart. 2016. Morphological evolution of the cave-, spring-, and swampfishes of the Amblyopsidae (Percopsiformes). Copeia 104(3):763–777.

Arnold, R. J. 2014. Evolutionary relationships of the enigmatic anglerfishes (Teleostei: Lophiiformes): can nuclear DNA provide resolution for conflicting morphological and mitochondrial phylogenies? [dissertation]. University of Washington. 92 pp.

Arratia, G. 1981. *Varasichthys ariasi* n. gen. et sp. from the Upper Jurassic of Chile (Pisces, Teleostei, Varasichthyidae n. fam.). Palaeontographica Abteilung A Palaeozoologie-Stratigraphie 175:107–139.

—1987a. *Anaethalion* and similar teleosts (Actinopterygii, Pisces) from the Late Jurassic (Tithonian) of southern Germany and their relationships. Palaeontographica Abteilung A 200:1–44.

—1987b. Description of the Primitive Family Diplomystidae (Siluriformes, Teleostei, Pisces): Morphology, Taxonomy and Phylogenetic Implications. Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig. 120 pp. (Bonner Zoologische Monographien 24.)

—1991. The caudal skeleton of Jurassic teleosts: a phylogenetic analysis. In: M.-M. Chang, Y.-H. Liu, and G.-R. Zhang, eds. Early Vertebrates and Related Problems in Evolutionary Biology. Beijing: Science Press. pp. 249–340.

—1992. Development and Variation of the Suspensorium of Primitive Catfishes (Teleostei: Ostariophysi) and Their Phylogenetic Relationships. Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig. 140 pp. (Bonner Zoologische Monographien 32.)

—1996a. The Jurassic and the early history of teleosts. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 243–259.

—1996b. Reassessment of the phylogenetic relationships of certain Jurassic teleosts and their implications on teleost phylogeny. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 219–242.

—1997. Basal Teleosts and Teleostean Phylogeny. Munich: Verlag Dr. Friedrich Pfeil. 168 pp. (Palaeo Ichthyologica 7.)

—1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record. Munich: Verlag Dr. Friedrich Pfeil. pp. 265–334.

—2000a. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the 'pholidophoriforms.' Paläontologische Zeitschrift 74:113–143.

—2000b. Phylogenetic relationships of Teleostei: past and present. Estudios Oceanologicos 19:19–51.

—2000c. Remarkable teleostean fishes from the Late Jurassic of southern Germany and their phylogenetic relationships. Fossil Record 3(1):137–179.

—2001. The sister-group of Teleostei: consensus and disagreements. Journal of Vertebrate Paleontology 21(4):767–773.

—2003a. Catfish head skeleton—an overview. In: G. Arratia, B. G. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes, Volume 1. Enfield, NH: Science Publishers. pp. 3–46.

—2003b. The siluriform postcranial skeleton—an overview. In: G. Arratia, B. G. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes, Volume 1. Enfield, NH: Science Publishers. pp. 121–157.

—2008. The varasichthyid and other crossognathiform fishes, and the break-up of Pangaea. In: L. Cavin, A. Longbottom, and M. Richter, eds. Fishes and the Break-up of Pangaea. London: Geological Society of London. pp. 71–92.

—2010a. The Clupeocephala re-visited: analysis of characters and homologies. Revista de Biología Marina y Oceanografía 45(S1):635–657.

—2010b. Critical analysis of the impact of fossils on teleostean phylogenies, especially that of basal teleosts. In: D. K. Elliot, J. G. Maisey, X. Yu, and D. Miao, eds. Morphology, Phylogeny, and Paleobiogeography of Fossil Fishes. Munich: Verlag Dr. Friedrich Pfeil. pp. 247–274.

—2013. Morphology, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). Journal of Vertebrate Paleontology 33(Suppl. 1):1–138.

—2016. New remarkable Late Jurassic teleosts from southern Germany: Ascalaboidae n. fam., its content, morphology, and phylogenetic relationships. Fossil Record 19(1):31–59.

—2017. New Triassic teleosts (Actinopterygii, Teleosteomorpha) from northern Italy and their phylogenetic relationships among the most basal teleosts. Journal of Vertebrate Paleontology 37(2):e1312690. https://doi.org/10.1080/02724634.2017.1312690

—2018. Otomorphs (=otocephalans or ostarioclupeomorphs) revisited. Neotropical Ichthyology 16(18):e180079. https://doi.org/10.1590/1982-0224-20180079

Arratia, G., and A. Cione. 1996. The record of fossil fishes of southern South America. In: G. Arratia, ed. Münchner Geowissenshaftliche Abhandlungen. Munich: Verlag Dr. Friedrich Pfeil. pp. 9–72.

Arratia, G., and M. Gayet. 1995. Sensory canals and related bones of Tertiary siluriform crania from Bolivia and North America and comparison with recent forms. Journal of Vertebrate Paleontology 15(3):482–505.

Arratia, G., and H.-P. Schultze. 2024. The oldest teleosts (Teleosteomorpha): their early taxonomic, phenotypic, and ecological diversification during the Triassic. Fossil Record 27(1):29–53.

Arratia, G., H.-P. Schultze, S. Gouiric-Cavalli, and C. Quezada-Romegialli. 2021. The intriguing †*Atacamichthys* fish from the Middle Jurassic of Chile—an amiiform or teleosteomorph? In: A. Pradel, J. S. S. Denton, and P. Janvier, eds. Ancient Fishes and Their Living

Relatives: A Tribute to John G. Maisey. Munich: Verlag Dr. Friedrich Pfeil. pp. 19–36.

Arratia, G., and D. Thies. 2001. A new teleost (Osteichthyes, Actinopterygii) from the Early Jurassic Posidonia shale of northern Germany. Fossil Record 4:167–187.

Arratia, G., and H. Tischlinger. 2010. The first record of Late Jurassic crossognathiform fishes from Europe and their phylogenetic importance for teleostean phylogeny. Fossil Record 13(2):317–341.

Arroyave, J., J. S. S. Denton, M. L. J. Stiassny, and W. J. Murphy. 2013. Are characiform fishes Gondwanan in origin? Insights from a time-scaled molecular phylogeny of the Citharinoidei (Ostariophysi: Characiformes). PLOS ONE 8(10):e77269. https://doi.org/10.1371/journal.pone.0077269

Arroyave, J., A. F. Mar-Silva, and P. Díaz-Jaimes. 2022. The complete mitochondrial genome of the Mexican blind brotula *Typhlias pearsei* (Ophidiiformes: Dinematichthydae): an endemic and troglomorphic cavefish from the Yucatán Peninsula karst aquifer. Mitochondrial DNA Part B 7:1151–1153.

Arroyave, J., and M. L. J. Stiassny. 2011. Phylogenetic relationships and the temporal context for the diversification of African characins of the family Alestidae (Ostariophysi: Characiformes): evidence from DNA sequence data. Molecular Phylogenetics and Evolution 60(3):385–397.

Artedi, P. 1738. Genera piscium. In: Quibus Systema Totum Ichthyologiæ Proponitus cum Classibus, Ordinibus, Generum Characteribus, Specierum Differentiis, Observationibus Plurimis. Redactis Speciebus 242 ad Genera 52. Ichthyologiæ Pars 3. Leiden: Lugduni Batavorum apud Conradum Wishoff. 88 pp.

Artyukhin, E. N. 2006. Morphological phylogeny of the order Acipenseriformes. Journal of Applied Ichthyology 22(Suppl. 1):66–69.

Ascanius, P. 1767. Icones rerum naturalium, ou figures enluminées d'histoire naturelle du Nord, premier cahier. Copenhagen: E. A. H. Möller. 22 pp.

—1772. Icones rerum naturalium, ou figures enluminées d'histoire naturelle du nord, second cahier. Copenhagen: E. A. H. Möller. 8 pp.

Aschliman, N. C., I. R. Tibbetts, and B. B. Collette. 2005. Relationships of sauries and needlefishes (Teleostei: Scomberesocoidea) to the internally fertilizing halfbeaks (Zenarchopteridae) based on the pharyngeal jaw apparatus. Proceedings of the Biological Society of Washington 118(2):416–427.

Astolfi, L., I. Dupanloup, R. Rossi, P. M. Bisol, E. Faure, and L. Congiu. 2005. Mitochondrial variability of sand smelt *Atherina boyeri* populations from north Mediterranean coastal lagoons. Marine Ecology Progress Series 297:233–243.

Astudillo-Clavijo, V., M. L. J. Stiassny, K. L. Ilves, Z. Musilova, W. Salzburger, and H. López-Fernández. 2023. Exon-based phylogenomics and the relationships of African cichlid fishes: tackling the challenges of reconstructing phylogenies with repeated rapid radiations. Systematic Biology 72(1):134–149.

Atta, C. J., H. Yuan, C. Li, D. Arcila, R. Betancur-R, L. C. Hughes, G. Ortí, and L. Tornabene. 2022. Exon-capture data and locus screening provide new insights into the phylogeny of flatfishes (Pleuronectoidei). Molecular Phylogenetics and Evolution 166:107315. https://doi.org/10.1016/j.ympev.2021.107315

Austin, C. M., M. H. Tan, L. J. Croft, M. P. Hammer, and H. M. Gan. 2015. Whole genome sequencing of the Asian Arowana (*Scleropages formosus*) provides insights into the evolution of ray-finned fishes. Genome Biology and Evolution 7(10):2885–2895.

Ayers, W. O. 1859 October 17. [Descriptions of fishes]. Proceedings of the California Academy of Sciences, Series 1, 2:25–32.

Azevedo, M. F. C., C. Oliveira, B. G. Pardo, P. Martinez, and F. Foresti. 2008. Phylogenetic analysis of the order Pleuronectiformes (Teleostei) based on sequences of 12S and 16S mitochondrial genes. Genetics and Molecular Biology 31(Suppl. 1):284–292.

Azpelicueta, M. D. L. M., and A. L. Cione. 2011. Redescription of the Eocene catfish *Bachmannia chubutensis* (Teleostei: Bachmanniidae) of southern South America. Journal of Vertebrate Paleontology 31(2):258–269.

Baciu, D. S., and B. Chanet. 2002. Les poissons plats fossils (Teleostei: Pleuronectiformes) de l'Oligocène de Piatra Neamt (Roumanie). Oryctos 4:17–38.

Baird, S. F., and C. Girard. 1853. Descriptions of new species of fishes collected by Mr. John H. Clark, on the U.S. and Mexican Boundary Survey, under Lt. Col. Jas. D. Graham. Proceedings of the Academy of Natural Science Philadelphia 6:387–390.

Bakke, I., and S. D. Johansen. 2005. Molecular phylogenetics of Gadidae and related Gadiformes based on mitochondrial DNA sequences. Marine Biotechnology 7:61–69.

Baldwin, C. C. 2013. The phylogenetic significance of colour patterns in marine teleost larvae. Zoological Journal of the Linnean Society 168(3):496–563.

Baldwin, C. C., and G. D. Johnson. 1995. A larva of the Atlantic flashlight fish, *Kryptophanaron alfredi* (Beryciformes, Anomalopidae), with a comparison of beryciform and stephanoberyciform larvae. Bulletin of Marine Science 56:1–24.

—1996. Interrelationships of Aulopiformes. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 355–404.

Baliga, V. B., and C. J. Law. 2016. Cleaners among wrasses: phylogenetics and evolutionary patterns of cleaning behavior within Labridae. Molecular Phylogenetics and Evolution 94(Part A):424–435.

Balushkin, A. V. 1992. Classification, phylogenetic relationships, and origins of the families of the suborder Notothenioidei (Perciformes). Journal of Ichthyology 32(7):90–110.

—1994. *Proeleginops grandeastmanorum* gen. et sp. nov. (Perciformes, Notothenioidei, Eleginopsidae) from the Late Eocene of Seymour Island (Antarctica) is a fossil notothenioid, not a gadiform. Journal of Ichthyology 34(8):10–23.

—2000. Morphology, classification, and evolution of notothenioid fishes of the Southern Ocean (Notothenioidei, Perciformes). Journal of Ichthyology 40(S1):S74–S109.

Bannikov, A. F. 1987. On the taxonomy, composition and origin of the family Carangidae. Journal of Ichthyology 27(1):1–8.

—1988. A new species of stromateoid fishes (Perciformes) the Lower Oligocene of the Caucasus. Paleontological Journal 22(4):107–112.

—1990. An Eocene veliferoid (Teleostei, Lampridiformes) from Bolca. Studi e Ricerche sui Giacimenti Terziari di Bolca 6:161–174.

—1998. New blennioid fishes of the families Blenniidae and Clinidae (Perciformes) from the Miocene of the Caucasus and Moldova. Paleonotological Journal 32(4):385–389.

—1999. Review of fossil Lampridiformes (Teleostei) finds with a description of a new Lophotidae genus and species from the Oligocene of the northern Caucasus. Paleontological Journal 33(1):68–76.

—2008. Revision of the atheriniform fish genera *Rhamphognathus* Agassiz and *Mesogaster* Agassiz (Teleostei) from the Eocene of Bolca, northern Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 9:65–76.

—2014a. A new genus of the family Palaeocentrotidae (Teleostei, Lampridiformes) from the Oligocene of the northern Caucasus and comments on other fossil Veliferoidei. Paleontological Journal 48(6):624–632.

—2014b. The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. Studi e Ricerche sui Giacimenti Terziari di Bolca 15:23–34.

Bannikov, A. F., and F. Bacchia. 2005. New species of the Cenomanian Eurypterygii (Pisces, Teleostei) from Lebanon. Paleontological Journal 39(5):514–522.

Bannikov, A. F., and D. Bellwood. 2015. A new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 16(13):5–16.

—2017. *Zorzinilabrus furcatus*, a new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 18(15):5–14.

Bannikov, A. F., and G. Carnevale. 2010. *Bellwoodilabrus landinii* n. gen., n. sp., a new genus and species of labrid fish (Teleostei, Perciformes) from the Eocene of Monte Bolca. Geodiversitas 32(2):201–220.

—2016. †*Carlomonnius quasigobius* gen. et sp. nov.: the first gobioid fish from the Eocene of Monte Bolca, Italy. Bulletin of Geosciences 91(1):13–22.

—2017. Eocene ghost pipefishes (Teleostei, Solenostomidae) from Monte Bolca, Italy. Bollettino della Società Paleontologica Italiana 56(3):319–331.

Bannikov, A. F., and T. H. Fraser. 2016. A new genus and species of cardinalfish (Percomorpha, Apogonidae) from the Eocene of Bolca, northern Italy (Monte Postale site). Studi e Ricerche sui Giacimenti Terziari di Bolca 17(14):13–23.

Bannikov, A. F., N. V. Parin, and J. Pinna. 1985. *Rhamphexocoetus volans*, gen. et sp. nov. a new beloniform fish (Beloniformes, Exocoetoidei) from the Lower Eocene of Italy. Journal of Ichthyology 25(2):150–155.

Bannikov, A. F., and L. Sorbini. 1990. *Eocoris bloti*, a new genus and species of labrid fish (Perciformes, Labroidei) from the Eocene of Monte Bolca, Italy. Studie Ricerche sui Giacimenti Terziari di Bolca 6:133–148.

—2000. Preliminary note on a Lower Paleocene fish fauna from Trebiciano (Trieste–north-eastern Italy). Atti del Museo Civico di Storia Naturale di Trieste 48:15–30.

Bannikov, A. F., and J. C. Tyler. 1995. Phylogenetic revision of the fish families Luvaridae and †Kushlukiidae (Acanthuroidei), with a new genus and two new species of Eocene luvarids. Washington, DC: Smithsonian Institution Press. 45 pp. (Smithsonian Contributions to Paleobiology 81.)

—2001. A new species of the luvarid fish genus †*Avitoluvarus* (Acanthuroidei: Perciformes) from the Eocene of the Caucasus in southwest Russia. Proceedings of the Biological Society of Washington 114(3):579–588.

Bannikov, A. F., J. C. Tyler, D. Arcila, and G. Carnevale. 2017. A new family of gymnodont fish (Tetraodontiformes) from the earliest Eocene of the Peri-Tethys (Kabardino-Balkaria, northern Caucasus, Russia). Journal of Systematic Palaeontology 15(2):129–146.

Bannikov, A., and R. Zorzin. 2019. *Paralabrus rossiae*, a new genus and species of putative labroid fish (Perciformes) from the Eocene of Bolca in northern Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 19:39–47.

Bargelloni, L., S. Marcato, L. Zane, and T. Patarnello. 2000. Mitochondrial phylogeny of notothenioids: a molecular approach to Antarctic fish evolution and biogeography. Systematic Biology 49(1):114–129.

Barros-García, D., E. Froufe, R. Bañón, J. C. Arronte, and A. de Carlos. 2018. Phylogenetic analysis shows the general diversification pattern of deep-sea notacanthiforms (Teleostei: Elopomorpha). Molecular Phylogenetics and Evolution 124:192–198.

Baskin, J. N. 1973. Structure and relationships of the Trichomycteridae [dissertation]. City University of New York. pp. 389.

Bean, L. 2021. Revision of the Mesozoic freshwater fish clade Archaeomaenidae. Alcheringa: An Australasian Journal of Palaeontology 45(2):217–259.

Bean, L. B., and G. Arratia. 2020. Anatomical revision of the Australian teleosts *Cavenderichthys talbragarensis* and *Waldmanichthys koonwarri* impacting on previous phylogenetic interpretations of teleostean relationships. Alcheringa: An Australasian Journal of Palaeontology 44(1):121–159.

Bean, T. H., and G. B. Goode. 1879. A catalogue of the fishes of Essex County, Massachusetts, including the fauna of Massachusetts Bay and the contiguous deep waters. Bulletin of the Essex Institute 11:1–38.

Beaulieu, J. M., R. H. Ree, J. Cavender-Bares, G. D. Weiblen, and M. J. Donoghue. 2012. Synthesizing phylogenetic knowledge for ecological research. Ecology 93(8):S4–S13.

Beckett, H. T., S. Giles, and M. Friedman. 2018. Comparative anatomy of the gill skeleton of fossil Aulopiformes (Teleostei: Eurypterygii). Journal of Systematic Palaeontology 16(14):1221–1245.

Beckett, H. T., S. Giles, Z. Johanson, and M. Friedman. 2018. Morphology and phylogenetic relationships of fossil snake mackerels and cutlassfishes (Trichiuroidea) from the Eocene (Ypresian) London Clay Formation. Papers in Palaeontology 4(4):577–603.

Beebe, W., and J. Crane. 1939. Deep-sea fishes of the Bermuda Oceanographic Expeditions. Family Melanostomiatidae. Zoologica 24:65–228.

Begle, D. P. 1991. Relationships of the osmeroid fishes and the use of reductive characters in phylogenetic analysis. Systematic Zoology 40(1):33–53.

—1992. Monophyly and relationships of the argentinoid fishes. Copeia 1992(2):350–366.

Bell, M. A., J. D. Stewart, and P. J. Park. 2009. The world's oldest fossil threespine stickleback fish. Copeia 2009(2):256–265.

Bellwood, D. R. 1990. A new fossil fish *Phyllopharyngodon longipinnis* gen. et sp. nov. (family Labridae) from the Eocene, Monte Bolca, Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 6:149–160.

Bellwood, D. R., L. van Herwerden, and N. Konow. 2004. Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). Molecular Phylogenetics and Evolution 33(1):140–155.

Belouze, A. 2002. Compréhension morphologique et phylogénétique des taxons actuels et fossiles rapportés aux Anguilliformes ("poissons," téléostéens). Lyon: U.F.R. des Sciences de la Terre, Université Claude-Bernard. 401 pp. (Documents des Laboratoires de Géologie, Lyon 158.)

Belouze, A., M. Gayet, and C. Atallah. 2003. Les premiers Anguilliformes: II. Paraphylie du genre *Urenchelys* Woodward, 1900 et relations phylogénétiques = The first Anguilliformes: II. Paraphyly of the genus *Urenchelys* Woodward, 1900 and phylogenetic relationships. Géobios 36(4):351–378.

Bemis, K. E., and B. B. Collette. 2019. Family Scomberesocidae. In: B. B. Collette, K. E. Bemis, N. V. Parin, and I. B. Shakhovskoy. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. B. B. Collette and T. J. Near, eds. New Haven, CT: Peabody Museum of Natural History, Yale University. pp. 79–88. (Memoir 1, Fishes of the Western North Atlantic 10.)

Bemis, W. E., E. K. Findeis, and L. Grande. 1997. An overview of Acipenseriformes. Environmental Biology of Fishes 48:25–72.

Benton, M. J., P. C. J. Donoghue, R. J. Asher, M. Friedman, T. J. Near, and J. Vinther. 2015. Constraints on the timescale of animal evolutionary history. Palaeontologia Electronica 18.1.1FC:1–106. https://doi.org/10.26879/424

Berendzen, P. B., and W. W. Dimmick. 2002. Phylogenetic relationships of pleuronectiformes based on molecular evidence. Copeia 2002(3):642–652.

Berg, L. S. 1937. A classification of fish-like vertebrates. Bulletin de l'Acadèmie des Sciences de l'URSS, Classe des Sciences Mathématiques et Naturelles 4:1277–1280.

—1940. Classification of fishes both Recent and fossil. Travaux de l'Institute de l'Academie des Sciences de l'URSS 5:87–517.

Berra, T. M. 2003. Nurseryfsh, *Kurtus gulliveri* (Perciformes: Kurtidae), from northern Australia: redescription, distribution, egg mass, and comparison with *K. indicus* from southeast Asia. Ichthyological Exploration of Freshwaters 14(4):295–306.

Berra, T. M., and J. D. Humphrey. 2002. Gross anatomy and histology of the hook and skin of forehead brooding male nurseryfish, *Kurtus gulliveri,* from northern Australia. Environmental Biology of Fishes 65:263–270.

Bertelsen, E., J. G. Nielsen, and D. G. Smith. 1989. Suborder Saccopharyngoidei. In: E. B. Böhlke, ed. Orders Anguilliformes and Saccopharyngiformes, Volume 1. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 636–655. (Memoir 1, Fishes of the Western North Atlantic 9.)

Bertin, L., and C. Arambourg. 1958. Super-ordre des téléostéens (Teleostei). In: P. Grassé, ed. Traité de zoologie, tome 13, fascicule 3. Paris: Libraires de L'académi de médecine. pp. 2204–2500.

Bertrand, S., and H. Escrivá. 2014. Chordates. In: P. Vargas and R. Zardoya, eds. The Tree of Life. Sunderland, MA: Sinauer Associates. pp. 458–468.

Betancur-R., R., D. Arcila, R. P. Vari, L. C. Hughes, C. Oliveira, M. H. Sabaj, and G. Ortí. 2019. Phylogenomic incongruence, hypothesis testing, and taxonomic sampling: the monophyly of characiform fishes. Evolution 73(2):329–345.

Betancur-R, R., R. E. Broughton, E. O. Wiley, K. Carpenter, J. A. López, C. Li, N. I. Holcroft, D. Arcila, M. Sanciangco, J. C. Cureton II, et al. 2013. The tree of life and a new classification of bony fishes. PLOS Currents 5. https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288.

Betancur-R, R., C. Li, T. A. Munroe, J. A. Ballesteros, and G. Ortí. 2013. Addressing gene tree discordance and non-stationarity to resolve a multi-locus phylogeny of the flatfishes (Teleostei: Pleuronectiformes). Systematic Biology 62(5):763–785.

Betancur-R, R., and G. Ortí. 2014. Molecular evidence for the monophyly of flatfishes (Carangimorpharia: Pleuronectiformes). Molecular Phylogenetics and Evolution 73:18–22.

Betancur-R, R., E. O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre, and G. Ortí. 2017. Phylogenetic classification of bony fishes. BMC Evolutionary Biology 17:162. https://doi.org/10.1186/s12862-017-0958-3

Betancur-R, R., E. O. Wiley, M. Miya, G. Lecointre, N. Bailly, and G. Ortí. 2014. New and revised classification of bony fishes. Version 2. Accessed 24 June 2014. http://www.deepfin.org/Classification_v2.htm.

Bi, X., K. Wang, L. Yang, H. Pan, H. Jiang, Q. Wei, M. Fang, H. Yu, C. Zhu, Y. Cai, et al. 2021. Tracing the genetic footprints of vertebrate landing in non-teleost ray-finned fishes. Cell 184(5):1377–1391.

Bian, C., Y. Hu, V. Ravi, I. S. Kuznetsova, X. Shen, X. Mu, Y. Sun, X. You, J. Li, X. Li, et al. 2016. The Asian arowana (*Scleropages formosus*) genome provides new insights into the evolution of an early lineage of teleosts. Scientific Reports 6:24501.

Bieńkowska-Wasiluk, M., and N. Bonde. 2015. A new Oligocene relative of the Caproidae (Teleostei: Acanthopterygii) from the Outer Carpathians, Poland. Bulletin of Geosciences 90(2):461–478.

Bieńkowska-Wasiluk, M., N. Bonde, P. R. Møller, and A. Gaździcki. 2013. Eocene relatives of cod icefishes

(Perciformes: Notothenioidei) from Seymour Island, Antarctica. Geological Quarterly 57(4):567–582.

Bigelow, H. B. 1963. Order Isospondyli: characters and keys to suborders and families. In: B. Bigelow and W. C. Schroeder, eds. Soft-rayed bony fishes. Class Osteichthyes. Sturgeons, Gars, Tarpon, Ladyfish, Bonefish, Salmon, Charrs, Anchovies, Herring, Shads, Smelt, Capelin, et al. New Haven, CT: Sears Foundation of Marine Research, Yale University. pp. 89–106. (Memoir 1, Fishes of the Western North Atlantic 3.)

Birge, T. L., G. M. Ralph, F. Di Dario, T. A. Munroe, R. W. Bullock, S. M. Maxwell, M. D. Santos, H. Hata, and K. E. Carpenter. 2021. Global conservation status of the world's most prominent forage fishes (Teleostei: Clupeiformes). Biological Conservation 253:108903. https://doi.org/10.1016/j.biocon.2020.108903

Bista, I., J. M. D. Wood, T. Desvignes, S. A. McCarthy, M. Matschiner, Z. Ning, A. Tracey, J. Torrance, Y. Sims, W. Chow, et al. 2023. Genomics of cold adaptations in the Antarctic notothenioid fish radiation. Nature Communications 14:3412. https://doi.org/10.1038/s41467-023-38567-6

Blainville, H. M. D. 1818. Des ichthyolites du bassin de la Méditerranée. a. Des ichthyolites de Monte-Bolca, ou Vestena-Nuova, dans le Véronais. In: Une société de naturalistes et d'agriculteurs. Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médicine, etc., tome 27. Paris: Deterville. pp. 334–361.

Bleeker, P. 1849. Bijdrage tot de kennis der ichthyologische fauna van het eiland Madura, met beschrijving van eenige nieuwe soorten. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 22(8):1–16.

—1852. Bijdrage tot de kennis der ichthijologische fauna van de Moluksche Eilanden. Visschen van Amboina en Ceram. Natuurkundig Tijdschrift voor Nederlandsch Indië 3:229–309.

—1853a. Derde bijdrage tot de kennis der ichthyologische fauna van Amboina. Natuurkundig Tijdschrift voor Nederlandsch Indië 4:91–130.

—1853b. Nalezingen op de ichthyologie van Japan. Verhandelingen van het Bataviaasch Genootschap van Kunsten en Wetenschappen 25(7):1–56.

—1855. Bijdrage tot de kennis der ichthyologische fauna van de Batoe Eilanden. Natuurkundig Tijdschrift voor Nederlandsch Indië 8:305–328.

—1856. Bijdrage tot de kennis der ichthyologische fauna van het eiland Boeroe. Natuurkundig Tijdschrift voor Nederlandsch Indië 11:383–414.

—1858. Siluri. Vol. 1 of Ichthyologiae Archipelagi Indici Prodromus. Batavia: Lange. 370 pp.

—1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. Acta Societatis Scientiarum Indo-Neerlandensis 6:1–276.

—1862. Conspectus generum Labroideorum analyticus. Proceedings of the Zoological Society of London 1861, pt. 3, pp. 408–418.

—1864a. Atlas ichthyologique des Indes orientales néêrlandaises: publié sous les auspices du gouvernement colonial néêrlandais, tome 4. Amsterdam: Frédéric Muller, editeur. 132 pp.

—1864b. Poissons inédits indo-archipélagiques de l'ordre des Murènes. Nederlandsch Tijdschrift voor de Dierkunde 2:38–54.

—1864c. Systema Muraenorum revisum. Nederlandsch Tijdschrift voor de Dierkunde. 2:113–122.

—1866. Systema Balistidorum, Ostracionidorum, Gymnodontidorumque revisum. Nederlandsch Tijdschrift voor de Dierkunde 3:8–19.

—1874. Poissons de Madagascar et de l'île la Réunion des collections de MM. Pollen et van Dam. In: P. L. Pollen and D. C. van Dam, eds. Recherches sur la faune de Madagascar et de ses dépendances d'après les découvertes de François. Leide [Leiden]: E. J. Brill. pp. 1–106.

Bloch, M. E. 1786. Naturgeschichte der ausländischen Fische, Volume 2. Berlin: Auf Kosten des Verfassers und in Commission bei dem Buchhändler Hr. Hesse. 160 pp.

—1788. Ueber zwey merkwürdige Fischarten. Abhandlungen der Böhmischen Gesellschaft der Wissenschaften 3:278–282.

—1792a. Beschreibung zweyer neuen Fische. Schriften der Gesellschaft Naturforschender Freunde zu Berlin 10:422–424.

—1792b. Naturgeschichte der ausländischen Fische, Volume 6. Berlin: Auf Kosten des Verfassers und in Commission bei dem Buchhändler Hr. Hesse. 174 pp.

—1795. Naturgeschichte der ausländischen Fische, Volume 9. Berlin: Auf Kosten des Verfassers und in Commission bei dem Buchhändler Hr. Hesse. 192 pp.

Bloch, M. E., and J. G. Schneider. 1801. Systema ichthyologiae iconibus cx illustratum. Berlin: Sumtibus auctoris impressum et Bibliopolio Sanderiano commissum. 584 pp.

Bloom, D. D., and J. P. Egan. 2018. Systematics of Clupeiformes and testing for ecological limits on species richness in a trans-marine/freshwater clade. Neotropical Ichthyology 16(3):e180095. https://doi.org/10.1590/1982-0224-20180095

Bloom, D. D., and N. R. Lovejoy. 2014. The evolutionary origins of diadromy inferred from a time-calibrated phylogeny for Clupeiformes (herring and allies). Proceedings of the Royal Society B, Biological Sciences 281(1778):20132081.

Bloom, D. D., P. J. Unmack, A. E. Gosztonyi, K. R. Piller, and N. R. Lovejoy. 2012. It's a family matter: molecular phylogenetics of Atheriniformes and the polyphyly of the surf silversides (family: Notocheiridae). Molecular Phylogenetics and Evolution 62(3):1025–1030.

Bloom, D. D., J. T. Weir, K. R. Piller, and N. R. Lovejoy. 2013. Do freshwater fishes diversify faster than marine fishes? A test using state-dependent diversification analyses and molecular phylogenetics of new world silversides (Atherinopsidae). Evolution 67(7):2040–2057.

Blot, J. 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie): catalogue systématique présentat l'état actuel des recherches concernant cette faune. Bulletin du Muséum National d'Histoire Naturelle 2(4):339–396.

Blum, S. D. 1988. The osteology and phylogeny of the Chaetodontidae (Pisces: Perciformes) [dissertation]. University of Hawaii. 365 pp.

—1991. *Dastilbe* Jordan, 1910. In: J. G. Maisey, ed. Santana Fossils: An Illustrated Atlas. Neptune City, NJ: T. F. H. Publications. pp. 274–283.

Boeseman, M. 1964. Notes on the fishes of western New Guinea: II. *Lophichthys boschmai*, a new genus and species from the Arafoera Sea. Zoologische Mededelingen 39(2):12–18.

Bogan, S., F. L. Agnolin, and A. Scanferla. 2018. A new Andinichthyidae catfish (Ostariophysi, Siluriformes) from the Paleogene of northwestern Argentina. Journal of Vertebrate Paleontology 38(3):e1449117. https://doi.org/10.1080/02724634.2018.1449117

Bohlen, J., and V. Šlechtová. 2009. Phylogenetic position of the fish genus *Ellopostoma* (Teleostei: Cypriniformes) using molecular genetic data. Ichthyological Exploration of Freshwaters 20:157–162.

Böhlke, J. E. 1966. Order Lyomeri. In: C. W. Mead, ed. Orders Iniomi and Lyomeri: Lizardfishes, Other Iniomi, Deepsea Gulpers. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 603–628. (Memoir 1, Fishes of the Western North Atlantic 5.)

Bonaparte, C. L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Giornale Arcadico di Scienze Lettere ed Arti 52:155–189.

—1840. Prodromus systematis ichthyologiae. Nuovi Annali delle Scienze naturali Bologna Series 1 Anno 2 4:181–196, 272–277.

—1845. Specchio generale del sistema ittiologico. Atti della sesta Riunione degli Scienziati Italiani 6:386–390.

Bonde, N. C. 1993. Osteoglossids (Teleostei: Osteoglossomorpha) of the Mesozoic—comments on their relationships. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology; proceedings of the international meeting, Eichstätt, 1993. Munich: Verlag Dr. Friedrich Pfeil. pp. 273–284.

Borden, W. C., T. Grande, and W. L. Smith. 2013. Comparative osteology and myology of the caudal fin in Paracanthopterygii (Teleostei: Acanthomorpha). In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Friedrich Pfeil. pp. 419–455.

Boulenger, G. A. 1891. Pisces. Zoological Record 28:1–41.

—1895. Catalogue of the Perciform Fishes in the British Museum. London: Taylor and Francis. 394 pp.

—1897. Descriptions of new fishes from the upper Congo. II. Annals and Magazine of Natural History, Series 6, 20:422–427.

—1904a. A synopsis of the suborders and families of teleostean fishes. Annals and Magazine of Natural History, Series 7, 13:161–190.

—1904b. Teleostei. Cambridge Natural History 7: 539–727.

—1906. Fourth contribution to the ichthyology of Lake Tanganyika.—Report on the collection of fishes made by Dr. W. A. Cunnington during the third Tanganyika Expedition, 1904–1905. Transactions of the Zoological Society of London 17:537–601.

—1909. Catalogue of the Fresh-water Fishes of Africa in the British Museum (Natural History), Volume 1. London: Taylor and Francis. 373 pp.

Bowne, P. S. 1994. Systematics and morphology of the Gasterosteiformes. In: M. A. Bell and S. A. Foster, eds. The Evolutionary Biology of the Threespine Stickleback. Oxford: Oxford University Press. pp. 28–60.

Braasch, I., A. R. Gehrke, J. J. Smith, K. Kawasaki, T. Manousaki, J. Pasquier, A. Amores, T. Desvignes, P. Batzel, J. Catchen, et al. 2016. The spotted gar genome illuminates vertebrate evolution and facilitates human-teleost comparisons. Nature Genetics 48:427–437.

Bragança, P. H. N., P. F. Amorim, and W. J. E. M. Costa. 2018. Pantanodontidae (Teleostei, Cyprinodontiformes), the sister group to all other cyprinodontoid killifishes as inferred by molecular data. Zoosystematics and Evolution 94:137–145.

Bragança, P. H. N., and W. J. E. M. Costa. 2018. Time-calibrated molecular phylogeny reveals a Miocene–Pliocene diversification in the Amazon miniature killifish genus *Fluviphylax* (Cyprinodontiformes: Cyprinodontoidei). Organisms Diversity and Evolution 18(3):345–353.

—2019. Multigene fossil-calibrated analysis of the African lampeyes (Cyprinodontoidei: Procatopodidae) reveals an early Oligocene origin and Neogene diversification driven by palaeogeographic and palaeoclimatic events. Organisms Diversity and Evolution 19(2):303–320.

Branson, B. A., and G. A. Moore. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. Copeia 1962(1):1–108.

Bravo, G. A., A. Antonelli, C. D. Bacon, K. Bartoszek, M. P. K. Blom, S. Huynh, G. Jones, L. L. Knowles, S. Lamichhaney, T. Marcussen, et al. 2019. Embracing heterogeneity: coalescing the tree of life and the future of phylogenomics. PeerJ 7:e6399. https://doi.org/10.7717/peerj.6399

Breder, C. M., Jr., and D. E. Rosen. 1966. Modes of Reproduction in Fishes. Garden City, NJ: Natural History Press. 941 pp.

Breining, T., and R. Britz. 2000. Egg surface structure of three clingfish species, using scanning electron microscopy. Journal of Fish Biology 56(5):1129–1137.

Bridge, T. W. 1904. Fishes. Cambridge Natural History 7:141–537.

Brinkman, D. B., M. G. Newbrey, and A. G. Neuman. 2014. Diversity and paleoecology of actinopterygian fish from vertebrate microfossil localities of the Maastrichtian Hell Creek Formation of Montana. In: G. P. Wilson, W. A. Clemens, J. R. Horner, and J. H. Hartman, eds. Through the End of the Cretaceous in the Type Locality of the Hell Creek Formation in Montana and Adjacent Areas. pp. 247–270. (Geological Society of America Special Papers 503.)

Brito, P. M., J. Alvarado-Ortega, and F. J. Meunier. 2017. Earliest known lepisosteoid extends the range of anatomically modern gars to the Late Jurassic. Scientific Reports 7:17830.

Brito, P. M., F. J. Figueiredo, and M. E. C. Leal. 2020. A revision of *Laeliichthys ancestralis* Santos, 1985

(Teleostei: Osteoglossomorpha) from the Lower Cretaceous of Brazil: phylogenetic relationships and biogeographical implications. PLOS ONE 15(10):e0241009. https://doi.org/10.1371/journal.pone.0241009

Britz, R. 1994. Ontogenic features of *Luciocephalus* (Perciformes, Anabantoidei) with a reversed hypothesis of anabantoid intrarelationships. Zoological Journal of the Linnean Society 112(4):491–508.

—1996. Ontogeny of the ethmoidal region and hyopalatine arch in *Macrognathus pancalus* (Percomorpha, Mastacembeloidei): with critical remarks on mastacembeloid inter- and intrarelationships. American Museum Novitates 3181:1–18.

—1997. Egg surface structure and larval cement glands in nandid and badid fishes, with remarks on phylogeny and biogeography. American Museum Novitates 3195:1–17.

—2001. The genus *Betta*—monophyly and intrarelationships, with remarks on the subfamilies Macropodinae and Luciocephalinae (Teleostei: Osphronemidae). Ichthyological Exploration of Freshwaters 12:305–318.

Britz, R., and P. Bartsch. 2003. The myth of dorsal ribs in gnathostome vertebrates. Proceedings of the Royal Society of London Series B, Biological Sciences 270(Suppl. 1):S1–S4.

Britz, R., and K. W. Conway. 2011. The Cypriniformes tree of confusion. Zootaxa 2946(1):73–78. https://doi.org/10.11646/zootaxa.2946.1.15

Britz, R., K. W. Conway, and L. Rüber. 2014. Miniatures, morphology and molecules: *Paedocypris* and its phylogenetic position (Teleostei, Cypriniformes). Zoological Journal of the Linnean Society 172:556–615.

Britz, R., N. Dahanukar, V. K. Anoop, S. Philip, B. Clark, R. Raghavan, and L. Rüber. 2020. Aenigmachannidae, a new family of snakehead fishes (Teleostei: Channoidei) from subterranean waters of South India. Scientific Reports 10:16081.

Britz, R., and G. D. Johnson. 2002. "Paradox Lost": skeletal ontogeny of *Indostomus paradoxus* and its signficance for the phylogenetic relationships of Indostomidae (Teleostei, Gasterosteiformes). American Museum Novitates 3383:1–43.

—2003. On the homology of the posteriormost gill arch in polypterids (Cladistia, Actinopterygii). Zoological Journal of the Linnean Society 138:495–503.

—2010. Occipito-vertebral fusion in actinopterygians: conjecture, myth and reality. Part 1, non-teleosts. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 77–93.

Britz, R., F. Kakkassery, and R. Raghavan. 2014. Osteology of *Kryptoglanis shajii*, a stygobitic catfish (Teleostei: Siluriformes) from peninsular India with diagnosis of a new family Kryptoglanidae. Ichthyological Exploration of Freshwaters 24:193–207.

Britz, R., and M. Kottelat. 1999. Two new species of the gasterosteiform fishes of the genus *Indostomus* (Teleostei: Indostomidae). Ichthyological Exploration of Freshwaters 10:327–336.

—2003. Descriptive osteology of the family Chaudhuriidae (Teleostei, Synbranchiformes, Mastacembeloidei), with a discussion of its relationships. American Museum Novitates 3418:1–62.

Britz, R., M. Kottelat, and T. H. Hui. 2011. *Fangfangia spinicleithralis*, a new genus and species of miniature cyprinid fish from the peat swamp forests of Borneo (Teleostei: Cyprinidae). Ichthyological Exploration of Freshwaters 22:327–335.

Britz, R., K. Kumar, and F. Baby. 2012. *Pristolepis rubripinnis*, a new species of fish from southern India (Teleostei: Percomorpha: Pristolepididae). Zootaxa 3345(1):59–68. https://doi.org/10.11646/zootaxa.3345.1.3

Brothers, E. B. 1984. Otolith studies. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 50–57. (Special Publication 1.)

Broughton, R. E. 2010. Phylogeny of teleosts based on mitochondrial sequences. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 61–76.

Broughton, R. E., R. Betancur-R, C. Li, G. Arratia, and G. Ortí. 2013. Multi-locus phylogenetic analysis reveals the pattern and tempo of bony fish evolution. PLOS Currents 5. https://doi.org/currents.tol.2ca8041495ffafd0c92756e75247483e

Broussonet, P. M. A. 1782. Ichtyologia, Sistens Piscium Descriptiones et Icones. London: Elmsy. 42 pp.

Brownstein, C. D. 2022. Unappreciated Cenozoic ecomorphological diversification of stem gars revealed by a new large species. Acta Palaeontologica Polonica 67(3):559–568.

—2023. Syngnathoid evolutionary history and the conundrum of fossil misplacement. Integrative Organismal Biology 5(1):obad011. https://doi.org/10.1093/iob/obad011

Brownstein, C. D., D. Kim, O. D. Orr, G. M. Hogue, B. H. Tracy, M. W. Pugh, R. Singer, C. Myles-McBurney, J. M. Mollish, J. W. Simmons, et al. 2022. Hidden species diversity in an iconic living fossil vertebrate. Biology Letters 18(11):20220395. https://doi.org/10.1098/rsbl.2022.0395

Brownstein, C. D., and T. R. Lyson. 2022. Giant gar from directly above the Cretaceous–Palaeogene boundary suggests healthy freshwater ecosystems existed within thousands of years of the asteroid impact. Biology Letters 18(6):20220118. https://doi.org/10.1098/rsbl.2022.0118

Brownstein, C. D., and T. J. Near. 2023. Evolutionary origins of the lampriform pelagic radiation. Zoological Journal of the Linnean Society, zlad142. https://doi.org/10.1093/zoolinnean/zlad142

Brownstein, C. D., L. Yang, M. Friedman, and T. J. Near. 2023. Phylogenomics of the ancient and species-depauperate gars tracks 150 million years of continental fragmentation in the Northern Hemisphere. Systematic Biology 72(1):213–227.

Brünnich, M. T. 1768. Ichthyologia Massiliensis, sistens piscium descriptiones eorumque apud incolas nomina. Accedunt Spolia Maris Adriatici. Hafniae et Lipsiae [Copenhagen and Leipzig]: Apud Rothii viduam et Proft. 110 pp.

—1788. Om en ny fiskart, den draabeplettede pladefish, fanget ved Helsingör i Nordsöen 1786. Kongelige Danske Videnskabernes Selskabs Skrivter, Nye Samling af det 3:398–407.

Buckup, P. A. 1993. The monophyly of the Characidiinae, a Neotropical group of characiform fishes (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 108:225–245.

—1998. Relationships of the Characidiinae and phylogeny of characiform fishes (Teleostei: Ostariophysi). In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 123–144.

Burgess, G. H. 1974. Evidence for the elevation to family status of the angelfishes (Pomacanthidae), previously considered to be a subfamily of the butterflyfish family, Chaetodontidae. Pacific Science 28(1):57–71.

Bürgin, T. 1989. The oral jaw apparatus of the Indian Halibut, *Psettodes erumei* (Bloch and Schneider, 1801) (Teleostei; Pleuronectiformes)—a formal description with functional considerations. Progress in Zoology 35:463–466.

Burns, M. D., and B. L. Sidlauskas. 2019. Ancient and contingent body shape diversification in a hyperdiverse continental fish radiation. Evolution 73(3):569–587.

Burridge, C. P., R. M. McDowall, D. Craw, M. V. H. Wilson, and J. M. Waters. 2012. Marine dispersal as a pre-requisite for Gondwanan vicariance among elements of the galaxiid fish fauna. Journal of Biogeography 39(2):306–321.

Burridge, C. P., and A. J. Smolenski. 2004. Molecular phylogeny of the Cheilodactylidae and Latridae (Perciformes: Cirrhitoidea) with notes on taxonomy and biogeography. Molecular Phylogenetics and Evolution 30(1):118–127.

Byrne, L., F. Chapleau, and S. Aris-Brosou. 2018. How the Central American Seaway and an ancient Northern Passage affected flatfish diversification. Molecular Biology and Evolution 35(8):1982–1989.

Cadenat, J. 1937. Recherches systématiques sur les poissons littoraux de la côte occidentale d'Afrique. Liste des poissons littoraux récoltés par le navire "Président Théodore-Tissier" au cours de sa cinquième croisière (1936). Revue des Travaux de l'Institut des Pêches Maritimes 10(fasc. 4, no. 40):425–462.

Calcagnotto, D., S. A. Schaefer, and R. DeSalle. 2005. Relationships among characiform fishes inferred from analysis of nuclear and mitochondrial gene sequences. Molecular Phylogenetics and Evolution 36(1):135–153.

Calzoni, P., J. Amalfitano, L. Giusberti, G. Marramà, and G. Carnevale. 2023. Eocene Rhamphosidae (Teleostei: Syngnathiformes) from the Bolca Lagerstätte, Italy. Rivista Italiana di Paleontologia e Stratigrafia 129(3):573–607.

Campanella, D., L. C. Hughes, P. J. Unmack, D. D. Bloom, K. R. Piller, and G. Ortí. 2015. Multi-locus fossil-calibrated phylogeny of Atheriniformes (Teleostei, Ovalentaria). Molecular Phylogenetics and Evolution 86:8–23.

Campbell, M. A., M. E. Alfaro, M. Belasco, and J. A. López. 2017. Early-branching euteleost relationships: areas of congruence between concatenation and coalescent model inferences. PeerJ 5:e3548. https://doi.org/10.7717/peerj.3548

Campbell, M. A., B. Chanet, J.-N. Chen, M.-Y. Lee, and W.-J. Chen. 2019. Origins and relationships of the Pleuronectoidei: molecular and morphological analysis of living and fossil taxa. Zoologica Scripta 48(5):640–656.

Campbell, M. A., W.-J. Chen, and J. A. López. 2013. Are flatfishes (Pleuronectiformes) monophyletic? Molecular Phylogenetics and Evolution 69(3):664–673.

—2014. Molecular data do not provide unambiguous support for the monophyly of flatfishes (Pleuronectiformes): a reply to Betancur-R and Ortí. Molecular Phylogenetics and Evolution 75:149–153.

Campbell, M. A., and J. A. Lopéz. 2014. Mitochondrial phylogeography of a Beringian relict: the endemic freshwater genus of blackfish *Dallia* (Esociformes). Journal of Fish Biology 84(2):523–538.

Campbell, M. A., J. A. López, T. Sado, and M. Miya. 2013. Pike and salmon as sister taxa: detailed intraclade resolution and divergence time estimation of Esociformes + Salmoniformes based on whole mitochondrial genome sequences. Gene 530(1):57–65.

Campbell, M. A., J. G. Nielsen, T. Sado, C. Shinzato, M. Kanda, T. P. Satoh, and M. Miya. 2017. Evolutionary affinities of the unfathomable Parabrotulidae: molecular data indicate placement of *Parabrotula* within the family Bythitidae, Ophidiiformes. Molecular Phylogenetics and Evolution 109:337–342.

Campbell, M. A., T. Sado, C. Shinzato, R. Koyanagi, M. Okamoto, and M. Miya. 2018. Multilocus phylogenetic analysis of the first molecular data from the rare and monotypic Amarsipidae places the family within the Pelagia and highlights limitations of existing data sets in resolving pelagian interrelationships. Molecular Phylogenetics and Evolution 124:172–180.

Campbell, M. A., P. Tongboonkua, B. Chanet, and W.-J. Chen. 2020. The distribution of the recessus orbitalis across flatfishes (order: Pleuronectiformes). Journal of Fish Biology 97(1):293–297.

Cantalice, K. M., and J. Alvarado-Ortega. 2016. *Eekaulostomus cuevasae* gen. and sp. nov., an ancient armored trumpetfish (Aulostomoidea) from Danian (Paleocene) marine deposits of Belisario Domínguez, Chiapas, southeastern Mexico. Palaeontologia Electronica 19.3.53A:1–24.

Cantalice, K. M., J. Alvarado-Ortega, and D. R. Bellwood. 2020. †*Chaychanus gonzalezorum* gen. et sp. nov.: a damselfish fossil (Percomorphaceae; Pomacentridae), from the Early Paleocene outcrop of Chiapas, southeastern Mexico. Journal of South American Earth Sciences 98:102322. https://doi.org/10.1016/j.jsames.2019.102322

Cantalice, K. M., J. Alvarado-Ortega, D. R. Bellwood, and A. C. Siqueira. 2022. Rising from the ashes: the biogeographic origins of modern coral reef fishes. BioScience 72(8):769–777.

Cantalice, K. M., B. A. Than-Marchese, and E. Villalobos-Segura. 2021. A new Cenomanian acanthomorph fish from the El Chango quarry (Chiapas, south-eastern Mexico) and its implications for the early diversification and evolutionary trends of acanthopterygians. Papers in Palaeontology 7(3):1699–1726.

Cantino, P. D., and K. de Queiroz. 2020. International Code of Phylogenetic Nomenclature (*PhyloCode*). Boca Raton: CRC Press. 149 pp.

Cantor, T. 1842. General features of Chusan, with remarks on the flora and fauna of that island. Annals and Magazine of Natural History, Series 1, 9(60):481–493.

Capobianco, A., and M. Friedman. 2019. Vicariance and dispersal in southern hemisphere freshwater fish clades: a palaeontological perspective. Biological Reviews 94(2):662–699.

Carmichael, D. 1819. Description of four species of fish found on the coast of Tristan da Cunha. Transactions of the Linnean Society of London 12(2):500–502.

Carnevale, G. 2007. Fossil fishes from the Serravallian (Middle Miocene) of Torricella Peligna, Italy. Palaeontographia Italica 91:1–67.

Carnevale, G., and A. F. Bannikov. 2019. A dragonet (Teleostei, Callionymoidei) from the Eocene of Monte Bolca, Italy. Bollettino della Società Paleontologica Italiana 58(3):295–307.

Carnevale, G., A. F. Bannikov, G. Marramà, J. C. Tyler, and R. Zorzin. 2014. 5. The Pesciara-Monte Postale Fossil Lagerstätte: 2. Fishes and other vertebrates. In: C. A. Papazzoni, L. Giusberti, G. Carnevale, G. Roghi, D. Bassi, and R. Zorzin, eds. The Bolca Fossil-Lagerstätten: A Window into the Eocene World. Milan: Rendiconti della Società Paleontologica Italiana. pp. 37–63.

Carnevale, G., and B. B. Collette. 2014. †*Zappaichthys harzhauseri*, gen. et sp. nov., a new Miocene toadfish (Teleostei, Batrachoidiformes) from the Paratethys (St. Margarethen in Burgenland, Austria), with comments on the fossil record of batrachoidiform fishes. Journal of Vertebrate Paleontology 34(5):1005–1017.

Carnevale, G., and G. D. Johnson. 2015. A Cretaceous cusk-eel (Teleostei, Ophidiiformes) from Italy and the Mesozoic diversification of percomorph fishes. Copeia 103(4):771–791.

Carnevale, G., L. Pellegrino, and J. C. Tyler. 2021. Evolution and fossil record of the ocean sunfishes. In: T. M. Thys, G. C. Hays, and J. D. R. Houghton, eds. The Ocean Sunfishes. Boca Raton, FL: CRC. pp. 1–17.

Carnevale, G., and T. W. Pietsch. 2009. An Eocene frogfish from Monte Bolca, Italy: the earliest known skeletal record for the family. Palaeontology 52(4):745–752.

—2010. Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae (Teleostei: Lophiiformes). Zoological Journal of the Linnean Society 160:621–647.

—2011. Batfishes from the Eocene of Monte Bolca. Geological Magazine 148(3):461–472.

—2012. †*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. Journal of Systematic Palaeontology 10(1):47–72.

Carnevale, G., T. W. Pietsch, N. Bonde, M. E. C. Leal, and G. Marramà. 2020. †*Neilpeartia ceratoi,* gen. et sp. nov., a new frogfish from the Eocene of Bolca, Italy. Journal of Vertebrate Paleontology 40(2):e1778711. https://doi.org/10.1080/02724634.2020.1778711

Carnevale, G., and A. Rindone. 2011. The teleost fish *Paravinciguerria praecursor* Arambourg, 1954 in the Cenomanian of north-eastern Sicily. Bollettino della Società Paleontologica Italiana 50(1):1–10.

Caron, A., V. Venkataraman, K. Tietjen, and M. I. Coates. 2023. A fish for Phoebe: a new actinopterygian from the Upper Carboniferous Coal Measures of Saddleworth, Greater Manchester, UK, and a revision of *Kansasiella eatoni*. Zoological Journal of the Linnean Society 198:957–981.

Carpenter, K. E. 1988. Fusilier Fishes of the World. Vol. 8 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 75 pp. (FAO Fisheries Synopsis 125.)

Carpenter, K. E., and G. R. Allen. 1989. Emperor Fishes and Large-eye Breams of the World (Family Lethrinidae). Vol. 8 of FAO Species Catalogue. 118 pp. (FAO Fisheries Synopsis 125.)

Carvalho, M., F. A. Bockmann, and M. R. de Carvalho. 2013. Homology of the fifth epibranchial and accessory elements of the ceratobranchials among gnathostomes: insights from the development of Ostariophysans. PLOS ONE 8(4):e62389. https://doi.org/10.1371/journal.pone.0062389

Casier, E. 1946. La faune ichthyologique de l'Ypresien de la Belgique. Brussells: Musée Royal d'Histoire Naturelle de Belgique. 267 pp. (Memoires 104.)

—1966. Faune Ichthyologique du London Clay. London: British Museum (Natural History). 496 pp.

Castle, P. H. J. 1977. Results of the research cruises of FRV "Walther Herwig" to South America. L. A new genus and species of bobtail eel (Anguilliformes, Cyemidae) from the South Atlantic. Archiv für Fischereiwissenschaft 28(2–3):69–79.

Cavagnetto, C., and J. Gaudant. 2000. A palynoflora of Palaeocene age from the fossiliferous sapropels of the Boltyshka depression, Central Ukraine. Newsletters on Stratigraphy 38(1):39–56.

Cavender, T. 1969. An Oligocene Mudminnow (Family Umbridae) from Oregon with Remarks on Relationships within the Esocoidei. Ann Arbor: University of Michigan Museum of Zoology. 33 pp. (Occasional Papers 660.)

Cavender, T. M., and M. M. Coburn. 1992. Phylogenetic relationships of North American Cyprinidae. In: R. L. Mayden, ed. Systematics, Historical Ecology, and North American Freshwater Fishes. Stanford, CA: Stanford University Press. pp. 293–327.

Cavin, L. 1999. A new Clupavidae (Teleostei, Ostariophysi) from the Cenomanian of Daoura (Morocco). Comptes rendus de l'Académie des sciences Série 2A: sciences de la terre et des planètes 329:689–695.

—2001. Osteology and phylogenetic relationships of the teleost *Goulmimichthys arambourgi* Cavin, 1995, from the Upper Cretaceous of Goulmima, Morocco. Eclogae Geologicae Helvetiae 94:509–535.

—2017. Freshwater Fishes: 250 Years of Evolutionary History. London: ISTE Press. 199 pp.

Cavin, L., A. Alexopoulos, and A. Piuz. 2012. Late Cretaceous (Maastrichtian) ray-finned fishes from the island of Gavdos, southern Greece, with comments on the evolutionary history of the aulopiform teleost

Enchodus. Bulletin de la Société Géologique de France 183(6):561–572.

Cavin, L., U. Deesri, and V. Suteethorn. 2013. Osteology and relationships of *Thaiichthys* nov. gen.: a Ginglymodi from the Late Jurassic–Early Cretaceous of Thailand. Palaeontology 56(1):183–208.

Cavin, L., and P. L. Forey. 2001. Osteology and systematic affinities of *Palaeonotopterus greenwoodi* Forey 1997 (Teleostei: Osteoglossomorpha). Zoological Journal of the Linnean Society 133:25–52.

Cavin, L., and V. Suteethorn. 2006. A new semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic–Lower Cretaceous deposits of north-east Thailand, with comments on the relationships of semionotiforms. Palaeontology 49(2):339–353.

Cellinese, N., and C. Dell. 2020. RegNum—the international clade names repository [online database]. Accessed 2 December 2023. https://www.phyloregnum.org.

Chakrabarty, P. 2010. The transitioning state of systematic ichthyology. Copeia 2010(3):513–515.

Chakrabarty, P., M. P. Davis, and J. S. Sparks. 2012. The first record of a trans-oceanic sister-group relationship between obligate vertebrate troglobites. PLOS ONE 7(8):e44083. https://doi.org/10.1371/journal.pone.0044083

Chakrabarty, P., B. C. Faircloth, F. Alda, W. B. Ludt, C. D. McMahan, T. J. Near, A. Dornburg, J. S. Albert, J. Arroyave, et al. 2017. Phylogenomic systematics of ostariophysan fishes: ultraconserved elements support the surprising non-monophyly of Characiformes. Systematic Biology 66(6):881–895.

Chakrabarty, P., J. A. Prejean, and M. L. Niemiller. 2014. The Hoosier cavefish, a new and endangered species (Amblyopsidae, *Amblyopsis*) from the caves of southern Indiana. ZooKeys 412:41–57.

Chanet, B. 1994. *Eobuglossus eocenicus* (Woodward 1910) from the Upper Lutetian of Egypt, one of the oldest soleids (Teleostei, Pleuronectiformes). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1994:391–398.

—1995. *Joleaudichthys sadeki* Chabanaud; 1937: Pleuronectiform fish from Egyptian Eocene. First steps on the history of Pleuronectiformes (Pisces; Teleostei). Géobios 28(Suppl. 2):189–191.

—1997. A cladistic reappraisal of the fossil flatfishes record consequences on the phylogeny of the Pleuronectiformes (Osteichthyes: Teleostei). Annales des Sciences naturelles—Zoologie et Biologie Animale, 13e Série, 18(3):105–117.

—1999. Supposed and true flatfishes [Teleostei: Pleuronectiformes] from the Eocene of Monte Bolca, Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 8:220–243.

—2003. Interrelationships of scophthalmid fishes (Pleuronectiformes: Scophthalmidae). Cybium 27(4):275–286.

Chanet, B., C. Guintard, E. Betti, C. Gallut, A. Dettaï, and G. Lecointre. 2013. Evidence for a close phylogenetic relationship between the teleost orders Tetraodontiformes and Lophiiformes based on an analysis of soft anatomy. Cybium 37(3):179–198.

Chanet, B., J. Mondéjar-Fernández, and G. Lecointre. 2020. Flatfishes interrelationships revisited based on anatomical characters. Cybium 44(1):9–18.

Chang, J., D. L. Rabosky, S. A. Smith, and M. E. Alfaro. 2019. An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. Methods in Ecology and Evolution 10(7):1118–1124.

Chang, M.-M., and G. Chen. 2008. Fossil cypriniformes from China and its adjacent areas and their paleobiogeographical implications. In: L. Cavin, A. Longbottom, and M. Richter, eds. Fishes and the Break-up of Pangaea. London: Geological Society of London. pp. 337–350. (Special Publications 295.)

Chang, M.-M., and J. G. Maisey. 2003. Redescription of †*Ellimma branneri* and †*Diplomystus shengliensis*, and relationships of some basal clupeomorphs. American Museum Novitates 3404:1–35.

Chapleau, F. 1993. Pleuronectiform relationships: a cladistic reassessment. Bulletin of Marine Science 52:516–540.

Chen, F., G. Xue, Y. Wang, H. Zhang, P. D. Clift, Y. Xing, J. He, J. S. Albert, J. Chen, and P. Xie. 2023. Evolution of the Yangtze River and its biodiversity. The Innovation 4(3):100417. https://doi.org/10.1016/j.xinn.2023.100417

Chen, G.-J., M.-M. Chang, and Q. Wang. 2010. Redescription of †*Cobitis longipectoralis* Zhou, 1992 (Cypriniformes: Cobitidae) from late early Miocene of East China. Science China Earth Sciences 53:945–955.

Chen, G.-J., W. Liao, and X.-Q. Lei. 2015. First fossil cobitid (Teleostei: Cypriniformes) from early-middle Oligocene deposits of South China. Vertebrata PalAsiatica 53(4):299–309.

Chen, J. N., J. A. López, S. Layoue, M. Miya, and W.-J. Chen. 2014. Phylogeny of the Elopomorpha (Teleostei): evidence from six nuclear and mitochondrial markers. Molecular Phylogenetics and Evolution 70:152–161.

Chen, M.-Y., D. Liang, and P. Zhang. 2015. Selecting question-specific genes to reduce incongruence in phylogenomics: a case study of jawed vertebrate backbone phylogeny. Systematic Biology 64(6):1104–1120.

Chen, W.-J., C. Bonillo, and G. Lecointre. 2003. Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. Molecular Phylogenetics and Evolution 26(2):262–288.

Chen, W.-J., S. Lavoué, L. B. Beheregaray, and R. L. Mayden. 2014. Historical biogeography of a new antitropical clade of temperate freshwater fishes. Journal of Biogeography 41(9):1806–1818.

Chen, W.-J., S. Lavoué, and R. L. Mayden. 2013. Evolutionary origin and early biogeography of otophysan fishes (Ostariophysi: Teleostei). Evolution 67(8):2218–2239.

Chen, W.-J., V. Lheknim, and R. L. Mayden. 2009. Molecular phylogeny of the Cobitoidea (Teleostei: Cypriniformes) revisited: position of enigmatic loach *Ellopostoma* resolved with six nuclear genes. Journal of Fish Biology 75(9):2197–2208.

Chen, W.-J., and R. L. Mayden. 2009. Molecular systematics of the Cyprinoidea (Teleostei: Cypriniformes), the world's largest clade of freshwater fishes: further evidence from six nuclear genes. Molecular Phylogenetics and Evolution 52(2):544–549.

Chen, W.-J., M. Miya, K. Saitoh, and R. L. Mayden. 2008. Phylogenetic utility of two existing and four novel nuclear gene loci in reconstructing tree of life of ray-finned fishes: the order Cypriniformes (Ostariophysi) as a case study. Gene 423(2):125–134.

Chen, W.-J., F. Santini, G. Carnevale, J. N. Chen, S. H. Liu, S. Lavoue, and R. L. Mayden. 2014. New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha). Frontiers in Marine Science 1:53. https://doi.org/10.3389/fmars.2014.00053

Chen, X. Y., and G. Arratia. 1994. Olfactory organ of acipenseriformes and comparison with other actinopterygians: patterns of diversity. Journal of Morphology 222(3):241–267.

Chereshnev, I. A., O. A. Radchenko, and A. V. Petrovskaya. 2013. Relationships and position of the taxa of the subfamily Xiphisterinae in the system of the suborder Zoarcoidei (Perciformes). Russian Journal of Marine Biology 39:276–286.

Cione, A. L. 1987. The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina, Part II: the fishes. Revista del Museo Argentino de ciencias naturales "Bernardino Rivadavia" e Instituto Nacional de Investigacion de als Ciencas Naturales: Paleontologia 3:111–120.

Cione, A. L., M. D. L. M. Azpelicueta, and D. R. Bellwood. 1995. An oplegnathid fish from the Eocene of Antarctica. Palaeontology 37(4):931–940.

Clardy, T. R. 2014. Phylogenetic systematics of the prickleback family Stichaeidae (Cottiformes: Zoarcidae) using morphological data [dissertation]. College of William and Mary. 188 pp. Dissertations, Theses, and Masters Projects, Paper 1539616612. https://doi.org/10.25773/v5-fyer-5n47

Clark, E., and M. Pohle. 1996. *Trichonotus halstead*, a new sand-diving fish from Papua New Guinea. Environmental Biology of Fishes 45:1–11.

Clark, H. W. 1937. New fishes from the Templeton Crocker expedition of 1934–35. Copeia 1937(2):88–91.

Clausen, H. S. 1959. Denticipitidae, a new family of primitive isospondylous teleosts from West African fresh-water. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 121:141–156.

Close, R. A., Z. Johanson, J. C. Tyler, R. C. Harrington, and M. Friedman. 2016. Mosaicism in a new Eocene pufferfish highlights rapid morphological innovation near the origin of crown tetraodontiforms. Palaeontology 59(4):499–514.

Coates, M. I. 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. Zoological Journal of the Linnean Society 122:27–59.

—1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 354(1382):435–462.

Coelho, M. V., C. Cupello, and P. Brito. 2018. Morphological variations in the dorsal fin finlets of extant polypterids raise questions about their taxonomical validity. PeerJ 6:e5083. https://doi.org/10.7717/peerj.5083

Cohen, D. M. 1984. Gadiformes: overview. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 259–265. (Special Publication 1.)

Cohen, D. M., T. Inada, T. Iwamoto, and N. Scialabba. 1990. Gadiform Fishes of the World (Order Gadiformes). Vol. 10 of FAO Species Catalogue. 442 pp. (FAO Fisheries Synopsis 125.)

Cohen, D. M., and J. G. Nielsen. 1978. Guide to the Identifcation of Genera of the Fish Order Ophidiiformes with a Tentative Classification of the Order. Washington, DC: National Oceanic and Atmospheric Administration. 72 pp. (NOAA Technical Report NMFS Circular 417.)

Colgan, D. J., C. G. Zhang, and J. R. Paxton. 2000. Phylogenetic investigations of the Stephanoberyciformes and Beryciformes, particularly whalefishes (Euteleostei: Cetomimidae), based on partial 12S rDNA and 16S rDNA sequences. Molecular Phylogenetics and Evolution 17(1):15–25.

Collar, D. C., S. Tremaine, R. C. Harrington, H. T. Beckett, and M. Friedman. 2022. Mosaic adaptive peak shifts underlie body shape diversification in pelagiarian fishes (Acanthomorpha: Percomorpha). Biological Journal of the Linnean Society 137(2):324–340.

Collette, B. B. 2003. Family Belonidae Bonaparte 1832: needlefishes. California Academy of Sciences Annotated Checklists of Fishes 16:1–22.

—2004a. Family Hemiramphidae Gill 1859: halfbeaks. California Academy of Sciences Annotated Checklists of Fishes 22:1–35.

—2004b. Family Scomberesocidae Müller 1843: sauries. California Academy of Sciences Annotated Checklists of Fishes 21:1–6.

Collette, B. B., and K. E. Bemis. 2019a. Family Belonidae. In: B. B. Collette, K. E. Bemis, N. V. Parin, and I. B. Shakhovskoy. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. B. B. Collette and T. J. Near, eds. New Haven, CT: Peabody Museum of Natural History, Yale University. pp. 5–77. (Memoir 1, Fishes of the Western North Atlantic 10.)

—2019b. Family Hemiramphidae. In: B. B. Collette, K. E. Bemis, N. V. Parin, and I. B. Shakhovskoy. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. B. B. Collette and T. J. Near, eds. New Haven, CT: Peabody Museum of Natural History, Yale University. pp. 89–147. (Memoir 1, Fishes of the Western North Atlantic 10.)

—2019c. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. In: B. B. Collette, K. E. Bemis, N. V. Parin, and I. B. Shakhovskoy. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. B. B. Collette and T. J. Near, eds. New Haven, CT: Peabody Museum of Natural History, Yale University. pp. 1–4. (Memoir 1, Fishes of the Western North Atlantic 10.)

Collette, B. B., G. E. McGowen, N. V. Parin, and S. Mito. 1984. Beloniformes: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 335–354. (Special Publication 1.)

Collette, B. B., and C. E. Nauen. 1983. Scombrids of the World. Vol. 2 of FAO Species Catalogue. 137 pp. (FAO Fisheries Synopsis 125.)

Collette, B. B., T. Potthoff, W. J. Richards, S. Ueyanagi, J. L. Russo, and Y. Nishikawa. 1984. Scombridei: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 591–620. (Special Publication 1.)

Collins, R. A., R. Britz, and L. Rüber. 2015. Phylogenetic systematics of leaffishes (Teleostei: Polycentridae, Nandidae). Journal of Zoological Systematics and Evolutionary Research 53(4):259–272.

Conway, K. W. 2011. Osteology of the South Asian genus *Psilorhynchus* McClelland, 1839 (Teleostei: Ostariophysi: Psilorhynchidae), with investigation of its phylogenetic relationships within the order Cypriniformes. Zoological Journal of the Linnean Society 163(1):50–154.

Conway, K. W., M. V. Hirt, L. Yang, R. L. Mayden, and A. M. Simons. 2010. Cypriniformes: systematics and paleontology. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 295–316.

Conway, K. W., and R. L. Mayden. 2007. The gill arches of *Psilorhynchus* (Ostariophysi: Psilorhynchidae). Copeia 2007(2):267–280.

Cooper, J. A., and F. Chapleau. 1998a. Monophyly and intrarelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. Fishery Bulletin 96:686–726.

—1998b. Phylogenetic status of *Paralichthodes algoensis* (Pleuronectiformes: Paralichthodidae). Copeia 1998(2):477–481.

Cope, E. D. 1865. Partial catalogue of the cold-blooded Vertebrata of Michigan. Part II. Proceedings of the Academy of Natural Science Philadelphia 17(2):78–88.

—1871a. Contribution to the ichthyology of the Lesser Antilles. Transactions of the American Philosophical Society 14:445–483.

—1871b. Observations on the systematic relations of the fishes. American Naturalist 5(8–9):579–593.

—1871c. On the fishes of the Tertiary shales of Green River, Wyoming Territory. In: F. V. Hayden, ed. Preliminary Report of the United States Geological Survey of Wyoming and Portions of Contiguous Territories. Washington, DC: Government Printing Office. pp. 425–431.

—1873. A contribution to the ichthyology of Alaska. Proceedings of the American Philosophical Society 13(90):24–32.

—1877a. A contribution to the knowledge of the ichthyological fauna of the Green River Shales. In: F. V. Hayden, ed. Bulletin of the United States Geological and Geographical Survey of the Territories, Volume 3. Washington, DC: Government Printing Office. pp. 807–819.

—1877b. On the classification of the extinct fishes of the lower types. Proceedings of the American Association for the Advancement of Science 26:292–300.

—1878. Descriptions of fishes from the cretaceous and tertiary deposits west of the Mississippi River. Bulletin of the United States Geological and Geographical Survey of the Territories, Volume 4. Washington, DC: Government Printing Office. pp. 67–77.

—1883. On a new and extinct genus and species of Percidae from Dakota Territory. American Journal of Science 25:414–416.

Costa, W. J. E. M. 1998. Phylogeny and classification of the Cyprinodontiformes (Euteleostei: Atherinomorpha): a reappraisal. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 537–560.

—2004. Relationships and redescription of *Fundulus brasiliensis* (Cyprinodontiformes: Rivulidae), with description of a new genus and notes on the classification of the Aplocheiloidei. Ichthyological Exploration of Freshwaters 15:105–120.

—2011. Redescription and phylogenetic position of the fossil killifish †*Carrionellus diumortuus* White from the Lower Miocene of Ecuador (Teleostei: Cyprinodontiformes). Cybium 35(3):181–187.

—2012a. The caudal skeleton of extant and fossil cyprinodontiform fishes (Teleostei: Atherinomorpha): comparative morphology and delimitation of phylogenetic characters. Vertebrate Zoology 62(2):161–180.

—2012b. Oligocene killifishes (Teleostei: Cyprinodontiformes) from southern France: relationships, taxonomic position, and evidence of internal fertilization. Vertebrate Zoology 62(3):371–386.

—2016. Comparative morphology and classification of South American cynopoeciline killifishes (Cyprinodontiformes: Aplocheilidae), with notes on family-group names used for aplocheiloids. Vertebrate Zoology 66(2):125–140.

Costa, W. J. E. M., P. F. Amorim, and J. L. O. Mattos. 2017. Molecular phylogeny and timing of diversification in South American *Cynolebiini* seasonal killifishes. Molecular Phylogenetics and Evolution 116:61–68.

Covain, R., S. Fisch-Muller, C. Oliveira, J. H. Mol, J. I. Montoya-Burgos, and S. Dray. 2016. Molecular phylogeny of the highly diversified catfish subfamily Loricariinae (Siluriformes, Loricariidae) reveals incongruences with morphological classification. Molecular Phylogenetics and Evolution 94(Part B):492–517.

Cowman, P. F., D. R. Bellwood, and L. van Herwerden. 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. Molecular Phylogenetics and Evolution 52(3):621–631.

Craig, M. T., and P. A. Hastings. 2007. A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. Ichthyological Research 54:1–17.

Cui, L., Y. Dong, R. Cao, X. Zhou, and S. Lu. 2020. Characterization of the complete mitochondrial genome of *Arius dispar* (Siluriformes: Ariidae) and phylogenetic analysis among sea catfishes. Journal of Ocean University of China 19:1198–1206.

Cunha, C., N. Mesquita, T. E. Dowling, A. Gilles, and M. M. Coelho. 2002. Phylogenetic relationships of Eurasian and American cyprinids using cytochrome *b* sequences. Journal of Fish Biology 61(4):929–944.

Cuvier, G. 1816. Le Règne Animal Distribué d'Après son Organisation pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée.

Tome 2, Les reptiles, les poissons, les mollusques et les annélides. 1st ed. Paris: Chez Déterville. 532 pp.

—1829. Le Règne Animal Distribué d'Après son Organisation, pour Servir de Base à l'Histoire Naturelle des Animaux et d'Introduction à l'Anatomie Comparée, Tome 2, Les reptiles, les poissons, les mollusques et les annélides. 2nd ed. Paris: Chez Déterville. 406 pp.

Cuvier, G., and A. Valenciennes. 1828. Histoire Naturelle des Poissons. Tome 2. Livre troisième, Des Poissons de la Famille des Perches, ou des Percoïdes. Paris: F. G. Levrault. 490 pp.

—1829a. Histoire Naturelle des Poissons. Tome 3. Suite du livre troisième, Des Percoïdes à Dorsale Unique à Sept Rayons Branchiaux et à Dents en Velours ou en Cardes. Paris: F. G. Levrault. 500 pp.

—1829b. Histoire Naturelle des Poissons. Tome 4. Livre quatrième, Des Acanthoptérygiens à Joue Cuirassée. Paris: F. G. Levrault. 518 pp.

—1830. Histoire Naturelle des Poissons. Tome 5. Livre cinquième, Des Sciénoïdes. Paris: F. G. Levrault. 499 pp.

—1831. Histoire Naturelle des Poissons. Tome 7. Livre septième, Des Squamipennes. Livre huitième, Des Poissons à Pharyngiens Labyrinthiformes. Paris: F. G. Levrault. 531 pp.

—1833. Histoire Naturelle des Poissons. Tome 9. Suite du livre neuvième, Des Scombéroïdes. Paris: F. G. Levrault. 512 pp.

—1837. Histoire Naturelle des Poissons. Tome 12. Suite du livre quatorzième, Gobioïdes. Livre quinzième, Acanthoptérygiens à Pectorales Pédiculées. Paris: F. G. Levrault. 507 pp.

—1846. Histoire Naturelle des Poissons. Tome 18. Suite du livre dix-huitième, Cyprinoïdes. Livre dix-neuvième, Des Ésoces ou Lucioïdes. Paris: P. Bertrand. 505 pp.

Daane, J. M., N. Blum, J. Lanni, H. Boldt, M. K. Iovine, C. W. Higdon, S. L. Johnson, N. R. Lovejoy, and M. P. Harris. 2021. Modulation of bioelectric cues in the evolution of flying fishes. Current Biology 31(22):5052–5061.e8. https://doi.org/10.1016/j.cub.2021.08.054

Daget, J. 1950. Révision des affinités phylogénétiques des Polyptéridés. Dakar, Senegal: Institut Français d'Afrique Noire. 178 pp. (Mémoires de l'Institut Français d'Afrique Noire 11.)

Daget, J., M. Gayet, F. J. Meunier, and J.-Y. Sire. 2001. Major discoveries on the dermal skeleton of fossil and Recent polypteriforms: a review. Fish and Fisheries 2(2):113–124.

Dai, W., M. Zou, L. Yang, K. Du, W. Chen, Y. Shen, R. L. Mayden, and S. He. 2018. Phylogenomic perspective on the relationships and evolutionary history of the major otocephalan lineages. Scientific Reports 8:205.

Damerau, M., M. Freese, and R. Hanel. 2018. Multigene phylogeny of jacks and pompanos (Carangidae), including placement of monotypic vadigo *Campogramma glaycos*. Journal of Fish Biology 92(1):190–202.

Danil'chenko, P. G. 1960. Kostistye ryby Maĭkopskikh otlozheniĭ Kavkaza. Moscow: Izdatel'stvo Akademii͡a nauk SSSR. 208 pp. (Trudy Paleontologicheskogo Instituta 78.)

—1968. Ryby verkhnego paleostena Turkmenii. In: D. V. Obruchev, ed. Ocherki po filogenii i sistematike iskopayemykh ryb i beschelyustnykh. Moscow: Nauka. pp. 113–156.

Danilit'chenko, P. G. 1962. Fishes from the Dabakhanian Formation of Georgia. Paleontologischeskii Zhurnal 1:111–126.

da Silva, J. P. C. B., A. Datovo, and G. D. Johnson. 2019. Phylogenetic interrelationships of the eel families Derichthyidae and Colocongridae (Elopomorpha: Anguilliformes) based on the pectoral skeleton. Journal of Morphology 280(7):934–947.

da Silva, J. P. C. B., and G. D. Johnson. 2018. Reconsidering pectoral girdle and fin morphology in Anguillidae (Elopomorpha: Anguilliformes). Journal of Fish Biology 93(2):420–423.

Datovo, A., and R. M. C. Castro. 2012. Anatomy and evolution of the mandibular, hyopalatine, and opercular muscles in characiform fishes (Teleostei: Ostariophysi). Zoology 115(2):84–116.

Datovo, A., M. C. C. de Pinna, and G. D. Johnson. 2014. The infrabranchial musculature and its bearing on the phylogeny of percomorph fishes (Osteichthyes: Teleostei). PLOS ONE 9(10):e110129. https://doi.org/10.1371/journal.pone.0110129

Datovo, A., and P. P. Rizzato. 2018. Evolution of the facial musculature in basal ray-finned fishes. Frontiers in Zoology 15:40.

Datovo, A., and R. P. Vari. 2014. The adductor mandibulae muscle complex in lower teleostean fishes (Osteichthyes: Actinopterygii): comparative anatomy, synonymy, and phylogenetic implications. Zoological Journal of the Linnean Society 171(3):554–622.

Davesne, D. 2017. A fossil unicorn crestfish (Teleostei, Lampridiformes, Lophotidae) from the Eocene of Iran. PeerJ 5:e3381. https://doi.org/10.7717/peerj.3381

Davesne, D., G. Carnevale, and M. Friedman. 2017. *Bajaichthys elegans* from the Eocene of Bolca (Italy) and the overlooked morphological diversity of Zeiformes (Teleostei, Acanthomorpha). Palaeontology 60(2):255–268.

Davesne, D., M. Friedman, V. Barriel, G. Lecointre, P. Janvier, C. Gallut, and O. Otero. 2014. Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). Zoological Journal of the Linnean Society 172(2):475–498.

Davesne, D., C. Gallut, V. Barriel, P. Janvier, G. Lecointre, and O. Otero. 2016. The phylogenetic intrarelationships of spiny-rayed fishes (Acanthomorpha, Teleostei, Actinopterygii): fossil taxa increase the congruence of morphology with molecular data. Frontiers in Ecology and Evolution 4:129. https://doi.org/10.3389/fevo.2016.00129

Davis, M. P. 2010. Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 431–470.

Davis, M. P., G. Arratia, and T. M. Kaiser. 2013. The first fossil shellear and its implications for the evolution and divergence of the Kneriidae (Teleostei: Gonorynchiformes). In: G. Arratia, H.-P. Schultze, and M.

V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Friedrich Pfeil. pp. 325–362.

Davis, M. P., and C. Fielitz. 2010. Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. Molecular Phylogenetics and Evolution 57(3):1194–1208.

Davis, M. P., N. I. Holcroft, E. O. Wiley, J. S. Sparks, and W. L. Smith. 2014. Species-specific bioluminescence facilitates speciation in the deep sea. Marine Biology 161:1139–1148.

Davis, M. P., J. S. Sparks, and W. L. Smith. 2016. Repeated and widespread evolution of bioluminescence in marine fishes. PLOS ONE 11(6):e0155154. https://doi.org/10.1371/journal.pone.0155154

Day, J. J., A. Fages, K. J. Brown, E. J. Vreven, M. L. J. Stiassny, R. Bills, J. P. Friel, and L. Rüber. 2017. Multiple independent colonizations into the Congo Basin during the continental radiation of African *Mastacembelus* spiny eels. Journal of Biogeography 44(10):2308–2318.

Dean, B. 1895. Fishes, Living and Fossil: An Outline of their Forms and Probable Relationships. New York: Macmillan and Co. 300 pp. (Columbia Biological Series 3.)

de Figueiredo, F. J. 2005. Reassessment of the morphology of *Scombroclupeoides scutata* Woodward, 1908, a teleostean fish from the Early Cretaceous of Bahia, with comments on its relationships. Arquivos do Museu Nacional do Rio de Janeiro 63(3):507–522.

—2009. A new clupeiform fish from the Lower Cretaceous (Barremian) of Sergipe-Alagoas Basin, northeastern Brazil. Journal of Vertebrate Paleontology 29(4):993–1005.

de Figueiredo, F. J., and V. Gallo. 2004. A new teleost fish from the Early Cretaceous of northeastern Brazil. Boletim do Museu Nacional do Rio de Janeiro 73:1–23.

de Figueiredo, F. J., V. Gallo, and A. F. P. Delarmelina. 2012. A new protacanthopterygian fish from the Upper Cretaceous (Turonian) of the Pelotas Basin, southern Brazil. Cretaceous Research 34:116–123.

de Figueiredo, F. J., V. Gallo, and M. E. C. Leal. 2012. Phylogenetic relationships of the elopomorph fish †*Paraelops cearensis* Silva Santos revisited: evidence from new specimens. Cretaceous Research 37:148–154.

Delbarre, D. J., D. Davesne, and M. Friedman. 2016. Anatomy and relationships of †*Aipichthys pretiosus* and †'*Aipichthys*' *nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. Journal of Systematic Palaeontology 14(7):545–567.

DeMartini, E. E., and T. J. Donaldson. 1996. Color morph-habitat relations to the arc-eye hawkfish *Paracirrhites arcatus* (Pisces: Cirrhitidae). Copeia 1996(2):362–371.

Denton, J. S. S. 2014. Seven-locus molecular phylogeny of Myctophiformes (Teleostei; Scopelomorpha) highlights the utility of the order for studies of deep-sea evolution. Molecular Phylogenetics and Evolution 76:270–292.

Denys, G. P. J., A. Dettaï, H. Persat, M. Hautecœur, and P. Keith. 2014. Morphological and molecular evidence of three species of pikes *Esox* spp. (Actinopterygii, Esocidae) in France, including the description of a new species. Comptes Rendus Biologies 337(9):521–534.

Denys, G. P. J., T. Lauga, G. B. Delmastro, and A. Dettaï. 2018. S7 characterization of Western European pikes *Esox* spp. (Actinopterygii, Esociformes). Cybium 42(3):221–228.

de Pinna, M. C. C. 1993. Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysi) [dissertation]. New York: City University of New York. pp. 482.

—1996. Teleostean monophyly. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 147–162.

—1998. Phylogenetic relationships of Neotropical Siluriformes (Teleostei: Ostariophysi): historical overview and synthesis of hypotheses. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 279–330.

de Pinna, M. C. C., and F. Di Dario. 2010. The branchial arches of the primitive clupeomorph fish *Denticeps clupeoides*, and their phylogenetic implication (Clupeiformes, Denticipitidae). In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 251–268.

de Pinna, M. C. C., J. Zuanon, L. Rapp Py-Daniel, and P. Petry. 2018. A new family of Neotropical freshwater fishes from deep fossorial Amazonian habitat, with a reappraisal of morphological characiform phylogeny (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 182(1):76–106.

de Queiroz, K., P. D. Cantino, and J. A. Gauthier. 2020a. Introduction. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode.* Boca Raton, FL: CRC Press. pp. xv–xxvii.

—, eds. 2020b. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC Press. 1324 pp.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definition of taxon names. Systematic Zoology 39(4):307–322.

—1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23:449–480.

—1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9(1):27–31.

Derome, N., W.-J. Chen, A. Dettaï, C. Bonillo, and G. Lecointre. 2002. Phylogeny of Antarctic dragonfishes (Bathydraconidae, Notothenioidei, Teleostei) and related families based on their anatomy and two mitochondrial genes. Molecular Phylogenetics and Evolution 24(1):139–152.

Derouen, V., W. B. Ludt, H.-C. Ho, and P. Chakrabarty. 2015. Examining evolutionary relationships and shifts in depth preferences in batfishes (Lophiiformes: Ogcocephalidae). Molecular Phylogenetics and Evolution 84(Part A):27–33.

de Sousa, R. P. C., G. C. Silva-Oliveira, I. O. Furo, A. B. de Oliveira-Filho, C. D. B. de Brito, L. Rabelo, A. Guimarães-Costa, E. H. C. de Oliveira, and M. Vallinoto. 2021. The role of the chromosomal rearrangements in the evolution and speciation of Elopiformes fishes (Teleostei; Elopomorpha). Zoologischer Anzeiger 290:40–48.

Dettaï, A., M. Berkani, A. C. Lautredou, A. Couloux, G. Lecointre, C. Ozouf-Costaz, and C. Gallut. 2012. Tracking the elusive monophyly of nototheniid fishes (Teleostei) with multiple mitochondrial and nuclear markers. In: Molecular and Genetic Advances to Understanding Evolution and Biodiversity in the Polar Regions, edited by C. Verde, P. Convey, and G. di Prisco. Special issue, Marine Genomics 8:49–58.

Dettaï, A., and G. Lecointre. 2004. In search of notothenioid (Teleostei) relatives. Antarctic Science 16:71–85.

—2005. Further support for the clades obtained by multiple molecular phylogenies in the acanthomorph bush. Comptes Rendus Biologies 328(7):647–689.

—2008. New insights into the organization and evolution of vertebrate IRBP genes and utility of IRBP gene sequences for the phylogenetic study of the Acanthomorpha (Actinopterygii: Teleostei). Molecular Phylogenetics and Evolution 48(1):258–269.

Díaz-Cruz, J. A., J. Alvarado-Ortega, and S. Giles. 2020. A long snout enchodontid fish (Aulopiformes: Enchodontidae) from the Early Cretaceous deposits at the El Chango quarry, Chiapas, southeastern Mexico: a multi-approach study. Palaeontolgia Electronica 23(2):a30. https://doi.org/10.26879/1065

Díaz-Cruz, J. A., J. Alvarado-Ortega, M. M. Ramírez-Sánchez, E. L. Bernard, L. Allington-Jones, and M. Graham. 2021. Phylogenetic morphometrics, geometric morphometrics and the Mexican fossils to understand evolutionary trends of enchodontid fishes. Journal of South American Earth Sciences 111:103492. https://doi.org/10.1016/j.jsames.2021.103492

Di Dario, F. 2004. Homology between the recessus lateralis and cephalic sensory canals, with the proposition of additional synapomorphies for the Clupeiformes and the Clupeoidei. Zoological Journal of the Linnean Society 141(2):257–270.

—2009. Chirocentrids as engrauloids: evidence from suspensorium, branchial arches, and infraorbital bones (Clupeomorpha, Teleostei). Zoological Journal of the Linnean Society 156(2):363–383.

Di Dario, F., and M. C. C. de Pinna. 2006. The supratemporal system and the pattern of ramification of cephalic sensory canals in *Denticeps clupeoides* (Denticipitoidei, Teleostei): additional evidence for monophyly of Clupeiformes and Clupeoidei. Papéis Avulsos de Zoologia 46(10):107–123.

Dietze, K. 2009. Morphology and phylogenetic relationships of certain neoteleostean fishes from the Upper Cretaceous of Sendenhorst, Germany. Cretaceous Research 30(3):559–574.

Dillman, C. B., D. E. Bergstrom, D. B. Noltie, T. P. Holtsford, and R. L. Mayden. 2011. Regressive progression, progressive regression or neither? Phylogeny and evolution of the Percopsiformes (Teleostei, Paracanthopterygii). Zoologica Scripta 40(1):45–60.

Dillman, C. B., B. L. Sidlauskas, and R. P. Vari. 2016. A morphological supermatrix-based phylogeny for the Neotropical fish superfamily Anostomoidea (Ostariophysi: Characiformes): phylogeny, missing data and homoplasy. Cladistics 32(3):276–296.

Dimmick, W. W., and A. Larson. 1996. A molecular and morphological perspective on the phylogenetic relationships of the otophysan fishes. Molecular Phylogenetics and Evolution 6(1):120–133.

Ding, Z., Y. Xu, W. Chen, Y. Liu, C. Wang, Y. Niu, K. Zhang, Y. Wang, and L. Yang. 2023. Stronger selective constraints on the mitochondrial genome in flying fishes. Frontiers in Marine Science 10:1168417. https://doi.org/10.3389/fmars.2023.1168417

Diogo, R. 2003. Higher-level phylogeny of Siluriformes—an overview. In: G. Arratia, B. G. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes, Volume 1. Enfield, NH: Science Publishers. pp. 353–384.

—2004. Morphological Evolution, Adaptations, Homoplasies, Constraints, and Evolutionary Trends: Catfishes as a Case Study on General Phylogeny and Macroevolution. Enfield, NH: Science Publishers. 491 pp.

—2007. The Origin of Higher Clades: Osteology, Myology, Phylogeny, and the Evolution of Bony Fishes and the Rise of Tetrapods. Enfield, NH: Science Publishers. 367 pp.

—2009. Origin, evolution and homologies of the Weberian apparatus: a new insight. International Journal of Morphology 27:333–354.

Diogo, R., I. Doadrio, and P. Vandewalle. 2008. Teleostean phylogeny based on osteological and myological characters. International Journal of Morphology 26:463–522.

Doiuchi, R., T. Sato, and T. Nakabo. 2004. Phylogenetic relationships of the stromateoid fishes (Perciformes). Ichthyological Research 51:202–212.

Dollo, L. 1904. Poissons. Expedition antarctique Belge. Resultats du voyage du S. Y. Belgica en 1897–1898–1899 sous le commandement de A. de Gerlache de Gomery. Antwerp: J.-E. Buschmann. 240 pp.

Dornburg, A., M. Friedman, and T. J. Near. 2015. Phylogenetic analysis of molecular and morphological data highlights uncertainty in the relationships of fossil and living species of Elopomorpha (Actinopterygii: Teleostei). Molecular Phylogenetics and Evolution 89:205–218.

Dornburg, A., and T. J. Near. 2021. The emerging phylogenetic perspective on the evolution of actinopterygian fishes. Annual Review of Ecology, Evolution, and Systematics 52:427–452.

Dornburg, A., J. P. Townsend, W. Brooks, E. Spriggs, R. I. Eytan, J. A. Moore, P. C. Wainwright, A. R. Lemmon, E. M. Lemmon, and T. J. Near. 2017. New insights on the sister lineage of percomorph fishes with an anchored hybrid enrichment dataset. Molecular Phylogenetics and Evolution 110:27–38.

Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, W. E. Browne, S. A. Smith, E. Seaver, G. W. Rouse, M. Obst, G. D. Edgecombe, et al. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452:745–749.

Dunn, J. R. 1989. A provisional phylogeny of gadid fishes based on adult and early life-history characters. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 209–235.

Duong, T. Y., L. T. K. Pham, X. T. K. Le, N. T. T. Nguyen, S. A. M. Nor, and T. H. Le. 2023. Mitophylogeny of pangasiid catfishes and its taxonomic implications for Pangasiidae and the suborder Siluroidei. Zoological Studies 62:48.

Dutheil, D. B. 1999. An overview of the freshwater fish fauna from the Kem Kem beds (Late Cretaceous: Cenomanian) of southeastern Morocco. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record. Munich: Verlag Dr. Friedrich Pfeil. pp. 553–563.

Dyer, B. S. 2006. Systematic revision of the South American silversides (Teleostei, Atheriniformes). Biocell 30:69–88.

Dyer, B. S., and B. Chernoff. 1996. Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). Zoological Journal of the Linnean Society 117(1):1–69.

Dyldin, Y., L. Hanel, R. Fricke, A. Orlov, V. Romanov, J. Plesnik, E. Interesova, D. Vorobiev, and M. Kochetkova. 2020. Fish diversity in freshwater and brackish water ecosystems of Russia and adjacent waters. Publications of the Seto Marine Biological Laboratory 45:47–116.

Eastman, J. T., and R. R. Eakin. 2021. Checklist of the species of notothenioid fishes. Antarctic Science 33(3):273–280.

Ebert, M. 2018. *Cerinichthys koelblae*, gen. et sp. nov., from the Upper Jurassic of Cerin, France, and its phylogenetic setting, leading to a reassessment of the phylogenetic relationships of Halecomorphi (Actinopterygii). Journal of Vertebrate Paleontology 38:e1420071. https://doi.org/10.1080/02724634.2017.1420071

Echelle, A. A., E. W. Carson, A. F. Echelle, R. A. Van Den Bussche, T. E. Dowling, and A. Meyer. 2005. Historical biogeography of the New-World pupfish genus *Cyprinodon* (Teleostei: Cyprinodontidae). Copeia 2005(2):320–339.

Echelle, A. A., L. Fuselier, R. A. Van Den Bussche, C. M. L. Rodriguez, and M. L. Smith. 2006. Molecular systematics of Hispaniolan pupfishes (Cyprinodontidae: *Cyprinodon*): implications for the biogeography of insular Caribbean fishes. Molecular Phylogenetics and Evolution 39(3):855–864.

Egan, J. P., D. D. Bloom, C.-H. Kuo, M. P. Hammer, P. Tongnunui, S. P. Iglésias, M. Sheaves, C. Grudpan, and A. M. Simons. 2018. Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies). Molecular Phylogenetics and Evolution 124:151–161.

Eigenmann, C. H. 1909. Reports on the expedition to British Guiana of the Indiana University and the Carnegie Museum, 1908. Report no. 1. Some new genera and species of fishes from British Guiana. Annals of the Carnegie Museum 6(1):4–54.

—1922. The Fishes of Western South America, Part I. The Fresh-water Fishes of Northwestern South America, Including Colombia, Panama, and the Pacific Slopes of Ecuador and Peru, Together with an Appendix upon the Fishes of the Rio Meta in Colombia. Pittsburgh: Carnegie Institute. 346 pp. (Memoirs of the Carnegie Museum 9, no. 1.)

Eigenmann, C. H., and R. S. Eigenmann. 1890. A Revision of the South American Nematognathi or Cat-fishes. San Francisco: California Academy of Sciences. 508 pp. (Occasional Papers 1.)

Endo, H. 2002. Phylogeny of the order Gadiformes (Teleostei, Paracanthopterygii). Memoirs of the Graduate School of Fisheries Sciences 49:75–149.

Espíndola, V. C., G. D. Johnson, and M. C. C. de Pinna. 2023. Facial and opercular muscles in the Anguilliformes (Elopomorpha: Teleostei): comparative anatomy and phylogenetic implications for the basal position of *Protanguilla*. Journal of Morphology 284(3):e21556. https://doi.org/10.1002/jmor.21556

Everly, A. W. 2002. Stages of development of the Goosefish, *Lophius americanus*, and comments on the phylogenetic significance of the development of the luring apparatus in Lophiiformes. Environmental Biology of Fishes 64:393–417.

Evseenko, S. A., N. V. Gordeeva, Y. Y. Bolshakova, and S. H. Kobyliansky. 2018. Morphology and molecular phylogenetic relationships of *Barathronus multidens* (Ophidiiformes: Bythitidae). Cybium 42(2):137–141.

Eytan, R. I., B. R. Evans, A. Dornburg, A. R. Lemmon, E. M. Lemmon, P. C. Wainwright, and T. J. Near. 2015. Are 100 enough? Inferring acanthomorph teleost phylogeny using Anchored Hybrid Enrichment. BMC Evolutionary Biology 15:113. https://doi.org/10.1186/s12862-015-0415-0

Fabricus, O. 1780. Fauna Groenlandica, Systematice Sistens Animalia Groenlandiae Occidentalis Hactenus Indagata, Quoad Nomen Specificum, Trivale, Vernaculumque. Copenhagen: I. G. Rothe. 452 pp.

Fahay, M. P., and D. F. Markle. 1984. Gadiformes: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 265–283. (Special Publication 1.)

Faircloth, B. C., F. Alda, K. Hoekzema, M. D. Burns, C. Oliveira, J. S. Albert, B. F. Melo, L. E. Ochoa, F. F. Roxo, P. Chakrabarty, et al. 2020. A target enrichment bait set for studying relationships among ostariophysan fishes. Copeia 108(1):47–60.

Faircloth, B. C., L. Sorenson, F. Santini, and M. E. Alfaro. 2013. A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). PLOS ONE 8(6): e65923. https://doi.org/10.1371/journal.pone.0065923

Fang, F., M. Norén, T.-Y. Liao, M. Källersjö, and S. O. Kullander. 2009. Molecular phylogenetic interrelationships of the south Asian cyprinid genera *Danio*, *Devario* and *Microrasbora* (Teleostei, Cyprinidae, Danioninae). Zoologica Scripta 38(3):237–256.

[FAO] Food and Agriculture Organization of the United Nations. 2020. The State of World Fisheries and Aquaculture 2020: Sustainability in Action. Rome: FAO. Accessed 3 November 2023. https://www.fao.org/state-of-fisheries-aquaculture/2020/en/

Fara, E., M. Gayet, and L. Taverne. 2010. The fossil record of Gonorynchiformes. In: T. Grande, F. J. Poyato-Ariza, and R. Diogo, eds. Gonorynchiformes and Ostariophysan Relationships: A Comprehensive Review. Enfield, NH: Science Publishers. pp. 173–226.

Feng, D.-H., G. H. Xu, X.-Y. Ma, and Y. Ren. 2023. Taxonomic revision of *Sinoeugnathus kueichowensis* (Halecomorphi, Holostei) from the Middle Triassic of Guizhou and Yunnan, China. Vertebrata PalAsiatica 61(3):161–181.

Ferraris, C. J. 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. Zootaxa 1418(1):1–628. https://doi.org/10.11646/zootaxa.1418.1.1

Ferraris, C. J., C. D. de Santana, and R. P. Vari. 2017. Checklist of Gymnotiformes (Osteichthyes: Ostariophysi) and catalogue of primary types. Neotropical Ichthyology 15:e160067. https://doi.org/10.1590/1982-0224-20160067

Ferrer Aledo, J. 1930. Catálogo de los peces de Menorca. Revista de Menorca 29:225–259.

Fessler, J. L., and M. W. Westneat. 2007. Molecular phylogenetics of the butterflyfishes (Chaetodontidae): taxonomy and biogeography of a global coral reef fish family. Molecular Phylogenetics and Evolution 45(1):50–68.

Fielitz, C. 2002. A new Late Cretaceous (Turonian) basal euteleostean fish from Lac des Bois of the Northwest Territories of Canada. Canadian Journal of Earth Sciences 39(11):1579–1590.

—2004. The phylogenetic relationships of the †Enchodontidae (Teleostei: Aulopiformes). In: G. Arratia, M. V. H. Wilson, and R. Cloutier, eds. Recent Advances in the Origin and Early Radiation of Vertebrates. Munich: Verlag Dr. Friedrich Pfeil. pp. 619–634.

Fielitz, C., and D. Bardack. 1992. *Deltaichthys albuloides*, a new and unusually preserved albulid (Teleostei) probably from the Cretaceous of Texas. Journal of Vertebrate Paleontology 12(2):133–141.

Fielitz, C., and K. A. González-Rodríguez. 2010. A new species of *Enchodus* (Aulopiformes: Enchodontidae) from the Cretaceous (Albian to Cenomanian) of Zimapan, Hidalgo, Mexico. Journal of Vertebrate Paleontology 30(5):1343–1351.

Filleul, A. 2000. *Baugeichthys caeruleus*, gen. et sp nov., a new albuliform fish from the Hauterivian of the Massif des Bauges (France). Journal of Vertebrate Paleontology 20(4):637–644.

Filleul, A., and S. Lavoue. 2001. Basal teleosts and the question of elopomorph monophyly. Morphological and molecular approaches. Comptes rendus de l'Académie des sciences Série 3: sciences de la vie 324(4):393–399.

Filleul, A., and J. G. Maisey. 2004. Redescription of *Santanichthys diasii* (Otophysi, Characiformes) from the Albian of the Santana formation and comments on its implications for otophysan relationships. American Museum Novitates 3455:1–21.

Fink, S. V., and W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei). Zoological Journal of the Linnean Society 72(4):297–353.

—1996. Interrelationships of ostariophysan fishes (Teleostei). In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 209–249.

Fink, W. L. 1984a. Basal euteleosts: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 202–206. (Special Publication 1.)

—1984b. Stomiiformes: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 181–184. (Special Publication 1.)

—1985. Phylogenetic Interrelationships of the Stomiid Fishes (Teleostei: Stomiiformes). Ann Arbor: University of Michigan Museum of Zoology. 127 pp. (Miscellaneous Publications 171.)

Fink, W. L., and S. H. Weitzman. 1982. Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. Bulletin of the Museum of Comparative Zoology 150(2):31–93.

Fitzinger, L. J. F. J. 1832. Ueber die Ausarbeitung einer Fauna des Erzherzogthumes Öesterreich, nebst einer systematischen Aufzählung der in diesem Lande vorkommenden Säugethiere, Reptilien und Fische, als Prodrum einer Fauna derfelben. Beiträge zur Landeskunde Österreichs unter der Enns 1:280–340.

Fletcher, G. L., M. A. Shears, M. J. King, M. H. Kao, P. L. Davies, and C. L. Hew. 1988. Antifreeze protein genes: physiological regulation and potential value to the genetic engineering of freeze resistant fish. In: R. C. Ryans, ed. Fish Physiology, Fish Toxicology, and Fisheries Management: Proceedings of an International Symposium, Guangzhou, PRC, September 14–16, 1988. Athens, GA: U.S. Environmental Protection Agency. pp. 228–247.

Forey, P. L. 1973a. Relationships of elopomorphs. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 351–368.

—1973b. A revision of the elopiform fishes, fossil and Recent. Bulletin of the British Museum (Natural History), Geology, Supplement 10:1–222.

—1980. *Latimeria*: a paradoxical fish. Proceedings of the Royal Society of London Series B, Biological Sciences 208(1172):369–384.

—1997. A Cretaceous notopterid (Pisces: Osteoglossomorpha) from Morocco. South African Journal of Science 93:564–569.

—2004. A three-dimensional skull of a primative clupeomorph from the Cenomanian English Chalk, and implications for the evolution of the clupeomorph acusticolateralis system. In: G. Arratia and A. Tintori, eds. Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity. Munich: Verlag Dr. Friedrich Pfeil. pp. 405–427.

Forey, P. L., and E. J. Hilton. 2010. Two new Tertiary osteoglossid fishes (Teleostei: Osteoglossomorpha) with notes on the history of the family. In: D. K. Elliot, J. G. Maisey, X. Yu, and D. Miao, eds. Morphology, Phylogeny, and Paleobiogeography of Fossil Fishes. Munich: Verlag Dr. Friedrich Pfeil. pp. 215–246.

Forey, P. L., D. T. J. Littlewood, P. Ritchie, and A. Meyer. 1996. Interrelationships of elopomorph fishes.

In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 174–191.

Forey, P. L., Y. Lu, C. Patterson, and C. E. Davis. 2003. Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. Journal of Systematic Palaeontology 1(4):230–330.

Forey, P. L., and J. G. Maisey. 2010. Structure and relationships of †*Brannerion* (Albuloidei), an Early Cretaceous teleost from Brazil. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 183–218.

Forster, J. R. 1773. An account of some curious fishes, sent from Hudson's Bay; by Mr. John Reinhold Forster, F. R. S. in a letter to Thomas Pennant, Esq; F. R. S. Philosophical Transactions of the Royal Society of London 63:149–160.

Fowler, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proceedings of the Academy of Natural Sciences of Philadelphia 85:233–367.

—1951. Analysis of the fishes of Chile. Revista Chilena de Historia Natural 51–53:263–326.

Francisco, S. M., L. Congiu, S. Stefanni, R. Castilho, A. Brito, P. P. Ivanova, A. Levy, H. Cabral, G. Kilias, I. Doadrio, and V. C. Almada. 2008. Phylogenetic relationships of the north-eastern Atlantic and Mediterranean forms of *Atherina* (Pisces, Atherinidae). Molecular Phylogenetics and Evolution 48(2):782–788.

Francisco, S. M., L. Congiu, S. von der Heyden, and V. C. Almada. 2011. Multilocus phylogenetic analysis of the genus *Atherina* (Pisces: Atherinidae). Molecular Phylogenetics and Evolution 61(1):71–78.

Fraser, T. H. 1972. Some thoughts about the teleostean fish concept—the Paracanthopterygii. Japanese Journal of Ichthyology 19(4):232–242.

—2013. A new genus of cardinalfish (Apogonidae: Percomorpha), redescription of Archamia and resemblances and relationships with *Kurtus* (Kurtidae: Percomorpha). Zootaxa 3714(1):1–63. https://doi.org/10.11646/zootaxa.3714.1.1

Freyhof, J., M. Özuluğ, and G. Saç. 2017. Neotype designation of *Aphanius iconii*, first reviser action to stabilise the usage of *A. fontinalis*, and *A. meridionalis* and comments on the family group names of fishes placed in Cyprinodontidae (Teleostei: Cyprinodontiformes). Zootaxa 4294(5):573–585. https://doi.org/10.11646/zootaxa.4294.5.6

Fricke, R., J.-N. Chen, and W.-J. Chen. 2017. New case of lateral asymmetry in fishes: a new subfamily, genus and species of deep water clingfishes from Papua New Guinea, western Pacific Ocean. Comptes Rendus Biologies 340(1):47–62.

Fricke, R., W. N. Eschmeyer, and J. D. Fong. 2023. Genera/species by family/subfamily. Eschmeyer's Catalog of Fishes [online database]. California Academy of Sciences. Accessed September 1, 2023. https://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp

Friedman, M. 2008. The evolutionary origin of flatfish asymmetry. Nature 454:209–212.

—2009. Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. Proceedings of the National Academy of Sciences of the United States of America 106:5218–5223.

—2010. Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. Proceedings of the Royal Society B, Biological Sciences 277(1688):1675–1683.

—2012. Osteology of †*Heteronectes chaneti* (Acanthomorpha, Pleuronectiformes), an Eocene stem flatfish, with a discussion of flatfish sister-group relationships. Journal of Vertebrate Paleontology 32(4):735–756.

Friedman, M., H. T. Beckett, R. A. Close, and Z. Johanson. 2016. The English chalk and London clay: two remarkable British bony fish Lagerstätten. In: Z. Johanson, P. M. Barrett, M. Richter, and M. Smith, eds. Arthur Smith Woodward: His Life and Influence on Modern Vetebrate Palaeontolology. London: Geological Society. pp. 165–200. (Special Publication 430.)

Friedman, M., K. L. Feilich, H. T. Beckett, M. E. Alfaro, B. C. Faircloth, D. Černý, M. Miya, T. J. Near, and R. C. Harrington. 2019. A phylogenomic framework for pelagiarian fishes (Acanthomorpha: Percomorpha) highlights mosaic radiation in the open ocean. Proceedings of the Royal Society B, Biological Sciences 286(1910):20191502.

Friedman, M., Z. Johanson, R. C. Harrington, T. J. Near, and M. R. Graham. 2013. An early fossil remora (Echeneoidea) reveals the evolutionary assembly of the adhesion disc. Proceedings of the Royal Society B, Biological Sciences 280(1766):20131200.

Friedman, M., and G. D. Johnson. 2005. A new species of *Mene* (Perciformes: Menidae) from the Paleocene of South America, with notes on paleoenvironment and a brief review of menid fishes. Journal of Vertebrate Paleontology 25(4):770–783.

Friedman, M., B. P. Keck, A. Dornburg, R. I. Eytan, C. H. Martin, C. D. Hulsey, P. C. Wainwright, and T. J. Near. 2013. Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. Proceedings of the Royal Society B, Biological Sciences 280(1770):20131733.

Friedman, S. T., and M. M. Muñoz. 2023. A latitudinal gradient of deep-sea invasions for marine fishes. Nature Communications 14:773.

Frost, G. A. 1928. Otoliths of fishes from the Tertiary formations of New Zealand, and from Balcombe Bay, Victoria. Transactions and Proceedings of the Royal Society of New Zealand 59:91–97.

Gago, F. J. 1997. Character evolution and phylogeny of the cutlassfishes: an ontogenetic perspective (Scombroidei: Trichiuridae). Bulletin of Marine Science 60:161–191.

—1998. Osteology and Phylogeny of the Cutlassfishes (Scombroidei: Trichiuridae). Los Angeles: Natural History Museum of Los Angeles. 79 pp. (Contributions in Science 476.)

Gallo, V., and P. M. Coelho. 2008. First occurrence of an aulopiform fish in the Barremian of the Sergipe-Alagoas Basin, northeastern Brazil. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 4: Homology and Phylogeny. Munich: Verlag Dr. Friedrich Pfeil. pp. 351–371.

Gallo, V., and F. J. de Figueiredo. 2002. †*Farinichthys gigas*, a new albulid fish (Teleostei: Elopomorpha) from the Paleocene of the Pernambuco-Paraíba Basin, northeastern Brazil. Journal of Vertebrate Paleontology 22(4):747–758.

Gallo, V., F. J. de Figueiredo, and S. A. Azevedo. 2009. *Santanasalmo elegans* gen. et sp nov., a basal euteleostean fish from the Lower Cretaceous of the Araripe Basin, northeastern Brazil. Cretaceous Research 30(6):1357–1366.

Gardiner, B. G. 1973. Interrelationships of teleostomes. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 105–135.

—1984. The relationships of the palaeoniscid fishes: a review based on new specimens of *Mimia* and *Moythomasia* from Upper Devonian of Western Australia. Bulletin of the British Museum (Natural History), Geology 37(4):173–428.

Gardiner, B. G., J. G. Maisey, and T. J. Littlewood. 1996. Interrelationships of basal neopterygians. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 117–146.

Gardiner, B. G., and B. Schaeffer. 1989. Interrelationships of lower actinopterygian fishes. Zoological Journal of the Linnean Society 97(2):135–187.

Gardiner, B. G., B. Schaeffer, and J. A. Masserie. 2005. A review of the lower actinopterygian phylogeny. Zoological Journal of the Linnean Society 144(4):511–525.

Garman, S. 1895. The Cyprinodonts. Cambridge, MA: Printed for the Museum. 179 pp. (Memoirs of the Museum of Comparative Zoölogy at Harvard College 19, no. 1.)

Garstang, W. 1931. A phyletic classification of Teleostei. Proceedings of the Leeds Philosophical and Literary Society, Scientific Section 2:240–260.

Gaudant, J. 1978. Essai de révision taxonomique des "*Pholidophorus*" (Poissons Actinoptérygiens) du Jurassique supérieur de Cerin (Ain). Nouvelles Archives du Muséum d'Histoire naturelle de Lyon, fascicule 16:101–121.

—1988. Les cyprinodontiformes (Poissons téléostéens) oligocènes de Ronzon, Le Puy-en-Velay (Haute-Loire): anatomie et signification paléoécologique. Géobios 21(6):773–785.

—2012. An attempt at the palaeontological history of the European mudminnows (Pisces, Teleostei, Umbridae). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 263:93–109.

Gaudant, M. 1969. Sur quelques nouveaux poisson Bérycoïdes crétacés du Mont Liban. Notes et Mémoires sur le Moyen-Orient 10:273–284.

—1978a. Contribution à la révision des Poissons crétacés du Jbel Tselfat (Rides prérifaines, Maroc). Première partie: Les Acanthoptérygiens. Notes et Mémoires du Service Géologique du Maroc 39(272):79–124.

—1978b. Recherches sur l'anatomie et la systématique de Cténothrissiformes et des Pattersonichthyiformes (Poisson Téléostéens) du Cénomanien du Liban. Paris: Éditions du Muséum. 124 pp. (Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série C, Sciences de la Terre 41.)

—1979. Recherches sur les relations phylogénétiques de certains poissons Eurypterygii du Crétacé de la Mésogée occidentale. Comptes rendus hebdomadaires des séances de l'Académie des sciences Série D: sciences naturelles 288:1047–1050.

Gayet, M. 1980a. Contribution a l'étude anatomique et systématique des poissons cénomaniens du Liban, anciennement placés dans les aeanthopterygiens. Paris: Éditions du Muséum. 149 pp. (Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série C, Sciences de la Terre 44.)

—1980b. Recherches sur l'ichthyofaune cenomanienne des Monts de Judee: les "acanthopterygiens." Annales de Paléontologie Vertébrés 66:75–128.

—1988a. Le plus ancien crâne de Siluriforme: *Andinichthys bolivianensis* nov. gen., nov. sp. (Andinichthyidae nov. fam.) du Maastrichtien de Tiupampa (Bolivie). Comptes rendus de l'Académie des sciences Série 2: Mécanique, physique, chimie, sciences de l'univers, sciences de la terre 307(7)":833–836.

—1988b. Relations phylogénétiques de *Barcarenichthys joneti* Gayet du Cénomanien de Barcarena (Portugal) au sein des "Salmoniformes." Comunicações dos Serviços Geológicos de Portugal 74:85–103.

—1989. *Barcarenichthys joneti* nov. gen., nov. sp., du Cénomanien marin de Barcarena (Portugal) et ses relations phylogénétiques au sein des "Salmoniformes." Comptes rendus de l'Académie des sciences Série 2: Mécanique, physique, chimie, sciences de l'univers, sciences de la terre 308(1):137–140.

—1990. Nouveaux Siluriformes du Maastrichtien de Tiupampa (Bolivie). Comptes rendus de l'Académie des sciences Série 2: Mécanique, physique, chimie, sciences de l'univers, sciences de la terre 310(7):867–872.

—1993. Relations phylogénétiques des Gonorynchiformes (Ostariophysi). Belgian Journal of Zoology 123:165–192.

—1994. Fishes from the Lower Cretaceous (Hauterivian?) of Wadi-el-Malih (Israel). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 194(1):73–94.

Gayet, M., M. Jégu, J. Bocquentin, and F. R. Negri. 2003. New characoids from the Upper Cretaceous and Paleocene of Bolivia and the Mio-Pliocene of Brazil: phylogenetic position and paleobiogeographic implications. Journal of Vertebrate Paleontology 23(1):28–46.

Gayet, M., and B. Lepicard. 1985. Salmoniforme nouveau du Maastrichtien supérieur des Petites Pyrénées (Haute-Garonne, France): *Pyrenichthys jauzaci* nov. gen. nov. sp. Bulletin du Muséum National d'Histoire Naturelle, 4e Série, Section C, Sciences de la Terre 7:131–141.

Gayet, M., L. G. Marshall, T. Sempere, F. J. Meunier, H. Cappetta, and J. C. Rage. 2001. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 169(1–2):39–68.

Gayet, M., and F. J. Meunier. 1991. First discovery of Polypteridae (Pisces, Cladistia, Polypteriformes) outside of Africa = Première découverte de Polypteridae (Pisces, Cladistia, Polypteriformes) hors d'Afrique. Géobios 24(4):463–466.

—1992. Polyptériformes (Pisces, Cladistia) du maastrichtien et du paléocène de Bolivie = Polyteriformes (Pisces, Cladistia) from Maastrichtian and Paleocene of Bolivia. Géobios 25(Suppl. 1):159–168.

—1998. Maastrichtian to Early Late Paleocene freshwater Osteichthyes of Bolivia: additions and comments. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 85–110.

—2000. Rectification of the nomenclature of the genus name *Ellisella* Gayet and Meunier 1991 (Teleostei, Ostarophysi, Gymnotiformes) in *Humboldtichthys* nom. nov. Cybium 24(1):104.

—2003. Palaeontology and palaeobiogeography of catfishes. In: G. Arratia, B. G. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes, Volume 2. Enfield, NH: Science Publishers. pp. 491–522.

Gayet, M., F. J. Meunier, and F. Kirshbaum 1994. *Ellisella kirschbaumi* Gayet and Meunier, 1991, Gymnotiforme fossile de Bolivie et ses relations phylogénétiques au sein des formes actuelles. Cybium 18(3):273–306.

Gayet, M., F. J. Meunier, and C. Werner. 2002. Diversification in Polypteriformes and special comparison with the Lepisosteiformes. Palaeontology 45(2):361–376.

Geoffroy St. Hilaire, E. 1809. Histoire naturelle des Poissons du Nil. In: France, Commission des sciences et arts d'Egypte. Description de l'Égypte ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'expedition de l'Armée français, publié par les ordres de sa Majesté l'Empereur Napoléon le Grand. Histoire Naturelle 1, part 1. Paris: Imprimerie Impériale. pp. 1–52, plates 18–27.

George, A. M., and V. G. Springer. 1980. Revision of the Clinid Fish Tribe *Ophiclinini*, Including Five New Species, and Definition of the Family Clinidae. Washington, DC: Smithsonian Institution Press. 31 pp. (Smithsonian Contributions to Zoology 307.)

Ghedotti, M. J. 2000. Phylogenetic analysis and taxonomy of the poecilioid fishes (Teleostei: Cyprinodontiformes). Zoological Journal of the Linnean Society 130(1):1–53.

Ghedotti, M. J., H. M. DeKay, A. J. Maile, W. L. Smith, and M. P. Davis. 2021. Anatomy and evolution of bioluminescent organs in the slimeheads (Teleostei: Trachichthyidae). Journal of Morphology 282(6):820–832.

Ghedotti, M. J., J. N. Gruber, R. W. Barton, M. P. Davis, and W. L. Smith. 2018. Morphology and evolution of bioluminescent organs in the glowbellies (Percomorpha: Acropomatidae) with comments on the taxonomy and phylogeny of Acropomatiformes. Journal of Morphology 279(11):1640–1653.

Ghezelayagh, A., R. C. Harrington, E. D. Burress, M. Campbell, J. Buckner, P. Chakrabarty, J. R. Glass, W. T. McCraney, P. Unmack, C. E. Thacker, et al. 2022. Prolonged morphological expansion of spiny-rayed fishes following the end-Cretaceous. Nature Ecology and Evolution 6:1211–1220. https://doi.org/10.1038/s41559-022-01801-3

Gierl, C., M. Dohrmann, P. Keith, W. F. Humphreys, H. R. Esmaeili, J. Vukić, R. Šanda, and B. Reichenbacher. 2022. An integrative phylogenetic approach for inferring relationships of fossil gobioids (Teleostei: Gobiiformes). PLOS ONE 17(7):e0271121. https://doi.org/10.1371/journal.pone.0271121

Gierl, C., and B. Reichenbacher. 2015. A new fossil genus of Gobiiformes from the Miocene characterized by a mosaic set of characters. Copeia 103(4):792–805.

—2017. Revision of so-called *Pomatoschistus* (Gobiiformes, Teleostei) from the Late Eocene and Early Oligocene. Palaeontologia Electronica 20.2.33A:1–17. https://doi.org/10.26879/721

Gierl, C., B. Reichenbacher, J. Gaudant, D. Erpenbeck, and A. Pharisat. 2013. An extraordinary gobioid fish fossil from Southern France. PLOS ONE 8(5):e64117. https://doi.org/10.1371/journal.pone.0064117

Gilbert, C. H. 1890. A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proceedings of the United States National Museum 13(879):49–126.

Giles, S., K. Feilich, R. C. M. Warnock, S. E. Pierce, and M. Friedman. 2023. A Late Devonian actinopterygian suggests high lineage survivorship across the end-Devonian mass extinction. Nature Ecology and Evolution 7:10–19. https://doi.org/10.1038/s41559-022-01919-4

Giles, S., G.-H. Xu, T. J. Near, and M. Friedman. 2017. Early members of 'living fossil' lineage imply later origin of modern ray-finned fishes. Nature 549:265–268.

Gill, A. C. 1996. Comments on an intercalar path for the glossopharyngeal (Cranial IX) nerve as a synapomorphy of the Paracanthopterygii and on the phylogenetic position on the Gobiesocidae (Teleostei: Acanthomorpha). Copeia 1996(4):1022–1029.

—2013. Classification and relationships of *Assiculus* and *Assiculoides* (Teleostei: Pseudochromidae). Zootaxa 3718(2):128–136. https://doi.org/10.11646/zootaxa.3718.2.2

Gill, A. C., and J. M. Leis. 2019. Phylogenetic position of the fish genera *Lobotes*, *Datnioides* and *Hapalogenys*, with a reappraisal of acanthuriform composition and relationships based on adult and larval morphology. Zootaxa 4680(1):1–81. https://doi.org/10.11646/zootaxa.4680.1.1

Gill, A. C., and R. D. Mooi. 1993. Monophyly of the Grammatidae and of the Notograptidae, with evidence for their phylogenetic positions among perciforms. Bulletin of Marine Science 52:327–350.

—2002. Phylogeny and systematics of fishes. In: P. J. B. Hart and J. D. Reynolds, eds. Handbook of Fish Biology and Fisheries. Malden, MA: Blackwell Science. pp. 15–42.

—2012. Thalasseleotrididae, new family of marine gobioid fishes from New Zealand and temperate Australia, with a revised definition of its sister taxon, the Gobiidae (Teleostei: Acanthomorpha). Zootaxa 3266(1):41–52. https://doi.org/10.11646/zootaxa.3266.1.3

Gill, T. N. 1861a. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. Proceedings of the Academy of Natural Sciences of Philadelphia 13:1–63.

—1861b. Observations on the genus *Cottus*, and descriptions of two new species (abridged from the forthcoming report of Capt. J. H. Simpson). Proceedings of the Boston Society of Natural History 8(1861–1862):40–42.

—1861c. On a new type of aulostomatoids, found in Washington Territory. Proceedings of the Academy of Natural Sciences of Philadelphia 13:168–170.

—1862. On a new genus of fishes allied to *Aulorhynchus* and on the affinities of the family Aulorhynchoidae, to which it belongs. Proceedings of the Academy of Natural Sciences of Philadelphia 14:233–235.

—1872. Arrangement of the Families of Fishes, or Classes Pisces, Marsipobranchii, and Leptocardii. Washington, DC: Smithsonian Institution. 95 pp. (Smithsonian Miscellaneous Collections 11.)

—1883. Deep-sea fishing fishes. Forest and Stream and Rod and Gun: The American Sportsman's Journal 21:284.

—1884a. Synopsis of the plectognath fishes. Proceedings of the United States National Museum 7(448): 411–427.

—1884b. Three new families of fishes added to the deep-sea fauna in a year. American Naturalist 18(4):433.

—1889. On the classification of the mail-cheeked fishes. Proceedings of the United States National Museum 11(756):567–592.

—1893. Families and subfamiles of fishes. Memoirs of the National Academy of Sciences 6:127–138.

Gill, T., and J. A. Ryder. 1883. On the anatomy and relations of the Eurypharyngidae. Proceedings of the United States National Museum 6(382):262–273.

Gilliams, J. 1824. Description of a new species of fish of the Linnean genus *Perca*. Journal of the Academy of Natural Sciences of Philadelphia 4:80–82.

Girard, C. 1854. Descriptions of new fishes, collected by Dr. A.L. Heermann, naturalist attached to the Survey of the Pacific Railroad Route, under Lieut. R.S. Williamson, U.S.A. Proceedings of the Academy of Natural Sciences of Philadelphia 7:129–140.

—1858a. Fishes. In: U. S. Congress, Senate. Reports of Explorations and Surveys, to Ascertain the Most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific Ocean, Volume 10, Part 4. 33rd Congress, 2nd session, S. Rep. 33-78, serial 767. Washington, DC: Beverley Tucker. pp. 1–400.

—1858b. Notice upon new genera and new species of marine and fresh-water fishes from western North America. Proceedings of the Academy of Natural Sciences of Philadelphia 9:200–202.

Girard, M. G., M. P. Davis, C. C. Baldwin, A. Dettaï, R. P. Martin, and W. L. Smith. 2022. Molecular phylogeny of the threadfin fishes (Polynemidae) using ultraconserved elements. Journal of Fish Biology 100(3):793–810.

Girard, M. G., M. P. Davis, and W. L. Smith. 2020. The phylogeny of carangiform fishes: morphological and genomic investigations of a new fish clade. Copeia 108(2):265–298.

Girard, M. G., M. P. Davis, H. H. Tan, D. J. Wedd, P. Chakrabarty, W. B. Ludt, A. P. Summers, and W. L. Smith. 2022. Phylogenetics of archerfishes (Toxotidae) and evolution of the toxotid shooting apparatus. Integrative Organismal Biology 4(1):obac013. https://doi.org/10.1093/iob/obac013

Girard, M. G., B. C. Mundy, A. Nonaka, and G. D. Johnson. 2023. Cusk-eel confusion: revisions of larval *Luciobrotula* and *Pycnocraspedum* and re-descriptions of two bythitid larvae (Ophidiiformes). Ichthyological Research 70:474–489.

Glass, J. R., R. C. Harrington, P. F. Cowman, B. C. Faircloth, and T. J. Near. 2023. Widespread sympatry in a species-rich clade of marine fishes (Carangoidei). Proceedings of the Royal Society B, Biological Sciences 290(2010):20230657.

Gmelin, J. F. 1789. Caroli a Linné…Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 13th ed., Volume 1, Part 3. Leipzig: Beer. 484 pp.

Goatley, C. H. R., and L. Tornabene. 2022. *Tempestichthys bettyae*, a new genus and species of ocean sleeper (Gobiiformes, Thalasseleotrididae) from the central Coral Sea. Systematics and Biodiversity 20(1):1–15.

Godkin, C. M., and R. Winterbottom. 1985. Phylogeny of the family Congrogadidae (Pisces, Perciformes) and its placement as a subfamily of the Pseudochromidae. Bulletin of Marine Science 36(3):633–671.

Goode, G. B., and T. H. Bean. 1879. Description of *Alepocephalus bairdii,* a new species of fish from the deep-sea fauna of the western Atlantic. Proceedings of the United States National Museum 2(68):55–57.

—1883. Reports on the results of dredging under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the U. S. coast survey steamer "Blake," Commander J. R. Bartlett, U.S.N., commanding. Bulletin of the Museum of Comparative Zoology 10:183–226.

—1896. Oceanic Ichthyology: A treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers "Blake," "Albatross," and "Fishhawk" in the northwestern Atlantic, with an atlas containing 417 figures. 2 vols. Cambridge, MA: Printed for the Museum. Published in connection with the National Museum and the Smithsonian Institution. (Memoirs of the Museum of Comparitive Zoölogy at Harvard College 22.)

Goodrich, E. S. 1909. Vertebrata Craniata (first fascicle: cyclostomes and fishes). Volume 9 of A Treatise on Zoology, edited by R. Lankester. London: Adam and Charles Black. 518 pp.

—1928. *Polypterus* a palaeoniscid? Palaeobiologica 1:87–92.

—1930. Studies on the Structure and Developtment of Vertebrates. London: Macmillan. 837 pp.

Gosline, W. A. 1960. Contributions toward a classification of modern isospondylous fishes. Bulletin of the British Museum (Natural History), Zoology 6:327–365.

—1961. Some osteological features of modern lower teleostean fishes. Smithsonian Miscellaneous Collections 142(3):1–42.

—1963a. Considerations Regarding the Relationships of the Percopsiform, Cyprinodontiform, and Gadiform Fishes. Ann Arbor: University of Michigan Museum of Zoology. 38 pp. (Occasional Papers 629.)

—1963b. Notes on the osteology and systematic position of *Hypoptychus dybowskii* Steindachner and other elongate perciform fishes. Pacific Science 17(1):90–101.

—1965. Teleostean phylogeny. Copeia 1965(2):186–194.

—1968. The suborders of perciform fishes. Proceedings of the United States National Museum 124(3647):1–78.

—1969. The morphology and systematic position of the alepocephaloid fishes. Bulletin of the British Museum (Natural History), Zoology 18:187–218.

—1971. Functional Morphology and Classification of Teleostean Fishes. Honolulu: University Press of Hawaii. 208 pp.

—1983. The relationships of the mastacembelid and synbranchid fishes. Japanese Journal of Ichthyology 29(4):323–328.

—1985. Relationships among some relatively deep bodied percoid fish groups. Japanese Journal of Ichthyology 31(4):351–357.

Gosline, W. A., N. B. Marshall, and G. W. Mead. 1966. Order Iniomi: characters and synopsis of the families. In: C. W. Mead, ed. Orders Iniomi and Lyomeri: Lizardfishes, Other Iniomi, Deepsea Gulpers. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 1–18. (Memoir 1, Fishes of the Western North Atlantic 5.)

Gottfried, M. D., R. E. Fordyce, and S. Rust. 2006. *Megalampris keyesi*, a giant moonfish (Teleostei, Lampridiformes) from the late oligocene of New Zealand. Journal of Vertebrate Paleontology 26(3):544–551.

Gouiric-Cavalli, S., and G. Arratia. 2022. A new †Pachycormiformes (Actinopterygii) from the Upper Jurassic of Gondwana sheds light on the evolutionary history of the group. Journal of Systematic Palaeontology 19(21):1517–1550.

Gradstein, F. M., and J. G. Ogg. 2020. The chronostratigraphic scale. In: F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg, eds. Geologic Time Scale 2020, Volume 1. Amsterdam: Elsevier. pp. 21–32.

Grand, A., R. Zaragüeta Bagils, L. M. Velez, and V. Ung. 2014. A cladistic re-analysis of the Gadiformes (Teleostei, Paracanthopterygii) using three-item analysis. Zootaxa 3889(4):525–552. https://doi.org/10.11646/zootaxa.3889.4.3

Grande, L. 1982. A revision of the fossil genus *Diplomystus*, with comments on the interrelationships of clupeomorph fishes. American Museum Novitates 2728:1–38.

—1984. Paleontology of the Green River Formation, with a Review of the Fish Fauna. Laramie, WY: Geological Survey of Wyoming. xvii, 333 pp. (Bulletin 63.)

—1985. Recent and fossil clupeomorph fishes with material for revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181(art. 2):231–272.

—1987. Redescription of †*Hypsidoris farsonensis* (Teleostei: Siluriformes), with a reassessment of its phylogenetic relationships. Journal of Vertebrate Paleontology 7(1):24–54.

—1988. A well preserved paracanthopterygian fish (Teleostei) from freshwater Lower Paleocene deposits of Montana. Journal of Vertebrate Paleontology 8(2):117–130.

—1999. The first *Esox* (Esocidae: Teleostei) from the Eocene Green River Formation, and a brief review of esocid fishes. Journal of Vertebrate Paleontology 19(2):271–292.

—2010. An empirical and synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy: the resurrection of Holostei. Lawrence, KS: American Society of Ichthyologists and Herpetologists. 871 pp. (Special Publication 6.)

Grande, L., and W. E. Bemis. 1991. Osteology and phylogenetic relationships of fossil and recent paddlefishes (Polyodontidae) with comments on the interrelationships of Acipenseriformes. Journal of Vertebrate Paleontology 11(1 Suppl.):1–121. (Society of Vertebrate Paleontology Memoir 1.)

—1996. Interrelationships of Acipenseriformes, with comments on "Chondrostei." In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 85–115.

—1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Journal of Vertebrate Paleontology 18(1 Suppl.):1–690. (Society of Vertebrate Paleontology Memoir 4.)

Grande, L., and M. C. C. de Pinna. 1998. Description of a second species of the catfish †*Hypsidoris* and a reevaluation of the genus and the family †Hypsidoridae. Journal of Vertebrate Paleontology 18(3):451–474.

Grande, L., and T. Grande. 1999. A new species of *Notogoneus* (Teleostei: Gonorynchidae) from the Upper Cretaceous Two Medicine Formation of Montana, and the poor Cretaceous record of freshwater fishes from North America. Journal of Vertebrate Paleontology 19(4):612–622.

Grande, L., and E. J. Hilton. 2006. An exquisitely preserved skeleton representing a primitive sturgeon from the Upper Cretaceous Judith River Formation of Montana (Acipenseriformes: Acipenseridae: n. gen. and sp). Journal of Paleontology 80(4 Suppl.):1–39. (Paleontological Society Memoir 65.)

Grande, T. 1994. Phylogeny and Paedomorphosis in an African Family of Freshwater Fishes (Gonorynchiformes: Kneriidae). Chicago: Field Museum of Natural History. 20 pp. (Fieldiana Zoology New Series 78.)

—1996. The interrelationships of fossil and Recent gonorynchid fishes with comments on two Cretaceous taxa from Israel. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 299–318.

—1999. Revision of the genus *Gonorynchus* Scopoli, 1777 (Teleostei: Ostariophysi). Copeia 1999(2):453–469.

Grande, T., W. C. Borden, and W. L. Smith. 2013. Limits and relationships of Paracanthopterygii: a molecular framework for evaluating past morphological hypotheses. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Fredrich Pfeil. pp. 385–418.

Grande, T., W. C. Borden, M. V. H. Wilson, and L. Scarpitta. 2018. Phylogenetic relationships among fishes in the order Zeiformes based on molecular and morphological data. Copeia 106(1):20–48.

Grande, T., and M. de Pinna. 2004. The evolution of the Weberian apparatus: a phylogenetic perspective. In: G. Arratia and A. Tintori, eds. Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity. Munich: Verlag Dr. Friedrich Pfeil. pp. 429–448.

Grande, T., H. Laten, and J. A. López. 2004. Phylogenetic relationships of extant esocid species (Teleostei: Salmoniformes) based on mophological and molecular characters. Copeia 2004(4):743–757.

Grande, T., and F. J. Poyato-Ariza. 1995. A cladistic analysis of fossil and living gonorynchiform ostariophysan fishes. Géobios 28(Suppl. 2):197–199.

—1999. Phylogenetic relationships of fossil and Recent gonorynchiform fishes (Teleostei: Ostariophysi). Zoological Journal of the Linnean Society 125(2):197–238.

Gray, J. E. 1831. Description of twelve new genera of fish, discovered by Gen. Hardwicke, in India, the greater part in the British Museum. Zoological Miscellany 1831:7–9.

Greenfield, D. W., R. Winterbottom, and B. B. Collette. 2008. Review of the toadfish genera (Teleostei: Batrachoididae). Proceedings of the California Academy of Sciences 59(15):665–710.

Greenwood, P. H. 1960. Fossil denticipitid fishes from East Africa. Bulletin of the British Museum (Natural History), Geology 5(1):1–11.

—1963. The swimbladder in African Notopteridae (Pisces) and its bearing on the taxonomy of the family. Bulletin of the British Museum (Natural History), Zoology 11(5):379–412.

—1968. The osteology and relationships of the Denticipitidae: a family of clupeomorph fishes. Bulletin of the British Museum (Natural History), Zoology 16(6):215–273.

—1973. Interrelationships of osteoglossomorphs. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 307–332.

—1977. Notes on the anatomy and classification of elopomorph fishes. Bulletin of the British Museum (Natural History), Zoology 32(4):65–102.

—1995. A revised familial classification for certain cirrhitoid genera (Teleostei, Percoidei Cirrhitoidea), with comments on the group's monophyly and taxonomic ranking. Bulletin of the Natural History Museum (Zoology) 61(1):1–10.

Greenwood, P. H., G. S. Myers, D. E. Rosen, and S. H. Weitzman. 1967. Named main divisions of teleostean fishes. Proceedings of the Biological Society of Washington 80:227–228.

Greenwood, P. H., and D. E. Rosen. 1971. Notes on the structure and relationships of alepocephaloid fishes. American Museum Novitates 2473:1–41.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131(art. 4):341–455.

Gregorová, R. 2011. Fossil fish fauna (Teleostei, Selachii) from the Dynów marlstone (Rupelian, NP 23) of the Menilitic Formation at the locality of Litenčice (Czech Republic). Acta Musei Moraviae, Scientiae Geologicae 96:3–33.

Gregory, W. K. 1907. The orders of teleostomus fishes. Annals of the New York Academy of Sciences 17(3):437–508.

—1933. Fish skulls: a study of the evolution of natural mechanisms. Transactions of the American Philosophical Society 23(2):75–481.

Gregory, W. K., and G. M. Conrad. 1936. Pictoral phylogenies of deep sea Isospondyli and Iniomi. Copeia 1936(1):21–36.

Guichenot, A. 1848. Fauna Chilena. Peces. In: C. Gay, ed. Historia fisica y politica de Chile. Zoología 2. Paris: Museo de historia natural de Santiago. pp. 137–370.

Guinot, G., and L. Cavin. 2018. Body size evolution and habitat colonization across 100 million years (Late Jurassic–Paleocene) of the actinopterygian evolutionary history. Fish and Fisheries 19(4):577–597.

Günther, A. 1859. Catalogue of the acanthopterygian fishes in the collection of the British Museum, Volume 1. London: British Museum. xxxi, 524 pp.

—1861. Catalogue of the Acanthopterygian Fishes in the Collection of the British Museum, Volume 3. London: British Museum. 586 pp.

—1863a. On new species of fishes from the Essequibo. Annals and Magazine of Natural History, Series 3, 12(72):441–443.

—1863b. On new species of fishes from Victoria, South Australia. Annals and Magazine of Natural History, Series 3, 12(68):114–117.

—1864a. Catalogue of the Fishes in the British Museum, Volume 5. London: British Museum. 455 pp.

—1864b. Report of a collection of fishes made by Messrs. Dow, Godman, and Salvin in Guatemala. Proceedings of the Zoological Society of London 1864, pt. 1 (art. 3), pp. 144–154.

—1868. Catalogue of the Fishes in the British Museum, Volume 7. London: British Museum. 512 pp.

—1870. Catalogue of the Fishes in the British Museum, Volume 8. London: British Museum. 549 pp.

—1878a. Preliminary notices of deep-sea fishes collected during the voyage of the H.M.S. "Challenger." Annals and Magazine of Natural History, Series 5, 2(7):17–28.

—1878b. Preliminary notices of deep-sea fishes collected during the voyage of the H.M.S. "Challenger." Annals and Magazine of Natural History, Series 5, 2(9):248–251.

—1880. An Introduction to the Study of Fishes. Edinburgh: Adam and Charles Black. 720 pp.

Gushiken, S. 1988. Phylogenetic relationships of the perciform genera of the family Carangidae. Japanese Journal of Ichthyology 34(4):443–461.

Haeckel, E. 1866. Generalle morphologie der organismen, Volume 2. Berlin: G. Reimer. clx, 462 pp.

Haedrich, R. L. 1967. The stromateoid fishes: systematics and a classification. Bulletin of the Museum of Comparative Zoology 135(2):31–139.

Hamilton, F. 1822. An Account of the Fishes Found in the River Ganges and Its Branches. Edinburgh: A. Constable and Company. 405 pp.

Hamilton, H., N. Saarman, G. Short, A. B. Sellas, B. Moore, T. Hoang, C. L. Grace, M. Gomon, K. Crow, and W. B. Simison. 2017. Molecular phylogeny and patterns of diversification in syngnathid fishes. Molecular Phylogenetics and Evolution 107:388–403.

Han, Z., C. Shou, M. Liu, and T. Gao. 2021. Large-scale phylogenomic analysis provides new insights into the phylogeny of the order Gadiformes and evolution of freshwater gadiform species Burbot (*Lota lota*) [preprint]. Preprints.org [online database]. https://doi.org/10.20944/preprints202106.0610.v1

Hao, C., Y. Liu, N. Wei, K. Arken, C. Shi, and C. Yue. 2023. The complete mitochondrial genomes of the *Leuciscus baicalensis* and *Rutilus rutilus*: a detailed genomic comparison among closely related species of the Leuciscinae subfamily. Gene 877:147535.

Hao, S., K. Han, L. Meng, X. Huang, W. Cao, C. Shi, M. Zhang, Y. Wang, Q. Liu, Y. Zhang, H. Sun, I. Seim, X. Xu, X. Liu, and G. Fan. 2020. African Arowana genome provides insights on ancient teleost evolution. iScience 23(11):101662. https://doi.org/10.1016/j.isci.2020.101662

Hardman, M. 2005. The phylogenetic relationships among non-diplomystid catfishes as inferred from mitochondrial cytochrome b sequences; the search for the ictalurid sister taxon (Otophysi: Siluriformes). Molecular Phylogenetics and Evolution 37(3):700–720.

Harold, A. S. 1993. Phylogenetic relationships of the sternoptychid *Argyropelecus* (Teleostei: Stomiiformes). Copeia 1993(1):123–133.

—1994. A taxonomic revision of the sternoptychid genus *Polyipnus* (Teleostei, Stromiiformes) with an analysis of phylogenetic relationships. Bulletin of Marine Science 54(2):428–534.

—1998. Phylogenetic relationships of the Gonostomatidae (Teleostei: Stomiiformes). Bulletin of Marine Science 62(3):715–741.

Harold, A. S., and S. H. Weitzman. 1996. Interrelationships of stomiiform fishes. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 333–353.

Harrington, R. C., B. C. Faircloth, R. I. Eytan, W. L. Smith, T. J. Near, M. E. Alfaro, and M. Friedman. 2016. Phylogenomic analysis of carangimorph fishes reveals flatfish asymmetry arose in a blink of the evolutionary eye. BMC Evolutionary Biology 16:224. https://doi.org/10.1186/s12862-016-0786-x

Harrington, R. C., M. Friedman, M. Miya, T. J. Near, and M. A. Campbell. 2021. Phylogenomic resolution of the monotypic and enigmatic *Amarsipus*, the Bagless Glassfish (Teleostei, Amarsipidae). Zoologica Scripta 50(4):411–422.

Harrington, R. C., M. A. Kolmann, J. J. Day, B. C. Faircloth, M. Friedman, and T. J. Near. 2023. Dispersal sweepstakes: biotic interchange propelled air-breathing fishes across the globe. Journal of Biogeography. Published ahead of print, 27 December. https://doi.org/10.1111/jbi.14781

Hart, P. B., R. J. Arnold, F. Alda, C. P. Kenaley, T. W. Pietsch, D. Hutchinson, and P. Chakrabarty. 2022. Evolutionary relationships of anglerfishes (Lophiiformes) reconstructed using ultraconserved elements. Molecular Phylogenetics and Evolution 171:107459.

Hart, P. B., M. L. Niemiller, E. D. Burress, J. W. Armbruster, W. B. Ludt, and P. Chakrabarty. 2020. Cave-adapted evolution in the North American amblyopsid fishes inferred using phylogenomics and geometric morphometrics. Evolution 74(5):936–949.

Hartel, K. E., and M. L. J. Stiassny. 1986. The identification of larval *Parasudis* (Teleostei, Chlorophthalmidae); with notes on the anatomy and relationships of aulopiform fishes. Breviora 487:1–23.

Harvey, V. L., J. N. Keating, and M. Buckley. 2021. Phylogenetic analyses of ray-finned fishes (Actinopterygii) using collagen type I protein sequences. Royal Society Open Science 8(8):201955. https://doi.org/10.1098/rsos.201955

Hastings, P. A. 1993. Relationships of fishes of the perciform suborder Notothenioidei. In: R. G. Miller, ed. A History and Atlas of the Fishes of the Antarctic Ocean. Carson City, NV: Foresta Institute for Ocean and Mountain Studies. pp. 99–107.

Hastings, P. A., and V. G. Springer. 2009. Systematics of the Blennioidei and the included families Dactyloscopidae, Chaenopsidae, Clinidae and Labrisomidae. In: R. A. Patzner, E. J. Goncalves, P. A. Hastings, and B. G. Kapoor, eds. The Biology of Blennies. Enfield, NH: Science Publishers. pp. 3–30.

Hay, O. P. 1903. Some remarks on the fossil fishes of Mount Lebanon, Syria. American Naturalist 37(442):685–695.

—1929. Second Bibliography and Catalogue of the Fossil Vertebrata of North America, Volume 1. Washington, DC: Carnegie Institution of Washington. 916 pp.

Haÿ, V., M. I. Mennesson, P. Keith, and C. Lord. 2022. Revision of the genus *Rhyacichthys* using integrative taxonomy. Pacific Science 76(2):123–137.

He, S. P., X. Gu, R. L. Mayden, W.-J. Chen, K. W. Conway, and Y. Y. Chen. 2008. Phylogenetic position of the enigmatic genus *Psilorhynchus* (Ostariophysi: Cypriniformes): evidence from the mitochondrial genome. Molecular Phylogenetics and Evolution 47(1):419–425.

He, S. P., R. L. Mayden, X. Z. Wang, W. Wang, K. L. Tang, W.-J. Chen, and Y. Y. Chen. 2008. Molecular phylogenetics of the family Cyprinidae (Actinopterygii: Cypriniformes) as evidenced by sequence variation in the first intron of S7 ribosomal protein-coding gene: further evidence from a nuclear gene of the systematic chaos in the family. Molecular Phylogenetics and Evolution 46(3):818–829.

Heckel, J. J. 1853. Berichtüber die vom Herrn Cavaliere Achille de Zigno hier angelangte Sammlung fossiler Fische. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 11:122–138.

Hector, J. 1871. On a new species of fish, *Coryphaenoides novae Zelandiae*; native name, Okarari. Transactions and Proceedings of the New Zealand Institute 3(21):136.

Heemstra, P. C., and T. Hecht. 1986. Dinopercidae, a new family for the percoid marine fish genera *Dinoperca* Boulenger and *Centrarchops* Fowler (Pisces: Perciformes). Grahamstown, South Africa: J. L. B. Smith Institute of Ichthyology. 21 pp. (Bulletin 51.)

Helmstetter, A. J., A. S. T. Papadopulos, J. Igea, T. J. M. Van Dooren, A. M. Leroi, and V. Savolainen. 2016.

Viviparity stimulates diversification in an order of fish. Nature Communications 7:11271.

Hensel, K. 1970. Review of the classification and of the opinions on the evolution of Cyprinoidei (Eventognathi) with an annotated list of genera and subgenera described since 1921. Annotationes Zoologicae et Botanice 57:1–45.

Hensley, D. A. 1997. An overview of the systematics and biogeography of the flatfishes. In: Proceedings of the Third International Symposium on Flatfish Ecology, Part I; 2–8 November 1996, Texel, The Netherlands. Special issue, Journal of Sea Research 37(3–4):187–194.

Hensley, D. A., and E. H. Ahlstrom. 1984. Pleuronectiformes: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 670–687. (Special Publication 1.)

Heras, S., and M. I. Roldán. 2011. Phylogenetic inference in *Odontesthes* and *Atherina* (Teleostei: Atheriniformes) with insights into ecological adaptation. Comptes Rendus Biologies 334(4):273–281.

Herler, J., S. Koblmüller, and C. Sturmbauer. 2009. Phylogenetic relationships of coral-associated gobies (Teleostei, Gobiidae) from the Red Sea based on mitochondrial DNA data. Marine Biology 156:725–739.

Hermann, J. 1781. Schreiben an den Herausgeber über eine neues amerikanisches Fischgeschlecht, *Sternoptyx diaphana*, der durchsichtige Brust-Falten-Fisch. Naturforscher 16:8–36.

Hernández-Guerrero, C., K. M. Cantalice, K. A. González-Rodríguez, and V. M. Bravo-Cuevas. 2021. The first record of a pterothrissin (Albuliformes, Albulidae) from the Muhi Quarry, mid-Cretaceous (Albian-Cenomanian) of Hidalgo, central Mexico. Journal of South American Earth Sciences 107:103032.

Hertwig, S. T. 2008. Phylogeny of the Cyprinodontiformes (Teleostei, Atherinomorpha): the contribution of cranial soft tissue characters. Zoologica Scripta 37(2):141–174.

Hidaka, K., Y. Tsukamoto, and Y. Iwatsuki. 2017. *Nemoossis*, a new genus for the eastern Atlantic long-fin bonefish *Pterothrissus belloci* Cadenat 1937 and a redescription of *P. gissu* Hilgendorf 1877 from the northwestern Pacific. Ichthyological Research 64:45–53.

Hilgendorf, F. M. 1877. *Pterothrissus*, eine neue Clupeidengattung. Leopoldina, Amtliches Organ der Kaiserlich Leopoldinisch-Carolinisch-Deutschen Akademie der Naturforscher 13:127–128.

—1878. Über das Vorkommen einer *Brama*-Art und einer neuen Fischgattung *Centropholis* aus der Nachbarschaft des Genus *Brama* in den japanischen Meeren. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin 1878:1–2.

Hilton, E. J. 2003. Comparative osteology and phylogenetic systematics of fossil and living bony-tongue fishes (Actinopterygii, Teleostei, Osteoglossomorpha). Zoological Journal of the Linnean Society 137(1):1–100.

—2009. Osteology of the Graveldiver *Scytalina cerdale* (Perciformes: Zoarcoidei: Scytalinidae). Journal of Morphology 270(12):1475–1491.

—2022. Origin and diversity of early teleostean fishes. In: P. C. Heemstra, E. Heemstra, D. A. Ebert, W. Hollerman, and J. E. Randall, eds. Coastal Fishes of the Western Indian Ocean, Volume 2. Makhanda, South Africa: South African Institute for Aquatic Biodiversity. pp. 4–19.

Hilton, E. J., and R. Britz. 2010. The caudal skeleton of osteglossomorph fishes, revisited: comparisons, homologies, and characters. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 219–237.

Hilton, E. J., and P. L. Forey. 2009. Redescription of †*Chondrosteus acipenseroides* Egerton, 1858 (Acipenseriformes, †Chondrosteidae) from the Lower Lias of Lyme Regis (Dorset, England), with comments on the early evolution of sturgeons and paddlefishes. Journal of Systematic Palaeontology 7(4):427–453.

Hilton, E. J., L. Grande, and W. E. Bemis. 2011. Skeletal anatomy of the Shortnose Sturgeon, *Acipenser brevirostrum* Lesueur, 1818, and the systematics of sturgeons (Acipenseriformes, Acipenseridae). Chicago: Field Museum of Natural History. 168 pp. (Fieldiana: Life and Earth Sciences 3.)

Hilton, E. J., P. Konstantinidis, and A. Williston. 2021. Osteology of *Parabrotula plagiophthalmus* (Ophidiiformes: Bythitoidei: Bythitidae). Breviora 569:1–18.

Hilton, E. J., and S. Lavoué. 2018. A review of the systematic biology of fossil and living bony-tongue fishes, Osteoglossomorpha (Actinopterygii: Teleostei). Neotropical Ichthyology 16(3):e180031.

Hilton, E. J., D. E. Stevenson, and A. C. Matarese. 2019. Osteology of *Ronquilus jordani* (Zoarcoidei: Bathymasteridae), with a discussion of the developmental osteology and systematics of bathymasterid fishes. Acta Zoologica 100(4):389–407.

Hinegardner, R., and D. E. Rosen. 1972. Cellular DNA content and the evolution of teleostean fishes. American Naturalist 106(951):621–644.

Hirt, M. V., G. Arratia, W.-J. Chen, R. L. Mayden, K. L. Tang, R. M. Wood, and A. M. Simons. 2017. Effects of gene choice, base composition and rate heterogeneity on inference and estimates of divergence times in cypriniform fishes. Biological Journal of the Linnean Society 121(2):319–339.

Hoese, D. F. 1984. Gobioidei: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 588–591. (Special Publication 1.)

Hoese, D. F., and A. C. Gill. 1993. Phylogenetic relationships of eleotridid fishes (Perciformes: Gobioidei). Bulletin of Marine Science 52:415–440.

Hoffmann, M., and R. Britz. 2006. Ontogeny and homology of the neural complex of otophysan Ostariophysi. Zoological Journal of the Linnean Society 147(3):301–330.

Hoganson, J., J. M. Erickson, and F. Holland. 2019. Chondrichthyan and Osteichthyan Paleofaunas of the Cretaceous (Late Maastrichtian) Fox Hills Formation of

North Dakota, USA: Paleoecology, Paleogeography, and Extinction. Ithaca, NY: Paleontological Research Institution. 94 pp. (Bulletins of American Paleontology 398.)

Holcroft, N. I. 2004. A molecular test of alternative hypotheses of tetraodontiform (Acanthomorpha: Tetraodontiformes) sister group relationships using data from the RAG1 gene. Molecular Phylogenetics and Evolution 32(3):749–760.

—2005. A molecular analysis of the interrelationships of tetraodontiform fishes (Acanthomorpha: Tetraodontiformes). Molecular Phylogenetics and Evolution 34(3):525–544.

Holcroft, N. I., and E. O. Wiley. 2008. Acanthuroid relationships revisited: a new nuclear gene-based analysis that incorporates tetraodontiform representatives. Ichthyological Research 55:274–283.

Hora, S. L. 1925. Notes on fishes of the Indian Museum. XII. The systematic position of cyprinoid genus *Psilorhynchus* McClelland. Records of the Indian Museum 27:457–460.

Horn, M. H. 1984. Stromateoidei: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 620–628. (Special Publication 1.)

Hoshino, K. 2001. Monophyly of the Citharidae (Pleuronectoidei: Pleuronectiformes: Teleostei) with considerations of pleuronectoid phylogeny. Ichthyological Research 48:391–404.

Hotaling, S., M. L. Borowiec, L. S. F. Lins, T. Desvignes, and J. L. Kelley. 2021. The biogeographic history of eelpouts and related fishes: linking phylogeny, environmental change, and patterns of dispersal in a globally distributed fish group. Molecular Phylogenetics and Evolution 162:107211. https://doi.org/10.1016/j.ympev.2021.107211

Howes, G. J. 1983. The cranial muscles of the loricarioid catfishes, their homologies and value as taxonomic characters (Teleostei: Siluroidei). Bulletin of the British Museum (Natural History), Zoology 45(6):309–345.

—1989. Phylogenetic relationships of macrouroid and gadoid fishes based on cranial myology and arthrology. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 113–128.

—1990. The syncranial osteology of the southern eelcod family Muraenolepididae, with comments on its phylogenetic-relationships and on the biogeography of sub-antarctic gadoid fishes. Zoological Journal of the Linnean Society 100(1):73–100.

—1991a. Anatomy, phylogeny and taxonomy of the gadoid fish genus *Macruronus* Günther, 1873, with a revised hypothesis of gadoid phylogeny. Bulletin of the British Museum (Natural History), Zoology 57(1):77–110.

—1991b. Systematics and biogeography: an overview. In: I. J. Winfield and J. S. Nelson, eds. Cyprinid Fishes: Systematics, Biology, and Exploitation. London: Chapman and Hall. pp. 1–33.

—1992. Notes on the anatomy and classification of ophidiiform fishes with particular reference to the abyssal genus *Acanthonus* Günther, 1878. Bulletin of the British Museum (Natural History), Zoology 58(2):95–131.

—1993. Anatomy of the Melanonidae (Teleostei: Gadiformes), with comments on its phylogenetic relationships. Bulletin of the British Museum (Natural History), Zoology 59(1):11–31.

Howes, G. J., and C. P. J. Sanford. 1987. The phylogenetic position of the Plecoglossidae (Teleostei, Salmoniformes), with comments on the Osmeridae and Osmeroidei. In: S. O. Kullander and B. Fernholm, eds. Proceedings V Congress of European Ichthyologists. Stockholm: Department of Vertebrate Zoology, Swedish Museum of Natural History. pp. 17–30.

Huang, Y., K. Zhu, Y. Yang, L. Fang, Z. Liu, J. Ye, C. Jia, J. Chen, and H. Jiang. 2023. Comparative analysis of complete mitochondrial genome of *Ariosoma meeki* (Jordan and Snider, 1900), revealing gene rearrangement and the phylogenetic relationships of Anguilliformes. Biology 12(3):348.

Hubbs, C. L. 1924. Studies of the Fishes of the Order Cyprinodontes. Ann Arbor: University of Michigan Museum of Zoology. 31 pp. (Miscellaneous Publications 13.)

—1927. Notes of the blennioid fishes of western North America. Papers of the Michigan Academy of Science, Arts, and Letters 7:351–394.

—1936. Fishes of the Yucatan Peninsula. Carnegie Institution of Washington Publications 457:157–287.

—1945. Phylogenetic Position of the Citharidae, a Family of Flatfishes. Ann Arbor: University of Michigan Museum of Zoology. 38 pp. (Miscellaneous Publications 63.)

—1952. A contribution to the classification of the blennioid fishes of the family Clinidae, with a partial revision of eastern Pacific forms. Stanford Ichthyological Bulletin 4(2):41–165.

Hubert, N., C. Bonillo, and D. Paugy. 2005a. Does elision account for molecular saturation: case study based on mitochondrial ribosomal DNA among Characiform fishes (Teleostei: Ostariophysii). Molecular Phylogenetics and Evolution 35(1):300–308.

—2005b. Early divergence among the Alestidae (Teleostei, Ostariophyses, Characiformes): mitochondrial evidences and congruence with morphological data. Comptes Rendus Biologies 328(5):477–491.

Huddleston, R. W., and K. M. Savoie. 1983. Teleostean otoliths from the Late Cretaceous (Maestrichtian age) Severn Formation of Maryland. Proceedings of the Biological Society of Washington 96(4):658–663.

Hughes, L. C., C. M. Nash, W. T. White, and M. W. Westneat. 2023. Concordance and discordance in the phylogenomics of the wrasses and parrotfishes (Teleostei: Labridae). Systematic Biology 72(3):530–543.

Hughes, L. C., G. Ortí, Y. Huang, Y. Sun, C. C. Baldwin, A. W. Thompson, D. Arcila, R. Betancur-R, C. Li, L. Becker, et al. 2018. Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. Proceedings of the National Academy of Sciences of the United States of America 115(24):6249–6254.

Huie, J. M., C. E. Thacker, and L. Tornabene. 2020. Co-evolution of cleaning and feeding morphology in western Atlantic and eastern Pacific gobies. Evolution 74(2):419–433.

Hulet, W. H., and C. R. Robins. 1989. The evolutionary significance of the lepotocephalus larva. In: E. B. Böhlke, ed. Orders Anguilliformes and Saccopharyngiformes, Volume 2. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 669–677. (Memoir 1, Fishes of the Western North Atlantic 9.)

Humboldt, F. H. A. v., and A. Valenciennes. 1821. Recherches sur les poissons fluviatiles de l'Amérique Équinoxiale. In: Voyage de Humboldt et Bonpland, deuxième partie. Observations de Zoologie et d'Anatomie comparée, Volume 2. Paris: J. Smith. pp. 145–216.

Hundt, P. J., S. P. Iglésias, A. S. Hoey, and A. M. Simons. 2014. A multilocus molecular phylogeny of combtooth blennies (Percomorpha: Blennioidei: Blenniidae): multiple invasions of intertidal habitats. Molecular Phylogenetics and Evolution 70:47–56.

Hundt, P. J., and A. M. Simons. 2018. Extreme dentition does not prevent diet and tooth diversification within combtooth blennies (Ovalentaria: Blenniidae). Evolution 72(4):930–943.

Hureau, J.-C. 1986. Relations phylogénétiques au sein des Notothenioidei. Oceanis 12(5):367–376.

Hurley, I. A., R. L. Mueller, K. A. Dunn, E. J. Schmidt, M. Friedman, R. K. Ho, V. E. Prince, Z. H. Yang, M. G. Thomas, and M. I. Coates. 2007. A new time-scale for ray-finned fish evolution. Proceedings of the Royal Society B, Biological Sciences 274(1609):489–498.

Ida, H. 1976. Removal of the family Hypoptychidae from the suborder Ammodytoidei, order Perciformes, to the suborder Gasterosteoidei, order Syngnathiformes. Japanese Journal of Ichthyology 23(1):33–42.

Ilves, K. L., and E. B. Taylor. 2009. Molecular resolution of the systematics of a problematic group of fishes (Teleostei: Osmeridae) and evidence for morphological homoplasy. Molecular Phylogenetics and Evolution 50(1):163–178.

Imamura, H. 1996. Phylogeny of the family Platycephalidae and related taxa (Pisces: Scorpaeniformes). Species Diversity 1(2):123–233.

—2000. An alternative hypothesis on the phylogenetic position of the family Dactylopteridae (Pisces: Teleostei), with a proposed new classification. Ichthyological Research 47:203–222.

—2004. Phylogenetic relationships and new classification of the superfamily Scorpaenoidea (Actinopterygii: Perciformes). Species Diversity 9(1):1–36.

Imamura, H., and K. Matsuura. 2003. Redefinition and phylogenetic relationships of the family Pinguipedidae (Teleostei: Perciformes). Ichthyological Research 50:259–269.

Imamura, H., and K. Odani. 2013. An overview of the phylogenetic relationships of the suborder Trachinoidei (Acanthomorpha: Perciformes). Ichthyological Research 60:1–15.

Imamura, H., and G. Shinohara. 1998. Scorpaeniform fish phylogeny: an overview. Bulletin of the National Science Museum, Tokyo, Series A, 24:185–212.

Imamura, H., S. M. Shirai, and M. Yabe. 2005. Phylogenetic position of the family Trichodontidae (Teleostei: Perciformes), with a revised classification of the perciform suborder Cottoidei. Ichthyological Research 52:264–274.

Imamura, H., and M. Yabe. 2002. Demise of the Scorpaeniformes (Actinopterygii: Percomorpha): an alternative phylogenetic hypothesis. Bulletin of Fisheries Sciences, Hokkaido University 53(3):107–128.

Inada, T. 1989. Current status of the systematics of Merlucciidae. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 197–207.

Inoue, J. G., Y. Kumazawa, M. Miya, and M. Nishida. 2009. The historical biogeography of the freshwater knifefishes using mitogenomic approaches: a Mesozoic origin of the Asian notopterids (Actinopterygii: Osteoglossomorpha). Molecular Phylogenetics and Evolution 51(3):486–499.

Inoue, J. G., M. Miya, M. J. Miller, T. Sado, R. Hanel, K. Hatooka, J. Aoyama, Y. Minegishi, M. Nishida, and K. Tsukamoto. 2010. Deep-ocean origin of the freshwater eels. Biology Letters 6(3):363–366.

Inoue, J. G., M. Miya, K. Tsukamoto, and M. Nishida. 2001. A mitogenomic perspective on the basal teleostean phylogeny: resolving higher-level relationships with longer DNA sequences. Molecular Phylogenetics and Evolution 20(2):275–285.

—2003a. Basal actinopterygian relationships: a mitogenomic perspective on the phylogeny of the "ancient fish." Molecular Phylogenetics and Evolution 26(1):110–120.

—2003b. Evolution of the deep-sea gulper eel mitochondrial genomes: large-scale gene rearrangements originated within the eels. Molecular Biology and Evolution 20(11):1917–1924.

—2004. Mitogenomic evidence for the monophyly of elopomorph fishes (Teleostei) and the evolutionary origin of the leptocephalus larva. Molecular Phylogenetics and Evolution 32(1):274–286.

[IPA] International Phonetic Association. 1999. Handbook of the International Phonetic Association: A Guide to the Use of the International Phonetic Alphabet. Cambridge: Cambridge University Press. 204 pp.

Ishida, M. 1994. Phylogeny of the suborder Scorpaenoidei (Pisces: Scorpaeniformes). Bulletin of Nansei National Fisheries Research Institute 27:1–112.

Ishiguro, N. B., M. Miya, and M. Nishida. 2003. Basal euteleostean relationships: a mitogenomic perspective on the phylogenetic reality of the "Protacanthopterygii." Molecular Phylogenetics and Evolution 27(3):476–488.

Ivantsoff, W., B. Said, and A. Williams. 1987. Systematic position of the family Dentatherinidae in relationship to Phallostethidae and Atherinidae. Copeia 1987(3):649–658.

Iwami, T. 1985. Osteology and Relationships of the Family Channichthyidae. Tokyo: National Institute of Polar Research. 69 pp. (Memoirs of the National Institute of Polar Research 36.)

Iwamoto, T. 1989. Phylogeny of grenadiers (suborder Macrouroidei). In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 159–173. (Science Series 32.)

Jackson, K. L. 2003. Contributions to the systematics of cottoid fishes (Teleostei: Scorpaenifromes) [dissertation]. University of Alberta. 181 pp. https://doi.org/10.7939/r3-4wnj-sn29

Jamieson, B. G. M. 1991. Fish Evolution and Systematics: Evidence from Spermatozoa. New York: Cambridge University Press. 319 pp.

Jarvik, E. 1980. Basic Structure and Evolution of Vertebrates. London: Academic Press. 2 volumes.

Ji, H.-S., J.-K. Kim, and B.-J. Kim. 2016. Molecular phylogeny of the families Pleuronectidae and Poecilopsettidae (Pisces, Pleuronectiformes) from Korea, with a proposal for a new classification. Ocean Science Journal 51:299–304.

Jiangyong, Z. 1990. The new materials of *Kuntulunia* and its systematic position. Vertebrata PalAsiatica 28(2):128–139.

Johansen, K. 1966. Air breathing in the teleost *Symbranchus marmoratus*. Comparative Biochemistry and Physiology 18(2):383–395.

Johnson, G. D. 1980. The limits and relationships of the Lutjanidae and associated families. Berkeley: University of California Press. 114 pp. (Bulletin of the Scrippps Institution of Oceanography 24.)

—1983. *Niphon spinosus*: a primitive epinepheline serranid, with comments on the monophyly and intrarelationships of the Serranidae. Copeia 1983(3):777–787.

—1984. Percoidei: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 464–498. (Special Publication 1.)

—1986. Scombroid phylogeny: an alternative hypothesis. Bulletin of Marine Science 39(1):1–41.

—1992. Monophyly of the euteleostean clades: Neoteleostei, Eurypterygii, and Ctenosquamata. Copeia 1992(1):8–25.

—1993. Percomorph phylogeny: progress and problems. Bulletin of Marine Science 52(1):3–28.

—2019. Revisions of anatomical descriptions of the pharyngeal jaw apparatus in moray eels of the family Muraenidae (Teleostei: Anguilliformes). Copeia 107(2):341–357.

Johnson, G. D., and E. B. Brothers. 1993. *Schindleria*: a paedomorphic goby (Teleostei: Gobioidei). Bulletin of Marine Science 52(1):441–471.

Johnson, G. D., H. Ida, J. Sakaue, T. Sado, T. Asahida, and M. Miya. 2012. A 'living fossil' eel (Anguilliformes: Protanguillidae, fam. nov.) from an undersea cave in Palau. Proceedings of the Royal Society B, Biological Sciences 279(1730):934–943.

Johnson, G. D., and C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52(1):554–626.

—1996. Relationships of lower euteleostean fishes. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 251–332.

—1997. The gill-arches of gonorynchiform fishes. South African Journal of Science 93(11–12):594–600.

Johnson, G. D., J. R. Paxton, T. T. Sutton, T. P. Satoh, T. Sado, M. Nishida, and M. Miya. 2009. Deep-sea mystery solved: astonishing larval transformations and extreme sexual dimorphism unite three fish families. Biology Letters 5(2):235–239.

Johnson, G. D., and B. B. Washington. 1987. Larvae of the Moorish idol, *Zanclus cornutus*, including a comparison with other larval acanthuroids. Bulletin of Marine Science 40(3):494–511.

Johnson, J. Y. 1862. Descriptions of some new genera and species of fishes obtained at Madeira. Proceedings of the Zoological Society of London 1862, pt. 2. (art. 2), pp. 167–180.

—1863. Descriptions of five new species of fishes obtained at Madeira. Proceedings of the Zoological Society of London 1863, pt. 1 (art. 5), pp. 36–46, pl. 7.

—1864. Descriptions of three new genera of marine fishes obtained at Madeira. Proceedings of the Zoological Society of London 1863, pt. 3 (art. 8), pp. 403–410.

Johnson, R. K. 1982. Fishes of the Families Evermannellidae and Scopelarchidae: Systmatics, Morphology, Interrelationships, and Zoogeography. Chicago: Field Museum of Natural History. 252 pp. (Fieldiana Zoology New Series 12.)

Jondeung, A., P. Sangthong, and R. Zardoya. 2007. The complete mitochondrial DNA sequence of the Mekong giant catfish (*Pangasianodon gigas*), and the phylogenetic relationships among Siluriformes. Gene 387:49–57.

Jones, J. M. 1874. A new fish. Zoologist, Series 2, 9:3837–3838.

Jones, W. J., and J. M. Quattro. 1999. Phylogenetic affinities of pygmy sunfishes (*Elassoma*) inferred from mitochondrial DNA sequences. Copeia 1999(2):470–474.

Jordan, D. S. 1896. Notes on fishes, little known or new to science. Proceedings of the California Academy of Sciences, Series 2, 6:201–244.

—1905. A Guide to the Study of Fishes, Volume 2. New York: Henry Holt and Company. 599 pp.

—1923. A classification of fishes including families and genera as far as known. Stanford University Publications University Series Biological Sciences 3(2):77–243.

Jordan, D. S., and B. W. Evermann. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bulletin of the United States National Museum 47:1–1240.

—1898. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part III. Bulletin of the United States National Museum 47:2184–3136.

Jordan, D. S., and H. W. Fowler. 1902. A review of the berycoid fishes of Japan. Proceedings of the United States National Museum 26(1306):1–21.

Jordan, D. S., and C. H. Gilbert. 1882a. Descriptions of thirty-three new species of fishes from Mazatlan, Mexico. Proceedings of the United States National Museum 4(237):338–365.

—1882b. Notes on fishes observed about Pensacola, Florida, and Galveston, Texas, with description of new species. Proceedings of the United States National Museum 5(282):241–307.

Jordan, D. S., and C. L. Hubbs. 1919. Studies in Ichthyology: A Monographic Review of the Family of Atherinidae or Silversides. Stanford, CA: Stanford University Press. 87 pp. (Stanford Junior University Publications, University Series 40,)

Jordan, D. S., and M. Sindo. 1902. A review of the pediculate fishes or anglers of Japan. Proceedings of the United States National Museum 24(1261):361–381.

Jordan, D. S., and J. O. Snyder. 1901. A review of the cardinal fishes of Japan. Proceedings of the United States National Museum 23(1240):891–913.

—1902. A review of the trachinoid fishes and their supposed allies found in the waters of Japan. Proceedings of the United States National Museum 24(1263):461–497.

Jordan, D. S., and E. C. Starks. 1895. The fishes of Puget Sound. Proceedings of the California Academy of Sciences, Series 2, 5:785–855.

—1901. A review of the atherine fishes of Japan. Proceedings of the United States National Museum 24(1250):199–206.

Kai, Y., and F. Tashiro. 2019. *Zenopsis filamentosa* (Zeidae), a new mirror dory from the western Pacific Ocean, with redescription of *Zenopsis nebulosa*. Ichthyological Research 66:340–352.

Kalumba, L. N., E. Abwe, F. D. B. Schedel, A. Chocha Manda, U. K. Schliewen, and E. J. W. M. N. Vreven. 2023. Two new shellear species (Gonorhynchiformes: Kneriidae), from the Luansa River (Upper Congo Basin): hidden diversity revealed by integrative taxonomy. Diversity 15(10):1044.

Kappas, I., S. Vittas, C. N. Pantzartzi, E. Drosopoulou, and Z. G. Scouras. 2016. A time-calibrated mitogenome phylogeny of catfish (Teleostei: Siluriformes). PLOS ONE 11(12):e0166988. https://doi.org/10.1371/journal.pone.0166988

Kartavtsev, Y. P., T. J. Park, J. S. Lee, K. A. Vinnikov, V. N. Ivankov, S. N. Sharina, and A. S. Ponomarev. 2008. Phylogenetic inferences introduced on cytochrome *b* gene sequences data for six flatfish species (Teleostei, Pleuronectidae) and species synonymy between representatives of genera *Pseudopleuronectes* and *Hippoglossoides* from far eastern seas. Russian Journal of Genetics 44(4):451–458.

Kaufman, L., and K. F. Liem. 1982. Fishes of the suborder Labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. Breviora 472:1–19.

Kaup, J. J. 1856. Catalogue of Apodal Fish, in the Collection of the British Museum. London: British Museum. 163 pp.

Kawahara, R., M. Miya, K. Mabuchi, S. Lavoué, J. G. Inoue, T. P. Satoh, A. Kawaguchi, and M. Nishida. 2008. Interrelationships of the 11 gasterosteiform families (sticklebacks, pipefishes, and their relatives): a new perspective based on whole mitogenome sequences from 75 higher teleosts. Molecular Phylogenetics and Evolution 46(1):224–236.

Kawahara, R., M. Miya, K. Mabuchi, T. J. Near, and M. Nishida. 2009. Stickleback phylogenies resolved: evidence from mitochondrial genomes and 11 nuclear genes. Molecular Phylogenetics and Evolution 50(2):401–404.

Keivany, Y., and J. S. Nelson. 2004. Phylogenetic relationships of sticklebacks (Gasterosteidae), with emphasis on ninespine sticklebacks (*Pungitius* spp.). Behaviour 141(11–12):1485–1497.

Kenaley, C. P., S. C. DeVaney, and T. T. Fjeran. 2014. The complex evolutionary history of seeing red: molecular phylogeny and the evolution of an adaptive visual system in deep-sea dragonfishes (Stomiiformes: Stomiidae). Evolution 68(4):996–1013.

Kendall, W. C., and L. Radcliffe. 1912. The shore fishes. Memoirs of the Museum of Comparative Zoology at Harvard College 35(3):75–171.

Keskin, E., and H. H. Atar. 2013. DNA barcoding commercially important fish species of Turkey. Molecular Ecology Resources 13(5):788–797.

Khajuria, C. K., and G. V. R. Prasad. 1998. Taphonomy of a late Cretaceous mammal-bearing microvertebrate assemblage from the Deccan inter-trappean beds of Naskal, peninsular India. Palaeogeography, Palaeoclimatology, Palaeoecology 137(1):153–172.

Khalloufi, B., D. Ouarhache, and H. Lelièvre. 2010. New paleontological and geological data about Jbel Tselfat (Late Cretaceous of Morocco). Historical Biology 22(1–3):57–70.

Kiernan, A. M. 1990. Systematics and zoogeography of the ronquils family Bathymasteridae (Teleostei:Perciformes) [dissertation]. University of Washington. 190 pp.

Kikugawa, K., K. Katoh, S. Kuraku, H. Sakurai, O. Ishida, N. Iwabe, and T. Miyata. 2004. Basal jawed vertebrate phylogeny inferred from multiple nuclear DNA-coded genes. BMC Biology 2:3. https://doi.org/10.1186/1741-7007-2-3

Kimura, K., H. Imamura, and T. Kawai. 2018. Comparative morphology and phylogenetic systematics of the families Cheilodactylidae and Latridae (Perciformes: Cirrhitoidea), and proposal of a new classification. Zootaxa 4536(1):1–72. https://doi.org/10.11646/zootaxa.4536.1.1

Klausewitz, W. 1968. Fische aus dem Roten Meer. IX. *Pseudochromis fridmani* n. sp. aus dem Golf von Aqaba (Pisces, Osteichthyes, Pseudochromidae). Senckenbergiana Biologica 49(6):443–450.

Klausewitz, W., and I. Eibl-Eibesfeldt. 1959. Neue Röhrenaale von den Maldiven und Nikobaren (Pisces, Apodes, Heterocongridae). Senckenbergiana Biologica 40(3–4):135–153.

Kner, R. 1868. Über neue Fische aus dem Museum der Herren Johann Cäsar Godeffroy and Sohn in Hamburg. (IV. Folge). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe 58:26–31.

Knudsen, S. W., J. H. Choat, and K. D. Clements. 2019. The herbivorous fish family Kyphosidae (Teleostei: Perciformes) represents a recent radiation from higher latitudes. Journal of Biogeography 46(9):2067–2080.

Knudsen, S. W., and K. D. Clements. 2016. World-wide species distributions in the family Kyphosidae (Teleostei: Perciformes). Molecular Phylogenetics and Evolution 101:252–266.

Kobyliansky, S. G., N. V. Gordeeva, and A. N. Kotlyar. 2020. New findings of the rare species *Rondeletia bicolor*

(Stephanoberycoidei) over the Mid-Atlantic Ridge and some peculiarities of the Rondeletiidae family's phylology. Journal of Ichthyology 60:13–21.

Koeda, K., and H.-C. Ho. 2019. A new tapertail species (family Radiicephalidae; Lampridiformes) from Taiwan, the first confirmed western Pacific Ocean record of the family. Ichthyological Research 66:207–214.

Konishi, Y., and M. Okiyama. 1997. Morphological development of four trachichthyoid larvae (Pisces: Beryciformes), with comments on trachichthyoid relationships. Bulletin of Marine Science 60:66–88.

Kontula, T., S. V. Kirilchik, and R. Väinölä. 2003. Endemic diversification of the monophyletic cottoid fish species flock in Lake Baikal explored with mtDNA sequencing. Molecular Phylogenetics and Evolution 27(1):143–155.

Kottelat, M. 1990. Synopsis of the endangered buntingi (Osteichthyes: Adrianichthyidae and Oryziidae) of Lake Poso, Central Sulawesi, Indonesia, with a new reproductive guild and descriptions of three new species. Ichthyological Exploration of Freshwaters 1:49–67.

—2012. Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidei). Raffles Bulletin of Zoology Suppl. 26:1–199.

Kottelat, M., R. Britz, T. H. Hui, and K.-E. Witte. 2006. *Paedocypris*, a new genus of Southeast Asian cyprinid fish with a remarkable sexual dimorphism, comprises the world's smallest vertebrate. Proceedings of the Royal Society B, Biological Sciences 273(1589):895–899.

Kriwet, J., and T. Hecht. 2008. A review of early gadiform evolution and diversification: first record of a rattail fish skull (Gadiformes, Macrouridae) from the Eocene of Antarctica, with otoliths preserved in situ. Naturwissenschaften 95:899–907.

Kuang, T., L. Tornabene, J. Li, J. Jiang, P. Chakrabarty, J. S. Sparks, G. J. P. Naylor, and C. Li. 2018. Phylogenomic analysis on the exceptionally diverse fish clade Gobioidei (Actinopterygii: Gobiiformes) and data-filtering based on molecular clocklikeness. Molecular Phylogenetics and Evolution 128:192–202.

Kuehne, L. M., and J. D. Olden. 2014. Ecology and conservation of mudminnow species worldwide. Fisheries 39(8):341–351.

Kullander, S., M. Norén, M. M. Rahman, and A. R. Mollah. 2019. Chameleonfishes in Bangladesh: hipshot taxonomy, sibling species, elusive species, and limits of species delimitation (Teleostei: Badidae). Zootaxa 4586(2):301–337. https://doi.org/10.11646/zootaxa.4586.2.7

Kullander, S., and R. Britz. 2002. Revision of the family Badidae (Teleostei: Perciformes), with description of a new genus and ten new species. Ichthyological Exploration of Freshwaters 13(4):295–372.

Kwun, H. J. 2013. Phylogenetic study on the genera *Eulophias* and *Zoarchias* (Zoarcoidei: Perciformes) [dissertation]. Pukyong National University. 90 pp.

Kwun, H. J., and J.-K. Kim. 2013. Molecular phylogeny and new classification of the genera *Eulophias* and *Zoarchias* (Pisces, Zoarcoidei). Molecular Phylogenetics and Evolution 69(3):787–795.

Lacépède, B. G. E. 1801. Histoire naturelle des poissons, Volume 3. Paris: Plassan. 558 pp.

—1802. Histoire naturelle des poissons, Volume 4. Paris: Plassan. 728 pp.

—1803. Histoire naturelle des poissons, Volume 5. Paris: Plassan. 803 pp.

Lambers, P. H. 1995. The monophyly of the Caturidae (Pisces; Actinopterygii) and the phylogeny of the Halecomorphi. Géobios 28(Suppl. 2):201–203.

Landi, M., M. Dimech, M. Arculeo, G. Biondo, R. Martins, M. Carneiro, G. R. Carvalho, S. L. Brutto, and F. O. Costa. 2014. DNA barcoding for species assignment: the case of Mediterranean marine fishes. PLOS ONE 9(9):e106135. https://doi.org/10.1371/journal.pone.0106135

Last, P. R. 2001. Leptoscopidae. In: K. E. Carpenter, and V. H. Niem, eds. Bony Fishes Part 4 (Labridae to Latimeriidae), Estuarine Crocodiles, Sea Turtles, Sea Snakes and Marine Mammals. Vol. 6 of FAO Species Identification Guide for Fishery Purposes: The Living Marine Resources of the Western Central Pacific. Rome: Food and Agriculture Organization of the United Nations. pp. 3517.

Latimer, A. E., and S. Giles. 2018. A giant dapediid from the Late Triassic of Switzerland and insights into neopterygian phylogeny. Royal Society Open Science 5(8):180497. https://doi.org/10.1098/rsos.180497

Lauder, G. V. 1980. Evolution of the feeding mechanism in primitive actionopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. Journal of Morphology 163(3):283–317.

—1983. Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. Zoological Journal of the Linnean Society 77(1):1–38.

Lauder, G. V., and K. F. Liem. 1982. Symposium summary: evolutionary patterns in actinopterygian fishes. American Zoologist 22(2):343–345.

—1983. The evolution and interrelationships of the actinopterygian fishes. Bulletin of the Museum of Comparative Zoology 150(3):95–197.

Lautredou, A.-C., H. Motomura, C. Gallut, C. Ozouf-Costaz, C. Cruaud, G. Lecointre, and A. Dettaï. 2013. New nuclear markers and exploration of the relationships among Serraniformes (Acanthomorpha, Teleostei): the importance of working at multiple scales. Molecular Phylogenetics and Evolution 67(1):140–155.

Lavoué, S. 2015. Testing a time hypothesis in the biogeography of the arowana genus *Scleropages* (Osteoglossidae). Journal of Biogeography 42(12):2427–2439.

—2016. Was Gondwanan breakup the cause of the intercontinental distribution of Osteoglossiformes? A time-calibrated phylogenetic test combining molecular, morphological, and paleontological evidence. Molecular Phylogenetics and Evolution 99:34–43.

Lavoué, S., M. E. Arnegard, D. L. Rabosky, P. B. McIntyre, D. Arcila, R. P. Vari, and M. Nishida. 2017. Trophic evolution in African citharinoid fishes (Teleostei: Characiformes) and the origin of intraordinal pterygophagy. Molecular Phylogenetics and Evolution 113:23–32.

Lavoué, S., P. Konstantinidis, and W.-J. Chen. 2014. Progress in clupeiform systematics. In: K. Ganias, ed. Biology and Ecology of Anchovies and Sardines. Boca Raton, FL: CRC. pp. 3–42.

Lavoué, S., M. Miya, M. E. Arnegard, P. B. McIntyre, V. Mamonekene, and M. Nishida. 2011. Remarkable morphological stasis in an extant vertebrate despite tens of millions of years of divergence. Proceedings of the Royal Society B, Biological Sciences 278(1708):1003–1008.

Lavoué, S., M. Miya, M. E. Arnegard, J. P. Sullivan, C. D. Hopkins, and M. Nishida. 2012. Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. PLOS ONE 7(5):e36287. https://doi.org/10.1371/journal.pone.0036287

Lavoué, S., M. Miya, J. G. Inoue, K. Saitoh, N. B. Ishiguro, and M. Nishida. 2005. Molecular systematics of the gonorynchiform fishes (Teleostei) based on whole mitogenome sequences: implications for higher-level relationships within the Otocephala. Molecular Phylogenetics and Evolution 37(1):165–177.

Lavoué, S., M. Miya, A. Kawaguchi, T. Yoshino, and M. Nishida. 2008. The phylogenetic position of an undescribed paedomorphic clupeiform taxon: mitogenomic evidence. Ichthyological Research 55:328–334.

Lavoué, S., M. Miya, T. Moritz, and M. Nishida. 2012. A molecular timescale for the evolution of the African freshwater fish family Kneriidae (Teleostei: Gonorynchiformes). Ichthyological Research 59:104–112.

Lavoué, S., M. Miya, P. Musikasinthorn, W.-J. Chen, and M. Nishida. 2013. Mitogenomic evidence for an Indo-West Pacific origin of the Clupeoidei (Teleostei: Clupeiformes). PLOS ONE 8(2):e56485. https://doi.org/10.1371/journal.pone.0056485

Lavoué, S., M. Miya, and M. Nishida. 2010. Mitochondrial phylogenomics of anchovies (family Engraulidae) and recurrent origins of pronounced miniaturization in the order Clupeiformes. Molecular Phylogenetics and Evolution 56(1):480–485.

Lavoué, S., M. Miya, J. Y. Poulsen, P. R. Møller, and M. Nishida. 2008. Monophyly, phylogenetic position and inter-familial relationships of the Alepocephaliformes (Teleostei) based on whole mitogenome sequences. Molecular Phylogenetics and Evolution 47(3):1111–1121.

Lavoué, S., M. Miya, K. Saitoh, N. B. Ishiguro, and M. Nishida. 2007. Phylogenetic relationships among anchovies, sardines, herrings and their relatives (Clupeiformes), inferred from whole mitogenome sequences. Molecular Phylogenetics and Evolution 43(3):1096–1105.

Lavoué, S., K. Nakayama, D. R. Jerry, Y. Yamanoue, N. Yagishita, N. Suzuki, M. Nishida, and M. Miya. 2014. Mitogenomic phylogeny of the Percichthyidae and Centrarchiformes (Percomorphaceae): comparison with recent nuclear gene-based studies and simultaneous analysis. Gene 549(1):46–57.

Lavoué, S., and J. P. Sullivan. 2004. Simultaneous analysis of five molecular markers provides a well-supported phylogenetic hypothesis for the living bony-tongue fishes (Osteoglossomorpha: Teleostei). Molecular Phylogenetics and Evolution 33(1):171–185.

Lê, H. L., G. Lecointre, and R. Perasso. 1993. A 28S rRNA-based phylogeny of gnathostomes: first steps in the analysis of conflict and congruence with morphologically based cladograms. Molecular Phylogenetics and Evolution 2(1):31–51.

Lecointre, G. 1995. Molecular and morphological evidence for a Clupeomorpha-Ostariophysi sister-group relationship (Teleostei). Géobios 28(Suppl. 2):205–210.

Lecointre, G., C. Bonillo, C. Ozouf-Costaz, and J.-C. Hureau. 1997. Molecular evidence for the origins of Antarctic fishes: paraphyly of the Bovichtidae and no indication for the monophyly of the Notothenioidei (Teleostei). Polar Biology 18:193–208.

Lecointre, G., and G. Nelson. 1996. Clupeomorpha, sister-group of Ostariophysi. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 193–207.

Leis, J. M. 1984. Tetraodontiformes: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 459–463. (Special Publication 1.)

Leslie, R. W., and W. S. Grant. 1994. Meristic and morphometric variation among anglerfish of the genus *Lophius* (Lophiiformes). Journal of Zoology 232(4):565–584.

Lesueur, C. A. 1817. A short description of five (supposed) new species of the genus *Muraena*, discovered by Mr. Le Sueur, in the year 1816. Journal of the Academy of Natural Sciences of Philadelphia 1(5):81–83.

—1818. Descriptions of several new species of North American fishes. Journal of the Academy of Natural Sciences of Philadelphia 1(2):222–235, 359–368.

Levin, B. A., and A. S. Golubtsov. 2018. New insights into the molecular phylogeny and taxonomy of mormyrids (Osteoglossiformes, Actinopterygii) in northern East Africa. Journal of Zoological Systematics and Evolutionary Research 56(1):61–76.

Li, B., A. Dettaï, C. Cruaud, A. Couloux, M. Desoutter-Meniger, and G. Lecointre. 2009. RNF213, a new nuclear marker for acanthomorph phylogeny. Molecular Phylogenetics and Evolution 50(1):345–363.

Li, C. H., R. Betancur-R, W. L. Smith, and G. Ortí. 2011. Monophyly and interrelationships of snook and barramundi (Centropomidae *sensu* Greenwood) and five new markers for fish phylogenetics. Molecular Phylogenetics and Evolution 60(3):463–471.

Li, C. H., G. Q. Lu, and G. Ortí. 2008. Optimal data partitioning and a test case for ray-finned fishes (Actinopterygii) based on ten nuclear loci. Systematic Biology 57(4):519–539.

Li, C. H., and G. Ortí. 2007. Molecular phylogeny of Clupeiformes (Actinopterygii) inferred from nuclear and mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 44(1):386–398.

Li, C. H., G. Ortí, and J. L. Zhao. 2010. The phylogenetic placement of sinipercid fishes ("Perciformes") revealed by 11 nuclear loci. Molecular Phylogenetics and Evolution 56(3):1096–1104.

Li, G.-Q. 1996. A new species of Late Cretaceous osteoglossid (Teleostei) from the Oldman Formation of Alberta, Canada, and its phylogenetic relationships. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 285–298.

Li, G.-Q., L. Grande, and M. V. H. Wilson. 1997. The species of †*Phareodus* (Teleostei: Osteoglossidae) from the Eocene of North America and their phylogenetic relationships. Journal of Vertebrate Paleontology 17:487–505.

Li, G.-Q., and M. V. H. Wilson. 1996. Phylogeny of Osteoglossomorpha. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 163–174.

—1999. Early divergence of Hiodontiformes *sensu stricto* in East Asia and phylogeny of some Late Mesozoic teleosts from China. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record. Munich: Verlag Dr. Friedrich Pfeil. pp. 369–384.

Li, G.-Q., M. V. H. Wilson, and L. Grande. 1997. Review of *Eohiodon* (Teleostei: Osteoglossomorpha) from western North America, with a phylogenetic reassessment of Hiodontidae. Journal of Paleontology 71(6):1109–1124.

Li, H., Y. He, J. Jiang, Z. Liu, and C. Li. 2018. Molecular systematics and phylogenetic analysis of the Asian endemic freshwater sleepers (Gobiiformes: Odontobutidae). Molecular Phylogenetics and Evolution 121:1–11.

Li, J., R. Xia, R. M. McDowall, J. A. López, G. C. Lei, and C. Z. Fu. 2010. Phylogenetic position of the enigmatic *Lepidogalaxias salamandroides* with comment on the orders of lower euteleostean fishes. Molecular Phylogenetics and Evolution 57(2):932–936.

Li, X., P. Musikasinthorn, and Y. Kumazawa. 2006. Molecular phylogenetic analyses of snakeheads (Perciformes: Channidae) using mitochondrial DNA sequences. Ichthyological Research 53:148–159.

Li, X., and W. Zhou. 2018. The species of *Clupisoma* from Yunnan, China (Teleostei: Siluriformes: Ailiidae), with a comment on the validity of the family Ailiidae. Zootaxa 4476(1):77–86. https://doi.org/10.11646/zootaxa.4476.1.7

Lichtenstein, M. H. C. 1819. Ueber einige neue Arten von Fischen aus der Gattung *Silurus*. Zoologisches Magazin 1(3):57–63.

Liddell, H. G., R. Scott, H. S. Jones, R. McKenzie, and E. A. Barber. 1968. A Greek-English Lexicon, with a Supplement. Oxford: Clarendon Press. 2042 pp; 153 pp.

Liem, K. F. 1970. Comparative Functional Anatomy of the Nandidae (Pisces: Teleostei). Chicago: Field Museum of Natural History. 166 pp. (Fieldiana: Zoology 56.)

Liem, K. F., and P. H. Greenwood. 1981. A functional-approach to the phylogeny of the pharyngognath teleosts. American Zoologist 21(1):83–101.

Lima, F. C. T., L. R. Malabarba, P. A. Buckup, J. F. Pezzi da Silva, R. P. Vari, A. Harold, R. Benine, O. T. Oyakawa, C. S. Pavanelli, N. A. Menezes, et al. 2003. Family Characidae (Characins, tetras). In: R. E. Reis, S. O. Kullander, and C. J. Ferraris, eds. Check List of the Freshwater Fishes of South and Central America. Porto Alegre, Brazil: EDIPUCRS. pp. 104–169.

Lin, H. C., and P. A. Hastings. 2013. Phylogeny and biogeography of a shallow water fish clade (Teleostei: Blenniiformes). BMC Evolutionary Biology 13:210. https://doi.org/10.1186/1471-2148-13-210

Lin, Q., S. Fan, Y. Zhang, M. Xu, H. Zhang, Y. Yang, A. P. Lee, J. M. Woltering, V. Ravi, H. M. Gunter, et al. 2016. The seahorse genome and the evolution of its specialized morphology. Nature 540:395–399.

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima, Reformata. Holmiae [Stockholm]: Impensis Direct. Laurentii Salvii. 824 pp.

—1761. Fauna Svecica, Sistens Animalia Sveciae Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes: Distributa per Classes and Ordines, Genera and Species, Cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarim, Locis Naturalium, Descriptionibus Insectorum. Altera Editio. Stockholmiae [Stockholm]: Sumtu and literis direct. Laurentii Salvii . 578 pp.

—1766. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus 1. Edition Duodecima, Reformata Holmiae [Stockholm]: Impensis Direct. Laurentii Salvii. 532 pp.

Little, A. G., S. C. Lougheed, and C. D. Moyes. 2010. Evolutionary affinity of billfishes (Xiphiidae and Istiophoridae) and flatfishes (Plueronectiformes): independent and trans-subordinal origins of endothermy in teleost fishes. Molecular Phylogenetics and Evolution 56(3):897–904.

Liu, J., M.-M. Chang, M. V. H. Wilson, and A. M. Murray. 2015. A new family of Cypriniformes (Teleostei, Ostariophysi) based on a redescription of †*Jianghanichthys hubeiensis* (Lei, 1977) from the Eocene Yangxi Formation of China. Journal of Vertebrate Paleontology 35(6):e1004073.

Liu, L., C. Li, Q. Liu, Z. Chen, and X. Fan. 2023. Genome-wide survey reveals the microsatellite characteristics and phylogenomic relationships of *Dictyosoma burgeri* (Zoarcales, Perciformes). Thalassas 39:609–619. https://doi.org/10.1007/s41208-023-00598-7

Liu, S.-Q., R. L. Mayden, J.-B. Zhang, D. Yu, Q.-Y. Tang, X. Deng, and H.-Z. Liu. 2012. Phylogenetic relationships of the Cobitoidea (Teleostei: Cypriniformes) inferred from mitochondrial and nuclear genes with analyses of gene evolution. Gene 508(1):60–72.

Liu, Z., X. Mu, H. Li, L. Gui, W. Zeng, and J. Zhang. 2016. Complete mitochondrial genome of the striped scat *Selenotoca multifasciata* (Perciformes: Scatophagidae). Mitochondrial DNA Part A 27(4):2691–2692.

Livy. 1919. History of Rome, Volume 1, Books 1 and 2. Translated by B. O. Foster. Cambridge, MA: Harvard University Press. 447 pp. (Loeb Classical Library 114.)

Lloris, D., J. Matallanas, and P. Oliver. 2005. Hakes of the World (Merlucciidae): An Annotated and Illustrated Catalogue of Hake Species Known to Date. Rome: Food and Agriculture Organization of the United Nations. 57 pp. (FAO Species Catalogue for Fishery Purposes 2.)

Lockington, W. N. 1880. Description of a new genus and some new species of California fishes (*Icosteus aenigmaticus* and *Osmerus attenuatus*). Proceedings of the United States National Museum 3(123):63–68.

Lofgren, D. L., J. A. Lillegraven, W. A. Clemens, P. D. Gingerich, and T. E. Williamson. 2004. Paleocene biochronology: the Puercan through Clarkforkian land mammal ages. In: M. O. Woodburne, ed. Late Cretaceous and Cenozoic Mammals of North America. New York: Columbia University Press. pp. 43–105.

Longo, S. J., B. C. Faircloth, A. Meyer, M. W. Westneat, M. E. Alfaro, and P. C. Wainwright. 2017. Phylogenomic analysis of a rapid radiation of misfit fishes (Syngnathiformes) using ultraconserved elements. Molecular Phylogenetics and Evolution 113:33–48.

López, J. A., P. Bentzen, and T. W. Pietsch. 2000. Phylogenetic relationships of esocoid fishes (Teleostei) based on partial cytochrome b and 16S mitochondrial DNA sequences. Copeia 2000(2):420–431.

López, J. A., W.-J. Chen, and G. Ortí. 2004. Esociform phylogeny. Copeia 2004(3):449–464.

López, J. A., M. W. Westneat, and R. Hanel. 2007. The phylogenetic affinities of the mysterious anguilliform genera *Coloconger* and *Thalassenchelys* as supported by mtDNA sequences. Copeia 2007(4):959–966.

López-Arbarello, A. 2012. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). PLOS ONE 7(7):e39370. https://doi.org/10.1371/journal.pone.0039370

López-Arbarello, A., T. Bürgin, H. Furrer, and R. Stockar. 2016. New holostean fishes (Actinopterygii: Neopterygii) from the Middle Triassic of the Monte San Giorgio (Canton Ticino, Switzerland). PeerJ 4:e2234. https://doi.org/10.7717/peerj.2234

—2019. Taxonomy and phylogeny of *Eosemionotus* Stolley, 1920 (Neopterygii: Ginglymodi) from the Middle Triassic of Europe. Palaeontologia Electronica 22.1.10:1–64. https://doi.org/10.26879/904

López-Arbarello, A., E. E. Maxwell, and G. Schweigert. 2020. New halecomorph (Actinopterygii, Neopterygii) from the Nusplingen Lithographic Limestone (Upper Jurassic, Late Kimmeridgian), Germany. Journal of Vertebrate Paleontology 40(2):e1771348.

López-Arbarello, A., and E. Sferco. 2018. Neopterygian phylogeny: the merger assay. Royal Society Open Science 5(3):172337. https://doi.org/10.1098/rsos.172337

López-Arbarello, A., R. Stockar, and T. Bürgin. 2014. Phylogenetic relationships of the Triassic *Archaeosemionotus* Deecke (Halecomorphi, Ionoscopiformes) from the 'Perledo Fauna.' PLOS ONE 9(10):e108665. https://doi.org/10.1371/journal.pone.0108665

Lovejoy, N. R. 2000. Reinterpreting recapitulation: systematics of needlefishes and their allies (Teleostei: Beloniformes). Evolution 54(4):1349–1362.

Lovejoy, N. R., M. Iranpour, and B. B. Collette. 2004. Phylogeny and jaw ontogeny of beloniform fishes. Integrative and Comparative Biology 44(5):366–377.

Løvtrup, S. 1977. The Phylogeny of Vertebrata. New York: John Wiley and Sons. 330 pp.

Lowe, R. T. 1833. Description of *Alepisaurus*, a new genus of fishes. Proceedings of the Zoological Society of London 1833. Part 1, p. 104.

—1843. Notices of fishes newly observed or discovered in Madeira during the years 1840, 1841, and 1842. Proceedings of the Zoological Society of London 1843. Part 11, pp. 81–95.

L-Recinos, M., K. M. Cantalice, C. Caballero-Viñas, and J. Alvarado-Ortega. 2023. A new Mesozoic teleost of the subfamily Albulinae (Albuliformes: Albulidae) highlights the proto-Gulf of Mexico in the early diversification of extant bonefishes. Journal of Systematic Palaeontology 21(1):2223797.

Lü, Z., L. Gong, Y. Ren, Y. Chen, Z. Wang, L. Liu, H. Li, X. Chen, Z. Li, H. Luo, et al. 2021. Large-scale sequencing of flatfish genomes provides insights into the polyphyletic origin of their specialized body plan. Nature Genetics 53:742–751.

Lü, Z., K. Zhu, H. Jiang, X. Lu, B. Liu, Y. Ye, L. Jiang, L. Liu, and L. Gong. 2019. Complete mitochondrial genome of *Ophichthus brevicaudatus* reveals novel gene order and phylogenetic relationships of Anguilliformes. International Journal of Biological Macromolecules 135:609–618.

Lucena, C. A. S., and N. A. Menezes. 1998. A phylogenetic analysis of *Roestes* Günther and *Gilbertolus* Eigenmann, with a hypothesis on the relationships of the Cynodontidae and Acestorhynchidae (Teleostei: Ostariophysi: Characiformes). In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 261–278.

Lucentini, L., M. E. Puletti, C. Ricciolini, L. Gigliarelli, D. Fontaneto, L. Lanfaloni, F. Bilò, M. Natali, and F. Panara. 2011. Molecular and phenotypic evidence of a new species of genus *Esox* (Esocidae, Esociformes, Actinopterygii): the Southern Pike, *Esox flaviae*. PLOS ONE 6(12):e25218. https://doi.org/10.1371/journal.pone.0025218

Ludt, W. B., C. P. Burridge, and P. Chakrabarty. 2019. A taxonomic revision of Cheilodactylidae and Latridae (Centrarchiformes: Cirrhitoidei) using morphological and genomic characters. Zootaxa 4585(1):121–141. https://doi.org/10.11646/zootaxa.4585.1.7

Lund, R. 2000. The new actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA). Geodiversitas 22(6):171–206.

Lundberg, J. G. 1993. African-South American freshwater fish clades and continental drift: problems with a paradigm. In: P. Goldblatt, ed. Biological Relationships between Africa and South America. New Haven, CT: Yale University Press. pp. 156–199.

—2020a. *Ostariophysi*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 725–726.

—2020b. *Otophysi*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 729–730.

—2020c. *Pan-Siluriformes*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 733–734.

—2020d. *Siluriformes*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 735–739.

Lundberg, J. G., K. R. Luckenbill, K. K. Subhash Babu, and H. H. Ng. 2014. A tomographic osteology of the taxonomically puzzling catfish *Kryptoglanis shajii* (Siluriformes, Siluroidei, *incertae sedis*): description and a first phylogenetic interpretation. Proceedings of the Academy of Natural Sciences of Philadelphia 163:1–41.

Lundberg, J. G., L. G. Marshall, J. Guerrero, B. Horton, M. C. Malabarba, and F. Wesselingh. 1998. The stage for Neotropical fish diversification: a history of tropical South American rivers. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 13–48.

Lundberg, J. G., J. P. Sullivan, R. Rodiles-Hernández, and D. A. Hendrickson. 2007. Discovery of African roots for the Mesoamerican Chiapas catfish, *Lacantunia enigmatica*, requires an ancient intercontinental passage. Proceedings of the Academy of Natural Sciences of Philadelphia 156:39–53.

Lundsten, L., S. B. Johnson, G. M. Cailliet, A. P. DeVogelaere, and D. A. Clague. 2012. Morphological, molecular, and in situ behavioral observations of the rare deep-sea anglerfish *Chaunacops coloratus* (Garman, 1899), order Lophiiformes, in the eastern North Pacific. Deep Sea Research Part 1: Oceanographic Research Papers 68:46–53.

Luo, T., Q. Yang, L. Wu, Y.-L. Wang, J.-J. Zhou, H.-Q. Deng, N. Xiao, and J. Zhou. 2023. Phylogenetic relationships of Nemacheilidae cavefish (*Heminoemacheilus*, *Oreonectes*, *Yunnanilus*, *Paranemachilus*, and *Troglonectes*) revealed by analysis of mitochondrial genome and seven nuclear genes. Zoological Research 44(4):693–697.

Ma, K. Y., M. T. Craig, J. H. Choat, and L. van Herwerden. 2016. The historical biogeography of groupers: clade diversification patterns and processes. Molecular Phylogenetics and Evolution 100:21–30.

Mabee, P. M., E. A. Grey, G. Arratia, N. Bogutskaya, A. Boron, M. M. Coburn, K. W. Conway, S. P. He, A. Naseka, N. Rios, et al. 2011. Gill arch and hyoid arch diversity and cypriniform phylogeny: distributed integration of morphology and web-based tools. Zootaxa 2877(1):1–40. https://doi.org/10.11646/zootaxa.2877.1.1

Mabuchi, K., T. H. Fraser, H. Song, Y. Azuma, and M. Nishida. 2014. Revision of the systematics of the cardinalfishes (Percomorpha: Apogonidae) based on molecular analyses and comparative reevaluation of morphological characters. Zootaxa 3846(2):151–203. https://doi.org/10.11646/zootaxa.3846.2.1

Mabuchi, K., M. Miya, Y. Azuma, and M. Nishida. 2007. Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. BMC Evolutionary Biology 7:10. https://doi.org/10.1186/1471-2148-7-10

Maddison, W. P., and D. R. Maddison. 2021. Mesquite: a modular system for evolutionary analysis [online analysis tool]. Version 3.70. http://www.mesquiteproject.org

Maduna, S. N., A. Vivian-Smith, Ó. D. B. Jónsdóttir, A. K. D. Imsland, C. F. C. Klütsch, T. Nyman, H. G. Eiken, and S. B. Hagen. 2022. Mitogenomics of the suborder Cottoidei (Teleostei: Perciformes): improved assemblies, mitogenome features, phylogeny, and ecological implications. Genomics 114(2):110297.

Mago-Leccia, F. 1978. Los peces de la familia Sternopygidae de Venezuela. Acta Científica Venezolana 29(Suppl. 1):1–51.

Mago-Leccia, F., and T. M. Zaret. 1978. The taxonomic status of *Rhabdolichops troscheli* (Kaup, 1856), and speculations on gymnotiform evolution. Environmental Biology of Fishes 3(4):379–384.

Maisey, J. G. 1986. Heads and tails: a chordate phylogeny. Cladistics 2(4):201–256.

—1993. A new clupeomorph fish from the Santana Formation (Albian) of NE Brazil. American Museum Novitates 3076:1–15.

Makushok, V. M. 1958. The morphology and classification of the northern blennioid fishes (Stichaeidae, Blennioidei, Pisces). Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR 25:3–129.

Malabarba, M. C., and F. Di Dario. 2017. A new predatory herring-like fish (Teleostei: Clupeiformes) from the early Cretaceous of Brazil, and implications for relationships in the Clupeoidei. Zoological Journal of the Linnean Society 180(1):175–194.

Malabarba, M. C., and L. R. Malabarba. 2010. Biogeography of Characiformes: an evaluation of the available information of fossil and extant taxa. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 317–336.

Malmstrøm, M., R. Britz, M. Matschiner, O. K. Tørresen, R. K. Hadiaty, H. Yaakob, H.-H. Tan, K. S. Jakobsen, W. Salzburger, and L. Rüber. 2018. The most developmentally truncated fishes show extensive *Hox* gene loss and miniaturized genomes. Genome Biology and Evolution 10(4):1088–1103.

Malmstrøm, M., M. Matschiner, O. K. Tørresen, K. S. Jakobsen, and S. Jentoft. 2017. Whole genome sequencing data and de novo draft assemblies for 66 teleost species. Scientific Data 4:160132.

Malmstrøm, M., M. Matschiner, O. K. Tørresen, B. Star, L. G. Snipen, T. F. Hansen, H. T. Baalsrud, A. J. Nederbragt, R. Hanel, W. Salzburger, et al. 2016. Evolution of the immune system influences speciation rates in teleost fishes. Nature Genetics 48:1204–1210.

Marić, S., D. Stanković, J. Wanzenböck, R. Šanda, T. Erős, P. Takács, A. Specziár, N. Sekulić, D. Bănăduc, M. Ćaleta, et al. 2017. Phylogeography and population genetics of the European mudminnow (*Umbra krameri*) with a time-calibrated phylogeny for the family Umbridae. Hydrobiologia 792:151–168.

Mar'ie, Z. A., and M. Allam. 2019. Molecular phylogenetic linkage for Nile and marine puffer fishes using mitochondrial DNA sequences of cytochrome *b* and 16S rRNA. Egyptian Journal of Aquatic Biology and Fisheries 23(5):67–80.

Markle, D. F. 1976. Preliminary studies on the systematics of deep-sea Alepocephaloidea (Pisces: Salmoniformes) [dissertation]. College of William and Mary. 240 pp.

—1989. Aspects of character homology and phylogeny of the Gadiformes. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 59–88.

Marramà, G., and G. Carnevale. 2017. Morphology, relationships and palaeobiology of the Eocene barracudina †*Holosteus esocinus* (Aulopiformes: Paralepididae) from Monte Bolca, Italy. Zoological Journal of the Linnean Society 181(1):209–228.

—2018. *Eoalosa janvieri gen*. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca, Italy. Paläontologische Zeitschrift 92:107–120.

Marramà, G., B. Khalloufi, and G. Carnevale. 2023. Redescription of '*Diplomystus*' *solignaci* Gaudant and Gaudant, 1971 from the Cretaceous of Tunisia, and a new hypothesis of double-armored herring relationships. Historical Biology 35(1):163–184.

Marshall, L. G., T. Sempere, and R. F. Butler. 1997. Chronostratigraphy of the mammal-bearing Paleocene of South America. Journal of South American Earth Sciences 10(1):49–70.

Marshall, N. B. 1962. Observations on the Heteromi: an order of teleost fishes. Bulletin of the British Museum (Natural History), Zoology 9(6):249–270.

—1965. Systematic and biological studies of the Macrourid fishes (Anacanthini-Teleostii). Deep-Sea Research and Oceanographic Abstracts 12(3):299–322.

—1966. The relationships of the anacanthine fishes, *Macruronus*, *Lyconus*, and *Steindachneria*. Copeia 1966(2):275–280.

Marshall, N. B., and D. M. Cohen. 1973. Order Anacanthini (Gadiformes): characters and synopsis of families. In: D. M. Cohen, J. W. Atz, R. H. Gibbs, F. H. Berry, E. A. Lachner, J. E. Böhlke, G. W. Mead, and D. Merriman, eds. Orders Heteromi (Notacanthiformes), Berycomorphi (Beryciformes), Xenoberyces (Stephanoberyciformes), and Anacanthini (Gadiformes): Halosuriforms, Killfishes, Squirrelfishes and other Beryciforms, Stephanoberyciforms, Grenadiers. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 479–495. (Memoir 1, Fishes of the Western North Atlantic 6.)

Martens, E. 1862. Über einen neuen *Polyodon* (*P. gladius*) aus dem Yangtsekiang und über die sogenannten Glaspolypen. Monatsberichte der Deutschen Akademie der Wissenschaften zu Berlin 1861:476–480.

Martin, C. H., and P. C. Wainwright. 2011. Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of *Cyprinodon* pupfish. Evolution 65(8):2197–2212.

Martin, J. M. 2015. Phylogeny, ontogeny and distribution of the ribbonfishes (Lampridiformes: Trachipteridae) [dissertation]. College of William and Mary. 217 pp.

Martin, R. P., E. E. Olson, M. G. Girard, W. L. Smith, and M. P. Davis. 2018. Light in the darkness: new perspective on lanternfish relationships and classification using genomic and morphological data. Molecular Phylogenetics and Evolution 121:71–85.

Matschiner, M., R. Hanel, and W. Salzburger. 2011. On the origin and trigger of the notothenioid adaptive radiation. PLOS ONE 6(4):e18911. https://doi.org/10.1371/journal.pone.0018911

Matsubara, K. 1955. Fish Morphology and Hierarchy. Tokyo: Ishizaki-Shoten. 3 volumes. [In Japanese.]

Matsunuma, M., and J. W. Johnson. 2023. Revision of the Indo-Pacific genus *Centrogenys* Richardson, 1842 (Centrogenyidae) with descriptions of two new species from Australia. Ichthyology and Herpetology 111(4):503–521.

Matsuura, K. 2015. Taxonomy and systematics of tetraodontiform fishes: a review focusing primarily on progress in the period from 1980 to 2014. Ichthyological Research 62:72–113.

Mattern, M. Y. 2004. Molecular phylogeny of the Gasterosteidae: the importance of using multiple genes. Molecular Phylogenetics and Evolution 30(2):366–377.

—2007. Phylogeny, systematics, and taxomony of sticklebacks. In: S. Östlund-Nilsson, I. Mayer, and F. A. Huntingford, eds. Biology of the Three-spined Stickleback. Boca Raton, FL: CRC Press. pp. 1–40.

Mattern, M. Y., and D. A. McLennan. 2004. Total evidence phylogeny of Gasterosteidae: combining molecular, morphological and behavioral data. Cladistics 20(1):14–22.

Matthei, C., and X. Matthei. 1975. Spermatogenesis and spermatozoa of the Elopomorpha (teleost fish). In: B. A. Afzelius, ed. The Functional Anatomy of the Spermatozoon. Oxford: Pergamon. pp. 211–221.

Mattox, G. M. T., and M. Toledo-Piza. 2012. Phylogenetic study of the Characinae (Teleostei: Characiformes: Characidae). Zoological Journal of the Linnean Society 165(4):809–915.

Mayden, R. L., and W.-J. Chen. 2010. The world's smallest vertebrate species of the genus *Paedocypris*: a new family of freshwater fishes and the sister group to the world's most diverse clade of freshwater fishes (Teleostei: Cypriniformes). Molecular Phylogenetics and Evolution 57(1):152–175.

Mayden, R. L., W.-J. Chen, H. L. Bart, M. H. Doosey, A. M. Simons, K. L. Tang, R. M. Wood, M. K. Agnew, L. Yang, M. V. Hirt, et al. 2009. Reconstructing the phylogenetic relationships of the earth's most diverse clade of freshwater fishes—order Cypriniformes (Actinopterygii: Ostariophysi): a case study using multiple nuclear loci and the mitochondrial genome. Molecular Phylogenetics and Evolution 51(3):500–514.

Mayden, R. L., K. L. Tang, R. M. Wood, W.-J. Chen, M. K. Agnew, K. W. Conway, L. Yang, A. M. Simons, H. L. Bart, P. M. Harris, et al. 2008. Inferring the tree of life of the order Cypriniformes, the earth's most diverse clade of freshwater fishes: implications of varied taxon and character sampling. Journal of Systematics and Evolution 46(2):424–438.

Mayrinck, D. 2011. Phylogenetic relationships of otophysan (Actinopterygii, Teleostei), notably the Characiformes, including fossil members [dissertation]. French Ichtyological Society–Cybium. 298 pp.

Mayrinck, D., P. M. Brito, and O. Otero. 2010. A new albuliform (Teleostei: Elopomorpha) from the Lower Cretaceous Santana Formation, Araripe Basin, northeastern Brazil. Cretaceous Research 31(2):227–236.

—2015a. Anatomical review of †*Salminops ibericus*, a Teleostei *incertae sedis* from the Cenomanian of Portugal, anciently assigned to Characiformes and possibly related to crossognathiform fishes. Cretaceous Research 56:66–75.

—2015b. Review of the osteology of the fossil fish formerly attributed to the genus †*Chanoides* and implications for the definition of otophysan bony characters. Journal of Systematic Palaeontology 13(5):397–420.

McAllister, D. E. 1968. The Evolution of Branchiostegals and Associated Opercular, Gular, and Hyoid Bones, and the Classification of Teleostome Fishes, Living and Fossil. Ottawa: National Museum of Canada. 239 pp. (Bulletin 221.)

McBride, R. S., C. R. Rocha, R. Ruiz-Carus, and B. W. Bowen. 2010. A new species of ladyfish, of the genus *Elops* (Elopiformes: Elopidae), from the western Atlantic Ocean. Zootaxa 2346(1):29–41. https://doi.org/10.11646/zootaxa.2346.1.3

McCraney, W. T. 2019. Phylogeny and divergence times of gobiarian fishes [dissertation]. University of California, Los Angeles. 111 pp.

McCraney, W. T., C. E. Thacker, and M. E. Alfaro. 2020. Supermatrix phylogeny resolves goby lineages and reveals unstable root of Gobiaria. Molecular Phylogenetics and Evolution 151:106862. https://doi.org/10.1016/j.ympev.2020.106862

McDougall, I. A. N., and C. S. Feibel. 1999. Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. Journal of the Geological Society 156:731–745.

McDowall, R. M. 1969. Relationships of galaxioid fishes with a further discussion of salmoniform classification. Copeia 1969(4):796–824.

—1973. Relationships and taxonomy of the New Zealand torrent fish, *Cheimarrichthys fosteri* Haast (Pisces: Mugiloididae). Journal of the Royal Society of New Zealand 3(2):199–217.

—1984. Southern hemisphere freshwater salmoniforms: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 150–153. (Special Publication 1.)

—2000. Biogeography of the New Zealand torrentfish, *Cheimarrichthys fosteri* (Teleostei: Pinguipedidae): a distribution driven mostly by ecology and behaviour. Environmental Biology of Fishes 58:119–131.

McDowall, R. M., and C. P. Burridge. 2011. Osteology and relationships of the southern freshwater lower euteleostean fishes. Zoosystematics and Evolution 87(1):7–185.

McKay, R. J. 1992. Sillaginid Fishes of the World (Order Gadiformes). Vol. 14 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 87 pp. (FAO Fisheries Synopsis 125.)

—1997. Pearl Perches of the World (Family Glaucosomatidae). Vol. 17 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 26 pp. (FAO Fisheries Synopsis 125.)

McLennan, D. A. 1993. Phylogenetic relationships in the Gasterosteidae: an updated tree based on behavioral characters with a discussion of homoplasy. Copeia 1993(2):318–326.

McLennan, D. A., and M. Y. Mattern. 2001. The phylogeny of the Gasterosteidae: combining behavioral and morphological data sets. Cladistics 17(1):11–27.

McMahan, C. D., D. J. Elías, Y. Li, O. Domínguez-Domínguez, S. Rodriguez-Machado, A. Morales-Cabrera, D. Velásquez-Ramírez, K. R. Piller, P. Chakrabarty, and W. A. Matamoros. 2021. Molecular systematics of the *Awaous banana* complex (river gobies; Teleostei: Oxudercidae). Journal of Fish Biology 99(3):970–979.

Mecklenburg, C. W. 2003a. Family Anarhichadidae Bonaparte 1846: wolffishes. California Academy of Sciences Annotated Checklists of Fishes 10:1–6.

—2003b. Family Bathymasteridae Jordan and Gilbert 1883: ronquils. California Academy of Sciences Annotated Checklists of Fishes 7:1–4.

—2003c. Family Cryptacanthodidae Gill 1861: wrymouths. California Academy of Sciences Annotated Checklists of Fishes 8:1–4.

—2003d. Family Ptilichthyidae Jordan and Gilbert 1883: quillfishes. California Academy of Sciences Annotated Checklists of Fishes 12:1–3.

—2003e. Family Scytalinidae Jordan and Evermann 1898: graveldivers. California Academy of Sciences Annotated Checklists of Fishes 11:1–3.

—2003f. Family Zaproridae Jordan and Evermann 1898: prowfishes. California Academy of Sciences Annotated Checklists of Fishes 13:1–3.

Mecklenburg, C. W., and B. Sheiko. 2004. Family Stichaeidae Gill 1864: pricklebacks. California Academy of Sciences Annotated Checklists of Fishes 35:1–36.

Mees, G. F. 1961. Description of a new fish of the family Galaxiidae from Western Australia. Journal of the Royal Society of Western Australia 44(pt. 2):33–38.

Meinema, E., and J. H. Huber. 2023. Review of Pantanodontidae (Cyprinodontiformes) and its fossil and extant genera *Pantanodon* Myers, 1955 and †*Paralebias* Gaudant, 2013 with descriptions of two new recent genera and five new species. In: J. H. Huber, ed. Killi-Data Series 2023 [pdf]. Killi-Data Online [online database]. pp. 21–73. Accessed 27 November 2023. https://www.killi-data.org

Melo, B. F., M. C. C. de Pinna, L. H. Rapp Py-Daniel, J. Zuanon, C. C. Conde-Saldaña, F. F. Roxo, and C. Oliveira. 2022. Paleogene emergence and evolutionary history of the Amazonian fossorial fish genus *Tarumania* (Teleostei: Tarumaniidae). Frontiers in Ecology and Evolution 10:924860.

Melo, B. F., B. L. Sidlauskas, K. Hoekzema, R. P. Vari, C. B. Dillman, and C. Oliveira. 2018. Molecular phylogenetics of Neotropical detritivorous fishes of the family Curimatidae (Teleostei: Characiformes). Molecular Phylogenetics and Evolution 127:800–812.

Melo, B. F., B. L. Sidlauskas, T. J. Near, F. F. Roxo, A. Ghezelayagh, L. E. Ochoa, M. L. J. Stiassny, J. Arroyave, J. Chang, B. C. Faircloth, et al. 2022. Accelerated diversification explains the exceptional species richness of tropical characoid fishes. Systematic Biology 71(1):78–92.

Melo, M. R. S. 2009. Taxonomic and phylogenetic revision of the family Chiasmodontidae (Perciformes: Acanthomorpha) [dissertation]. Auburn University. pp. 540.

Meunier, F. J., and M. Gayet. 1996. A new polypteriform from the Late Cretaceous and the Middle Paleocene of South America. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 95–105.

Meyer, H. W. 2003. The Fossils of Florissant. Washington, DC: Smithsonian Institution Press. 258 pp.

Mickle, K. E., R. Lund, and E. D. Grogan. 2009. Three new palaeoniscoid fishes from the Bear Gulch Limestone (Serpukhovian, Mississippian) of Montana (USA) and the relationships of lower actinopterygians. Geodiversitas 31(3):623–668.

Milec, L. J. M., M. P. M. Vanhove, F. M. Bukinga, E. L. R. De Keyzer, V. L. Kapepula, P. M. Masilya, N. S. Mulimbwa, C. E. Wagner, and J. A. M. Raeymaekers. 2022. Complete mitochondrial genomes and updated divergence time of the two freshwater clupeids endemic to Lake Tanganyika (Africa) suggest intralacustrine speciation. BMC Ecology and Evolution 22:127. https://doi.org/10.1186/s12862-022-02085-8

Miller, E. C., C. M. Martinez, S. T. Friedman, P. C. Wainwright, S. A. Price, and L. Tornabene. 2022. Alternating regimes of shallow and deep-sea diversification explain a species-richness paradox in marine fishes. Proceedings of the National Academy of Sciences 119:e2123544119.

Miller, P. J. 1973. The osteology and adaptive features of *Rhyacichthys aspro* (Teleostei: Gobioidei) and the classification of gobioid fishes. Journal of Zoology 171(3):397–434.

—1986. Reproductive biology and systematic problems in gobioid fishes. In: T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura, eds. Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes. Tokyo: Ichthyological Society of Japan. pp. 640–647.

—1992. The sperm duct gland: a visceral synapomorphy for gobioid fishes. Copeia 1992(1):253–256.

Miller, R. R. 1947. A new genus and species of deep-sea fish of the family Myctophidae from the Philippine Islands. Proceedings of the United States National Museum 97(3211):81–90.

Milliken, D. M., and E. D. Houde. 1984. A new species of Bregmacerotidae (Pisces), *Bregmaceros cantori*, from the western Atlantic Ocean. Bulletin of Marine Science 35:11–19.

Miranda Ribeiro, A. de. 1915. Fauna Brasiliense. Peixes. Tomo 5. Part 2. *Eleutherobranchios aspirophoros* (Physoclisti). Arquivos do Museu Nacional de Rio de Janeiro 17(1):679.

Mirande, J. M. 2009. Weighted parsimony phylogeny of the family Characidae (Teleostei: Characiformes). Cladistics 25(6):574–613.

—2010. Phylogeny of the family Characidae (Teleostei: Characiformes): from characters to taxonomy. Neotropical Ichthyology 8:385–568.

—2017. Combined phylogeny of ray-finned fishes (Actinopterygii) and the use of morphological characters in large-scale analyses. Cladistics 33(4):333–350.

Mitchill, S. L. 1814. Report, in Part, of Samuel L. Mitchill, M. D., Professor of Natural History, &c, on the Fishes of New-York. New York: D. Carlisle. 28 pp.

—1815. The fishes of New-York, described and arranged. Transactions of the Literary and Philosophical Society of New-York 1(5):.355–492.

—1818a. Description of three species of fish. Journal of the Academy of Natural Sciences of Philadelphia 1:407–412.

—1818b. Memoir on ichthyology. The fishes of New York, described and arranged. In a supplement to the Memoir... (continued). American Monthly Magazine and Critical Review 2(5):321–328.

Miya, M., M. Friedman, T. P. Satoh, H. Takeshima, T. Sado, W. Iwasaki, Y. Yamanoue, M. Nakatani, K. Mabuchi, J. G. Inoue, et al. 2013. Evolutionary origin of the Scombridae (tunas and mackerels): members of a Paleogene adaptive radiation with 14 other pelagic fish families. PLOS ONE 8(9):e73535. https://doi.org/10.1371/journal.pone.0073535

Miya, M., N. I. Holcroft, T. P. Satoh, M. Yamaguchi, M. Nishida, and E. O. Wiley. 2007. Mitochondrial genome and a nuclear gene indicate a novel phylogenetic position of deep-sea tube-eye fish (Stylephoridae). Ichthyological Research 54:323–332.

Miya, M., A. Kawaguchi, and M. Nishida. 2001. Mitogenomic exploration of higher teleostean phylogenies: a case study for moderate-scale evolutionary genomics with 38 newly determined complete mitochondrial DNA sequences. Molecular Biology and Evolution 18(11):1993–2009.

Miya, M., and J. Nielsen. 1991. A new species of the deep-sea fish genus *Parabrotula* (Parabrotulidae) from Sagami Bay with notes on its ecology. Japanese Journal of Ichthyology 38(1):1–5.

Miya, M., and M. Nishida. 2015. The mitogenomic contributions to molecular phylogenetics and evolution of fishes: a 15-year retrospect. Ichthyological Research 62:29–71.

Miya, M., T. W. Pietsch, J. W. Orr, R. J. Arnold, T. P. Satoh, A. M. Shedlock, H.-C. Ho, M. Shimazaki, M. Yabe, and M. Nishida. 2010. Evolutionary history of anglerfishes (Teleostei: Lophiiformes): a mitogenomic perspective. BMC Evolutionary Biology 10:58. https://doi.org/10.1186/1471-2148-10-58

Miya, M., T. R. Satoh, and M. Nishida. 2005. The phylogenetic position of toadfishes (order Batrachoidiformes) in the higher ray-finned fish as inferred from partitioned Bayesian analysis of 102 whole mitochondrial genome sequences. Biological Journal of the Linnean Society 85(3):289–306.

Miya, M., M. Takahashi, H. Endo, N. B. Ishiguro, J. G. Inoue, T. Mukai, T. P. Satoh, M. Yamaguchi, A. Kawaguchi, K. Mabuchi, et al. 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 26(1): 121–138.

Mo, T. 1991. Anatomy, Relationships and Systematics of the Bagridae (Teleostei: Siluroidei) with a Hypothesis of Siluroid Phylogeny. Koenigstein: Koeltz Scientific Books. 216 pp.

Mok, H.-K., and S.-C. Shen. 1983. Osteology and Phylogeny of the Squamipinnes. Taipei: Taiwan Museum. 87 pp. (Special Publication 1.)

Molina, G. I. 1782. Saggio sulla Storia Naturale del Chili. Bologna: S. Tommaso d'Aquino. 367 pp.

Møller, P. R., A. D. Jordan, P. Gravlund, and J. F. Steffensen. 2002. Phylogenetic position of the cryopelagic codfish genus *Arctogadus* Drjagin, 1932 based on partial mitochondrial cytochrome b sequences. Polar Biology 25:342–349.

Møller, P. R., S. W. Knudsen, W. Schwarzhans, and J. G. Nielsen. 2016. A new classification of viviparous brotulas (Bythitidae)—with family status for Dinematichthyidae—based on molecular, morphological and fossil data. Molecular Phylogenetics and Evolution 100:391–408.

Monsch, K. A., and A. F. Bannikov. 2011. New taxonomic synopses and revision of the scombroid fishes (Scombroidei, Perciformes), including billfishes, from the Cenozoic of territories of the former USSR. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 102(4):253–300.

Mooi, R. D. 1990. Egg surface morphology of pseudochromoids (Perciformes: Percoidei), with comments on its phylogenetic implications. Copeia 1990(2):455–475.

Mooi, R. D., and G. D. Johnson. 1997. Dismantling the Trachinoidei: evidence of a scorpaenoid relationship for the Champsodontidae. Ichthyological Research 44:143–176.

Moore, J. A. 1993a. The phylogeny and evolution of the Trachichthyiformes (Teleostei: Percomorpha), with comments on the intrarelationships of the Acanthomorpha [dissertation]. Yale University. pp. 271.

—1993b. Phylogeny of the Trachichthyiformes (Teleostei: Percomorpha). Bulletin of Marine Science 52:114–136.

Moore, J. A., and T. J. Near. 2020a. *Actinopteri*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 705–708.

—2020b. *Actinopterygii*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 695–699.

—2020c. *Neopterygii*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 711–714.

—2020d. *Osteichthyes*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 685–689.

—2020e. *Pan-Teleostei*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 715–717.

—2020f. *Teleostei*. In: K. de Queiroz, P. D. Cantino, and J. A. Gauthier, eds. Phylonyms: A Companion to the *PhyloCode*. Boca Raton, FL: CRC. pp. 719–723.

Moreira, D. A., P. A. Buckup, C. Furtado, A. L. Val, R. Schama, and T. E. Parente. 2017. Reducing the information gap on Loricarioidei (Siluriformes) mitochondrial genomics. BMC Genomics 18:345. https://doi.org/10.1186/s12864-017-3709-3

Moritz, T., and R. Britz. 2019. Revision of the extant Polypteridae (Actinopterygii: Cladistia). Ichthyological Exploration of Freshwaters 29(2):97–192.

Mthethwa, S., A. E. Bester-van der Merwe, and R. Roodt-Wilding. 2023a. Addressing the complex phylogenetic relationship of the Gempylidae fishes using mitogenome data. Ecology and Evolution 13:e10217.

—2023b. The complete mitochondrial genome of the South African snoek *Thyrsites atun* (Euphrasén, 1791) (Perciformes, Gempylidae). Mitochondrial DNA Part B 8:288–291.

Mu, X., Y. Yang, J. Sun, l. Yi, M. Xu, C. Shao, K. H. Chu, W. Li, C. Liu, D. Gu, et al. 2022. FishPIE: a universal phylogenetically informative exon markers set for ray-finned fishes. iScience 25(9):105025.

Müller, J. 1845a. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Bericht der Akademie der Wissenschaften Berlin 1844:416–422.

—1845b. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Archiv für Naturgeschichte 11:91–141.

Müller, J., and F. H. Troschel. 1848. Fische. In: M. R. Schomburgk, ed. Reisen in Britisch-Guiana in den Jahren 1840–1844, vol. 3. Leipzig: J. J. Weber. pp. 618–644.

Muller, T. A. 2023. Taxonomic revision of the pirate perches (Percopsiformes: Aphredoderidae) reveals three new species and elevates two subspecies [dissertation]. University of Minnesota. 52 pp. ProQuest (order no. 30630998). https://www.proquest.com/

Muñoz, M. 2010. Reproduction in Scorpaeniformes. In: K. S. Cole, ed. Reproduction and Sexuality in Marine Fishes: Patterns and Processes. Berkeley: University of California Press. pp. 64–89.

Munroe, T. A. 2015. Systematic diversity of the Pleuronectiformes. In: R. N. Gibson, R. Nash, A. Geffen, and H. van der Veer, eds. Flatfishes: Biology and Exploitation. 2nd ed. Chichester, UK: Wiley Blackwell. pp. 13–51.

Murphy, W. J., and G. E. Collier. 1997. A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinodontiformes): the role of vicariance and the origins of annualism. Molecular Biology and Evolution 14:790–799.

Murray, A. M. 1996. A new Paleocene genus and species of percopsid, †*Massamorichthys wilsoni* (Paracanthopterygii) from Joffre Bridge, Alberta, Canada. Journal of Vertebrate Paleontology 16(4):642–652.

—2003. A new Eocene citharinoid fish (Ostariophysi: Characiformes) from Tanzania. Journal of Vertebrate Paleontology 23(3):501–507.

—2016. Mid-Cretaceous acanthomorph fishes with the description of a new species from the Turonian of Lac des Bois, Northwest Territories, Canada. Vertebrate Anatomy Morphology Palaeontology 1:101–115.

—2019. Redescription of *Barbus megacephalus* Günther, 1876 and *Thynnichthys amblyostoma* von der Marck, 1876 (Cypriniformes: Cyprinidae) from probable Eocene deposits of Southeast Asia, and an assessment of their taxonomic positions. Journal of Systematic Palaeontology 17(17):1433–1455.

—2020. Early Cenozoic cyprinoids (Ostariophysi: Cypriniformes: Cyprinidae and Danionidae) from Sumatra, Indonesia. Journal of Vertebrate Paleontology 40(1):e1762627.

—2022. Re-description and phylogenetic relationships of †*Protosyngnathus sumatrensis* (Teleostei: Syngnathoidei), a freshwater pipefish from the Eocene of Sumatra, Indonesia. Journal of Systematic Palaeontology 20(1):2113832.

Murray, A. M., D. B. Brinkman, M. G. Newbrey, and A. G. Neuman. 2020. Earliest North American articulated freshwater acanthomorph fish (Teleostei: Percopsiformes) from Upper Cretaceous deposits of Alberta, Canada. Geological Magazine 157(7):1087–1096.

Murray, A. M., and S. L. Cumbaa. 2013. Early Turonian acanthomorphs from Lac Des Bois, Northwest Territories, Canada. Journal of Vertebrate Paleontology 33(2):293–300.

Murray, A. M., L. E. Nelson, and D. B. Brinkman. 2023. A new sturgeon from the Upper Cretaceous Horseshoe Canyon Formation in central Alberta, Canada. Journal of Vertebrate Paleontology 43(1):e2232846.

Murray, A. M., and J. G. M. Thewissen. 2008. Eocene actinopterygian fishes from Pakistan, with the description of a new genus and species of channid (Channiformes). Journal of Vertebrate Paleontology 28(1):41–52.

Murray, A. M., and M. V. H. Wilson. 1996. A new Paleocene genus and species of percopsiform (Teleostei: Paracanthopterygii) from the Paskapoo Formation, Smoky Tower, Alberta. Canadian Journal of Earth Science 33(3):429–438.

—1999. Contributions of fossils to the phylogenetic relationships of the percopsiform fishes (Teleostei: Paracanthopterygii): order restored. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record. Munich: Verlag Dr. Friedrich Pfeil. pp. 397–411.

—2013. Two new paraclupeid fishes (Clupeomorpha: Ellimmichthyiformes) from the Upper Cretaceous of Morocco. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Friedrich Pfeil. pp. 267–290.

—2014. Four new basal acanthomorph fishes from the Late Cretaceous of Morocco. Journal of Vertebrate Paleontology 34(1):34–48.

Murray, A. M., D. K. Zelenitsky, D. B. Brinkman, and A. G. Neuman. 2018. Two new Palaeocene osteoglossomorphs from Canada, with a reassessment of the relationships of the genus †*Joffrichthys*, and analysis of diversity from articulated versus microfossil material. Zoological Journal of the Linnean Society 183(4):907–944.

Musilova, Z., F. Cortesi, M. Matschiner, W. I. L. Davies, J. S. Patel, S. M. Stieb, F. de Busserolles, M. Malmstrøm, O. K. Tørresen, C. J. Brown, et al. 2019. Vision using multiple distinct rod opsins in deep-sea fishes. Science 364(6440):588–592.

Myers, G. S., and C. B. Wade. 1946. New fishes of the families Dactyloscopidae, Microdesmidae, and Antennariidae from the west coast of Mexico and the Galapagos Islands, with a brief account of the use of rotenone fish poisons in ichthyological collecting. Allan Hancock Pacific Expeditions 9, no. 6. Los Angeles: University of Southern California Press. pp. 151–179. (Allan Hancock Foundation Publications of the University of Southern California Series 1.)

Nakae, M., and K. Sasaki. 2010. Lateral line system and its innervation in Tetraodontiformes with outgroup comparisons: descriptions and phylogenetic implications. Journal of Morphology 271(5):559–579.

Nakatani, M., M. Miya, K. Mabuchi, K. Saitoh, and M. Nishida. 2011. Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. BMC Evolutionary Biology 11:177. https://doi.org/10.1186/1471-2148-11-177

Nam, K.-S., and M. V. Nazarkin. 2018. Fossil prowfish, *Zaprora koreana*, sp. nov. (Pisces, Zaproridae), from the Neogene of South Korea. Journal of Vertebrate Paleontology 38(5):e1514616. https://doi.org/10.1080/02724634.2018.1514616

Nazarkin, M. V. 1997. A new genus and species of greenling (Hexagrammidae) from the Miocene of Sakhalin Island. Journal of Ichthyology 37(1):5–13.

—2002. Gunnels (Perciformes, Pholidae) from the Miocene of Sakhalin Island. Journal of Ichthyology 42(4):279–288.

Nazarkin, M. V., G. Carnevale, and A. F. Bannikov. 2013. A new greenling (Teleostei, Cottoidei) from the Miocene of Sakhalin Island, Russia. Journal of Vertebrate Paleontology 33(4):794–803.

Near, T. J., D. I. Bolnick, and P. C. Wainwright. 2004. Investigating phylogenetic relationships of sunfishes and black basses (Actinopterygii: Centrarchidae) using DNA sequences from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 32(1):344–357.

Near, T. J., A. Dornburg, R. I. Eytan, B. P. Keck, W. L. Smith, K. L. Kuhn, J. A. Moore, S. A. Price, F. T. Burbrink, M. Friedman, and P. C. Wainwright. 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. Proceedings of the National Academy of Sciences of the United States of America 110(31):12738–12743.

Near, T. J., A. Dornburg, and M. Friedman. 2014. Phylogenetic relationships and timing of diversification in gonorynchiform fishes inferred using nuclear gene DNA sequences (Teleostei: Ostariophysi). Molecular Phylogenetics and Evolution 80:297–307.

Near, T. J., A. Dornburg, R. C. Harrington, C. Oliveira, T. W. Pietsch, C. E. Thacker, T. P. Satoh, E. Katayama, P. C. Wainwright, et al. 2015. Identification of the notothenioid sister lineage illuminates the biogeographic history of an Antarctic adaptive radiation. BMC Evolutionary Biology 15:109. https://doi.org/10.1186/s12862-015-0362-9

Near, T. J., A. Dornburg, K. L. Kuhn, J. T. Eastman, J. N. Pennington, T. Patarnello, L. Zane, D. A. Fernández, and C. D. Jones. 2012. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. Proceedings of the National Academy of Sciences of the United States of America 109(9):3434–3439.

Near, T. J., A. Dornburg, M. Tokita, D. Suzuki, M. C. Brandley, and M. Friedman. 2014. Boom and bust: ancient and recent diversification in bichirs (Polypteridae: Actinopterygii), a relictual lineage of ray-finned fishes. Evolution 68(4):1014–1026.

Near, T. J., R. I. Eytan, A. Dornburg, K. L. Kuhn, J. A. Moore, M. P. Davis, P. C. Wainwright, M. Friedman, and W. L. Smith. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. Proceedings of the National Academy of Sciences of the United States of America 109(34):13698–13703.

Near, T. J., and D. Kim. 2021. Phylogeny and time scale of diversification in the fossil-rich sunfishes and black basses (Teleostei: Percomorpha: Centrarchidae). Molecular Phylogenetics and Evolution 161:107156. https://doi.org/10.1016/j.ympev.2021.107156

Near, T. J., D. J. MacGuigan, E. Parker, C. D. Struthers, C. D. Jones, and A. Dornburg. 2018. Phylogenetic analysis of Antarctic notothenioids illuminates the utility of RADseq for resolving Cenozoic adaptive radiations. Molecular Phylogenetics and Evolution 129:268–279.

Near, T. J., J. J. Pesavento, and C.-H. C. Cheng. 2004. Phylogenetic investigations of Antarctic notothenioid fishes (Perciformes: Notothenioidei) using complete gene sequences of the mitochondrial encoded 16S rRNA. Molecular Phylogenetics and Evolution 32(3):881–891.

Near, T. J., M. Sandel, K. L. Kuhn, P. J. Unmack, P. C. Wainwright, and W. L. Smith. 2012. Nuclear gene-inferred phylogenies resolve the relationships of the enigmatic pygmy sunfishes, *Elassoma* (Teleostei: Percomorpha). Molecular Phylogenetics and Evolution 63(2):388–395.

Near, T. J., and C. E. Thacker. 2023. Phylogenetic classification of living and fossil ray-finned fishes (Actinopterygii) [online dataset]. Dryad. https://doi.org/10.5061/dryad.80gb5mkwp

Neilson, M. E., and C. A. Stepien. 2009. Escape from the Ponto-Caspian: evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). Molecular Phylogenetics and Evolution 52(1):84–102.

Nelson, G. J. 1967. Gill arches of teleostean fishes of the family Clupeidae. Copeia 1967(2):389–399.

—1968. Gill arches of teleosteanfishes of the division Osteoglossomorpha. Journal of the Linnean Society, Zoology 47(312):261–277.

—1969a. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bulletin of the American Museum of Natural History 141:475–552.

—1969b. Infraorbital bones and their bearing on the phylogeny and geography of osteoglossomorph fishes. American Museum Novitates 2394:1–37.

—1969c. Origin and diversification of teleostean fishes. Annals of the New York Academy of Sciences 167(1):18–30.

—1970a. Gill arches of some teleostean fishes of the families Salangidae and Argentinidae. Japanese Journal of Ichthyology 17(2):61–66.

—1970b. The hyobranchial apparatus of teleostean fishes of the families Engraulidae and Chirocentridae. American Museum Novitates 2410:1–30.

—1972. Cephalic sensory canals, pitlines, and the classification of esocoid fishes, with notes on galaxiids and other teleosts. American Museum Novitates 2492:1–49.

—1973. Relationships of clupeomorphs with remarks on the structure of the lower jaw in fishes. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 333–349.

—1989. Phylogeny of major fish groups. In: B. Fernholm, K. Bremer, and H. Jôrnvall, eds. The Hierarchy of Life: Molecules and Morphology in Phylogenetic Analysis. Amsterdam: Elsevier. pp. 325–336.

Nelson, J. S. 1976. Fishes of the World, 1st ed. New York: Wiley. 416 pp.

—1978. Review of The Biology of Sticklebacks, by R. J. Wootton. Copeia 1978(3):552–554.

—1984. Fishes of the World, 2nd ed. New York: Wiley. 523 pp.

—1986. Some characters of Trichonotidae, with emphasis to those distinguishing it from Creediidae (Perciformes, Trachinoidei). Japanese Journal of Ichthyology 33(1):1–6.

—1994. Fishes of the World, 3rd ed. New York: Wiley. 600 pp.

—2006. Fishes of the World, 4th ed. Hoboken, NJ: John Wiley. 601 pp.

Nelson, J. S., T. C. Grande, and M. V. H. Wilson. 2016. Fishes of the World, 5th ed. Hoboken, NJ: John Wiley and Sons. 707 pp.

Newbrey, M. G., and T. Konishi. 2015. A new lizardfish (Teleostei, Aulopiformes) from the Late Cretaceous Bearpaw Formation of Alberta, Canada, with a revised diagnosis of *Apateodus* (Aulopiformes, Ichthyotringoidei). Journal of Vertebrate Paleontology 35(3):e918042. https://doi.org/10.1080/02724634.2014.918042

Newbrey, M. G., A. M. Murray, M. V. H. Wilson, D. B. Brinkman, and A. G. Neuman. 2013. A new species of the paracanthopterygian *Xenyllion* (Sphenocephaliformes) from the Mowry Formation (Cenomanian) of Utah, USA. In: G. Arratia, H.-P. Schultze, and M. V. H. Wilson, eds. Mesozoic Fishes 5: Global Diversity and Evolution. Munich: Verlag Dr. Fredrich Pfeil. pp. 363–384.

Niebuhr, C. 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Post mortem auctoris edidit Carsten Niebuhr. Hauniæ: ex officina Mölleri. 164 pp.

Nielsen, J. G. 1968. Re-description and reassignment of *Parabrotula* and *Leucobrotula* (Pisces, Zoarcidae). Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening, Kjøbenhavnsk 131:225–250.

Nielsen, J. G., J. Badcock, and N. R. Merrett. 1990. New data elucidating the taxonomy and ecology of the Parabrotulidae (Pisces: Zoarcoidei). Journal of Fish Biology 37(3):437–448.

Nielsen, J. G., D. M. Cohen, D. F. Markle, and C. R. Robins. 1999. Ophidiiform Fishes of the World (Order Ophidiiformes). Vol. 18 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 178 pp. (FAO Fisheries Synopsis 125.)

Niemiller, M. L., B. M. Fitzpatrick, P. Shah, L. Schmitz, and T. J. Near. 2013. Evidence for repeated loss of selective constraint in rhodopsin of amblyopsid cavefishes (Teleostei: Amblyopsidae). Evolution 67:732–748.

Nolf, D. 1972. Les otolithes du Calcaire Grossier à Fercourt (Éocène du Bassin de Paris). Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie 81:139–157.

—1988. Les Otolithes de Téléostéens Éoeènes d'Aquitaine (Sud-Ouest de la France) et Leur Intérêt Stratigraphique. Brussels: Académie Royale de Belgique. 147 pp. (Mémoires de la Classe des Sciences 19.)

Nolf, D., and H. Lapierre. 1979. Otolithes de Poissons nouveaux ou peu connus du Calcaire Grossier et de la formation d'Auvers (Éocène du Bassin parisien). Bulletin du Muséum National d'Histoire Naturelle, Section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie, Series 4, 1(2):79–125.

Nolf, D., R. S. Rana, and H. Singh. 2006. Fish otoliths from the Ypresian (early Eocene) of Vastan, Gujarat, India. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre 76:105–118.

Nolf, D., and E. Steurbaut. 1989. Evidence from otoliths for establishing relationships within gadiforms. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 89–111.

Nolf, D., and G. Stringer. 1996. Cretaceous fish otoliths—a synthesis of the North American record. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 433–459.

Norman, J. R. 1934. A Systematic Monograph of the Flatfishes (Heterosomata). Vol. I of Psettodidæ, Bothidæ, Pleruonectidæ. London: Printed by order of the Trustees of the British Museum. 459 pp.

—1938a. Coast fishes. Part III. The Antarctic zone. Discovery Reports 18:1–104.

—1938b. On the affinities of the Chilean fish, Normanichthys crockeri Clark. Copeia 1938(1):29–32.

Normark, B. B., A. R. McCune, and R. G. Harrison. 1991. Phylogenetic relationships of neopterygian fishes inferred from mitochondrial DNA sequences. Molecular Biology and Evolution 8:819–834.

Nybelin, O. 1971. On the caudal Skeleton in *Elops* with remarks on other teleostean fishes. Acta Regiae Societatis Scientiarum et Litterarum Gothoburgensis Zoologica 7:1–52.

Nyegaard, M., E. Sawai, N. Gemmell, J. Gillum, N. R. Loneragan, Y. Yamanoue, and A. L. Stewart. 2018. Hiding in broad daylight: molecular and morphological data reveal a new ocean sunfish species (Tetraodontiformes: Molidae) that has eluded recognition. Zoological Journal of the Linnean Society 182(3):631–658.

Obermiller, L. E., and E. Pfeiler. 2003. Phylogenetic relationships of elopomorph fishes inferred from mitochondrial ribosomal DNA sequences. Molecular Phylogenetics and Evolution 26(2):202–214.

Oelschläger, H. 1983. Vergleichende und funktionelle anatomie der Allotriognathi (=Lampridiformes), ein beitrag zur evolutionsmorphologie der knochenfische. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 541:1–127.

Oh, D.-J., J.-C. Lee, Y.-M. Ham, and Y.-H. Jung. 2021. The mitochondrial genome of *Stereolepis doederleini* (Pempheriformes: Polyprionidae) and mitogenomic phylogeny of Pempheriformes. Genetics and Molecular Biology 44:e20200166. https://doi.org/10.1590/1678-4685-GMB-2020-0166

Ohashi, S. 2018. Morphology of a unique ophidiid, *Hypopleuron caninum* Radcliffe 1913 (Ophidiiformes, Ophidiidae, Neobythitinae), suggesting a close relationship with the family Carapidae. Zootaxa 4521(4):499–538. https://doi.org/10.11646/zootaxa.4521.4.2

Okamura, O. 1989. Relationships of the suborder Macrouroidei and related groups, with comments on Merlucciidae and *Steindachneria*. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 129–142.

Okiyama, M. 1984. Myctophiformes: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 254–259. (Special Publication 1.)

Oliveira, C., G. S. Avelino, K. T. Abe, T. C. Mariguela, R. C. Benine, G. Ortí, R. P. Vari, and R. M. Corrêa e Castro. 2011. Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. BMC Evolutionary Biology 11:275. https://doi.org/10.1186/1471-2148-11-275

Olney, J. E., G. D. Johnson, and C. C. Baldwin. 1993. Phylogeny of lampridiform fishes. Bulletin of Marine Science 52:137–169.

Olsen, P. E. 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the early Triassic Sakamena group of Madagascar, with comments on the relationships of the holostean fishes. Essays Presented to Dr. Bobb Schaeffer, Journal of Vertebrate Paleontology 4(3):481–499.

Olsen, P. E., and A. R. McCune. 1991. Morphology of the *Semionotus elegans* species group from the early Jurassic part of the Newark supergroup of eastern North America with comments on the family Semiontidae (Neopterygii). Journal of Vertebrate Paleontology 11(3):269–292.

Orr, J. W. 1995. Phylogenetic relationships of gasterosteiform fishes (Teleostei: Acanthomorpha) [dissertation]. University of Washington. 813 pp.

Orrell, T. M., B. B. Collette, and G. D. Johnson. 2006. Molecular data support separate scombroid and xiphioid clades. Bulletin of Marine Science 79:505–519.

Ortí, G. 1997. Radiation of characiform fishes: evidence from mitochondrial and DNA sequences. In: T. D. Kocher and C. A. Stepien, eds. Molecular Systematics of Fishes. San Diego: Academic Press. pp. 219–314.

Ortí, G., and A. Meyer. 1996. Molecular evolution of ependymin and the phylogenetic resolution of early divergences among euteleost fishes. Molecular Biology and Evolution 13:556–573.

—1997. The radiation of characiform fishes and the limits of resolution of mitochondrial ribosomal DNA sequences. Systematic Biology 46(1):75–100.

Ørvig, T. O. R. 1978. Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Nephrotus* and *Colobodus*, with remarks on the dentition in other forms. Zoologica Scripta 7(1–4):297–326.

Osinov, A., and V. Lebedev. 2004. Salmonid fishes (Salmonidae, Salmoniformes): the systematic position in the superorder Protacanthopterygii, the main stages of evolution, and molecular dating. Journal of Ichthyology 44:690–715.

Östlund-Nilsson, S., and G. E. Nilsson. 2004. Breathing with a mouth full of eggs: respiratory consequences of mouthbrooding in cardinalfish. Proceedings of the Royal Society B, Biological Sciences 271(1543):1015–1022.

Otero, O. 2004. Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae). Zoological Journal of the Linnean Society 141(1):81–133.

Otero, O., and M. Gayet. 1995. Étude phylogénétique des Aipichthyides; poissons téléostéens de la Téthys cénomanienne. Géobios 28(Suppl. 2):221–224.

—1996. Anatomy and phylogeny of the Aipichthyoidea nov. of the Cenomanian Tethys and their place in the Acanthomorpha (Teleostei). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 202:313–344.

Otero, O., A. Pinton, H. T. Mackaye, A. Likius, P. Vignaud, and M. Brunet. 2009. First description of a Pliocene ichthyofauna from Central Africa (site KL2, Kolle area, Eastern Djurab, Chad): what do we learn? Journal of African Earth Sciences 54:62–74.

O'Toole, B. 2002. Phylogeny of the species of the superfamily Echeneoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behaviour. Canadian Journal of Zoology 80(4):596–623.

Pallas, P. S. 1769. Spicilegia zoologica: quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur, Volume 1 (fasc. 7). Berolini: Prostant apud Gottl. August. Lange. 42 pp.

—1810. Labraces, novum genus piscium, oceani orientalis. Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg 2:382–398.

Pan, Q., R. Feron, E. Jouanno, H. Darras, A. Herpin, B. Koop, E. Rondeau, F. W. Goetz, W. A. Larson, L. Bernatchez, et al. 2021. The rise and fall of the ancient northern pike master sex-determining gene. eLife 10:e62858. https://doi.org/10.7554/eLife.62858

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei: Atherinomorpha). Bulletin of the American Museum of Natural History 168:335–557.

—1984. On the relationships of phallostethid fishes (Atherinomorpha): with notes on the anatomy of *Phallostethus dunckeri* Regan, 1913. American Museum Novitates 2779:1–12.

—1986. The phylogenetic significance of bone types in euteleost fishes. Zoological Journal of the Linnean Society 87(1):37–51.

—1987. Phylogenetic aspects of tooth and jaw structure of the Medaka, *Oryzias latipes*, and other beloniform fishes. Journal of Zoology 211(3):561–572.

—1989. A phylogenetic revision of the phallostethid fishes (Atherinomorpha, Phallostethidae). Proceedings of the California Academy of Sciences, 4th series, 46(11):243–277.

—1993. Relationships of atherinomorph fishes (Teleostei). Bulletin of Marine Science 52:170–196.

—2005. The phylogeny of atherinomorphs: evolution of a novel fish reproductive system. In: M. C. Uribe, and H. J. Grier, eds. Viviparous Fishes. Homestead, FL: New Life. pp. 13–30.

—2008. A phylogenetic analysis and taxonomic revision of ricefishes, *Oryzias* and relatives (Beloniformes, Adrianichthyidae). Zoological Journal of the Linnean Society 154(3):494–610.

Parenti, L. R., and H. J. Grier. 2004. Evolution and phylogeny of gonad morphology in bony fishes. Integrative and Comparative Biology 44(5):333–348.

Parenti, P., and J. E. Randall. 2020. An annotated checklist of the fishes of the family Serranidae of the world with description of two new related families of fishes. FishTaxa 15:1–170.

Parey, E., A. Louis, J. Montfort, O. Bouchez, C. Roques, C. Iampietro, J. Lluch, A. Castinel, C. Donnadieu, T. Desvignes, et al. 2023. Genome structures resolve the early diversification of teleost fishes. Science 379(6632):572–575.

Parin, N. V., I. B. Shakhovskoy, K. E. Bemis, and B. B. Collette. 2019. Family Exocoetidae. In: B. B. Collette, K. E. Bemis, N. V. Parin, and I. B. Shakhovskoy. Order Beloniformes: Needlefishes, Sauries, Halfbeaks, and Flyingfishes. B. B. Collette and T. J. Near, eds. New Haven, CT: Peabody Museum of Natural History, Yale University. pp. 149–239. (Memoir 1, Fishes of the Western North Atlantic 10.)

Parker, A., and I. Kornfield. 1995. Molecular perspective on evolution and zoogeography of cyprinodontid killifishes (Teleostei: Atherinomorpha). Copeia 1995(1):8–21.

Parker, E., A. Dornburg, C. D. Struthers, C. D. Jones, and T. J. Near. 2022. Phylogenomic species delimitation dramatically reduces species diversity in an Antarctic adaptive radiation. Systematic Biology 71(1):58–77.

Parker, E., and T. J. Near. 2022. Phylogeny reconciles classification in Antarctic plunderfishes. Ichthyology and Herpetology 110(4):662–674.

Parr, A. E. 1951. Preliminary revision of the Alepocephalidae, with the introduction of a new family, Searsidae. American Museum Novitates 1531:1–21.

Pastana, M. N. L., G. D. Johnson, and A. Datovo. 2022. Comprehensive phenotypic phylogenetic analysis supports the monophyly of stromateiform fishes (Teleostei: Percomorphacea). Zoological Journal of the Linnean Society 195(3):841–963.

Patterson, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 247(739):213–482.

—1967. New Cretaceous berycoid fishes from the Lebanon. Bulletin of The British Museum (Natural History) Geology 14(3):67–109.

—1968. The caudal skeleton in Mesozoic acanthopterygian fishes. Bulletin of the British Museum (Natural History), Geology 17(2):47–102.

—1970. A clupeomorph fish from the Gault (Lower Cretaceous). Zoological Journal of the Linnean Society 49(3):161–182.

—1973. Interrelationships of holosteans. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 233–305.

—1975. Braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 269(899):275–579.

—1977. The contribution of paleontology to teleostean phylogeny. In: P. C. Hecht, P. C. Goody, and B. M. Hecht, eds. Major Patterns in Vertebrate Evolution. New York: Plenum Press. pp. 579–643.

—1982. Morphology and interrelationships of primitive actinopterygian fishes. American Zoologist 22(2):241–259.

—1984a. *Chanoides*, a marine Eocene otophysan fish (Teleostei: Ostariophysi). Journal of Vertebrate Paleontology 4(3):430–456.

—1984b. Family Chanidae and other teleostean fishes as living fossils. In: N. Eldredge, and S. M. Stanley, eds. Living Fossils. New York: Springer. pp. 132–139.

—1993. An overview of the early fossil record of acanthomorphs. Bulletin of Marine Science 52:29–59.

—1994. Bony fishes. In: D. R. Prothero and R. M. Schoch, eds. Major Features of Vertebrate Evolution. Knoxville, TN: Paleontological Society. pp. 57–84.

—1997. Peter Humphry Greenwood. 21 April 1927–3 March 1995. Biographical Memoirs of Fellows of the Royal Society 43:195–213.

Patterson, C., and G. D. Johnson. 1995. The Intermuscular Bones and Ligaments of Teleostean Fishes. Washington, DC: Smithsonian Institution Press. 83 pp. (Smithsonian Contributions to Zoology 559.)

Patterson, C., and D. E. Rosen. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158:85–172.

—1989. The Paracanthopterygii revisited: order and disorder. In: D. M. Cohen, ed. Papers on the Systematics of Gadiform Fishes. Los Angeles: Natural History Museum of Los Angeles County. pp. 5–36.

Paucă, M. 1929. Vorläufige Mitteilung über eine fossile Fischfauna aus den Oligozänschiefern von Sŭslanesti (Muscel). Bulletin de la Section Scientifique Académie Roumaine 12(4–5):112–120.

Paxton, J. R., E. H. Ahlstrom, and H. G. Moser. 1984. Myctophidae: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 239–244. (Special Publication 1.)

Paxton, J. R., and P. A. Hulley. 1999a. Myctophidae. Lanternfishes. In: K. E. Carpenter and V. H. Niem, eds. Batoid Fishes, Chimaeras and Bony Fishes Part 1 (Elopidae to Linophrynidae), Vol. 3 of FAO Species Identification Guide for Fishery Purposes: The Living Marine Resources of the Western Central Pacific. Rome: Food and Agriculture Organization of the United Nations. pp. 1957–1965.

—1999b. Neoscopelidae. Neoscopelids. In: K. E. Carpenter and V. H. Niem, eds. Batoid Fishes, Chimaeras and Bony Fishes Part 1 (Elopidae to Linophrynidae), Vol. 3 of FAO Species Identification Guide for Fishery Purposes: The Living Marine Resources of the Western Central Pacific. Rome: Food and Agriculture Organization of the United Nations. pp. 1955–1956.

Paxton, J. R., G. D. Johnson, and T. Trnski. 2001. Larvae and juveniles of the deepsea "whalefishes" *Barbourisia* and *Rondeletia* (Stephanoberyciformes: Barbourisiidae, Rondeletiidae), with comments on family relationships. Records of the Australian Museum 53(3):407–425.

[PBDB] The Paleobiology Database. 2023. *Cottus otiakensis* [online dataset]. Accessed 15 November 2022. https://paleobiodb.org

Peng, Z. G., S. P. He, J. Wang, W. Wang, and R. Diogo. 2006. Mitochondrial molecular clocks and the origin of the major otocephalan clades (Pisces: Teleostei): a new insight. Gene 370:113–124.

Pérez-Rodríguez, R., O. Domínguez-Domínguez, A. F. Mar-Silva, I. Doadrio, and G. Pérez-Ponce de León. 2016. The historical biogeography of the southern group of the sucker genus *Moxostoma* (Teleostei: Catostomidae) and the colonization of central Mexico. Zoological Journal of the Linnean Society 177(3):633–647.

Peskin, B., K. Henke, N. Cumplido, S. Treaster, M. P. Harris, M. Bagnat, and G. Arratia. 2020. Notochordal signals establish phylogenetic identity of the teleost spine. Current Biology 30(14):2805–2814.

Peters, W. 1852. Diagnosen von neuen Flussfischen aus Mossambique. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1852:275–276, 681–685.

—1876. Über eine merkwürdige von Hrn. Professor Dr. Buchholz entdeckte neue Gattung von Süsswasserfischen, Pantodon Buchholzi, welche zugleich eine neue, den Malacopterygii abdominales angehörige Gruppe von Fischen, Pantodontes, repräsentirt. Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 1876:195–200.

Peterson, R. D., J. P. Sullivan, C. D. Hopkins, A. Santaquiteria, C. B. Dillman, S. Pirro, R. Betancur-R, D. Arcila, L. C. Hughes, and G. Ortí. 2022. Phylogenomics of bony-tongue fishes (Osteoglossomorpha) shed light on the craniofacial evolution and biogeography of the weakly electric clade (Mormyridae). Systematic Biology 71(5):1032–1044.

Pfaff, C., R. Zorzin, and J. Kriwet. 2016. Evolution of the locomotory system in eels (Teleostei: Elopomorpha). BMC Evolutionary Biology 16:159. https://doi.org/10.1186/s12862-016-0728-7

Pfeiffer, W. 1977. The distribution of fright reaction and alarm substance cells in fishes. Copeia 1977(4):653–665.

Pickett, B. D., E. M. Wallace, P. G. Ridge, and J. S. K. Kauwe. 2020. Lingering taxonomic challenges hinder conservation and management of global bonefishes. Fisheries 45(7):347–358.

Pietsch, T. W. 1978. Evolutionary relationships of the sea moths (Teleostei: Pegasidae) with a classification of the gasterosteiform families. Copeia 1978(3):517–529.

—1981. The osteology and relationships of the anglerfish genus *Tetrabrachium* with comments on lophiiform classification. Fishery Bulletin 79(3):387–419.

—1984. Lophiiformes: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 320–325. (Special Publication 1.)

—1989. Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989(2):253–303.

—2005. Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes

(Teleostei: Lophiiformes). Ichthyological Research 52:207–236.

—2009. Oceanic Anglerfishes: Extraordinary Diversity in the Deep Sea. Berkeley: University of California Press. 557 pp.

Pietsch, T. W., and R. J. Arnold. 2020. Frogfishes: Biodiversity, Zoogeography, and Behavioral Ecology. Baltimore: John Hopkins University Press. 601 pp.

Pietsch, T. W., and G. Carnevale. 2011. A new genus and species of anglerfish (Teleostei: Lophiiformes: Lophiidae) from the Eocene of Monte Bolca, Italy. Copeia 2011(1):64–71.

Pietsch, T. W., and D. B. Grobecker. 1987. Frogfishes of the World. Stanford, CA: Stanford University Press. 420 pp.

Pietsch, T. W., and J. W. Orr. 2007. Phylogenetic relationships of deep-sea anglerfishes of the suborder Ceratioidei (Teleostei: Lophiiformes) based on morphology. Copeia 2007(1):1–34.

Pietsch, T. W., and C. P. Zabetian. 1990. Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). Copeia 1990(1):78–100.

Piller, K. R., E. Parker, A. R. Lemmon, and E. M. Lemmon. 2022. Investigating the utility of anchored hybrid enrichment data to investigate the relationships among the killifishes (Actinopterygii: Cyprinodontiformes), a globally distributed group of fishes. Molecular Phylogenetics and Evolution 173:107482. https://doi.org/10.1016/j.ympev.2022.107482

Pinion, A. K., R. Britz, K. M. Kubicek, D. S. Siegel, and K. W. Conway. 2023. The larval attachment organ of the bowfin *Amia ocellicauda* Richardson, 1836 (Amiiformes: Amiidae) and its phylogenetic significance. Journal of Fish Biology 103(6):1300–1311. Published ahead of print, 18 August 2023. https://doi.org/10.1111/jfb.15528

Pohl, M., F. Milvertz, A. Meyer, and M. Vences. 2015. Multigene phylogeny of cyprinodontiform fishes suggests continental radiations and a rogue taxon position of Pantanodon. Vertebrate Zoology 65(1):37–44.

Poll, M., and D. J. Stewart. 1975. Un Mochocidae et un Kneriidae nouveaux de la rivière Luongo (Zambia), affluent du bassin du Congo (Pisces). Revue de Zoologie Africaine 89:151–158.

Poly, W. J. 2004a. Family Aphredoderidae Bonaparte 1846: pirate perches. California Academy of Sciences Annotated Checklists of Fishes 24:1–5.

—2004b. Family Percopsidae Bonaparte 1846: trout perches and sand rollers. California Academy of Sciences Annotated Checklists of Fishes 23:1–5.

Poly, W. J., and G. S. Proudlove. 2004. Family Amblyopsidae Bonaparte 1846: cavefishes. California Academy of Sciences Annotated Checklists of Fishes 25:1–7.

Posner, M., and R. J. Lavenberg. 1999. Kasatkia seigeli: a new species of stichaeid (Perciformes: Stichaeidae) from California. Copeia 1999(4):1035–1040.

Postel, E. 1959. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du Cap Spartel au Cap Roxo, suivie d'un bref aperçu sur leur répartition bathymétrique et géographique. Bulletin de la Société Scientifique de Bretagne 34:129–179.

Poulsen, J. Y. 2019. New observations and ontogenetic transformation of photogenic tissues in the tubeshoulder *Sagamichthys schnakenbecki* (Platytroctidae, Alepocephaliformes). Journal of Fish Biology 94(1):62–76.

Poulsen, J. Y., I. Byrkjedal, E. Willassen, D. Rees, H. Takeshima, T. P. Satoh, G. Shinohara, M. Nishida, and M. Miya. 2013. Mitogenomic sequences and evidence from unique gene rearrangements corroborate evolutionary relationships of Myctophiformes (Neoteleostei). BMC Evolutionary Biology 13:111. https://doi.org/10.1186/1471-2148-13-111

Poulsen, J. Y., M. J. Miller, T. Sado, R. Hanel, K. Tsukamoto, and M. Miya. 2018. Resolving deep-sea pelagic saccopharyngiform eel mysteries: identification of *Neocyema* and Monognathidae leptocephali and establishment of a new fish family "Neocyematidae" based on larvae, adults and mitogenomic gene orders. PLOS ONE 13(7):e0199982. https://doi.org/10.1371/journal.pone.0199982

Poulsen, J. Y., P. R. Møller, S. Lavoué, S. W. Knudsen, M. Nishida, and M. Miya. 2009. Higher and lower-level relationships of the deep-sea fish order Alepocephaliformes (Teleostei: Otocephala) inferred from whole mitogenome sequences. Biological Journal of the Linnean Society 98(4):923–936.

Poyato-Ariza, F. J. 1994. A New Early Cretaceous Gonorynchiform Fish (Teleostei: Ostariophysi) from Las Hoyas (Cuenca, Spain). Lawrence, KS: Museum of Natural History University of Kansas. 37 pp. (Occasional Papers of the Museum of Natural History University of Kansas 164.)

—1995. *Ichthyemidion*, a new genus for the elopiform fish "*Anaethalion*" *vidali*, from the Early Cretaceous of Spain: phylogenetic comments. Comptes rendus de l'Académie des sciences Série 2A: sciences de la terre et des planètes 320':133–139.

—1996a. A revision of *Rubiesichthys gregalis* WENZ 1984 (Ostariophysi, Gonorynchiformes), from the Early Cretaceous of Spain. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 319–328.

—1996b. A Revision of the Ostariophysan Fish Family Chanidae, with Special Reference to the Mesozoic Forms. Munich: Verlag Dr. Friedrich Pfeil. 52 pp. (Palaeo Ichthyologica 6.)

—2015. Studies on pycnodont fishes (I): evaluation of their phylogenetic position among actinopterygians. Rivista Italiana di Paleontologia e Stratigrafia 121(3):329–343.

Poyato-Ariza, F. J., T. Grande, and R. Diogo. 2010. Gonorynchiform interrelationships: historic overview, analysis, and revised systematics of the group. In: T. Grande, F. J. Poyato-Ariza, and R. Diogo, eds. Gonorynchiformes and Ostariophysan Relationships: A Comprehensive Review. Enfield, NH: Science Publishers. pp. 227–337.

Prashad, B., and D. D. Mukerji. 1929. The fish of the Indawgyi Lake and the streams of the Myitkyina District (Upper Burma). Records of the Indian Museum 31(3):161–223.

Přikryl, T. 2014. A new species of the sleeper goby (Gobioidei, Eleotridae) from the České Středohoří Mountains

(Czech Republic, Oligocene) and analysis of the validity of the family Pirskeniidae. Paläontologische Zeitschrift 88:187–196.

Přikryl, T., and G. Carnevale. 2017. An Oligocene toadfish (Teleostei, Percomorpha) from Moravia, Czech Republic: the earliest skeletal record for the order Batrachoidiformes. Bulletin of Geosciences 92(1):123–130.

—2019. An Oligocene tubeshoulder (Teleostei, Alepocephaliformes) from the Central Paratethys (Czech Republic): the first skeletal record for the family Platytroctidae. Journal of Vertebrate Paleontology 39(6):e1719123. https://doi.org/10.1080/02724634.2019.1719123

Přikryl, T., I. Kania, and W. Krzemiński. 2016. Synopsis of fossil fish fauna from the Hermanowa locality (Rupelian; Central Paratethys; Poland): current state of knowledge. Swiss Journal of Geosciences 109:429–443.

Prokofiev, A. M. 2002a. A remarkable new genus of Carangidae from the Upper Paleocene of Turkmenistan (Osteichthyes: Perciformes). Zoosystematica Rossica 11(1):219–228.

—2002b. A new genus of cutlassfish from the Upper Paleocene of Turkmenistan (Scombroidei: Trichiuroidea). Zoosystematica Rossica 11(1):229–233.

Prokofiev, A. M. 2006a. Fossil myctophid fishes (Myctophiformes: Myctophoidei) from Russia and adjacent regions. Journal of Ichthyology 46(Suppl. 1):S38–S83.

—2006b. A new genus of cardinalfishes (Perciformes: Apogonidae) from the South China Sea, with a discussion of the relationships between the families Apogonidae and Kurtidae. Journal of Ichthyology 46(4):279–291.

Quast, J. C. 1965. Osteological characteristics and affinities of the hexagrammid fishes, with a synopsis. Proceedings of the California Academy of Sciences, Series 4, 31(21):563–600.

Quoy, J. R. C., and J. P. Gaimard. 1824. Description des poissons. In: L. C. D. de Freycinet, ed. Voyage autour du Monde, entrepris par ordre du roi,…exécuté sur les corvettes de S. M. L'Uranie et La Physicienne, pendant les années 1817, 1818, 1819 et 1820. Paris: Pillet Ainé. pp. 192–401.

—1825. Description des Poissons. In: L. C. D. de Freycinet, ed. Voyage autour du Monde, entrepris par ordre du roi,…exécuté sur les corvettes de S. M. L'Uranie et La Physicienne, pendant les années 1817, 1818, 1819 et 1820. Paris: Pillet Ainé. pp. 329–616.

Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, et al. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559:392–395.

—2019. Data from: An inverse latitudinal gradient in speciation rate for marine fishes [online dataset]. Dryad. https://doi.org/10.5061/dryad.fc71cp4

Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. Nature Communications 4:1958. https://doi.org/10.1038/ncomms2958

Radchenko, O. A. 2015. The system of the suborder Zoarcoidei (Pisces, Perciformes) as inferred from molecular genetic data. Russian Journal of Genetics 51(11):1096–1112.

—2016. Timeline of the evolution of eelpouts from the suborder Zoarcoidei (Perciformes) based on DNA variability. Journal of Ichthyology 56(4):556–568.

—2017. Molecular Systematics and Phylogeny of Zoarcoid Fishes. Moscow: GEOS. 383 pp. [In Russian.]

Radchenko, O. A., I. A. Chereshnev, and A. V. Petrovskaya. 2010. Relationships and position of the genus *Neozoarces* of the subfamily neozoarcinae in the system of the suborder Zoarcoidei (Pisces, Perciformes) by molecular-genetic data. Journal of Ichthyology 50(3):246–251.

—2012. Position of neck banded blenny *Leptostichaeus pumilus* (Perciformes: Zoarcoidei) in the system of the suborder Zoarcoidei as inferred from molecular genetic data. Journal of Ichthyology 52(9):592–598.

—2014. Genetic differentiation of species and taxonomic structure of the superfamily Stichaeoidea (Perciformes: Zoarcoidei). Russian Journal of Marine Biology 40(6):473–485.

Radchenko, O. A., I. A. Chereshnev, A. V. Petrovskaya, A. A. Balanov, and S. V. Turanov. 2014. Position of the genus *Azygopterus* (Stichaeidae, Perciformes) in the system of the suborder Zoarcoidei as inferred from sequence variation of mitochondrial and nuclear genes. Russian Journal of Genetics 50(3):280–287.

Radovčič, J. 1975. Some new upper Cretaceous teleosts from Yugoslavia with special reference to localities, geology and palaeoenvironment. Palaeontolgia Jugoslavica 17:7–55.

Rafinesque, C. S. 1810a. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia: con varie osservazioni sopra i medesim. Palermo: Sanfilippo. 70 pp.

—1810b. Indice d'ittiologia siciliana: ossia, catalogo metodico dei nomi Latini, Italiani, e Siciliani dei pesci, che si rinvengono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione de alcuni nuovi pesci Siciliani. Messina: Giovanni del Nobolo. 70 pp.

—1815. Analyse de la nature, ou tableau d' l'univers et des corps organisés. Palerme: Aux dépens d' l'auteur. 224 pp.

Raju, S. N. 1974. Three new species of the genus *Monognathus* and the leptocephali of the order Saccopharyngiformes. Fishery Bulletin 72(2):547–562.

Randall, J. E., and B. C. Victor. 2015. Descriptions of thirty-four new species of the fish genus *Pempheris* (Perciformes: Pempheridae), with a key to the species of the western Indian Ocean. Journal of the Ocean Science Foundation 18:1–77.

Randall, Z. S., and L. M. Page. 2015. On the paraphyly of *Homaloptera* (Teleostei: Balitoridae) and description of a new genus of hillstream loaches from the Western Ghats of India. Zootaxa 3926(1):57–86. https://doi.org/10.11646/zootaxa.3926.1.2

Rasquin, P. 1958. Ovarian morphology and early embryology of the pediculate fishes *Antennarius* and *Histrio*. Bulletin of the American Museum of Natural History 114:327–372.

Reed, D. L., K. E. Carpenter, and M. J. deGravelle. 2002. Molecular systematics of the Jacks (Perciformes: Carangidae) based on mitochondrial cytochrome *b* sequences using parsimony, likelihood, and Bayesian approaches. Molecular Phylogenetics and Evolution 23(3):513–524.

Regan, C. T. 1903. On the classification of the fishes of the suborder Plectognathi; with notes and descriptions of new species from specimens in the British Museum Collection. Proceedings of the Zoological Society of London 1902, vol. 2, pp. 284–303.

—1904a. A monograph of the fishes of the family Loricariidae. Transactions of the Zoological Society of London 17(pt. 3):191–350.

—1904b. The phylogeny of Teleostomi. Annals and Magazine of Natural History, Series 7, 13(7):329–349.

—1907a. Descriptions of the teleostean fish *Velifer hypselopterus*, and of a new species of the genus Velifer. Proceedings of the Zoological Society of London 1907, pt. 3 (art. 4), pp. 633–634.

—1907b. On the anatomy, classification and systematic position of the Teleostean fishes of the sub-order Allotriognathi. Proceedings of the Zoological Society of London 1907, pt. 3 (art. 4), pp. 634–643.

—1908. The systematic position of *Stylophorus caudatus*. Annals and Magazine of Natural History, Series 8, 2(11):447–449.

—1909a. The classification of teleostean fishes. Annals and Magazine of Natural History, Series 8, 3(13):75–86.

—1909b. On the anatomy and classification of the scombroid fishes. Annals and Magazine of Natural History, Series 8, 3(13):66–75.

—1910a. The anatomy and classification of the teleostean fishes of the order Zeomorphi. Annals and Magazine of Natural History, Series 8, 6(35):481–484.

—1910b. The origin and evolution of the teleostean fishes of the order Heterosomata. Annals and Magazine of Natural History, Series 8, 6(35):484–496.

—1911a. The anatomy and classification of the teleostean fishes of the order Iniomi. Annals and Magazine of Natural History, Series 8, 7(37):120–133.

—1911b. The anatomy and classification of the teleostean fishes of the order Salmopercae. Annals and Magazine of Natural History, Series 8, 7(39):294–296.

—1911c. The anatomy and classification of the teleostean fishes of the orders Berycomorphi and Xenoberyces. Annals and Magazine of Natural History, Series 8, 7(37):1–9.

—1911d. The classification of the teleostean fishes of the order Ostariophysi.—1. Cyprinoidea. Annals and Magazine of Natural History, Series 8, 8(43):13–32.

—1911e. The classification of the teleostean fishes of the order Ostariophysi.—2. Siluroidea. Annals and Magazine of Natural History, Series 8, 8(47):553–577.

—1911f. The classification of the teleostean fishes of the order Synentognathi. Annals and Magazine of Natural History, Series 8, 7(40):327–335.

—1911g. The osteology and classification of the teleostean fishes of the order Microcyprini. Annals and Magazine of Natural History, Series 8, 7(40):320–327.

—1912a. The anatomy and classification of the teleostean fishes of the order Lyomeri. Annals and Magazine of Natural History, Series 8, 10(57):347–349.

—1912b. The classification of the blennioid fishes. Annals and Magazine of Natural History, Series 8, 10(57):265–280.n bvc

—1912c. The classification of the teleostean fishes of the order Pediculati. Annals and Magazine of Natural History, Series 8, 9(51):277–289.

—1912d. Description of two new eels from West Africa, belonging to a new genus and family. Annals and Magazine of Natural History, Series 8, 10(57): 323–324.

—1912e. The osteology and classification of the teleostean fishes of the order Apodes. Annals and Magazine of Natural History, Series 8, 10(58):377–387.

—1912f. A revision of the Pæciliid fishes of the genera *Rivulus*, *Pterolebias*, and *Cynolebias*. Annals and Magazine of Natural History, Series 8, 10(59):494–508.

—1913a. The Antarctic fishes of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 49:229–292.

—1913b. The classification of the percoid fishes. Annals and Magazine of Natural History, Series 8, 12(67):111–145.

—1913c. The osteology and classification of the teleostean fishes of the order Scleroparei. Annals and Magazine of Natural History, Series 8, 11(62):169–184.

—1914a. Description of a new cyprinodont fish of the genus *Mollienisia* from Yucatan. Annals and Magazine of Natural History, Series 8, 13(75):338.

—1914b. Fishes. British Antarctic ("Terra Nova") expedition, 1910. Natural history report. Zoology 1(1):1–54.

—1923a. The classification of the stomiatoid fishes. Annals and Magazine of Natural History, Series 9, 11(65):612–614.

—1923b. The skeleton of *Lepidosteus*, with remards on the origin and evolution of the lower neopterygian fishes. Proceedings of the Zoological Society of London 1923 (art. 24), pp. 445–461.

—1924. The morphology of a rare oceanic fish, *Stylephorus chordatus*, Shaw; based on specimens collected in the Atlantic by the "Dana" Expeditions, 1920–1922. Proceedings of the Royal Society of London B, Biological Sciences 96(674):193–207.

—1925. Dwarfed males parasitic on the females in oceanic angler-fishes (Pediculati Ceratioidea). Proceedings of the Royal Society of London B, Biological Sciences 97(684):386–400.

—1926. The Pediculate Fishes of the Suborder Ceratioidea. Copenhagen: Gyldendalske Boghandel. 45 pp. (Danish "Dana"—Expeditions in the North Atlantic and the Gulf of Panama [1920–1922] Oceanographical Reports 2.)

—1929. Fishes. In: Encyclopaedia Britannica. 14th ed. Volume 9. London: Encyclopaedia Britannica Company. pp. 305–329.

Reichenbacher, B., T. Přikryl, A. F. Cerwenka, P. Keith, C. Gierl, and M. Dohrmann. 2020. Freshwater gobies 30 million years ago: new insights into character evolution and phylogenetic relationships of †Pirskeniidae (Gobioidei, Teleostei). PLOS ONE 15(8):e0237366. https://doi.org/10.1371/journal.pone.0237366

Reinhardt, J. C. H. 1837. Ichthyologiske bidrag til den Grönlandske fauna. Indledning, indeholdende tillaeg og forandringer I den fabriciske fortegnelse paa Grönlandske hvirveldyr. Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 7:83–196.

Reis, R. E. 1998. Systematics, biogeography, and the fossil record of the Callichthyidae: a review of the available data. In: L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C. A. S. Lucena, eds. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brazil: EDIPUCRS. pp. 351–362.

Reist, J. D. 1987. Comparative morphometry and phenetics of the genera of esocoid Fishes (Salmoniformes). Zoological Journal of the Linnean Society 89(3):275–294.

Ren, Y., and G.-H. Xu. 2021. A new species of *Pteronisculus* from the Middle Triassic (Anisian) of Luoping, Yunnan, China, and phylogenetic relationships of early actinopterygian fishes. Vertebrata PalAsiatica 59(3):169–199.

Reznick, D. N., A. I. Furness, R. W. Meredith, and M. S. Springer. 2017. The origin and biogeographic diversification of fishes in the family Poeciliidae. PLOS ONE 12(3):e0172546. https://doi.org/10.1371/journal.pone.0172546

Ribeiro, A. C., F. J. Poyato-Ariza, F. A. Bockmann, and M. R. de Carvalho. 2018. Phylogenetic relationships of Chanidae (Teleostei: Gonorynchiformes) as impacted by *Dastilbe moraesi*, from the Sanfranciscana basin, Early Cretaceous of Brazil. Neotropical Ichthyology 16:e180059. https://doi.org/10.1590/1982-0224-20180059

Ribeiro, E., A. M. Davis, R. A. Rivero-Vega, G. Ortí, and R. Betancur-R. 2018. Post-Cretaceous bursts of evolution along the benthic-pelagic axis in marine fishes. Proceedings of the Royal Society B, Biological Sciences 285(1893):20182010.

Rice, A. N., and A. H. Bass. 2009. Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: insights into the diversity of the Batrachoididae. Journal of Experimental Biology 212(pt. 9):1377–1391.

Richardson, J. 1843. Contributions to the ichthyology of Australia (continued). Annals and Magazine of Natural History, Series 1, 11 (67–68, 71–72):22–28, 169–182, 352–359, 422–428.

—1844. Ichthyology of the voyage of H. M. S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R. N., F. R. S. In: J. Richardson and J. E. Gray, eds. The Zoology of the Voyage of H. M. S. Erebus and Terror, under the Command of Captain Sir J. C. Ross, R. N., F. R. S., during the Years 1839 to 1843, Volume 2. London: Longman, Brown, Green, and Longmans. pp. 1–16.

—1845. Ichthyology of the voyage of H. M. S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R. N., F. R. S. In: J. Richardson and J. E. Gray, eds. The Zoology of the Voyage of H. M. S. Erebus and Terror, under the Command of Captain Sir J. C. Ross, R. N., F. R. S., during the Years 1839 to 1843, Volume 2. London: Longman, Brown, Green, and Longmans. pp. 17–52.

—1846. Ichthyology of the voyage of H. M. S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R. N., F. R. S. In: J. Richardson and J. E. Gray, eds. The Zoology of the Voyage of H. M. S. Erebus and Terror, under the Command of Captain Sir J. C. Ross, R. N., F. R. S., during the Years 1839 to 1843, Volume 2. London: Longman, Brown, Green, and Longmans. pp. 53–74.

Ridewood, W. G. 1904. On the cranial osteology of the fishes of the families Mormyridae, Notopteridae and Hyodontidae. Zoological Journal of the Linnean Society 29(190):188–217.

—1905. On the cranial osteology of the fishes of the families Osteoglossidae, Pantodontidae, and Phractolaemidae. Zoological Journal of the Linnean Society 29(191):252–282.

Rincon-Sandoval, M., E. Duarte-Ribeiro, A. M. Davis, A. Santaquiteria, L. C. Hughes, C. C. Baldwin, L. Soto-Torres, A. Acero P, H. J. Walker, K. E. Carpenter, et al. 2020. Evolutionary determinism and convergence associated with water-column transitions in marine fishes. Proceedings of the National Academy of Sciences 117(52):33396–33403.

Risso, A. 1810. Ichthyologie de Nice, ou Histoire Naturelle des Poissons du Département des Alpes Maritimes. Paris: F. Schoell. 388 pp.

—1820. Mémoire sur un nouveau genre de poisson nommé Alépocéphale vivant dans les grandes profondeurs de la mer de Nice. Memorie della Reale Accademia delle Scienze di Torino 25:270–272.

Rivera-Rivera, C. J., and J. I. Montoya-Burgos. 2017. Trunk dental tissue evolved independently from underlying dermal bony plates but is associated with surface bones in living odontode-bearing catfish. Proceedings of the Royal Society B, Biological Sciences 284(1865):20171831.

—2018. Back to the roots: reducing evolutionary rate heterogeneity among sequences gives support for the early morphological hypothesis of the root of Siluriformes (Teleostei: Ostariophysi). Molecular Phylogenetics and Evolution 127:272–279.

Roa-Varón, A., R. B. Dikow, G. Carnevale, L. Tornabene, C. C. Baldwin, C. Li, and E. J. Hilton. 2021. Confronting sources of systematic error to resolve historically contentious relationships: a case study using gadiform fishes (Teleostei, Paracanthopterygii, Gadiformes). Systematic Biology 70(4):739–755.

Roa-Varón, A., and G. Ortí. 2009. Phylogenetic relationships among families of Gadiformes (Teleostei, Paracanthopterygii) based on nuclear and mitochondrial data. Molecular Phylogenetics and Evolution 52(3):688–704.

Roberts, C. D. 1993. Comparative morphology of spined scales and their phylogenetic significance in the Teleostei. Bulletin of Marine Science 52:60–113.

Roberts, T. R. 1973. Interrelationships of ostariophysans. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 373–395.

—2012. Systematics, biology,and distribution of the species of the oceanic oarfish genus *Regalecus*: Teleostei, Lampridiformes, Regalecidae. Mémoires du Muséum Nationa' d'Histoire Naturelle 202:1–268.

Robins, C. H., and C. R. Robins. 1989. Family Synaphobranchidae. In: E. B. Böhlke, ed.. Orders Anguilliofrmes and Saccopharyngiformes, Volume 1. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 207–253. (Memoir 1, Fishes of the Western North Atlantic 9.)

Robins, C. R. 1989. The phylogenetic relationships of anguilliform fishes. In: E. B. Böhlke, ed. Orders Anguilliofrmes and Saccopharyngiformes, Volume 1. New

Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 9–23. (Memoir 1, Fishes of the Western North Atlantic 9.)

Rodiles-Hernández, R., D. A. Hendrickson, J. G. Lundberg, and J. M. Humphries. 2005. *Lacantunia enigmatica* (Teleostei: Siluriformes): a new and phylogenetically puzzling freshwater fish from Mesoamerica. Zootaxa 1000(1):1–24. https://doi.org/10.11646/zootaxa.1000.1.1

Roe, L. J. 1991. Phylogenetic and ecological significance of Channidae (Osteichthyes, Teleostei) from the early Eocene Kuldana Formation of Kohat, Pakistan. Contributions from the Museum of Paleontology University of Michigan 28(5):93–100.

Rosas Puchuri, U. F. 2021. What is Protacanthopterygii? A phylogenomic perspective of early-branching lineages of euteleost fishes [master's thesis]. George Washington University. 101 pp.

Rosen, D. E. 1962. Comments on the relationships of the North American cave fishes of the family Amblyopsidae. American Museum Novitates 2109:1–35.

—1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides and their relatives. Bulletin of the American Museum of Natural History 127:217–268.

—1973. Interrelationships of higher euteleostean fishes. In: P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of Fishes. London: Academic Press. pp. 397–513.

—1974. Phylogeny and zoogeography of salmoniform fishes and relationships of *Lepidogalaxias salamandroides*. Bulletin of the American Museum of Natural History 153:269–325.

—1982. Teleostean interrelationships, morphological function and evolutionary inference. American Zoologist 22(2):261–273.

—1984. Zeiforms as primitive plectognath fishes. American Museum Novitates 2782:1–45.

—1985. An essay on euteleostean classification. American Museum Novitates 2827:1–57.

Rosen, D. E., P. L. Forey, B. G. Gardiner, and C. Patterson. 1981. Lungfishes, tetrapods, paleontology, and plesiomorphy. Bulletin of the American Museum of Natural History 167:163–275.

Rosen, D. E., and P. H. Greenwood. 1970. Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorynchiform fishes. American Museum Novitates 2428:1–25.

—1976. A fourth Neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes. Bulletin of the American Museum of Natural History 157:1–69.

Rosen, D. E., and L. R. Parenti. 1981. Relationships of *Oryzias* and the groups of atherinomorph fishes. American Museum Novitates 2719:1–25.

Rosen, D. E., and C. Patterson. 1969. The structure and relationships of the paracanthopterygian fishes. Bulletin of the American Museum of Natural History 141:357–474.

—1990. On Müller's and Cuvier's concepts of pharyngognath and labyrinth fishes and the classification of percomorph fishes, with an atlas of percomorph dorsal gill arches. American Museum Novitates 2983:1–57.

Roth, O., M. H. Solbakken, O. K. Tørresen, T. Bayer, M. Matschiner, H. T. Baalsrud, S. N. K. Hoff, M. S. O. Brieuc, D. Haase, R. Hanel, et al. 2020. Evolution of male pregnancy associated with remodeling of canonical vertebrate immunity in seahorses and pipefishes. Proceedings of the National Academy of Sciences 117(17):9431–9439.

Rüber, L., R. Britz, S. O. Kullander, and R. Zardoya. 2004. Evolutionary and biogeographic patterns of the Badidae (Teleostei: Perciformes) inferred from mitochondrial and nuclear DNA sequence data. Molecular Phylogenetics and Evolution 32(3):1010–1022.

Rüber, L., R. Britz, and R. Zardoya. 2006. Molecular phylogenetics and evolutionary diversification of labyrinth fishes (Perciformes: Anabantoidei). Systematic Biology 55(3):374–397.

Rüber, L., M. Kottelat, H. H. Tan, P. K. L. Ng, and R. Britz. 2007. Evolution of miniaturization and the phylogenetic position of *Paedocypris*, comprising the wo'ld's smallest vertebrate. BMC Evolutionary Biology 7:38. https://doi.org/10.1186/1471-2148-7-38

Rüber, L., H. H. Tan, and R. Britz. 2020. Snakehead (Teleostei: Channidae) diversity and the Eastern Himalaya biodiversity hotspot. Journal of Zoological Systematics and Evolutionary Research 58(1):356–386.

Rüber, L., J. L. Van Tassell, and R. Zardoya. 2003. Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny. Evolution 57(7):1584–1598.

Russell, A. 1794. Natural History of Aleppo. 2nd ed. London: Millar. 430 pp.

Russell, B. C. 1990. Nemipterid Fishes of the World (Threadfin Breams, Whiptail Breams, Monocle Breams, Dwarf Monocle Breams and Coral Breams). Vol. 12 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 303 pp. (FAO Fisheries Synopsis 125.)

Rutenko, O. A., S. V. Turanov, and Y. Ph. Kartavtsev. 2019. Complete mitochondrial genome of ocellated blenny, *Opisthocentrus ocellatus* (Tilesius, 1811) (Zoarcales: Opisthocentidae). Mitochondrial DNA Part B 4(1):1553–1555.

Sabaj, M. H., M. Arce H, D. Donahue, A. Cramer, and L. M. Sousa. 2022. *Synbranchus* of the Middle to Lower Xingu Basin, Brazil, with the description of a new rheophilic species, *S. royal* (Synbranchiformes: Synbranchidae). Proceedings of the Academy of Natural Sciences of Philadelphia 166(1):1–24.

Saeed, B., W. Ivantsoff, and L. E. L. M. Crowley. 1994. Systematic relationships of atheriniform families within Division I of the Series Atherinomorpha (Acanthopterygii) with relevant historical perspectives. Journal of Ichthyology 34:27–72.

Sagemehl, M. 1885. Beiträge zur vergleichenden anatomie der fische. III. Das Cranium der Characiniden nebst allgemeinen Bemerkungen über die mit einem 'Weber'schen Apparat versehenen Physostomenfamilien. Morphologisches Jahrbuch 10:1–119.

Saitoh, K., M. Miya, J. G. Inoue, N. B. Ishiguro, and M. Nishida. 2003. Mitochondrial genomics of ostrariophysan fishes: perspectives on phylogeny and biogeography. Journal of Molecular Evolution 56(4):464–472.

Saitoh, K., T. Sado, M. H. Doosey, H. L. Bart, J. G. Inoue, M. Nishida, R. L. Mayden, and M. Miya. 2011. Evidence from mitochondrial genomics supports the lower Mesozoic of South Asia as the time and place of basal divergence of cypriniform fishes (Actinopterygii: Ostariophysi). Zoological Journal of the Linnean Society 161(3):633–662.

Saitoh, K., T. Sado, R. L. Mayden, N. Hanzawa, K. Nakamura, M. Nishida, and M. Miya. 2006. Mitogenomic evolution and interrelationships of the Cypriniformes (Actinopterygii: Ostariophysi): the first evidence toward resolution of higher-level relationships of the 'world's largest freshwater fish clade based on 59 whole mitogenome sequences. Journal of Molecular Evolution 63:826–841.

Sakamoto, K., T. Uyeno, and N. Micklich. 2004. *Oligopleuronectes germanicus* gen. et sp. nov., an Oligocene pleuronectid flatfish from Frauenweiler, S-Germany. Bulletin of the National Science Museum, Series C, Geology and Paleontology 30:89–94.

Sanciangco, M. D., K. E. Carpenter, and R. Betancur-R. 2016. Phylogenetic placement of enigmatic percomorph families (Teleostei: Percomorphaceae). Molecular Phylogenetics and Evolution 94(Part B):565–576.

Sanford, C. P. J. 1990. The phylogenetic relationships of salmonoid fishes. Bulletin of the British Museum (Natural History), Zoology 56:145–153.

Santaquiteria, A., A. C. Siqueira, E. Duarte-Ribeiro, G. Carnevale, W. T. White, J. J. Pogonoski, C. C. Baldwin, G. Ortí, D. Arcila, and R. Betancur-R. 2021. Phylogenomics and historical biogeography of seahorses, dragonets, goatfishes, and allies (Teleostei: Syngnatharia): assessing factors driving uncertainty in biogeographic inferences. Systematic Biology 70(6):1145–1162.

Santini, F., and G. Carnevale. 2015. First multilocus and densely sampled timetree of trevallies, pompanos and allies (Carangoidei, Percomorpha) suggests a Cretaceous origin and Eocene radiation of a major clade of piscivores. Molecular Phylogenetics and Evolution 83:33–39.

Santini, F., L. J. Harmon, G. Carnevale, and M. E. Alfaro. 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. BMC Evolutionary Biology 9:194. https://doi.org/10.1186/1471-2148-9-194

Santini, F., X. H. Kong, L. Sorenson, G. Carnevale, R. S. Mehta, and M. E. Alfaro. 2013. A multi-locus molecular timescale for the origin and diversification of eels (order: Anguilliformes). Molecular Phylogenetics and Evolution 69(3):884–894.

Santini, F., M. T. T. Nguyen, L. Sorenson, T. B. Waltzek, J. W. L. Alfaro, J. M. Eastman, and M. E. Alfaro. 2013. Do habitat shifts drive diversification in teleost fishes? An example from the pufferfishes (Tetraodontidae). Journal of Evolutionary Biology 26(5):1003–1018.

Santini, F., L. Sorenson, and M. E. Alfaro. 2013. A new phylogeny of tetraodontiform fishes (Tetraodontiformes, Acanthomorpha) based on 22 loci. Molecular Phylogenetics and Evolution 69(1):177–187.

Santini, F., and J. C. Tyler. 2003. A phylogeny of the families of fossil and extant tetraodontiform fishes (Acanthomorpha, Tetraodontiformes), Upper Cretaceous to Recent. Zoological Journal of the Linnean Society 139(4):565–617.

—2004. The importance of even highly incomplete fossil taxa in reconstructing the phylogenetic relationships of the Tetraodontiformes (Acanthomorpha: Pisces). Integrative and Comparative Biology 44(5):349–357.

Santini, F., J. C. Tyler, A. F. Bannikov, and D. S. Baciu. 2006. A phylogeny of extant and fossil buckler dory fishes, family Zeidae (Zeiformes, Acanthomorpha). Cybium 30(2):99–107.

Sato, M. 2022. Morphological diversity of the lateral line system in Teleostei. In: Y. Kai, H. Motomura, and K. Matsuura, eds. Fish Diversity of Japan: Evolution, Zoogeography, and Conservation. Singapore: Springer Nature Singapore. pp. 283–310.

Sato, T., and T. Nakabo. 2002. Paraulopidae and *Paraulopus*, a new family and genus of aulopiform fishes with revised relationships within the order. Ichthyological Research 49:25–46.

Satoh, T. P. 2018. Complete mitochondrial genome sequence of *Glaucosoma buergeri* (Pempheriformes: Glaucosomatidae) with implications based on the phylogenetic position. Mitochondrial DNA Part B 3(1):107–109.

Satoh, T. P., and E. Katayama. 2022. Complete mitochondrial genomes of two sand diver species (Perciformes, Trichonotidae): novel gene orders and phylogenetic position within Gobiiformes. Mitochondrial DNA Part B 7(1):12–14.

Sawada, Y. 1982. Phylogeny and zoogeography of the superfamily Cobitoidea (Cyprinoidei, Cypriniformes). Memoirs of the Faculty of Fisheries, Hokkaido University 28(2):65–223.

Schaefer, S. A. 1990. Anatomy and relationships of the scoloplacid catfishes. Proceedings of the Academy of Natural Sciences of Philadelphia 142:167–210.

—2006. Morphological Evolution, Aptations, Homoplasies, Constraints and Evolutionary Trends: Catfishes as a Case Study on General Phylogeny and Macroevolution. By Rui Diogo [book review]. Quarterly Review of Biology 81(3):276–278.

Schaefer, S. A., and G. V. Lauder. 1986. Historical transformation of functional design: evolutionary morphology of feeding mechanisms in loricarioid catfishes. Systematic Zoology 35(4):489–508.

Schaeffer, B., and C. Patterson. 1984. Jurassic fishes from the western United States, with comments on Jurassic fish distribution. American Museum Novitates 2796:1–86.

Schedel, F. D. B., A. Chakona, B. L. Sidlauskas, M. O. Popoola, N. Usimesa Wingi, D. Neumann, E. J. W. M. N. Vreven, and U. K. Schliewen. 2022. New phylogenetic insights into the African catfish families Mochokidae and Austroglanididae. Journal of Fish Biology 100(5):1171–1186.

Schlesinger, G. 1909. Zur phylogenie und ethologie der scombresociden. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien 59:302–339.

Schomburgk, R. H. 1848. The History of Barbados: Comprising a Geographical and Statistical Description of the Island; a Sketch of the Historical Events Since the Settlement; and an Account of Its Geology and Natural Productions. London: Longman, Brown, Green and Longmans. 722 pp.

Schrøder, A. E., and G. Carnevale. 2023. The argentiniform *Surlykus longigracilis* gen. et sp. nov., the most abundant fish from the Eocene Fur Formation of Denmark. Bulletin of the Geological Society of Denmark 72:1–18.

Schrøder, A. E., J. A. Rasmussen, P. R. Møller, and G. Carnevale. 2022. A new beardfish (Teleostei, Polymixiiformes) from the Eocene Fur Formation, Denmark. Journal of Vertebrate Paleontology 42(2):e2142914. https://doi.org/10.1080/02724634.2022.2142914

Schultz, L. P. 1948. A revision of six subfamilies of Atherine fishes, with descriptions of new genera and species. Proceedings of the United States National Museum 98(3220):1–48.

Schultze, H.-P., and G. Arratia. 1988. Reevaluation of the caudal skeleton of some actinopterygian fishes. II. *Hiodon*, *Elops*, and *Albula*. Journal of Morphology 195(3):257–303.

Schultze, H.-P., and E. O. Wiley. 1984. The neopterygian *Amia* as a living fossil. In: N. Eldredge and S. M. Stanley, eds. Living Fossils. New York: Springer. pp. 153–159.

Schwarzhans, W. 2003. Fish Otoliths from the Paleocene of Denmark. Copenhagen: Danmarks og Grønlands geologiske undersøgelse. 94 pp. (Geologic Survey of Denmark and Greenland Bulletin 2.)

—2007. The otoliths from the middle Eocene of Osteroden near Bramsche, north-western Germany. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 244:299–369.

—2010. Otolithen aus den Gerhartsreiter Schichten (Oberkreide: Maastricht) des Gerhartsreiter Grabens (Oberbayern). Munich: Verlag Dr. Friedrich Pfeil. 100 pp. (Palaeo Ichthyologica 4.)

—2019. Reconstruction of the fossil marine bony fish fauna (Teleostei) from the Eocene to Pleistocene of New Zealand by means of otoliths. With studies of Recent congroid, morid and trachinoid otoliths. Memorie della Società Italianan de Scienze Naturali e del Museo Civico di Storia Naturale di Milano 46:1–326.

Schwarzhans, W., and A. Bratishko. 2011. The otoliths from the middle Paleocene of Luzanivka (Cherkasy district, Ukraine). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 261:83–110.

Schwarzhans, W., and G. Carnevale. 2021. The rise to dominance of lanternfishes (Teleostei: Myctophidae) in the oceanic ecosystems: a paleontological perspective. Paleobiology 47(3):446–463.

Schwarzhans, W., and J. W. M. Jagt. 2021. Silicified otoliths from the Maastrichtian type area (Netherlands, Belgium) document early gadiform and perciform fishes during the Late Cretaceous, prior to the K/Pg boundary extinction event. Cretaceous Research 127:104921. https://doi.org/10.1016/j.cretres.2021.104921

Schwarzhans, W., and G. Stringer. 2020. Fish otoliths from the Late Maastrichtian Kemp Clay (Texas, USA) and the Early Dannian Clayton Formation (Arkansas, USA) and an assessment of extinction and survival of teleost lineages across the K-Pg boundary based on otoliths. Rivista Italiana di Paleontologia e Stratigrafia 126(2):395–446.

Semple, G. P. 1985. Reproductive behaviour and development of the Glassperchlet, *Ambassis agrammus* Gunther (Pisces: Ambassidae), from the Alligator rivers system, northern territory. Australian Journal of Marine and Freshwater Research 36(6):797–805.

Setiamarga, D. H. E., M. Miya, Y. Yamanoue, K. Mabuchi, T. P. Satoh, J. G. Inoue, and M. Nishida. 2008. Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes, silversides, and their relatives): the first evidence based on whole mitogenome sequences. Molecular Phylogenetics and Evolution 49(2):598–605.

Sferco, E., A. López-Arbarello, and A. M. Báez. 2015. Phylogenetic relationships of †*Luisiella feruglioi* (Bordas) and the recognition of a new clade of freshwater teleosts from the Jurassic of Gondwana. BMC Evolutionary Biology 15:1–15. https://doi.org/10.1186/s12862-015-0551-6

Shaw, G. 1791. Description of the *Stylephorus chordatus*, a new fish. Transactions of the Linnean Society of London 1:90–92.

Shaw, G., and F. P. Nodder. 1799. The Naturalist's Miscellany, or Coloured Figures of Natural Objects; Drawn and Described from Nature, Volume 10. London: J. Cooper. 297 pp.

Shedko, S. V. 2022. Molecular dating of phylogeny of sturgeons (Acipenseridae) based on total evidence analysis. Russian Journal of Genetics 58(6):718–729.

Shedlock, A. M., T. W. Pietsch, M. G. Haygood, P. Bentzen, and M. Hasegawa. 2004. Molecular systematics and life history evolution of anglerfishes (Teleostei: Lophiiformes): evidence from mitochondrial DNA. Steenstrupia 28(2):129–144.

Shen, C., and G. Arratia. 2021. Re-description of the sexually dimorphic peltopleuriform fish *Wushaichthys exquisitus* (Middle Triassic, China): taxonomic implications and phylogenetic relationships. Journal of Systematic Palaeontology 19(19):1317–1342.

Shen, Y., N. Yang, Z. Liu, Q. Chen, and Y. Li. 2020. Phylogenetic perspective on the relationships and evolutionary history of the Acipenseriformes. Genomics 112(5):3511–3517.

Shi, W., S. Chen, X. Kong, L. Si, L. Gong, Y. Zhang, and H. Yu. 2018. Flatfish monophyly refereed by the relationship of *Psettodes* in Carangimorphariae. BMC Genomics 19:400. https://doi.org/10.1186/s12864-018-4788-5

Shinohara, G. 1994. Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). Memoirs of the Faculty of Fisheries, Hokkaido University 41:1–97.

Siebert, D. J. 1987. Interrelationships among families of the order Cypriniformes (Teleostei) [dissertation]. City University of New York. 380 pp.

—1990. Papers on the Systematics of Gadiform Fishes. D. M. Cohen (ed.) [book review]. Copeia 1990(3):889–893.

Silva, G. S. C., B. F. Melo, F. F. Roxo, L. E. Ochoa, O. A. Shibatta, M. H. Sabaj, and C. Oliveira. 2021. Phylogenomics of the bumblebee catfishes (Siluriformes:

Pseudopimelodidae) using ultraconserved elements. Journal of Zoological Systematics and Evolutionary Research 59(8):1662–1672.

Silva, H. M. A., and V. Gallo. 2011. Taxonomic review and phylogenetic analysis of Enchodontoidei. Anais da Academia Brasileira de Ciências 83:483–511.

Silva Santos, R. 1985. *Laeliichthys ancestralis*, novo gênero e espécie de Osteoglossiformes do Aptiano da Formação Areado, Estado de Minas Gerais, Brasil. Série Geologia. Seção Paleontologia e Estratigrafia 27:151–167.

Simion, P., F. Delsuc, and H. Philippe. 2020. To what extent current limits of phylogenomics can be overcome? In: C. Scornavacca, F. Delsuc, and N. Galtier, eds. Phylogenetics in the Genomic Era. HAL Open Science [online archive].. 35 pp. https://hal.science/hal-02535366

Simons, A. M., and N. J. Gidmark. 2010. Systematics and phylogenetic relationships of Cypriniformes. In: T. Grande, F. J. Poyato-Ariza, and R. Diogo, eds. Gonorynchiformes and Ostariophysan Relationships: A Comprehensive Review. Enfield, NH: Science Publishers. pp. 409–440.

Siqueira, A. C., D. R. Bellwood, and P. F. Cowman. 2019. Historical biogeography of herbivorous coral reef fishes: the formation of an Atlantic fauna. Journal of Biogeography 46(7):1611–1624.

Skelton, P. H., L. Risch, and L. D. G. de Vos. 1984. On the generic identity of the *Gephyroglanis* catfishes from southern Africa (Pisces, Siluroidei, Bagridae). Revue de Zoologie Africaine 98(2):337–372.

Šlechtová, V., J. Bohlen, and H.-H. Tan. 2007. Families of Cobitoidea (Teleostei; Cypriniformes) as revealed from nuclear genetic data and the position of the mysterious genera *Barbucca*, *Psilorhynchus*, *Serpenticobitis* and *Vaillantella*. Molecular Phylogenetics and Evolution 44(3):1358–1365.

Smith, C. L. 1975. The evolution of hermaphroditism in fishes. In: R. Reinboth, ed. Intersexuality in the Animal Kingdom. Berlin: Springer. pp. 295–310.

Smith, D. G. 1984. A redescription of the rare eel *Myroconger compressus* (Pisces: Myrocongridae), with notes on its osteology, relationships and distribution. Copeia 1984(3):585–594.

Smith, D. G., and G. D. Johnson. 2007. A new species of *Pteropsaron* (Teleostei: Trichonotidae: Hemerocoetinae) from the western Pacific, with notes on related species. Copeia 2007(2):364–377.

Smith, J. A. 1865 March 23. Report in [Edinburgh] Daily Review, no. 1242, 2.

Smith, J. L. B. 1935. The “Galjoen” fishes of South Africa. Transactions of the Royal Society of South Africa 23(3):265–276.

Smith, J. L. B. 1955a. The fishes of Aldabra. Part II. Annals and Magazine of Natural History, Series 12, 8(93):689–697.

Smith, J. L. B. 1955b. The fishes of the family Pomacanthidae in the western Indian Ocean. Annals and Magazine of Natural History, Series 12, 8(89):377–384.

Smith, M. L., and M. W. Hahn. 2022. The frequency and topology of pseudoorthologs. Systematic Biology 71(3):649–659.

Smith, W. L. 2005. The limits and relationships of mail-cheeked fishes (Teleostei: Percomorpha) and the evolution of venom in fishes [dissertation]. Columbia University. 414 pp.

Smith, W. L., and M. S. Busby. 2014. Phylogeny and taxonomy of sculpins, sandfishes, and snailfishes (Perciformes: Cottoidei) with comments on the phylogenetic significance of their early-life-history specializations. Molecular Phylogenetics and Evolution 79:332–352.

Smith, W. L., and M. T. Craig. 2007. Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. Copeia 2007(1):35–55.

Smith, W. L., E. Everman, and C. Richardson. 2018. Phylogeny and taxonomy of flatheads, scorpionfishes, sea robins, and stonefishes (Percomorpha: Scorpaeniformes) and the evolution of the lachrymal saber. Copeia 106(1):94–119.

Smith, W. L., M. J. Ghedotti, O. Domínguez-Domínguez, C. D. McMahan, E. Espinoza, R. P. Martin, M. G. Girard, and M. P. Davis. 2022. Investigations into the ancestry of the Grape-eye Seabass (*Hemilutjanus macrophthalmos)* reveal novel limits and relationships for the Acropomatiformes (Teleostei: Percomorpha). Neotropical Ichthyology 20(3):e210160. https://doi.org/10.1590/1982-0224-2021-0160

Smith, W. L., J. H. Stern, M. G. Girard, and M. P. Davis. 2016. Evolution of venomous cartilaginous and ray-finned fishes. Integrative and Comparative Biology 56(5):950–961.

Smith, W. L., and W. C. Wheeler. 2004. Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. Molecular Phylogenetics and Evolution 32(2):627–646.

—2006. Venom evolution widespread in fishes: a phylogenetic road map for the bioprospecting of piscine venoms. Journal of Heredity 97(3):206–217.

Smith-Vaniz, W. F. 1984. Carangidae: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 522–530. (Special Publication 1.)

Song, H. Y., K. Mabuchi, T. P. Satoh, J. A. Moore, Y. Yamanoue, M. Miya, and M. Nishida. 2014. Mitogenomic circumscription of a novel percomorph fish clade mainly comprising “Syngnathoidei“ (Teleostei). Gene 542(2):146–155.

Song, S., J. Zhao, and C. Li. 2017. Species delimitation and phylogenetic reconstruction of the sinipercids (Perciformes: Sinipercidae) based on target enrichment of thousands of nuclear coding sequences. Molecular Phylogenetics and Evolution 111:44–55.

Sorbini, L. 1970. Un nuovo genere fossile nell’ittiofauna di M. Bolca: *Eolates* nov. gen. Memorie del Museo Civico di Storia Naturale di Verona, prima serie 18:11–29.

—1981. The Cretaceous fishes of Nardò. I. Order Gasterosteiformes (Pisces). Bollettino del Museo Civico di Storia Naturale di Verona 8:1–27.

Sparks, J. S., P. V. Dunlap, and W. L. Smith. 2005. Evolution and diversification of a sexually dimorphic luminescent system in ponyfishes (Teleostei: Leiognathidae), including diagnoses for two new genera. Cladistics 21(4):305–327.

Sparks, J. S., R. C. Schelly, W. L. Smith, M. P. Davis, D. Tchernov, V. A. Pieribone, and D. F. Gruber. 2014. The covert world of fish biofluorescence: a phylogenetically widespread and phenotypically variable phenomenon. PLOS ONE 9(1):e83259. https://doi.org/10.1371/journal.pone.0083259

Sparks, J. S., and W. L. Smith. 2004a. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). Cladistics 20(6):501–517.

—2004b. Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Melanotaenioidei): Gondwanan vicariance and evolution in freshwater. Molecular Phylogenetics and Evolution 33(3):719–734.

Speijer, R. P., H. Pälike, C. J. Hollis, J. J. Hooker, and J. G. Ogg. 2020. The Paleogene Period. In: F. M. Gradstein, J. G. Ogg, M. D. Schmitz, and G. M. Ogg, eds. Geologic Time Scale 2020, Volume 2. Amsterdam: Elsevier. pp. 1087–1140.

Springer, V. G. 1983. *Tyson belos*, New Genus and Species of Western Pacific Fish (Gobiidae, Xenisthminae), with Discussions of Gobioid Osteology and Classification. Washington, DC: Smithsonian Institution Press. 40 pp. (Smithsonian Contributions to Zoology 390.)

—1993. Definition of the suborder Blennioidei and its included families (Pisces: Perciformes). Bulletin of Marine Science 52:472–495.

Springer, V. G., and W. C. Freihofer. 1976. Study of the Monotypic Fish Family Pholidichthyidae (Perciformes). Washington, DC: Smithsonian Institution Press. 43 pp. (Smithsonian Contributions to Zoology 216.)

Springer, V. G., and G. D. Johnson. 2004. Study of the Dorsal Gill-arch Musculature of Teleostome Fishes, with Special Reference to the Actinopterygii. Washington, DC: Biological Society of Washington, Smithsonian Institution. 260 pp. (Bulletin of the Biological Society of Washington 11.)

—2015. The gill-arch musculature of *Protanguilla*, the morphologically most primitive eel (Teleostei: Anguilliformes), compared with that of other putatively primitive extant eels and other elopomorphs. Copeia 103(3):595–620.

Springer, V. G., and T. M. Orrell. 2004. Appendix: phylogenetic analysis of 147 families of acanthomorph fishes based primarily on dorsal gill-arch muscles and skeleton. In: V. G. Springer, G. D. Johnson, T. M. Orrell, and K. Darrow, eds. Study of the Dorsal Gill-arch Musculature of Teleostome Fishes, with Special Reference to the Actinopterygii. Washington, DC: Biological Society of Washington, Smithsonian Institution. pp. 236–260. (Bulletin of the Biological Society of Washington 11.)

Stanhope, M. J., V. G. Waddell, O. Madsen, W. de Jong, S. B. Hedges, G. C. Cleven, D. Kao, and M. S. Springer. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proceedings of the National Academy of Sciences of the United States of America 95(17):9967–9972.

Starks, E. C. 1904. The osteology of some berycoid fishes. Proceedings of the United States National Museum 27(1366):601–619.

—1908. The characters of Atelaxia, a new suborder of fishes. Bulletin of the Museum of Comparative Zoology 52(2):1–22.

Steindachner, F. 1867. Notizen. Anzeiger der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 4:119–120.

—1875. Ichthyologische Beiträge (II). I. Die Fische von Juan Fernandez in den Sammlungen des Wiener Museums. II. Über einige neue Fischarten von der Ost- und Westküste Süd-Amerikas. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 71(1. Abth.):443–480.

—1878. Ichthyologische Beiträge (VII). Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 78(1. Abth.):377–400.

—1880. Beitäge zur Kenntniss der Flussfische Südamerikas (II) und Ichthyologische Beiträge (IX). Anzeiger der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Classe 17(19):157–159.

—1908. Über eine während der brasilianischen Expedition entdeckte Brachyplatystoma-Art aus dem Rio Parnahyba und über eine dicht gefleckte und gestrichelte Varietät von Giton fasciatus aus den Gewässern von Santos (Staat Sao Paulo). Anzeiger der Kaiserlichen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Classe 45(9):126–130.

Stewart, D. J. 2013a. A new species of *Arapaima* (Osteoglossomorpha: Osteoglossidae) from the Solimões River, Amazonas State, Brazil. Copeia 2013(3):470–476.

—2013b. Re-description of *Arapaima agassizii* (Valenciennes), a rare fish from Brazil (Osteoglossomorpha: Osteoglossidae). Copeia 2013(1):38–51.

Stewart, K. M. 2001. The freshwater fish of Neogene Africa (Miocene–Pleistocene): systematics and biogeography. Fish and Fisheries 2(3):177–230.

—2003. Fossil fish remains from the Mio-Pliocene deposits at Lothagam, Kenya. In: M. G. Leakey and J. M. Harris, eds. Lothagam: The Dawn of Humanity in Eastern Africa. New York: Columbia University Press. pp. 75–111.

Steyskal, G. C. 1980. The grammar of family-group names as exemplified by those of fishes. Proceedings of the Biological Society of Washington 93(1):168–177.

Stiassny, M. L. J. 1986. The limits and relationships of acanthomorph teleosts. Journal of Zoology 1(2):411–460.

—1990. Notes on the anatomy and relationships of the bedotiid fishes of Madagascar, with a taxonomic revision of the genus *Rheocles* (Atherinomorpha: Bedotiidae). American Museum Novitates 2979:1–33.

—1993. What are grey mullets? Bulletin of Marine Science 52:197–219.

—1996. Basal ctenosquamate relationships and the interrelationships of the myctophiform (Scopelomorph) fishes. In: M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson, eds. Interrelationships of Fishes. San Diego: Academic Press. pp. 174–191.

Stiassny, M. L. J., and J. S. Jensen. 1987. Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. Bulletin of the Museum of Comparative Zoology 151(5):269–319.

Stiassny, M. L. J., and J. A. Moore. 1992. A review of the pelvic girdle of acanthomorph fishes, with comments on hypotheses of acanthomorph intrarelationships. Zoological Journal of the Linnean Society 104(3):209–242.

Stiassny, M. L. J., R. C. Schelly, and V. Mamonekene. 2009. A new *Alestes* (Characiformes, Alestidae) from the Mpozo River in the Democratic Republic of Congo. Copeia 2009(1):110–116.

Stiassny, M. L. J., E. O. Wiley, G. D. Johnson, and M. R. de Carvalho. 2004. Gnathostome fishes. In: J. Cracraft and M. J. Donoghue, eds. Assembling the Tree of Life. New York: Oxford University Press. pp. 410–429.

Stiller, J., G. Short, H. Hamilton, N. Saarman, S. Longo, P. Wainwright, G. W. Rouse, and W. B. Simison. 2022. Phylogenomic analysis of Syngnathidae reveals novel relationships, origins of endemic diversity and variable diversification rates. BMC Biology 20:75. https://doi.org/10.1186/s12915-022-01271-w

Stout, C. C., M. Tan, A. R. Lemmon, E. M. Lemmon, and J. W. Armbruster. 2016. Resolving Cypriniformes relationships using an anchored enrichment approach. BMC Evolutionary Biology 16:244. https://doi.org/10.1186/s12862-016-0819-5

Straube, N., C. Li, M. Mertzen, H. Yuan, and T. Moritz. 2018. A phylogenomic approach to reconstruct interrelationships of main clupeocephalan lineages with a critical discussion of morphological apomorphies. BMC Evolutionary Biology 18:158. https://doi.org/10.1186/s12862-018-1267-1

Streelman, J. T., and S. A. Karl. 1997. Reconstructing labroid evolution with single-copy nuclear DNA. Proceedings of the Royal Society of London B, Biological Sciences 264(1384):1011–1020.

Stringer, G., and W. Schwarzhans. 2021. Upper Cretaceous teleostean otoliths from the Severn Formation (Maastrichtian) of Maryland, USA, with an unusual occurrence of Siluriformes and Beryciformes and the oldest Atlantic coast Gadiformes. Cretaceous Research 125:104867. https://doi.org/10.1016/j.cretres.2021.104867

Stundl, J., A. Pospisilova, D. Jandzik, P. Fabian, B. Dobiasova, M. Minarik, B. D. Metscher, V. Soukup, and R. Cerny. 2019. Bichir external gills arise via heterochronic shift that accelerates hyoid arch development. eLife 8:e43531. https://doi.org/10.7554/eLife.43531

Su, Y., H.-C. Lin, and H.-C. Ho. 2022a. *Hoplostethus roseus*, a new roughy fish from the western Pacific based on morphology and DNA barcoding (family Trachichthyidae). Journal of Fish Biology 101(3):441–452.

—2022b. A new cryptic species of the pineapple fish genus *Monocentris* (family Monocentridae) from the western Pacific Ocean, with redescription of *M. japonica* (Houttuyn, 1782). Zootaxa 5189(1):180–203. https://doi.org/10.11646/zootaxa.5189.1.18

Sullivan, J. P., S. Lavoué, and C. D. Hopkins. 2000. Molecular systematics of the African electric fishes (Mormyroidea: Teleostei) and a model for the evolution of their electric organs. Journal of Experimental Biology 203:665–683.

—2016. *Cryptomyrus*: a new genus of Mormyridae (Teleostei, Osteoglossomorpha) with two new species from Gabon, West-Central Africa. ZooKeys 561:117–150.

Sullivan, J. P., J. G. Lundberg, and M. Hardman. 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. Molecular Phylogenetics and Evolution 41(3):636–662.

Sullivan, J. P., J. Muriel-Cunha, and J. G. Lundberg. 2013. Phylogenetic relationships and molecular dating of the major groups of catfishes of the Neotropical superfamily Pimelodoidea (Teleostei, Siluriformes). Proceedings of the Academy of Natural Sciences of Philadelphia 162(1):89–110.

Sullivan, J. P., Z. Peng, J. G. Lundberg, J. Peng, and S. He. 2008. Molecular evidence for diphyly of the Asian catfish family Amblycipitidae (Teleostei: Siluriformes) and exclusion of the South American Aspredinidae from Sisoroidea. Proceedings of the Academy of Natural Sciences of Philadelphia 157(1):51–65.

Sun, Z. Y., A. Tintori, X. Yaozhong, C. Lombardo, N. Peigang, and J. Dayong. 2017. A new non-parasemionotiform order of the Halecomorphi (Neopterygii, Actinopterygii) from the Middle Triassic of Tethys. Journal of Systematic Palaeontology 15(3):223–240.

Suttkus, R. D. 1963. Order Lepisostei. In: B. Bigelow, and W. C. Schroeder, eds. Soft-rayed bony fishes. Class Osteichthyes. Sturgeons, Gars, Tarpon, Ladyfish, Bonefish, Salmon, Charrs, Anchovies, Herring, Shads, Smelt, Capelin, et al. New Haven, CT: Sears Foundation of Marine Research, Yale University. pp. 61–88. (Memoir 1, Fishes of the Western North Atlantic 3.)

Suzuki, D., M. C. Brandley, and M. Tokita. 2010. The mitochondrial phylogeny of an ancient lineage of ray-finned fishes (Polypteridae) with implications for the evolution of body elongation, pelvic fin loss, and craniofacial morphology in Osteichthyes. BMC Evolutionary Biology 10:21. https://doi.org/10.1186/1471-2148-10-21

Swainson, W. 1838. On the Natural History and Classification of Fishes, Amphibians, and Reptiles, or Monocardian Animals, Volume 1. London: Longman, Orme, Brown, Green, and Longmans. 368 pp.

Swann, J. B., S. J. Holland, M. Petersen, T. W. Pietsch, and T. Boehm. 2020. The immunogenetics of sexual parasitism. Science 369(6511):1608–1615.

Sytchevskaya, E. K. 1999. Freshwater fish fauna from the Triassic of northern Asia. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record. Munich: Verlag Dr. Friedrich Pfeil. pp. 445–468.

Sytchevskaya, E. K., and A. M. Prokofiev. 2002. First findings of Xiphioidea (Perciformes) in the late Paleocene of Turkmenistan. Journal of Ichthyology 42(3):227–237.

Tagliacollo, V. A., M. J. Bernt, J. M. Craig, C. Oliveira, and J. S. Albert. 2016. Model-based total evidence phylogeny of Neotropical electric knifefishes (Teleostei, Gymnotiformes). Molecular Phylogenetics and Evolution 95:20–33.

Takezaki, N. 2021. Resolving the early divergence pattern of teleost fish using genome-scale data. Genome Biology and Evolution 13(5):evab052. https://doi.org/10.1093/gbe/evab118

Tan, M., and J. W. Armbruster. 2018. Phylogenetic classification of extant genera of fishes of the order

Cypriniformes (Teleostei: Ostariophysi). Zootaxa 4476(1):6–39. https://doi.org/10.11646/zootaxa.4476.1.4

Tang, K. L., M. K. Agnew, M. V. Hirt, T. Sado, L. M. Schneider, J. Freyhof, Z. Sulaiman, E. Swartz, C. Vidthayanon, M. Miya, K. Saitoh, A. M. Simons, R. M. Wood, and R. L. Mayden. 2010. Systematics of the subfamily Danioninae (Teleostei: Cypriniformes: Cyprinidae). Molecular Phylogenetics and Evolution 57(1):189–214.

Tang, K. L., P. B. Berendzen, E. O. Wiley, J. F. Morrissey, R. Winterbottom, and G. D. Johnson. 1999. The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes) based on molecular and morphological evidence. Molecular Phylogenetics and Evolution 11(3):415–425.

Tang, K. L., and C. Fielitz. 2013. Phylogeny of moray eels (Anguilliformes: Muraenidae), with a revised classification of true eels (Teleostei: Elopomorpha: Anguilliformes). Mitochondrial DNA 24(1):55–66.

Tang, K. L., D. N. Lumbantobing, and R. L. Mayden. 2013. The phylogenetic placement of *Oxygaster* van Hasselt, 1823 (Teleostei: Cypriniformes: Cyprinidae) and the taxonomic status of the family-group Name Oxygastrinae Bleeker, 1860. Copeia 2013(1):13–22.

Tang, Q., H. Liu, R. Mayden, and B. Xiong. 2006. Comparison of evolutionary rates in the mitochondrial DNA cytochrome *b* gene and control region and their implications for phylogeny of the Cobitoidea (Teleostei: Cypriniformes). Molecular Phylogenetics and Evolution 39(2):347–357.

Tang, T., Y. Huang, C. Peng, Y. Liao, Y. Lv, Q. Shi, and B. Gao. 2023. A chromosome-level genome assembly of the Reef Stonefish (*Synanceia verrucosa*) provides novel insights into stonustoxin (sntx) genes. Molecular Biology and Evolution 40(10):msad215.

Tao, W., R. L. Mayden, and S. He. 2013. Remarkable phylogenetic resolution of the most complex clade of Cyprinidae (Teleostei: Cypriniformes): a proof of concept of homology assessment and partitioning sequence data integrated with mixed model Bayesian analyses. Molecular Phylogenetics and Evolution 66(3):603–616.

Tao, W., L. Yang, R. L. Mayden, and S. He. 2019. Phylogenetic relationships of Cypriniformes and plasticity of pharyngeal teeth in the adaptive radiation of cyprinids. Science China Life Sciences 62:553–565.

Tate, M., R. E. McGoran, C. R. White, and S. J. Portugal. 2017. Life in a bubble: the role of the labyrinth organ in determining territory, mating and aggressive behaviours in anabantoids. Journal of Fish Biology 91(3):723–749.

Taverne, L. 1979. Ostéologie, phylogénèse, et systématique des téléostéens fossils et actuels du super-orde de ostéoglossomorphes, troisième partie. Évolution des structures ostéologiques et conclusions générales relatives à la phylogénèse et à la systématique du super-ordre. Addendum. Académie Royale de Belgique Mémoires de la Classe des Sciences 43:1–168.

—1981. Les actinopterygiens de l'Aptien Inférieur (Tock) d'Helgoland. Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 51:43–82.

—1982. Sur *Pattersonella formosa* (Traquair R.H. 1911) et *Nybelinoides brevis* (Traquair R.H. 1911), téléosténs salmoniformes argentinoides du Wealdien inférieur de Bernissart, Belgique, précédemment attribués au genre Leptolepis Agassiz L. 1832. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 54(3):1–27.

—1992. Révision de *Kermichthys daguini* (Arambourg, 1954) nov. gen., téléostéen salmoniforme du Crétacé de la Mésogée eurafricaine. Biologisch Jaarboek Dodonaea 60:76–95.

—1995. Description de l'appareil de weber du téléostéen crétacé marin *Clupavus maroccanus* et ses implications phylogénétiques. Belgian Journal of Zoology 125(2):267–282.

—1997a. Les Clupéomorphes (Pisces, Teleostei) du Cénomanien (Crétace) de Kipala (Kwango, Zaire): ostéologie et phylogénie. Belgian Journal of Zoology 127(1):75–97.

—1997b. Ostéologie et position systématique d'*Audenaerdia* casieri, téléostéen clupéomorphe (Pisces) du Santonien (Crétacé) de Vonso, Bas-Zaire. Annales du Musee Royal de l'Afrique Centrale, Serie 8, Sciences Zoologiques (Tervuren, Belgium) 1997:203–213.

—1998. Les ostéoglossomorphes marins de l'Éocène du Monte Bolca (Italie): *Monopterus* Volta 1796, *Thrissopterus* Heckel, 1856 et *Foreyichthys* Taverne, 1979. Considérations sur la phylogénie de téléostéens ostéoglossomorphes. Studi e Ricerche sui Giacimenti Terziari di Bolca 7:67–158.

—2002. Les poissons crétacés de Nardò. 18°. *Nardoclupea granderi* gen. et sp. nov. et (Teleostei, Clupeiformes, Dussumieriinae). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 26:3–23.

—2004. Les poissons crétacés de Nardò. 18°. *Pugliaclupea nolardi* gen. et sp. nov. et (Teleostei, Clupeiformes, Clupeidae). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 28:17–28.

—2007a. Les poissons crétacés de Nardò. 25°. *Italoclupea nolfi* gen. et sp. nov. (Teleostei, Clupeidae). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 31:21–35.

—2007b. Les poissons crétacés de Nardò. 26°. Un second Dussumieriinae: *Portoselvaggioclupea whiteheadi* gen. et sp. nov. et complément a l'étude de *Pugliaclupea nolardi* (Teleostei, Clupeidae). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 31:37–42.

—2011a. Les poissons crétacés de Nardò. 33°. *Lecceclupea ehiravaensis* gen. et sp. nov. (Teleostei, Clupeidae). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 35:3–17.

—2011b. Ostéologie et relations de *Catervariolus* (Teleostei, "Pholidophoriformes") du Jurassique moyen de Kisangani (Formation de Stanleyville) en République Démocratique du Congo. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 81:175–212.

—2013. Osteology and relationships of *Songaichthys luctacki* gen. and sp. nov. (Teleostei, Ankylophoriformes ord. nov.) from the Middle Jurassic (Songa Limestones) of Kisangani (Democratic Republic of Congo). Geo-Eco-Trop 37:33–52.

Taverne, L., and A. Filleul. 2003. Osteology and relationships of the genus *Spaniodon* (Teleostei, Salmoniformes) from the Santonian (Upper Cretaceous) of Lebanon. Palaeontology 46(5):927–944.

Tchernavin, V. V. 1947. Further notes on the structure of the bony fishes of the order Lyomeri (*Eurypharynx*). Zoological Journal of the Linnean Society 41(280):377–393.

Tedesco, P. A., E. Paradis, C. Lévêque, and B. Hugueny. 2017. Explaining global-scale diversification patterns in actinopterygian fishes. Journal of Biogeography 44(4):773–783.

Teletchea, F., V. Laudet, and C. Hänni. 2006. Phylogeny of the Gadidae (*sensu* Svetovidov, 1948) based on their morphology and two mitochondrial genes. Molecular Phylogenetics and Evolution 38(1):189–199.

Temminck, C. J., and H. Schlegel. 1846. Pisces. In: P. F. von Siebold, ed. Fauna Japonica, sive, Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis, superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 [Parts 10–14]. Lugduni Batavorum [Leiden]: Apud Auctorem. pp. 173–269.

—1850. Pisces. In: P. F. von Siebold, ed. Fauna Japonica, sive, Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis, superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 [Part 15]. Lugduni Batavorum [Leiden]: Apud Auctorem. pp. 270–324.

Teugels, G. 2003. State of the art of recent siluriform systematics. In: G. Arratia, B. G. Kapoor, M. Chardon, and R. Diogo, eds. Catfishes, Volume 1. Enfield, NH: Science Publishers. pp. 317–352.

Thacker, C. E. 2003. Molecular phylogeny of the gobioid fishes (Teleostei: Perciformes: Gobioidei). Molecular Phylogenetics and Evolution 26(3):354–368.

—2009. Phylogeny of Gobioidei and placement within Acanthomorpha, with a new classification and investigation of diversification and character evolution. Copeia 2009(1):93–104.

—2013. Phylogenetic placement of the European sand gobies in Gobionellidae and characterization of gobionellid lineages (Gobiiformes: Gobioidei). Zootaxa 3619(1):369–382. https://doi.org/10.11646/zootaxa.3619.3.6

—2014. Species and shape diversification are inversely correlated among gobies and cardinalfishes (Teleostei: Gobiiformes). Organisms Diversity and Evolution 14(4):419–436.

—2015. Biogeography of goby lineages (Gobiiformes: Gobioidei): origin, invasions and extinction throughout the Cenozoic. Journal of Biogeography 42(9):1615–1625.

—2017. Patterns of divergence in fish species separated by the Isthmus of Panama. BMC Evolutionary Biology 17:111. https://doi.org/10.1186/s12862-017-0957-4

Thacker, C. E., and C. Gkenas. 2019. Morphometric convergence among European sand gobies in freshwater (Gobiiformes: Gobionellidae). Ecology and Evolution 9(14):8087–8103.

Thacker, C. E., C. Gkenas, A. Triantafyllidis, S. Malavasi, and I. Leonardos. 2019. Phylogeny, systematics and biogeography of the European sand gobies (Gobiiformes: Gobionellidae). Zoological Journal of the Linnean Society 185(1):212–225.

Thacker, C. E., and M. A. Hardman. 2005. Molecular phylogeny of basal gobioid fishes: Rhyacichthyidae, Odontobutidae, Xenisthmidae, Eleotridae (Teleostei: Perciformes: Gobioidei). Molecular Phylogenetics and Evolution 37(3):858–871.

Thacker, C. E., W. T. McCraney, R. C. Harrington, T. J. Near, J. J. Shelley, M. Adams, M. P. Hammer, and P. J. Unmack. 2023. Diversification of the sleepers (Gobiiformes: Gobioidei: Eleotridae) and evolution of the root gobioid families. Molecular Phylogenetics and Evolution 186:107841. https://doi.org/10.1016/j.ympev.2023.107841

Thacker, C. E., and D. M. Roje. 2009. Phylogeny of cardinalfishes (Teleostei: Gobiiformes: Apogonidae) and the evolution of visceral bioluminescence. Molecular Phylogenetics and Evolution 52(3):735–745.

—2011. Phylogeny of Gobiidae and identification of gobiid lineages. Systematics and Biodiversity 9(4):329–347.

Thacker, C. E., T. P. Satoh, E. Katayama, R. C. Harrington, R. I. Eytan, and T. J. Near. 2015. Molecular phylogeny of Percomorpha resolves *Trichonotus* as the sister lineage to Gobioidei (Teleostei: Gobiiformes) and confirms the polyphyly of Trachinoidei. Molecular Phylogenetics and Evolution 93:172–179.

Thacker, C. E., J. J. Shelley, W. T. McCraney, M. Adams, M. P. Hammer, and P. J. Unmack. 2022. Phylogeny, diversification, and biogeography of a hemiclonal hybrid system of native Australian freshwater fishes (Gobiiformes: Gobioidei: Eleotridae: Hypseleotris). BMC Ecology and Evolution 22:22. https://doi.org/10.1186/s12862-022-01981-3

Thacker, C. E., J. J. Shelley, W. T. McCraney, P. J. Unmack, and M. D. McGee. 2022. Delayed adaptive radiation among new zealand stream fishes: joint estimation of divergence time and trait evolution in a newly delineated island species flock. Systematic Biology 71(1):13–23.

Thieme, P., N. K. Schnell, K. Parkinson, and T. Moritz. 2022. Morphological characters in light of new molecular phylogenies: the caudal-fin skeleton of Ovalentaria. Royal Society Open Science 9(1):211605. https://doi.org/10.1098/rsos.211605

Thompson, A. W., M. B. Hawkins, E. Parey, D. J. Wcisel, T. Ota, K. Kawasaki, E. Funk, M. Losilla, O. E. Fitch, Q. Pan, et al. 2021. The bowfin genome illuminates the developmental evolution of ray-finned fishes. Nature Genetics 53:1373–1384.

Thompson, D. W. 1947. A Glossary of Greek Fishes. London: Oxford University Press. 302 pp.

Tibbetts, I. R. 1991. The trophic ecology, functional morphology and phylogeny of the Hemiramphidae (Beloniformes) [dissertation]. University of Queensland. 388 pp.

Tominaga, Y. 1968. Internal morphology, mutual relationships and systematic position of the fishes belonging to the family Pempheridae. Japanese Journal of Ichthyology 15(2):43–95.

Tornabene, L., Y. J. Chen, and F. Pezold. 2013. Gobies are deeply divided: phylogenetic evidence from nuclear

DNA (Teleostei: Gobioidei: Gobiidae). Systematics and Biodiversity 11(3):345–361.

Tornabene, L., R. Manning, D. R. Robertson, J. L. Van Tassell, and C. C. Baldwin. 2023. A new lineage of deep-reef gobies from the Caribbean, including two new species and one new genus (Teleostei: Gobiidae: Gobiosomatini). Zoological Journal of the Linnean Society 197(2):322–343.

Tornabene, L., J. L. Van Tassell, D. R. Robertson, and C. C. Baldwin. 2016. Repeated invasions into the twilight zone: evolutionary origins of a novel assemblage of fishes from deep Caribbean reefs. Molecular Ecology 25(15):3662–3682.

Travers, R. A. 1981. The interarcual cartilage; a review of its development, distribution and value as an indicator of phyletic relationships in euteleostean fishes. Journal of Natural History 15(5):853–871.

—1984. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part 2: Phylogenetic analysis. Bulletin of the British Museum (Natural History), Zoology 47(2):83–150.

Trewavas, E. 1932. A contribution to the classification of the fishes of the order Apodes, based on the osteology of some rare eels. Proceedings of the Zoological Society of London 102(3):639–659.

Triques, M. L. 1993. Filogenia dos gêneros de Gymnotiformes (Actinopterygii, Ostariophysi), com base em caracteres esqueléticos. Comunicações do Museu de Ciências de PUCRS, série Zoologia 6:85–130.

Troyer, E. M., R. Betancur-R, L. C. Hughes, M. Westneat, G. Carnevale, W. T. White, J. J. Pogonoski, J. C. Tyler, C. C. Baldwin, G. Ortí, et al. 2022. The impact of paleoclimatic changes on body size evolution in marine fishes. Proceedings of the National Academy of Sciences 119(29):e2122486119. https://doi.org/10.1073/pnas.2122486119

Tsuneki, K. 1992. A systematic survey of the occurrence of the hypothalamic saccus vasculosus in teleost fish. Acta Zoologica 73(1):67–77.

Turanov, S., Y. Kartavtsev, and V. Zemnukhov. 2012. Molecular phylogenetic study of several eelpout fishes (Perciformes, Zoarcoidei) from Far Eastern seas on the basis of the nucleotide sequences of the mitochondrial cytochrome oxidase 1 gene (*Co-1*). Russian Journal of Genetics 48(2):208–223.

Turanov, S. V., Y. P. Kartavtsev, Y. H. Lee, and D. Jeong. 2017. Molecular phylogenetic reconstruction and taxonomic investigation of eelpouts (Cottoidei: Zoarcales) based on *Co-1* and *Cyt-b* mitochondrial genes. Mitochondrial DNA Part A 28:547–557.

Tyler, J. C. 2005a. A new genus for the surgeon fish *Acanthurus gaudryi* De Zigno 1887 from the Eocene of Monte Bolca, Italy, a morphologically primitive basal taxon of Acanthuridae (Acanthuroidea, Perciformes). Studi e Ricerche sui Giacimenti Terziari di Bolca 11:149–163.

—2005b. Redescription and basal phylogenetic placement of the acanthurid surgeon fish *Gazolaichthys vestenanovae* from the Eocene of Monte Bolca, Italy (Perciformes; Acanthuroidea). Studi e Ricerche sui Giacimenti Terziari di Bolca 11:97–117.

Tyler, J. C., and A. F. Bannikov. 1992. A Remarkable New Genus of Tetraodontiform Fish with Features of both Balistids and Ostraciids from the Eocene of Turkmenistan. Washington, DC: Smithsonian Institution Press. 14 pp. (Smithsonian Contributions to Paleobiology 72.)

—1997. Relationships of the Fossil and Recent Genera of Rabbitfishes (Acanthuroidei: Siganidae). Washington, DC: Smithsonian Institution Press. 35 pp. (Smithsonian Contributions to Paleobiology 84.)

—2005. *Massalongius*, gen. and fam. nov., a new clade of acanthuroid fishes (Perciformes, Acanthuridae) from the Eocene of Monte Bolca, Italy, related to Zanclidae. Studi e Ricerche sui Giaciamenti Terziari di Bolca 11:75–95.

Tyler, J. C., P. Bronzi, and A. Ghiandoni. 2000. The Cretaceous fishes of Nardò. 11°. A new genus and species of Zeiformes, *Cretazeus rinaldii*, the earliest record for the order. Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 24:11–28.

Tyler, J. C., G. D. Johnson, I. Nakamura, and B. B. Collette. 1989. Morphology of *Luvarus imperialis* (Luvaridae), with a Phylogenetic Analysis of the Acanthuroidei (Pisces). Washington, DC: Smithsonian Institution Press. 78 pp. (Smithsonian Contributions to Zoology 485.)

Tyler, J. C., and M. Križnar. 2013. A new genus and species, *Slovenitriacanthus saksidai*, from southwestern Slovenia, of the Upper Cretaceous basal tetraodontiform fish family Cretatriacanthidae (Plectocretacicoidea). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 37:45–56.

Tyler, J. C., M. Mirzaie, and A. Nazemi. 2006. New genus and species of basal tetraodontoid puffer fish from the Oligocene of Iran, related to the Zignoichthydae (Tetraodontiformes). Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria 30:49–58.

Tyler, J. C., B. O'Toole, and R. Winterbottom. 2003. Phylogeny of the Genera and Families of Zeiform Fishes, with Comments on Their Relationships with Retraodontiforms and Caproids. Washington, DC: Smithsonian Institution Press. 110 pp. (Smithsonian Contributions to Zoology 618.)

Tyler, J. C., and F. Santini. 2002. Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. Studi e Ricerche sui Giancimenti Terziari di Bolca 9:47–119.

—2005. A phylogeny of the fossil and extant zeiform-like fishes, Upper Cretaceous to Recent, with comments on the putative zeomorph clade (Acanthomorpha). Zoologica Scripta 34(2):157–175.

Tyler, J. C., and C. Sorbini. 1999. Phylogeny of the fossil and recent genera of fishes of the family Scatophagidae (Squamipinnes). Bollettino del Museo Civico di Storia Naturale di Verona 23:353–393.

Tyler, J. C., and L. Sorbini. 1996. New Superfamily and Three New Families of Tetraodontiform Fishes from the Upper Cretaceous: The Earliest and Most Morphologically Primitive Plectognaths. Washington, DC: Smithsonian Institution Press. 59 pp. (Smithsonian Contributions to Paleobiology 82.)

Underkoffler, K. E., M. A. Luers, J. R. Hyde, and M. T. Craig. 2018. A taxonomic review of *Lampris guttatus* (Brünnich 1788) (Lampridiformes; Lampridae) with descriptions of three new species. Zootaxa 4413(3):551–565. https://doi.org/10.11646/zootaxa.4413.3.9

Uribe, M. C., H. J. Grier, and V. Mejía-Roa. 2014. Comparative testicular structure and spermatogenesis in bony fishes. Spermatogenesis 4(3):e983400. https://doi.org/10.4161/21565562.2014.983400

Vaillant, L. 1902. Résultats zoologiques de l'expédition scientifique Néerlandaise au Bornéo central. Poissons. Notes from the Leyden Museum 24(1–3):1–166.

Van der Laan, R., W. N. Eschmeyer, and R. Fricke. 2014. Family-group names of Recent fishes. Zootaxa 3882(1):1–230. https://doi.org/10.11646/zootaxa.3882.1.1

Van der Laan, R., R. Fricke, and W. N. Eschmeyer, eds. 2023. Eschmeyer's Catalog of Fishes: Classification [online database]. Accessed 3 November 2023. http://www.calacademy.org/scientists/catalog-of-fishes-classification/

Vari, R. P. 1979. Anatomy, relationships, and classification of the families Citharinidae and Distichodontidae (Pisces, Characoidea). Bulletin of the British Museum (Natural History), Zoology 36(5):261–344.

—1983. Phylogenetic Relationships of the Families Curimatidae, Prochilodontidae, Anostomidae, and Chilodontidae (Pisces: Characiformes). Washington, DC: Smithsonian Institution Press. 60 pp. (Smithsonian Contributions to Zoology 378.)

—1995. The Neotropical Fish Family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial Phylogenetic Relationships, with a Revisionary Study. Washington, DC: Smithsonian Institution Press. 97 pp. (Smithsonian Contributions to Zoology 564.)

Vaz, D. F. B. 2020. Morphology and systematics of Batrachoidiformes (Percomorphacea: Teleostei) [dissertation]. College of William and Mary. pp. 456.

Vaz, D. F. B., and E. J. Hilton. 2020. The caudal skeleton of Batrachoidiformes (Teleostei: Percomorphacea): a study of morphological diversity, intraspecific variation, and phylogenetic inferences. Zoological Journal of the Linnean Society 189(1):228–286.

—2023. Skeletal ontogeny of the Plainfin Midshipman, *Porichthys notatus* (Percomorphacea: Batrachoidiformes). Journal of Anatomy 242(3):447–494.

Vecchioni, L., F. Marrone, E. Belaiba, F. Tiralongo, L. Bahri-Sfar, and M. Arculeo. 2019. The DNA barcoding of Mediterranean combtooth blennies suggests the paraphyly of some taxa (Perciformes, Blenniidae). Journal of Fish Biology 94(2):339–344.

Velez, J. A., W. Watson, E. M. Sandknop, W. Arntz, and M. Wolff. 2003. Larval and osteological development of the mote sculpin (*Normanichthys crockeri*) (Pisces: Normanichthyidae) from the Independencia Bight, Pisco, Peru. Journal of Plankton Research 25(3):279–290.

Vernygora, O. 2020. Systematics of Clupeomorpha (Osteichthyes: Teleostei) with methodological considerations for morphological phylogenetics [dissertation]. University of Alberta. 388 pp.

Vernygora, O., A. M. Murray, and M. V. H. Wilson. 2016. A primitive clupeomorph from the Albian Loon River Formation (Northwest Territories, Canada). Canadian Journal of Earth Sciences 53(4):331–342.

Veysey, A. J., P. M. Brito, and D. M. Martill. 2020. A new crossognathiform fish (Actinopterygii, Teleostei) from the Upper Cretaceous (Turonian) of southern Morocco with hypertrophied fins. Cretaceous Research 114:104207. https://doi.org/10.1016/j.cretres.2019.104207

Vialle, R. A., J. E. S. de Souza, K. de Paiva Lopes, D. G. Teixeira, P. de Azevedo Alves Sobrinho, A. M. Ribeiro-dos-Santos, C. Furtado, T. Sakamoto, F. A. Oliveira Silva, E. Herculano Corrêa de Oliveira, et al. 2018. Whole genome sequencing of the Pirarucu (*Arapaima gigas*) supports independent emergence of major teleost clades. Genome Biology and Evolution 10(9):2366–2379.

Vincent, M., and J. T. Thomas. 2011. *Kryptoglanis shajii*, an enigmatic subterranean-spring catfish (Siluriformes, *incertae sedis*) from Kerala, India. Ichthyological Research 58:161–165.

Vinnikov, K. A., R. C. Thomson, and T. A. Munroe. 2018. Revised classification of the righteye flounders (Teleostei: Pleuronectidae) based on multilocus phylogeny with complete taxon sampling. Molecular Phylogenetics and Evolution 125:147–162.

Voigt, E. 1926. Über ein bemerkenswertes Vorkommen neuer Fischotolithen in einem Senongeschiebe von Cöthen in Anhalt. Zeitschrift für Geschiebeforschung 2:172–187.

Volta, G. S. 1796. Ittiolitologia Veronese del Museo Bozziano: Ora Annesso a Quello del Conte Giovambattista Gazola e di altri Gabinetti di Fossili Veronesi. Verona: Dalla Stamperia Giuliari. 323 pp.

von der Heyden, S., and C. A. Matthee. 2008. Towards resolving familial relationships within the Gadiformes, and the resurrection of the Lyconidae. Molecular Phylogenetics and Evolution 48(2):764–769.

Voskoboinikova, O. S. 2004. Ontogenetic bases of the origin and relationships of the fishes from the suborder Notothenioidei (Perciformes). Journal of Ichthyology 44(6):418–432.

Wainwright, P. C., W. L. Smith, S. A. Price, K. L. Tang, J. S. Sparks, L. A. Ferry, K. L. Kuhn, R. I. Eytan, and T. J. Near. 2012. The evolution of pharyngognathy: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. Systematic Biology 61(6):1001–1027.

Walbaum, J. J. 1792. Petri Artedi Sueci Genera Piscium: In Quibus Systema Totum Ichthyologiae Proponitur Cum Classibus, Ordinibus, Generum Characteribus, Specierum Differentiis, Observationibus Plurimis. Redactis Speciebus 242 Ad Genera 52. Ichthyologiae Pars III. Grypeswaldiae [Greifswald]: Ant. Ferdin, Rose. 723 pp.

Walters, V. 1957. *Protolophotus*, a new genus of allotriognath fish from the Oligocene of Iran. Copeia 1957(1):60–61.

Walters, V., and J. E. Fitch. 1960. The families and genera of the lampridiform (Allotriognath) suborder Trachipteroidei. California Fish and Game 46(4):441–451.

Wang, C.-H., C.-H. Kuo, H.-K. Mok, and S.-C. Lee. 2003. Molecular phylogeny of elopomorph fishes inferred from mitochondrial 12S ribosomal RNA sequences. Zoologica Scripta 32(3):231–241.

Wang, J., B. Lu, R. Zan, J. Chai, W. Ma, W. Jin, R. Duan, J. Luo, R. W. Murphy, et al. 2016. Phylogenetic relationships of five Asian schilbid genera including *Clupisoma* (Siluriformes: Schilbeidae). PLOS ONE 11(1):e0145675. https://doi.org/10.1371/journal.pone.0145675

Wang, J.-F., H.-Y. Yu, S.-B. Ma, Q. Lin, D.-Z. Wang, and X. Wang. 2023. Phylogenetic and evolutionary comparison of mitogenomes reveal adaptive radiation of lampriform fishes. International Journal of Molecular Sciences 24(10):8756. https://doi.org/10.3390/ijms24108756

Wang, Q., L. Purrafee Dizaj, J. Huang, K. Kumar Sarker, C. Kevrekidis, B. Reichenbacher, H. Reza Esmaeili, N. Straube, T. Moritz, and C. Li. 2022. Molecular phylogenetics of the Clupeiformes based on exon-capture data and a new classification of the order. Molecular Phylogenetics and Evolution 175:107590. https://doi.org/10.1016/j.ympev.2022.107590

Wang, Q., C. Xu, C. Xu, and R. J. Wang. 2015. Complete mitochondrial genome of the southern catfish (*Silurus meridionalis* Chen) and Chinese catfish (*S. asotus* Linnaeus): structure, phylogeny, and intraspecific variation. Genetics and Molecular Research 14(4):18198–18209.

Wang, X. Z., X. N. Gan, J. B. Li, R. L. Mayden, and S. He. 2012. Cyprinid phylogeny based on Bayesian and maximum likelihood analyses of partitioned data: implications for Cyprinidae systematics. Science China Life Sciences 55:761–773.

Wang, X., J. Li, and S. He. 2007. Molecular evidence for the monophyly of East Asian groups of Cyprinidae (Teleostei: Cypriniformes) derived from the nuclear recombination activating gene 2 sequences. Molecular Phylogenetics and Evolution 42(1):157–170.

Washington, B. B., W. M. Eschmeyer, and K. M. Howe. 1984. Sorpaeniformes: relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 438–447. (Special Publication 1.)

Waters, J. M., T. Saruwatari, T. Kobayashi, I. Oohara, R. M. McDowall, and G. P. Wallis. 2002. Phylogenetic placement of retropinnid fishes: data set incongruence can be reduced by using asymmetric character state transformation costs. Systematic Biology 51(3):432–449.

Watson, W., A. C. Matarese, and E. G. Stevens. 1984. Trachinoidei: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 554–561. (Special Publication 1.)

Wcisel, D. J., J. T. Howard, J. A. Yoder, and A. Dornburg. 2020. Transcriptome Ortholog Alignment Sequence Tools (TOAST) for phylogenomic dataset assembly. BMC Evolutionary Biology 20:41. https://doi.org/10.1186/s12862-020-01603-w

Webb, S. A., J. A. Graves, C. Macias-Garcia, A. E. Magurran, D. O. Foighil, and M. G. Ritchie. 2004. Molecular phylogeny of the livebearing Goodeidae (Cyprinodontiformes). Molecular Phylogenetics and Evolution 30(3):527–544.

Weber, M. 1895. Fische von Ambon, Java, Thursday Island, dem Burnett-Fluss und von der Süd-Küste von Neu-Guinea. In: R. W. Semon, ed. Zoologische Forschungsreisen in Australien und dem Malayischen Archipel. Mit Unterstützung des Herrn Dr. Paul von Ritter ausgeführt in den Jahren 1891–1893, von Richard Semon, Volume 8. Jena: G. Fischer. pp. 257–276.

Weitzman, S. H. 1967. The origin of the stomiatoid fishes, with comments on the classification of salmoniform fishes. Copeia 1967(3):507–540.

—1974. Osteology and evolutionary relationships of the Sternoptychidae with a new classification of stomiatoid families. Bulletin of the American Museum of Natural History 153:327–478.

Wenz, S. 1999. *Pliodetes nigeriensis*, gen. nov. et. sp. nov., a new semionotid fish from the Lower Cretaceous of Gadoufaoua (Niger Republic): phylogenetic comments. In: G. Arratia and H.-P. Schultze, eds. Mesozoic Fishes 2: Systematics and Fossil Record –. Munich: Verlag Dr. Friedrich Pfeil. pp. 107–120.

Westneat, M. W., and M. E. Alfaro. 2005. Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Molecular Phylogenetics and Evolution 36(2):370–390.

Wettstein, A. 1886. Über die Fischfauna des tertiären Glarnerschiefers. Mémoires de la Société Paléontologique Suisse, Bâle 13:5–103.

White, B. N. 1985. Evolutionary Relationships of the Atherinopsinae (Pisces: Atherinidae). Los Angeles: Natural History Museum of Los Angeles County. 20 pp. (Contributions in Science 368.)

White, B. N., R. J. Lavenberg, and G. E. McGowen. 1984. Atheriniformes: development and relationships. In: H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, J. A.W. Kendall, and S. L. Richardson, eds. Ontogeny and Systematics of Fishes. Lawrence, KS: American Society of Ichthyologists and Herpetologists. pp. 355–362. (Special Publication 1.)

Whitehead, P. J. P. 1962. A contribution to the classification of Clupeoid fishes. Annals and Magazine of Natural History, Series 13, 5(60):737–750.

—1985. Clupeiod Fishes of the World (Suborder Clupeioidei). Part 1. Chirocentridae, Clupeidae and Pristigasteridae. Vol. 7 of FAO Species Catalogue. Rome: Food and Agriculture Organization of the United Nations. 303 pp. (FAO Fisheries Synopsis 125.)

Whitley, G. P. 1945. New sharks and fishes from Western Australia. Part 2. Australian Zoologist 11:1–42.

Wiley, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). Lawrence, KS: University of Kansas Museum of Natural History. 111 pp. (Miscellaneous Publications 64.)

—1979. Ventral gill arch muscles and the interrelationships of gnathostomes, with a new classification of the Vertebrata. Zoological Journal of the Linnean Society 67(2):149–179.

Wiley, E. O., and G. D. Johnson. 2010. A teleost classification based on monophyletic groups. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and

Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 123–182.

Wiley, E. O., G. D. Johnson, and W. W. Dimmick. 1998. The phylogenetic relationships of lampridiform fishes (Teleostei: Acanthomorpha), based on a total-evidence analysis of morphological and molecular data. Molecular Phylogenetics and Evolution 10(3):417–425.

—2000. The interrelationships of acanthomorph fishes: a total evidence approach using molecular and morphological data. Biochemical Systematics and Ecology 28(4):319–350.

Wiley, E. O., and H.-P. Schultze. 1984. Family Lepisosteidae (gars) as living fossils. In: N. Eldredge and S. M. Stanley, eds. Living Fossils. New York: Springer. pp. 160–165.

Williams, J. T. 1990. Phylogenetic Relationships and Revision of the Blenniid Fish Genus *Scartichthys*. Washington, DC: Smithsonian Institution Press. 30 pp. (Smithsonian Contributions to Zoology 492.)

Williams, R. R. G. 1987. The phylogenetic relationships of the salmoniform fishes based on the suspensorium and its muscles [dissertation]. University of Alberta. 752 pp.

Williford, D., N. S. Beeken, J. Anderson, P. Hajovsky, and R. Weixelman. 2022. Phylogenetic origins and age-based proportions of Malacho (*Elops smithi*) relative to Ladyfish (*Elops saurus*): species on the move in the western Gulf of Mexico. Gulf and Caribbean Research 33(1):46–59.

Wilson, A. B., and J. W. Orr. 2011. The evolutionary origins of Syngnathidae: pipefishes and seahorses. Journal of Fish Biology 78(6):1603–1623.

Wilson, C. D., C. F. Mansky, and J. S. Anderson. 2021. A platysomid occurrence from the Tournaisian of Nova Scotia. Scientific Reports 11:8375. https://doi.org/10.1038/s41598-021-87027-y

Wilson, M. V. H. 1977. Middle Eocene Freshwater Fishes from British Columbia. Toronto: Royal Ontario Museum. 61 pp. (Life Sciences Contributions 113.)

—1980. Oldest known *Esox* (Pisces: Esocidae) part of a new Paleocene teleost fauna from western Canada. Canadian Journal of Earth Sciences 17(3):307–312.

Wilson, M. V. H., D. B. Brinkman, and A. G. Neuman. 1992. Cretaceous Esocoidei (Teleostei): early radiation of the pikes in North American fresh waters. Journal of Paleontology 66(5):839–846.

Wilson, M. V. H., and A. M. Murray. 1996. Early Cenomanian acanthomorph teleost in the Cretaceous Fish Scale Zone, Albian/Cenomanian boundary, Alberta, Canada. In: G. Arratia and G. Viohl, eds. Mesozoic Fishes: Systematics and Paleoecology. Munich: Verlag Dr. Friedrich Pfeil. pp. 369–382.

—2008. Osteoglossomorpha: phylogeny, biogeography, and fossil record and the significance of key African and Chinese fossil taxa. In: L. Calvin, A. Longbottom, and M. Richter, eds. Fishes and the Break-Up of Pangaea. London: Geological Society of London. pp. 185–219. (Special Publications 295.)

Wilson, M. V. H., and P. Veilleux. 1982. Comparative osteology and relationships of the Umbridae (Pisces: Salmoniformes). Zoological Journal of the Linnean Society 76(4):321–352.

Wilson, M. V. H., and R. R. G. Williams. 1991. New Paleocene genus and species of smelt (Teleostei: Osmeridae) from freshwater deposits of the Paskapoo Formation, Alberta, Canada, and comments on osmerid phylogeny. Journal of Vertebrate Paleontology 11(4):434–451.

—2010. Salmoniform fishes: key fossils, supertree, and possible morphological synapomorphies. In: J. S. Nelson, H.-P. Schultze, and M. V. H. Wilson, eds. Origin and Phylogenetic Interrelationships of Teleosts. Munich: Verlag Dr. Friedrich Pfeil. pp. 379–409.

Winterbottom, R. 1974. The Familial Phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as Evidenced by Their Comparative Myology. Washington, DC: Smithsonian Institution Press. 201 pp. (Smithsonian Contributions to Zoology 155.)

—1993a. Myological evidence for the phylogeny of recent genera of surgeonfishes (Percomorpha, Acanthuridae), with comments on the Acanthuroidei. Copeia 1993(1):21–39.

—1993b. Search for the gobioid sister group (Actinopterygii: Percomorpha). Bulletin of Marine Science 52:395–414.

Winterbottom, R., and D. A. McLennan. 1993. Cladogram versatility: evolution and biogeography of acanthuroid fishes. Evolution 47(5):1557–1571.

Wirtz, P. 1993. Does the larva of *Pholidichthys leucotaenia* give a clue to the systematic position of the monotypic fish family Pholidichthyidae? In: J. H. Schröder, J. Bauer, and M. Schartl, eds. Trends in Ichthyology: An International Perspective. Oxford: Blackwell Scientific. pp. 237–238.

Woese, C. R., and G. E. Fox. 1977. Phylogenetic structure of prokaryotic domain: the primary kingdoms. Proceedings of the National Academy of Sciences of the United States of America 74:5088–5090.

Woodburne, M. O. 2004. Global events and the North American mammalian biochronology. In: M. O. Woodburne, ed. Late Cretaceous and Cenozoic Mammals of North America. New York: Columbia University Press. pp. 315–343.

Woods, L. P., and P. M. Sonoda. 1973. Order Berycomorphi (Beryciformes). In: D. M. Cohen, J. W. Atz, R. H. Gibbs, F. H. Berry, E. A. Lachner, J. E. Böhlke, G. W. Mead, and D. Merriman, eds. Orders Heteromi (Notacanthiformes), Berycomorphi (Beryciformes), Xenoberyces (Stephanoberyciformes), and Anacanthini (Gadiformes): Halosuriforms, Killfishes, Squirrelfishes and other Beryciforms, Stephanoberyciforms, Grenadiers. New Haven, CT: Sears Foundation for Marine Research, Yale University. pp. 263–396. (Memoir 1, Fishes of the Western North Atlantic 6.)

Woodward, A. S. 1891. Catalogue of the Fossil Fishes in the British Museum (Natural History), Volume 2. London: British Museum (Natural History). 567 pp.

—1901. Catalogue of the Fossil Fishes in the British Museum (Natural History), Volume 4. London: British Museum (Natural History). 639 pp.

Wu, F., D. He, G. Fang, and T. Deng. 2019. Into Africa via docked India: a fossil climbing perch from the Oligocene of Tibet helps solve the anabantid biogeographical puzzle. Science Bulletin 64(7):455–463.

Wu, F., D. Miao, M.-M. Chang, G. Shi, and N. Wang. 2017. Fossil climbing perch and associated plant megafossils indicate a warm and wet central Tibet during the late Oligocene. Scientific Reports 7:878. https://doi.org/10.1038/s41598-017-00928-9

Wu, X.-W., Y.-Y. Chen, X.-L. Chen, and J.-X. Chen. 1981. A taxonomical system and phylogenetic relationship of the families of the suborder Cyprinoidei (Pisces). Scientia Sinica 24(4):563–572.

Xu, G.-H. 2021. A new stem-neopterygian fish from the Middle Triassic (Anisian) of Yunnan, China, with a reassessment of the relationships of early neopterygian clades. Zoological Journal of the Linnean Society 191(2):375–394.

Xu, G.-H., and M.-M. Chang. 2009. Redescription of †*Paralycoptera wui* Chang and Chou, 1977 (Teleostei: Osteoglossoidei) from the Early Cretaceous of eastern China. Zoological Journal of the Linnean Society 157(1):83–106.

Xu, G.-H., and K.-Q. Gao. 2011. A new scanilepiform from the Lower Triassic of northern Gansu Province, China, and phylogenetic relationships of non-teleostean Actinopterygii. Zoological Journal of the Linnean Society 161(3):595–612.

Xu, G.-H., K.-Q. Gao, and J. A. Finarelli. 2014. A revision of the middle Triassic scanilepiform fish *Fukangichthys longidorsalis* from Xinjiang, China, with comments on the phylogeny of the Actinopteri. Journal of Vertebrate Paleontology 34(4):747–759.

Xu, G.-H., and X.-Y. Ma. 2016. A Middle Triassic stem-neopterygian fish from China sheds new light on the peltopleuriform phylogeny and internal fertilization. Science Bulletin 61(22):1766–1774.

Xu, G.-H., X.-Y. Ma, and Y. Ren. 2018. *Fuyuanichthys wangi* gen. et sp. nov. from the Middle Triassic (Ladinian) of China highlights the early diversification of ginglymodian fishes. PeerJ 6:e6054. https://doi.org/10.7717/peerj.6054

Xu, G.-H., X.-Y. Ma, F.-X. Wu, and Y. Ren. 2019. A Middle Triassic kyphosichthyiform from Yunnan, China, and phylogenetic reassessment of early ginglymodians. Vertebrata PalAsiatica 57(3):181–204.

Xu, G.-H., and C.-C. Shen. 2015. *Panxianichthys imparilis* gen. et sp. nov., a new ionoscopiform (Halecomorphi) from the Middle Triassic of Guizhou, China. Vertebrata Palasiatica 53(1):1–15.

Xu, G.-H., and F.-X. Wu. 2012. A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. Chinese Science Bulletin 57:111–118.

Xu, G.-H., and L.-J. Zhao. 2016. A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics. Science Bulletin 61(4):338–344.

Xu, G.-H., L.-J. Zhao, and M. I. Coates. 2014. The oldest ionoscopiform from China sheds new light on the early evolution of halecomorph fishes. Biology Letters 10:20140204. https://doi.org/10.1098/rsbl.2014.0204

Xu, G.-H., L.-J. Zhao, K.-Q. Gao, and F.-X. Wu. 2012. A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates. Proceedings of the Royal Society B,Biological Sciences 280(1750):20122261.

Yabe, M. 1985. Comparative osteology and myology of the superfamily Cottoidea (Pisces: Scorpaeniformes), and its phylogenetic classification. Memoirs of the Faculty of Fisheries, Hokkaido University 32:1–130.

Yabe, M., and T. Uyeno. 1996. Anatomical description of *Normanichthys crockeri* (Scorpaeniformes, *incertae sedis*: family Normanichthyidae). Bulletin of Marine Science 58:494–510.

Yagishita, N., T. Kobayashi, and T. Nakabo. 2002. Review of monophyly of the Kyphosidae (*sensu* Nelson, 1994), inferred from the mitochondrial ND2 gene. Ichthyological Research 49:103–108.

Yagishita, N., M. Miya, Y. Yamanoue, S. M. Shirai, K. Nakayama, N. Suzuki, T. P. Satoh, K. Mabuchi, M. Nishida, and T. Nakabo. 2009. Mitogenomic evaluation of the unique facial nerve pattern as a phylogenetic marker within the perciform fishes (Teleostei: Percomorpha). Molecular Phylogenetics and Evolution 53(1):258–266.

Yamada, T., T. Sugiyama, N. Tamaki, A. Kawakita, and M. Kato. 2009. Adaptive radiation of gobies in the interstitial habitats of gravel beaches accompanied by body elongation and excessive vertebral segmentation. BMC Evolutionary Biology 9:145. https://doi.org/10.1186/1471-2148-9-145

Yamaguchi, M. 2000. Phylogenetic analyses of myctophid fishes using morphological characters: progress, problems, and future perspectives. Japanese Journal of Ichthyology 47(2):87–107.

Yamanoue, Y., M. Miya, K. Matsuura, N. Yagishita, K. Mabuchi, H. Sakai, M. Katoh, and M. Nishida. 2007. Phylogenetic position of tetraodontiform fishes within the higher teleosts: Bayesian inferences based on 44 whole mitochondrial genome sequences. Molecular Phylogenetics and Evolution 45(1):89–101.

Yang, X., Y. Song, R. Zhang, M. Yu, X. Guo, H. Guo, X. Du, S. Sun, C. Li, X. Mao, G. Fan, and X. Liu. 2023. Unraveling the genomic features, phylogeny and genetic basis of tooth ontogenesis in Characiformes through analysis of four genomes. DNA Research 30(5):dsad022. https://doi.org/10.1093/dnares/dsad022

Yedİer, S., and D. Bostanci. 2022. Molecular and otolith shape analyses of *Scorpaena* spp. in the Turkish seas. Turkish Journal of Zoology 46(1):78–92.

Yokoyama, R., and A. Goto. 2005. Evolutionary history of freshwater sculpins, genus *Cottus* (Teleostei; Cottidae) and related taxa, as inferred from mitochondrial DNA phylogeny. Molecular Phylogenetics and Evolution 36(3):654–668.

Yuan, Z., G.-H. Xu, X. Dai, F. Wang, X. Liu, E. Jia, L. Miao, and H. Song. 2022. A new perleidid neopterygian fish from the Early Triassic (Dienerian, Induan) of South China, with a reassessment of the relationships of Perleidiformes. PeerJ 10:e13448. https://doi.org/10.7717/peerj.13448

Zanata, A. M., and R. P. Vari. 2005. The family Alestidae (Ostariophysi, Characiformes): a phylogenetic analysis of a trans-Atlantic clade. Zoological Journal of the Linnean Society 145(1):1–144.

Zaragüeta Bagils, R. 2004. Basal clupeomorphs and ellimmichthyiform phylogeny. In: G. Arratia and A. Tintori, eds. Mesozoic Fishes 3: Systematics, Paleoenvironments and Biodiversity. Munich: Verlag Dr. Friedrich Pfeil. pp. 391–404.

Zehren, S. J. 1979. The Comparative Osteology and Phylogeny of the Beryciformes. Chicago: University of Chicago. 389 pp. (Evolutionary Monographs 1.)

—1987. Osteology and evolutionary relationships of the boarfish genus *Antigonia* (Teleostei, Caproidae). Copeia 1987(3):564–592.

Zemnukhov, V. V. 2012. Genus *Leptostichaeus* and its position in the taxonomy of fishes (Perciformes: Zoarcoidei, Stichaeidae). Journal of Ichthyology 52:363–368.

Zhang, H., I. Jarić, D. L. Roberts, Y. He, H. Du, J. Wu, C. Wang, and Q. Wei. 2020. Extinction of one of the world's largest freshwater fishes: lessons for conserving the endangered Yangtze fauna. Science of the Total Environment 710:136242. https://doi.org/10.1016/j.scitotenv.2019.136242

Zhang, J.-Y. 1998. Morphology and phylogenetic relationships of †*Kuntulunia* (Teleostei: Osteoglossomorpha). Journal of Vertebrate Paleontology 18(2):280–300.

—2006. Phylogeny of Osteoglossomorpha. Vertebrata PalAsiatica 44(1):43–59.

Zhang, K., Y. Liu, J. Chen, H. Zhang, L. Gong, L. Jiang, L. Liu, Z. Lü, and B. Liu. 2021. Characterization of the complete mitochondrial genome of *Macrotocinclus affinis* (Siluriformes; Loricariidae) and phylogenetic studies of Siluriformes. Molecular Biology Reports 48:677–689.

Zhang, K., K. Zhu, Y. Liu, H. Zhang, L. Gong, L. Jiang, L. Liu, Z. Lü, and B. Liu. 2021. Novel gene rearrangement in the mitochondrial genome of *Muraenesox cinereus* and the phylogenetic relationship of Anguilliformes. Scientific Reports 11:2411. https://doi.org/10.1038/s41598-021-81622-9

Zhou, J.-J. 1990. The Cyprinidae fossil from middle Miocene of Shanwang Basin. Vertebrata PalAsiatica 28(2):95–127.

Zhuang, X., M. Qu, X. Zhang, and S. Ding. 2013. A comprehensive description and evolutionary analysis of 22 grouper (Perciformes, Epinephelidae) mitochondrial genomes with emphasis on two novel genome organizations. PLOS ONE 8(8):e73561. https://doi.org/10.1371/journal.pone.0073561

Zugmayer, E. 1914. Diagnoses de quelques poissons nouveaux provenant des campagnes du yacht *Hirondelle II* (1911–1913). Bulletin de l'Institut Océanographique de Monaco 288:1–4.