



# Phylogeny, biology, and evolution of acanthopterygian fish clades

Christine E. Thacker · Thomas J. Near

Received: 11 May 2024 / Accepted: 22 February 2025 / Published online: 13 March 2025  
© The Author(s) 2025

**Abstract** The advent of molecular phylogenetics has rapidly transformed the understanding of relationships within *Acanthopterygii*, the spiny-rayed fishes. *Acanthopterygii* includes most of the marine fish diversity as well as several lineages in freshwater and contains such iconic groups as tunas, cichlids, seahorses, flatfishes, anglerfishes, and most fishes found on coral reefs. The robust and well-resolved phylogeny resulting from more than two decades of molecular studies includes some highly novel placements as well as unprecedented resolution of the lineages within *Percomorpha*. In this review, we highlight the patterns of morphology, ecology, biology, and biogeography within and among the major clades

of *Acanthopterygii* using an evolutionary perspective that has been made possible by this emergent phylogenetic consensus. Our aim is to provide a comprehensive summary of each clade's characteristics, serving as a reorientation for those familiar with previous conceptions of acanthopterygian phylogeny and as an introduction for those new to the biology, evolution, and biogeography of the major acanthopterygian groups.

---

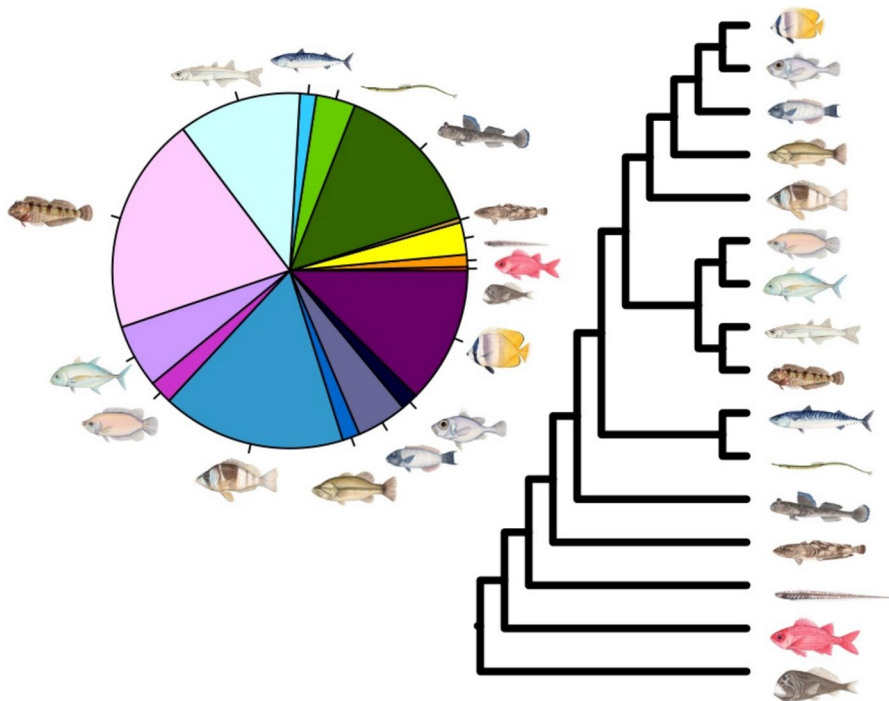
C. E. Thacker (✉)  
Vertebrate Zoology, Santa Barbara Museum of Natural  
History, Santa Barbara, CA 93105, USA  
e-mail: christine.e.thacker@gmail.com

C. E. Thacker  
Research and Collections, Department of Ichthyology,  
Natural History Museum of Los Angeles County,  
Los Angeles, CA 90007, USA

T. J. Near  
Department of Ecology and Evolutionary Biology,  
Osborn Memorial Labs, Yale University, New Haven,  
CT 06520-8106, USA  
e-mail: thomas.near@yale.edu

T. J. Near  
Yale Peabody Museum, Yale University, New Haven,  
CT 06520-8118, USA

## Graphical abstract



**Keywords** *Acanthopterygii* · *Actinopterygii* · Phylogeny · Diversity · Evolution · Fish

### Introduction

*Acanthopterygii*, the spiny-rayed fishes, contains 19,188 species classified in 313 taxonomic families (Fricke et al. 2023; Near and Thacker 2024) and includes most of the fish diversity in marine environments as well as a substantial fraction of species in fresh and brackish waters. Phylogenies based on analyses of morphological characters have provided insights into the evolutionary relationships of many acanthopterygian clades, but those efforts were unavoidably hampered by the incredible species diversity, the many instances of convergent phenotypic similarity, and the paucity of morphological characters informative at large phylogenetic scales (Lauder and Liem 1983; Johnson 1993; Johnson and Patterson 1993). In contrast, molecular data have provided an abundant source of phylogenetic characters applicable across the entire radiation, enabling resolution within

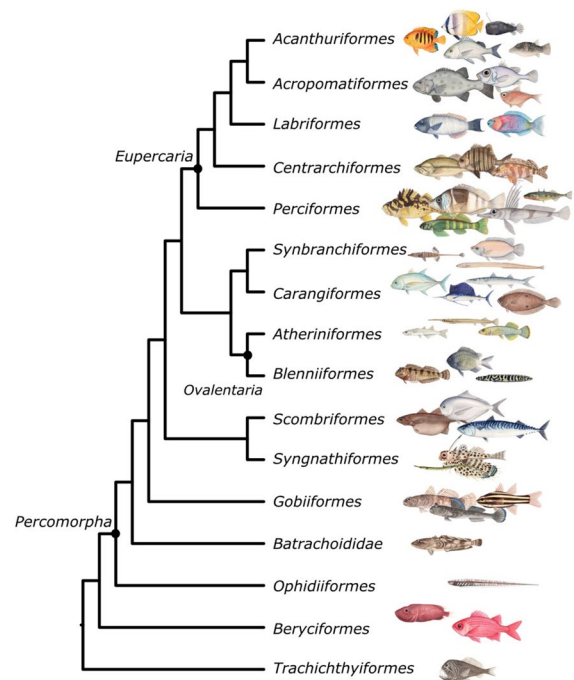
and among the large clades that form the backbone of acanthopterygian phylogeny. Comprehensive efforts based on a variety of DNA sequence markers (Near et al. 2012b, 2013; Betancur-R et al. 2013, 2017; Faircloth et al. 2013; Alfaro et al. 2018; Hughes et al. 2018; Rabosky et al. 2018; Dornburg and Near 2021; Ghezelayagh et al. 2022) have largely converged on the same 16 major clades, with some ambiguity as to the relationships among lineages within those clades. This concision among multiple studies has provided a consistent broader picture of higher-level fish relationships that is partially consistent with previous estimations based on morphology but also contains many novel groupings (Dornburg and Near 2021).

We recently published a monographic phylogenetic classification of ray-finned fishes (*Actinopterygii*) that reassessed the taxonomy of actinopterygians based on the relationships inferred primarily from molecular data (Near and Thacker 2024). In addition to providing a new taxonomy, our monograph discussed phylogenetic and taxonomic history of the major clades, listed species diversity, reviewed synonyms and known synapomorphic characters for each major

clade, and provided summary phylogenetic trees for all extant family-rank taxonomic groups along with more than 285 fossil taxa. However, our monograph did not delve into the biology and ecology of these clades. In this review we cover the 16 major clades of *Acanthopterygii*; for each we list all the family-rank taxa and their common names, display the relationships of their living lineages with summary phylogenetic trees, and review their morphology, ecology, biology, and biogeography. We provide information on salinity tolerance, depth, and habitat preference, available details on their reproductive biology, and discuss the distribution of notable characteristics including bioluminescence, venom, air-breathing, mutualisms, endothermy, sound production, viviparity, and parental care. Our accounts reveal the phenotypic, ecological, geographic, and phylogenetic patterns within clades and serve as a review as well as a starting point for research exploring the evolution and biogeography of acanthopterygian fishes in their evolutionary context.

Following the classification of Near and Thacker (2024), we italicize all clade names and denote redundant family names (those containing a single genus) with asterisks in the taxon lists. We italicize all taxonomic names to facilitate their identification in the text, in accordance with the principles of rank-free phylogenetic nomenclature and recent taxonomic practice (deQueroiz and Cantino 2020; Thines et al. 2020; Brownstein et al. 2024). Common names for families are from the classification of Fricke et al. (2023); in rare cases where a common name is not given, we suggest one. All the phylogenetic trees shown here are derived from the hypothesis of Ghezelayagh et al. (2022) and the consensus trees shown in Near and Thacker (2024); we modify the trees presented in Near and Thacker (2024) to show only the living lineages, excluding fossil taxa. Species diversity estimates are those in Near and Thacker (2024) and are derived from the information given in Fricke et al. (2023), however, species counts are continually changing as groups are revised and new species are described.

The relationships among the 16 major acanthopterygian clades are shown in Fig. 1. *Trachichthyiformes* and *Beryciformes* resolve as sequential sister taxa to *Percomorpha* although *Holocentridae* has sometimes been placed outside *Beryciformes* (with ambiguous support; Betancur-R et al. 2013, 2017). Within



**Fig. 1** Phylogenetic relationships among the major clades of *Acanthopterygii*

*Percomorpha* the first major clade to diverge is *Ophidiiformes*, then *Batrachoididae*, followed by *Gobiiformes* and the clade containing *Syngnathiformes* and *Scombriformes*, although the relative placements of *Gobiiformes* and the clade containing *Syngnathiformes* and *Scombriformes* vary among phylogenetic analyses (Near et al. 2013; Betancur-R et al. 2013, 2017; Alfaro et al. 2018; Hughes et al. 2018; Dornburg and Near 2021; Ghezelayagh et al. 2022). Two large clades comprise the remainder of *Percomorpha*, one containing *Atheriniformes*, *Blenniiformes*, *Synbranchiformes*, and *Carangiformes*, and *Eupercaria* that includes *Perciformes*, *Centrarchiformes*, *Labriformes*, *Acropomatiformes*, and *Acanthuriformes*. These clades are resolved with broad agreement across molecular phylogenetic studies, although relationships within some of the clades are less confidently resolved.

## *Acanthopterygii* (313 families and lineages, 19,188 species)

### *Trachichthyiformes* (5 families, 71 species)

*Anomalopidae* (flashlight fishes), *Anoplogasteridae*\* (fangtooths), *Diretmidae* (spinyfins), *Monocentridae* (pinecone fishes), *Trachichthyidae* (roughies).

*Trachichthyiformes* is a species-depauperate clade of robust, laterally compressed species with forked tails and often with small spines on the head and operculum; species of *Monocentridae* are covered with thick, ridged scales (Paxton 1999a, b, c). All *Trachichthyiformes* are marine, with a worldwide distribution from shallow nearshore habitats to the mesopelagic zone. Little is known about their reproduction, but it is likely they are broadcast spawners; spawning aggregations and pelagic eggs and larvae have been documented from a few species (Mace et al. 1990; Watson 1996a, b). Many species of *Anomalopidae*, *Monocentridae*, and *Trachichthyidae* possess cutaneous bioluminescent organs that host symbiotic bacteria, located under the eye in *Anomalopidae*, on the lower jaw in *Monocentridae*, and around the anus in *Trachichthyidae* (Davis et al. 2016a, b; Ghedotti et al. 2021). *Anomalopidae* and *Monocentridae* are associated with coral reefs, from shallow depths to 350 M and occur in schools (Paxton and Johnson 1999; Paxton 1999c). *Anoplogasteridae* and *Diretmidae* are meso- to bathypelagic (200–3000 M; Paxton 1999a, b), and *Trachichthyidae* span the range from 2 to 1500 M (Moore and Paxton 1999a). *Trachichthyidae* is the most species-rich lineage, with 51 species; all other families have nine or fewer species (Fricke et al. 2023; Near and Thacker 2024). The stem age of *Trachichthyiformes* is estimated as 137.42 Ma (95% credible interval 129.12–147.3 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Trachichthyiformes* are shown in Fig. 2.

### *Beryciformes* (9 families, 213 species)

*Berycoidei*: *Barbouriidae*\* (Red Velvet Whalefish), *Berycidae* (alfonsinos), *Cetomimidae* (flabby whalefishes), *Gibberichthyidae*\* (gibberfishes), *Hispidoberycidae*\* (Spinyscale Pricklefish), *Melamphaidae*



**Fig. 2** Phylogenetic relationships among the living lineages of *Acanthopterygii*, focusing on *Trachichthyiformes*, *Beryciformes*, *Ophidiiformes*, and *Gobiiformes* (representative *Apogonoidei* shown at left of tree; modified from Fig. 14 of Near and Thacker 2024)

(bigscale), *Rondeletiidae*\* (redmouth whalefishes), *Stephanoberycidae* (pricklefishes).

### *Holocentridae* (squirrelfishes).

Species of *Beryciformes* are all marine, and except for *Berycidae* and *Holocentridae*, they occupy meso- to bathypelagic depths. The deepwater species are generally ovoid, with single dorsal fins and forked tails (Hastings et al. 2014). Unlike the deep-dwelling beryciform lineages, *Holocentridae* and *Berycidae* are strong swimmers with large eyes and robust spines; they are nocturnal and range into shallower waters (25 to 1,300 M for *Berycidae* and 1 to 100 M in *Holocentridae*; Moore and Paxton 1999b). *Berycidae* and *Holocentridae* generally have red, yellow, or silvery coloration; red pigments appear black in deeper waters due to the differential filtration of longer wavelengths at depth. *Holocentridae* is the most species-rich lineage (90 species), followed by *Melamphaidae* (76 species) and *Cetomimidae* (27 species) (Fricke et al. 2023; Near and Thacker 2024).

The monophyly of *Beryciformes* is supported in some but not all molecular phylogenetic analyses of *Acanthopterygii* (Smith and Wheeler 2006; Alfaro et al. 2009; Santini et al. 2009; Near et al. 2012b, 2013; Davis et al. 2016a, b), and in particular, there are differing resolutions of *Holocentridae* (Betancur-R et al. 2013, 2017; Chen et al. 2014b; Dornburg et al. 2017; Hughes et al. 2018; Rabosky et al. 2018; Ghezelayagh et al. 2022). Species of *Holocentridae* are known from tropical reef and near-reef habitats in the Indo-Pacific and Atlantic and have been recorded in the Mediterranean as Lessepsian immigrants that transited the Suez Canal (Golani and Ben-Tuvia 1985; Farrag et al. 2018; Deef 2021). Phylogenetic reconstruction of biogeography that incorporates fossil taxa indicates that *Holocentridae* originated in the West Tethys reef biodiversity hotspot in the earliest Eocene, approximately 55 Ma, followed by multiple instances of divergence between the Western Atlantic and Eastern Pacific as well as the Indo-Pacific and Western Indian oceans as the West Tethys hotspot collapsed and the global center of reef fish diversity moved eastward to its present location in the Indo-Australian archipelago (Renema et al. 2008; Dornburg et al. 2014). Genetic connectivity among populations of cosmopolitan holocentrid species is generally high, with structure primarily evident only among ocean basins (Craig et al. 2007; Copus et al. 2022).

*Beryciformes* includes one of the most dramatic examples of sexual dimorphism and ontogenetic transformation known among fishes, in which the females, males, and larvae of some species of *Cetomimidae* exhibit morphologies so drastically different that they had previously been classified in different families. The connection between the forms was first suggested based on molecular data (Miya et al. 2003, 2005) and later confirmed based on the morphology of specimens of intermediate (transforming) larval stages (Johnson et al. 2009). Phylogenetic analysis calibrated with the earliest known holocentrid fossil places the origin of *Holocentridae* in the Paleocene (61.3 Ma), and the origin of *Beryciformes* in the Cretaceous (110.7 Ma) (Andrews et al. 2023). The stem age of *Beryciformes* is estimated as 132.91 Ma (95% credible interval 123.97–143.13 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships

among the living lineages of *Beryciformes* are shown in Fig. 2.

### ***Percomorpha* (299 families and lineages, 18,904 species)**

#### ***Ophidiiformes* (3 families, 569 species)**

***Bythitoidei:*** *Bythitidae* (viviparous brotulas), *Dinematichthyidae* (dwarf brotulas).

*Ophidiidae* (cusk-eels and pearlfishes).

*Ophidiiformes* contains three lineages of demersal, almost exclusively marine fishes with a worldwide distribution in tropical and temperate habitats. Species of *Bythitidae* and *Dinematichthyidae* are live-bearers with internal fertilization and intromittent organs present in males. This group also includes the pearlfishes in *Ophidiidae*, which lack the pelvic fins and girdle and are commensal with sea cucumbers, starfish, clams, and tunicates. They are generally slender, in most cases with the dorsal, caudal, and anal fins conjoined and the tail pointed, without a distinct caudal peduncle or fin (Hastings et al. 2014). Pelvic fins are often absent in species of *Ophidiidae* and some species have barbels on the chin. Scaled and scaleless species are found throughout *Ophidiiformes*. The livebearing lineages *Bythitidae* and *Dinematichthyidae* resolve as a clade that is the sister lineage of *Ophidiidae* (Betancur-R et al. 2013, 2017; Near et al. 2013; Møller et al. 2016). *Ophidiidae* contains 323 species; *Bythitidae* includes 129 species and *Dinematichthyidae* has 117 (Fricke et al. 2023; Near and Thacker 2024). An alternative taxonomy of *Ophidiiformes* includes the families *Carapidae* (37 species), *Brotulidae* (7 species), and *Acanthonidae* (3 species) (Wong and Chen 2024); however, we include these lineages in *Ophidiidae* (Near and Thacker 2024).

*Ophidiiformes* includes several species known from abyssal depths, including *Thermichthys hollii* (*Bythitidae*) found on hydrothermal vents in the Galapagos as well as *Abyssobrotula galatheae* and *Holomyxeronotus profundissimus* (*Ophidiidae*), known from depths of 3000–8000 m worldwide (Møller et al. 2016). Species of the cosmopolitan bathydemersal and abyssal ophidiid genus *Porogadus* are segregated by depth in tropical and subtropical oceans and include species pairs in the Atlantic and Eastern Pacific split by the Isthmus of Panama

(Schwarzahns and Møller 2021). *Bythitidae* also contains several paedomorphic lineages (*Aphyonus*, *Barathronus*, and their relatives) that are small, scaleless, blind, have reductions and simplifications throughout their skeletal, muscular, and sensory systems and inhabit deep waters. Taxonomic and revisionary work on this group is active, with many new species being described, particularly from museum collections (Schwarzahns et al. 2005; Schwarzahns and Møller 2007, 2011, 2021). The stem age of *Ophidiiformes* is estimated as 126.76 Ma (95% credible interval 116.96–135.68 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Ophidiiformes* are shown in Fig. 2.

### ***Batrachoididae* (toadfishes; 84 species)**

Species of *Batrachoididae* are distributed worldwide, mostly in nearshore marine environments but with a few freshwater species including one species of *Thalassophryne* in the Amazon River. Toadfishes are benthic, with flattened heads and tapering bodies, and they are generally found hidden on or buried in the substrate (Hastings et al. 2014). The distributions of toadfish genera are roughly equally split between the Eastern Pacific and Atlantic vs. the Indo-Pacific (Greenfield et al. 2008). Spines in the anterior dorsal fin and on the opercle are hollow and venomous in species of *Daector* (Eastern Pacific) and *Thalassophryne* (Western Atlantic) (Smith and Wheeler 2006). Pectoral fins are large, some bearing axillary pores and secretory glandular tissue. The function of this tissue is unknown, and analyses of secretions of the Western Atlantic *Opsanus beta* revealed no toxic or pheromonal function (Maina et al. 1998), although it has been suggested that the pectoral gland supplies venom to the opercular spines in *Porichthys* (Lopes-Ferreira et al. 2014).

Toadfishes have a unique mechanism of sound production in which contractions of swim bladder muscles are used to create grunts, whistles, and croaks that are used both as mating calls and warnings (Rice and Bass 2009). They are also among the few shallow-water bioluminescent species known, with cutaneous photophores arranged in several ventral rows in *Porichthys*. Species of *Porichthys* are facultatively bioluminescent; those in the northern extent of their range lack adequate luciferin sources in their diet and

so do not luminesce like their southern conspecifics (toadfish luminescence is endogenous and does not involve hosting symbiotic luminescent bacteria). The light organs are under voluntary control by the toadfish. The photophores produce light of the same intensity as ambient downwelling light, consistent with a function of counterillumination (Harper and Case 1999).

Toadfish females lay demersal eggs in a nest that is constructed and guarded by the male. After hatching, the larvae remain benthic and do not have a planktonic dispersal phase. Species tend to have restricted, neighboring, minimally overlapping distributions (Greenfield et al. 2008), consistent with speciation in allopatry following uncommon dispersal events. Due to the age and restricted dispersal abilities of species in this clade, inference of biogeographic history among toadfishes is very likely to show high concordance with vicariant events such as the closure of the Isthmus of Panama, even on very fine scales. The stem age of *Batrachoididae* is estimated as 121.82 Ma (95% credible interval 113.37–130.94 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). The phylogenetic relationship of *Batrachoididae* within *Percomorpha* is shown in Fig. 2.

### ***Gobiiformes* (12 families, 2,740 species)**

***Apogonoidei:*** *Apogonidae* (cardinalfishes), *Kurtidae*\* (nurseryfishes).

***Gobioidi:*** *Butidae* (gudgeons), *Eleotridae* (sleepers), *Gobiidae* (gobies), *Milyeringidae* (cave gudgeons), *Odontobutidae* (Asian freshwater sleepers), *Oxudercidae* (mudskippers and allies), *Rhyacichthyidae* (loach gobies), *Thalasseleotrididae* (ocean sleepers), *Xenisthmidae* (collared wrigglers).

***Trichonotidae***\* (sand divers).

*Gobiiformes* is a worldwide radiation of small, usually benthic fishes that inhabit inshore marine habitats as well as fresh and brackish waters. The species are generally less than 200 mm in length (often less than 100 mm in *Gobiidae*) but vary in their body shapes. *Kurtidae* and *Apogonidae* are laterally compressed and nektonic, *Trichonotidae* are eel-like and bury themselves in sand, and *Eleotridae*, *Butidae*, *Oxudercidae*, and *Gobiidae* are variously laterally compressed or more commonly cylindrical in shape and benthic, many with fused pelvic fins that function

as an attachment disc. Within *Gobiiformes*, *Apogonidae* and *Kurtidae* are sister lineages, and *Trichonotidae* and *Gobioidei* form a clade (Thacker 2009; Near et al. 2013; Thacker et al. 2015; Betancur-R et al. 2017). The most species-rich lineages are *Gobiidae* (1387 species) and *Oxudercidae* (703 species); within those families, 19 clades have also been delineated (Thacker and Roje 2011; Agorreta et al. 2013; Thacker 2013).

Gobiiform species engage in complex reproductive behaviors that involve parental care by the male. Eggs are laid in a benthic nest (*Gobioidei*), carried on the forehead of the male (*Kurtidae*), or brooded in the oral cavity (*Apogonidae*) or gill chamber (*Trichonotidae*). The eggs are adhesive, and bear elaborate caps and filaments (Thacker et al. 2015). Within *Gobiidae*, several species are hermaphroditic, including protogyny or either sequential or bidirectional sex change (Cole 1990; Maxfield et al. 2012; Kuwamura et al. 2020). In *Eleotridae*, the freshwater genus *Hypseleotris* includes several wide-ranging species in Australia that interbreed and form a hemiclinal hybrid complex (Thacker et al. 2022). In this system, parental species persist alongside their hemiclone hybrids; hemiclones retain half of their genome in each generation without recombination and reproduce by mating with one of their sexual parental species and likely also with other hemiclone hybrids. At reproduction, the hemiclone passes the haploid genome from one parent only, with the other haploid genome supplied by the sexual parent species and then discarded in the next generation during gametogenesis (Unmack et al. 2019; Majtánová et al. 2021).

Paedomorphosis (small size coupled with juvenile morphology) and miniaturization (small size alone) are common in *Gobiidae* and *Oxudercidae*, with several species attaining adult lengths of only 17–25 mm (Giovannotti et al. 2007; Iwata et al. 2001; Kon and Yoshino 2002). *Gobiidae* includes some of the smallest vertebrates known, including the paedomorphic *Schindleria brevipinguis* (Watson and Walker 2004). Paedomorphic gobies feature comprehensive simplifications in the skeleton and soft tissues including drastic rearrangements in the gonads (Thacker and Grier 2005; La Mesa 2012). All the paedomorphic species are transparent and pelagic, resembling larval *Gobiidae* as mature adults. In *Schindleria*, few morphological characters are useful in distinguishing species, but many

cryptic taxa have been delineated based on phylogenetic analysis of DNA sequences (Kon et al. 2007). *Schindleria* species also exhibit complex variation in the shapes of the male genital papillae, raising the possibility that fertilization is internal, and that genital variation may promote speciation among otherwise very similar forms. *Schindleria* species perform the diel migrations typical of fish larvae, descending in the day and rising to the surface at night. They are most abundant in near-reef habitats during the new moon when they aggregate, presumably to mate and possibly to deposit their eggs on or in the reef substrate (Thacker and Grier 2005; Robitzsch et al. 2021).

Gobies frequently participate in mutualistic associations, ranging from simply occupying a living substrate such as a coral or a sponge to complex cleaning behaviors and intimate mutualisms with burrowing alpheid shrimp (Rüber et al. 2003; Herler et al. 2009; Duchene et al. 2013; Tornabene et al. 2013). The obligate mutualism between shrimp and gobies has evolved several times (Thacker et al. 2011) although there are many fewer shrimp than goby species that participate in the mutualism and there is not a strict pattern of cospeciation (Thompson et al. 2013). The mutualism features a tactile communication system in which the shrimp keeps its long antennae in contact with the goby's flank and the goby communicates by means of body movements and tail flicks (Kaplus and Thompson 2011). Gobies also communicate with fin-flaring displays and several Mediterranean goby species in *Oxudercidae* and *Gobiidae* produce clicking and humming sounds both for courtship and aggression. The sounds are likely produced with the buccal and opercular bones and muscles given that adult gobies do not have swim bladders (Malavasi et al. 2008).

*Kurtidae* and several species of *Apogonidae* inhabit estuaries and mangroves, but most species of *Apogonidae* are nocturnal and occupy coral reef habitats (Berra et al. 2007; Thacker and Roje 2009). Some reef *Apogonidae* possess a visceral bioluminescent system consisting of pouches elaborated from the gut; in some species the bioluminescent organs host symbiotic bacteria, in others they do not. Bioluminescence in *Apogonidae* is ventral and provides counterillumination, camouflaging the fish in low light conditions and potentially also used for attracting prey. Luminescent adaptations vary among species

and have evolved several times within *Apogonidae* (Thacker and Roje 2009; Davis et al. 2016a, b).

Biogeography and phylogeography have been investigated for several gobiiform clades, in particular the divergences within and among species of *Apogonidae*, *Eleotridae*, and *Gobiidae* in the Caribbean and Eastern Pacific (Taylor and Hellberg 2005; Maxfield et al. 2012; Galván-Quesada et al. 2016; Tornabene et al. 2016; Thacker 2017; Piñeros et al. 2019; Huie et al. 2020; Thacker et al. 2023). In those groups, the closure of the Isthmus of Panama promoted both speciation and morphological diversification and revealed that gobies may exhibit phylogeographic differentiation on surprisingly small spatial scales as well as along depth gradients. Similarly, genetic structure within complexes of Indo-Pacific reef gobies (*Eviota*; Tornabene et al. 2015), mudskippers (*Periophthalmus*; Polgar et al. 2014) and gudgeons (*Eleotris*; Mennesson et al. 2018) indicates that new species, often cryptic, are arising both allopatrically and sympatrically in the Coral Triangle. Gobies comprise a large portion of the cryptobenthic reef fauna (Brandl et al. 2018): small fishes that are morphologically cryptic but vital to the biodiversity and functioning of reef environments (Brandl et al. 2019).

Phylogeographic studies of Australian and New Zealand freshwater *Gobiidae*, *Eleotridae*, and *Apogonidae* (Cook et al. 2017; Hammer et al. 2019; Mossop et al. 2015; Shelley et al. 2020a; Thacker et al. 2007, 2008) confirm that many cryptic species are present among freshwater lineages and indicate that currently isolated freshwater systems may have experienced periods of high connectivity in the past. Similarly, phylogenetic analyses of *Oxudercidae* in the marine and freshwaters of Europe and Western Asia have revealed previously unrecognized diversity, prompted taxonomic adjustments, and shown that independently derived freshwater lineages share convergent similarities in body form (Huysse et al. 2004; Vanhove et al. 2012; Thacker and Gkenas 2019; Thacker et al. 2019). Reconstruction of continental-scale biogeographic patterns in *Gobiidae* and *Oxudercidae* by Thacker (2015) inferred a Tethyan-Indo-Pacific origin for gobies, with seven independent invasions of the Americas along multiple routes over the course of the past 50 million years.

Gobies are notoriously hardy, often euryhaline, and excellent invaders both through natural pathways and human-mediated introductions (Neilson and Stepien

2009). Expansions in immune system gene families in both amphibious mudskippers and invasive round gobies are hypothesized to allow both groups to contend with unfamiliar pathogens in novel environments (You et al. 2014; Adrian-Kalchhauser et al. 2020). The stem age of *Gobiiformes* is estimated as 117.81 Ma (95% credible interval 108.89–126.63 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Gobiiformes* are shown in Fig. 2.

### ***Scombriformes* (17 families and lineages, 287 species)**

*Amarsipidae*\* (Bagless Glassfish), *Ariommatidae*\* (ariommatids), *Arripidae*\* (Australian salmon), *Bramidae* (pomfrets), *Caristiidae* (manefishes), *Centrolophidae* (medusafishes), *Chiasmodontidae* (swallowers), *Gempylidae* (snake mackerels), *Icosteidae*\* (Ragfish), *Lepidocybium flavobrunneum* (Escolar), *Nomeidae* (driftfishes), *Pomatomidae*\* (Bluefish), *Scombridae* (mackerels, tunas and bonitos), *Scombrolabracidae*\* (Longfin Escolar), *Stromateidae* (butterfishes), *Tetragonuridae*\* (squaretails), *Trichiuridae* (cutlassfishes).

*Scombriformes* is a worldwide group of marine predators occupying open ocean habitats as well as the deep sea. Disparate molecular phylogenies all resolve *Scombriformes* as monophyletic but agree on little else beyond clades that include *Gempylidae* and *Trichiuridae*, *Caristiidae* and *Bramidae*, and a clade containing *Stromateidae*, *Ariommatidae*, and *Nomeidae* (Miya et al. 2013; Near et al. 2013; Betancur-R et al. 2017; Hughes et al. 2018; Friedman et al. 2019; Arcila et al. 2021; Ghezelayagh et al. 2022). The most species-rich lineages are *Scombridae* (52 species) and *Trichiuridae* (47 species; Fricke et al. 2023; Near and Thacker 2024).

Overall body shape in *Scombriformes* ranges from the elongate, ribbon-like profiles of *Gempylidae* and *Trichiuridae* to the stout forms of *Scombridae* and the laterally compressed ovoid shapes of *Stromateidae* and *Ariommatidae*. Dorsal fins are paired or single, with a series of small finlets following the dorsal and anal fins in *Scombridae* and *Gempylidae*; most have forked tails. *Icosteidae* and *Chiasmodontidae* are known from deeper waters and are drab and darkly colored (Hastings

et al. 2014; Friedman et al. 2019). *Scombriformes* are pelagic and often found in schools, and some undertake long distance migrations across ocean basins (Miya et al. 2013), yielding high connectivity among populations (Thiesen et al. 2008; Barth et al. 2017). Most are predators of bony fish except for *Centrolophidae*, *Nomeidae*, *Ariommatidae*, *Tetragonuridae*, and *Stromateidae* which consume jellyfishes, siphonophores, salps and other small invertebrates (Miya et al. 2013; Friedman et al. 2019; some *Nomeidae* are commensal with siphonophores). Reproductive mode has only been observed in some of the scombriform lineages, but it is likely that they are all broadcast spawners. Lineages in which reproduction has been documented exhibit a prolonged spawning period containing one or two peaks; they form spawning aggregations in coastal waters and have high fecundity (Dadzie et al. 2008; Juan-Jordá et al. 2013; de Souza et al. 2021).

*Scombridae* species are endothermic, and most utilize a countercurrent circulation system that retains metabolic heat; *Gasterochisma* employs a slightly different mechanism in which a heater organ derived from eye muscles maintains warmth only in the brain (Block et al. 1993; Block and Finnerty 1994; Dickson and Graham 2004; Little et al. 2010; Wu et al. 2021). These adaptations have enabled tunas to perform long migrations in both tropical and temperate waters, migrate vertically in the water column, and maintain visual acuity in low-light conditions (Block et al. 1993; Dickson and Graham 2004).

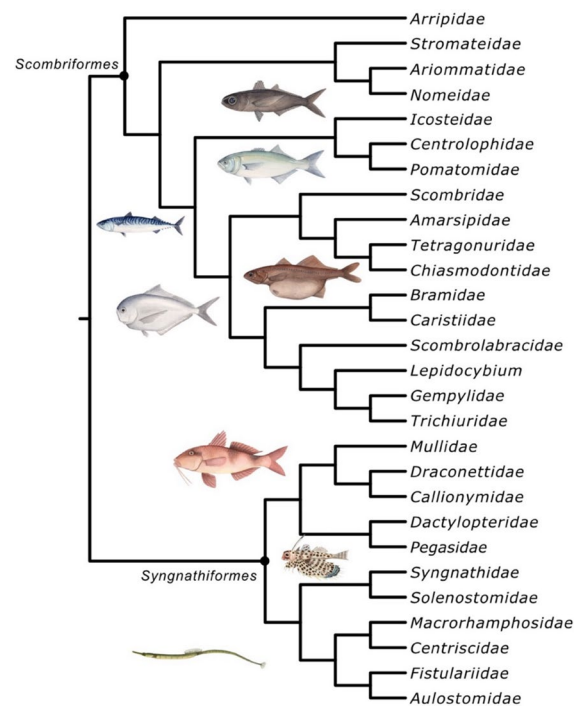
Calibrated phylogenetic hypotheses of *Scombriformes* infer a crown age in the latest Cretaceous, approximately 65–73 Ma, and infer a rapid divergence of scombriform lineages around that time (Miya et al. 2013; Near et al. 2013; Friedman et al. 2019; Harrington et al. 2021; Ghezelayagh et al. 2022). Collar et al. (2022) examined the evolution of scombriform body shapes and showed that the ancestral (and most common) shape is the streamlined, torpedo-shaped form of tunas. Deeper, flat bodied shapes arose twice (in *Stromateidae* and *Bramidae*), and similarly, elongate morphologies developed independently in *Gempylidae* and *Trichiuridae*, each with different modifications to the vertebral column. The stem age of *Scombriformes* is estimated as 110.3 Ma (95% credible interval 101.51–120.65 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships

among the living lineages of *Scombriformes* are shown in Fig. 3.

### *Syngnathiformes* (11 families, 690 species)

*Aulostomidae*\* (trumpetfishes), *Callionymidae* (dragonets), *Centriscidae* (shrimpfishes), *Dactylopteridae* (flying gurnards), *Draconettidae* (slope dragonets), *Fistulariidae*\* (cornetfishes), *Macrorhamphosidae*\* (snipefishes), *Mullidae* (goatfishes), *Pegasidae* (sea moths), *Solenostomidae*\* (ghost pipefishes), *Syngnathidae* (pipefishes and seahorses).

*Syngnathiformes* is a charismatic group of small-bodied species found in temperate and tropical habitats worldwide, mostly in shallow nearshore marine environments. They are characterized by having small mouths that are sometimes terminal and borne on a tubular snout and varying degrees of bony armor in the skin (Longo et al. 2017; Santaquiteria et al. 2021). Molecular phylogenetic and phylogenomic analyses agree in resolving two clades within *Syngnathiformes*, one composed of *Pegasidae*, *Dactylopteridae*, *Mullidae*, *Callionymidae* and *Draconettidae*



**Fig. 3** Relationships among the living lineages of *Scombriformes* and *Syngnathiformes* (modified from Fig. 15 of Near and Thacker 2024)

and a second including *Syngnathidae*, *Solenostomidae*, *Aulostomidae*, *Fistulariidae*, *Centriscidae*, and *Macrorhamphosidae* (Near et al. 2013; Betancur-R et al. 2017; Longo et al. 2017; Santaquiteria et al. 2021; Ghezelayagh et al. 2022). The most species-rich lineages are *Syngnathidae* (328 species) and *Callionymidae* (201 species; Fricke et al. 2023; Near and Thacker 2024).

*Syngnathiformes* comprises two distinct clades with different characteristics and ecological adaptations. The first clade includes benthic lineages with varying degrees of body armor; *Mullidae* lack body scutes entirely, while *Callionymidae* and *Draconettidae* feature spines only on their heads and opercles. *Dactylopteridae* exhibit more extensive armor, with bony plates and spines on the head and scute-like scales covering the body. *Pegasidae* stand out as the most heavily armored species of *Syngnathiformes*, being completely covered in bony plates and characterized by an elongated rostrum. Both *Pegasidae* and *Dactylopteridae* share a notable feature of dramatically enlarged, wing-like pectoral fins. The second clade exhibits a more nektonic lifestyle and includes *Syngnathidae*, *Solenostomidae*, *Aulostomidae*, *Fistulariidae*, *Centriscidae*, and *Macrorhamphosidae*. This group displays remarkable morphological diversity, ranging from the elongated forms of *Aulostomidae* and *Fistulariidae* to the distinctively long-snouted *Centriscidae* and *Macrorhamphosidae* and the unique seahorses and pipefishes in *Syngnathidae*. Despite their varied appearances, members of this nektonic clade share several common characteristics. They all possess a long snout terminating in a small suction mouth and are generally weak swimmers. Armor configurations vary within this group: *Aulostomidae* have small scutes on the posterior head region, *Fistulariidae* display lines of scutes along their bodies, and *Syngnathidae*, *Centriscidae*, and *Macrorhamphosidae* feature extensive body armor composed of bony plates and rings. These distinctive morphological and ecological characteristics highlight the remarkable evolutionary adaptations within *Syngnathiformes* (Longo et al. 2017; Santaquiteria et al. 2021; Kawahara et al. 2008).

Species of *Syngnathiformes* employ a variety of reproductive strategies. Most syngnathiform species are pelagic spawners: *Mullidae* spawn in aggregations, *Fistulariidae*, *Aulostomidae*, and *Dactylopteridae* are pelagic spawners but the specific behavior is

unknown, and the males engage in courting behaviors, pair with females, and rise into the water to spawn in species of *Pegasidae*, *Callionymidae*, *Draconettidae*, *Centriscidae* and *Macrorhamphosidae* (de Oliveira et al. 1993; Awata et al. 2010; Pavlov et al. 2011; Bariche et al. 2013; Zhang et al. 2020). Among species of *Solenostomidae*, the eggs are brooded by the female in a pouch supported by the pelvic fins. All species of *Syngnathidae* display male parental care of the eggs, ranging from brooding on an open patch of skin on the underside of the tail to protection of embryos in partially or completely enclosed brood pouches on the abdomen. The location of the brooding structure is diagnostic for the two major clades within *Syngnathidae*: tail brooders (nine pipefish genera) are distinct from trunk brooders (all other pipefish species, seahorses, seadragons, and pygmy pipefishes), and it is in the trunk-brooding seahorses that truly viviparous male pregnancies occur (Wilson and Orr 2011; Hamilton et al. 2017).

Species of *Syngnathiformes* are distributed worldwide, with the highest species diversity in the Indo-Pacific and with species of *Syngnathidae* particularly abundant on both the temperate and tropical coasts of Australia (Hamilton et al. 2017). Lineages within *Syngnathiformes* originated in the Tethys reef hotspot in the late Cretaceous roughly 87 Ma and from there populated the Indo-Pacific, with multiple invasions of the Atlantic and Eastern Pacific (Hamilton et al. 2017; Santaquiteria et al. 2021). Species of *Syngnathidae* are concentrated in the central Indo-Pacific and have undergone several long-distance dispersal events (Li et al. 2021; Stiller et al. 2022). The stem age of *Syngnathiformes* is estimated as 110.3 Ma (95% credible interval 101.51–120.65 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Syngnathiformes* are shown in Fig. 3.

### ***Atheriniformes* (32 families and lineages, 2,126 species)**

***Atherinoidei*:** *Atherinidae* (Old World silversides), *Atherinopsidae* (New World silversides), *Atherionidae*\* (pricklenose silversides), *Bedotiidae* (Malagasy rainbowfishes), *Isonidae*\* (surf sardines), *Melanotaeniidae* (rainbowfishes), *Phallostethidae* (priapum

fishes), *Pseudomugilidae* (blue eyes), *Telmatherinidae* (sailfin silversides).

**Belonoidei:** *Adrianichthyidae* (ricefishes), *Belonidae* (needlefishes), *Euleptorhamphidae* (ribbon halfbeaks), *Exocoetidae* (flyingfishes), *Hemiramphidae* (halfbeaks), “hyporhamphids” (*Arrhamphus* + *Chriodorus* + *Hyporhamphus* + *Melapedalion*), *Zenarchopteridae* (viviparous halfbeaks).

**Cyprinodontoidei:** *Anablepidae* (four-eyed fishes), *Aphaniidae* (Oriental killifishes), *Aplocheilidae* (Old World rivulins), *Cubanichthyidae* (island pupfishes), *Cyprinodontidae* (pupfishes), *Fluviphylacidae*\* (American lampeyes), *Fundulidae* (topminnows and killifishes), *Goodeidae* (splitfins), *Nothobranchiidae* (African rivulins), *Orestiidae* (Andean killifishes), *Pantanodontidae* (spine killifishes), *Poeciliidae* (livebearers), *Procatopodidae* (African lampeyes), *Profundulidae* (Middle American killifishes), *Rivulidae* (rivulins), *Valenciidae*\* (European killifishes).

*Atheriniformes* includes a variety of inshore marine and freshwater fishes, some of which are diadromous, that are generally small-bodied and live in shallow habitats. Species of *Atheriniformes* either lay demersal eggs with adhesive filaments, often mouth-brooded or guarded in a substrate nest, or are viviparous (Mabuchi et al. 2007; Wainwright et al. 2012). *Atheriniformes* is also characterized by a restricted spermatogonial testis type in which sperm are generated from spermatogonia only at the ends of the testicular lobes rather than throughout the entire organ (Uribe et al. 2014). The most species-rich lineages are *Rivulidae* (476 species), *Nothobranchiidae* (314 species), and *Poeciliidae* (274 species) (Fricke et al. 2023; Near and Thacker 2024). *Atheriniformes* contains three subclades: *Atherinoidei*, *Belonoidei*, and *Cyprinodontoidei* (Near and Thacker 2024).

*Atherinoidei* and *Belonoidei* are most frequently found in inshore marine habitats, in contrast to the generally freshwater *Cyprinodontoidei*. Species of *Atherinoidei* are all small, laterally compressed, usually with an overall silvery coloration and sometimes with a black lateral stripe. They have two separate dorsal fins, with flexible spines in the first and at the start of the second. The unusual species of *Phallostethidae* have internal fertilization, in which the male clasps and inseminates the female by means of an elaborate copulatory organ modified from the pelvic girdle (Dyer and Chernoff 1996). *Atherinopsidae* includes beach-spawning grunion species in both the

temperate Western Atlantic (*Menidia*) and Eastern Pacific (*Leuresthes*). The California grunion *Leuresthes tenuis* performs coordinated spawning rituals in which fishes swim up onto beaches at high tide during full or new moons, the female burrows tail-first into the sand and lays eggs and the male curls around the female and fertilizes the clutch. Eggs incubate into the sand for roughly two weeks until the eggs hatch and the larvae are carried out to sea by the next high tide (Martin and Swiderski 2001).

*Atherinoidei* includes several remarkable radiations of brightly colored fishes in Australia, New Guinea, Sulawesi (and neighboring islands) and Madagascar, including species in *Bedotiidae*, *Melanotaeniidae*, *Telmatherinidae*, and *Pseudomugilidae* (the atherinid genus *Craterocephalus* is also diverse in Australia and New Guinea). Phylogenetic hypotheses based on both morphological and molecular data resolve *Atherinopsidae* (distributed in the Americas) as sister to the remaining lineages, which are distributed in Europe, Africa, Asia, Australia, and the Indo-Pacific (Dyer and Chernoff 1996; Setiamarga et al. 2008; Bloom et al. 2012; Campanella et al. 2015; Betancur-R et al. 2017; Ghezelayagh et al. 2022), and in most phylogenetic analyses the colorful Indo-Pacific *Bedotiidae*, *Melanotaeniidae*, *Telmatherinidae*, and *Pseudomugilidae* are resolved as the crown clade.

*Belonoidei* is distributed worldwide, mostly in marine habitats except for some freshwater *Belonidae*, *Hemiramphidae*, and *Zenarchopteridae*. Species of *Adrianichthyidae* occupy freshwater and brackish habitats in the Indo-Pacific region. Molecular phylogenies resolve well-supported relationships among the belonoid lineages and agree in resolving *Adrianichthyidae* as the sister taxon to a clade containing *Belonidae* plus *Zenarchopteridae* as then sister lineage of a clade containing *Hemiramphidae* and *Exocoetidae* (Lovejoy et al. 2004; Near et al. 2013; Betancur-R et al. 2017; Ghezelayagh et al. 2022). A phylogenomic analysis of *Belonoidei* resolves a paraphyletic *Hemiramphidae*, with separate resolution of three clades including *Euleptorhamphus* and *Rhynchorhamphus* (*Euleptorhamphidae*); *Arrhamphus*, *Chriodorus*, *Hyporhamphus*, and *Melapedalion* (“hyporamphids”; Near and Thacker 2024); and *Hemiramphidae* restricted to *Hemiramphus* and *Oxyporhamphus* (Daane et al. 2021). Lovejoy et al. (2004) investigated the evolutionary and ontogenetic patterns of upper and lower jaw elongation among

*Belonidae*, *Hemiramphidae*, *Zenarchopteridae*, and *Exocoetidae* and refuted the hypothesis that the half-beaked condition in *Hemiramphidae* is a pedomorphic reduction of the symmetric jaw elongation in *Belonidae*. A phylogenomic analysis of *Belonoidei* revealed that aerial gliding in *Exocoetidae* is linked to elevated rates of evolution in genes associated with pectoral fin size and musculature, neuromuscular control of the propulsive caudal fin, corneal adaptations for vision in air, and enlargement of the semicircular canals (Daane et al. 2021).

Species of *Cyprinodontoidei* are distributed worldwide, mostly in fresh or brackish water, and are characterized by having small, terminal mouths and a single spineless dorsal fin placed far back on the body. Many species of *Cyprinodontoidei* feature pronounced sexual dimorphism, with the males brightly colored and sometimes with elaborately extended fins (Hastings et al. 2014). Lineages of *Cyprinodontoidei* have radiated extensively in freshwaters of the Western Hemisphere (*Fundulidae*, *Profundulidae*, *Goodeidae*, *Anablepidae*, *Poeciliidae*, and most *Cyprinodontidae*), with the remaining lineages known from Europe, North Africa, and Asia (Parenti 1981; Pohl et al. 2015; Bragança et al. 2018). Pupfishes (*Cyprinodon*) are distributed patchily in Southern and Western North America and islands in the Caribbean. They include the endangered Devil's Hole Pupfish, Desert Pupfish, and Owens Pupfish, all restricted to small waterholes and springs in California, Nevada, Arizona, and Mexico, relicts of distributions in larger ancient drainages or potentially the products of vectored overland dispersal (Martin and Turner 2018). Pupfishes are highly tolerant of extremes in both salinity and temperature but are threatened by habitat degradation and reduction due to water diversion and introduction of non-native species. Analysis of *Cyprinodon* phylogeny and trait data indicates that accelerations in morphological change are correlated with transitions from generalist to specialist feeding strategies (including scale-eating, molluscivory, planktivory and piscivory) in two lineages known from inland lakes in Mexico and the Bahamas (Martin and Wainwright 2011).

*Cyprinodontoidei* also includes livebearing species with internal fertilization, independently evolved in *Anablepidae*, *Poeciliidae*, and *Goodeidae* (Parenti 1981; Ghedotti and Davis 2013; Reznick et al. 2017; Amorim and Costa 2018; Bragança et al. 2018).

Phylogenies of *Cyprinodontoidei* consistently resolve two clades within the group, one containing *Aplocheilidae*, *Nothobranchiidae*, and *Rivulidae* as the sister clade to the remaining lineages (Pohl et al. 2015; Betancur-R et al. 2017; Bragança et al. 2018; Ghezelayagh et al. 2022). Resolution among the deeper nodes in the phylogeny is weak, but *Goodeidae*, *Profundulidae*, and *Cubanichthyidae* are resolved as a clade, as are *Cyprinodontidae*, *Orestiidae*, and *Fundulidae*. *Poeciliidae* and *Anablepidae* are sister lineages, but the interrelationships of *Fluviophylacidae*, *Procatopodidae*, *Aphaniidae*, and *Valenciidae* are less clear (Ghedotti and Davis 2013; Reznick et al. 2017; Amorim and Costa 2018). Within *Poeciliidae*, most genera are monophyletic, and they are resolved into four subclades (Hrbek et al. 2007; Reznick et al. 2017; Rodríguez-Machado et al. 2024).

The stem age of *Atheriniformes* is estimated as 96.2 Ma (95% credible interval 86.23–105.98 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Atheriniformes* are shown in Fig. 4.

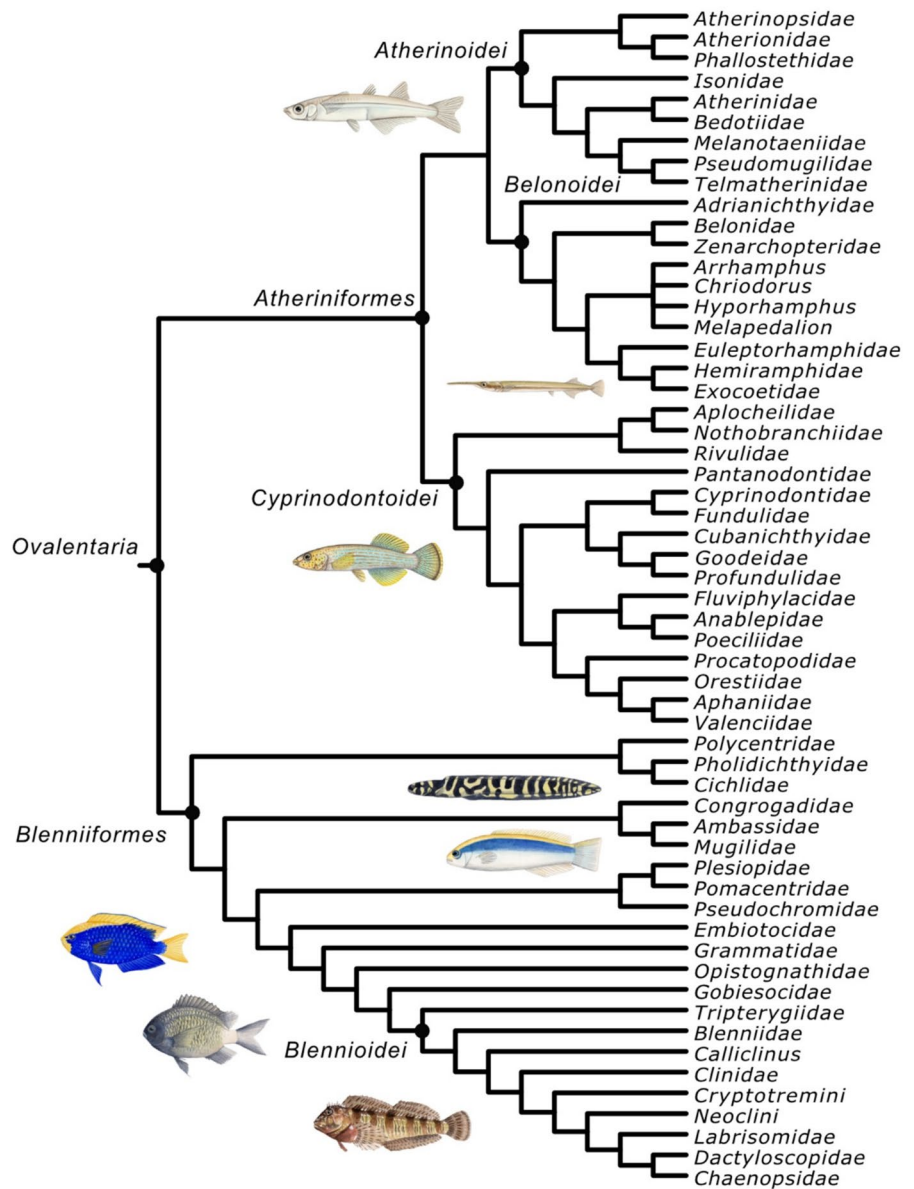
### ***Blenniiformes* (22 families and lineages, 3,814 species)**

*Ambassidae* (Asiatic glassfishes), *Cichlidae* (cichlids), *Congrogadidae* (eelblennies), *Embiotocidae* (surfperches), *Gobiesocidae* (clingfishes), *Grammatidae* (gramma basslets), *Mugilidae* (mulletts), *Opistognathidae* (jawfishes), *Pholidichthyidae*\* (convictblennies), *Plesiopidae* (roundheads), *Polycentridae* (leaffishes), *Pomacentridae* (damsel-fishes and anemonefishes), *Pseudochromidae* (dottybacks).

***Blennioidei*:** *Blenniidae* (combtooth blennies), *Calliclinus* (*Calliclinus* blennies), *Chaenopsidae* (pikeblennies), *Clinidae* (kelp blennies), *Cryptotremiini* (cryptotremines), *Dactyloscopidae* (sand stargazers), *Labrisomidae* (labrisomid blennies), *Neoclini* (fringeheads), *Tripterygiidae* (triplefins).

*Blenniiformes* is the most species-rich major clade of acanthopterygians. The most species-rich lineage of *Blenniiformes* is *Cichlidae* (1,755 species), distributed in freshwater habitats in Madagascar, India, Africa, and the Neotropics with notable adaptive radiations in African Rift Valley Lakes. The other lineages in *Blenniiformes* are mostly marine and feature a variety of colorful benthic and reef-associated

**Fig. 4** Phylogenetic relationships among the living lineages of *Ovalentaria*, including *Atheriniformes* and *Blenniiformes* (modified from Fig. 16 of Near and Thacker 2024)



groups including *Pomacentridae* (426 species), *Pseudochromidae* (131 species), *Plesiopidae* (52 species), *Congrogadidae* (24 species), *Grammatidae* (18 species), *Opistognathidae* (106 species), *Gobiesocidae* (191 species), and *Blennioidei* (948 species) (Fricke et al. 2023; Near and Thacker 2024). Most blenniiform species have elongate single dorsal fins. Body shapes vary widely among lineages, including laterally compressed ovoid *Pomacentridae*, eel-like *Congrogadidae* and *Pholidichthyidae*, and large-finned, brightly colored *Opistognathidae*, *Grammatidae*,

*Pseudochromidae*, and *Plesiopidae*. *Embiotocidae*, *Ambassidae*, *Cichlidae*, and *Polycentridae* attain more typical rhomboid shapes, while *Blennioidei* are elongate and often have cirri on the head. *Gobiesocidae* are highly modified benthic species, with large heads and modified pelvic fins that function as an adhesive disc (Hastings et al. 2014). Species of *Blenniiformes*, in common with *Atheriniformes*, produce eggs with adhesive strands; eggs are guarded in demersal nests or mouthbrooded (by males in both cases), or are internally fertilized and retained

by females (Mabuchi et al. 2007; Wainwright et al. 2012).

Phylogenetic hypotheses for this group, primarily based on molecular data (Setiamarga et al. 2008; Wainwright et al. 2012; Near et al. 2013; Betancur-R et al. 2017), have revealed unexpected phylogenetic relationships including the placement of *Pholidichthyidae* and *Polycentridae* as sequential sister lineages of *Cichlidae*. Cichlids are globally distributed in tropical freshwaters but most of their diversity is found in the Rift Valley Lakes of Eastern Africa where they form an exceptionally large adaptive radiation. Cichlids are sexually dimorphic with bright coloration and share a suite of pharyngeal modifications that increase feeding efficiency and versatility, characteristics that facilitate divergence in sympatry (Stiassny 1981; Wainwright et al. 2012; Ronco et al. 2021). There is also genomic evidence for historic hybridization and numerous insertion and deletion polymorphisms among cichlids, both of which are implicated as contributing to their history of rapid lineage diversification (Meier et al. 2017; Kautt et al. 2020; McGee et al. 2020; Svoldal et al. 2020; Ronco et al. 2021). The elongate, marine reef-dwelling *Pholidichthys* is an unlikely sister lineage of *Cichlidae*, but that placement is consistently resolved in molecular phylogenies and supported by the morphology of the pharyngeal jaw apparatus (Wainwright et al. 2012). Molecular phylogenies also support the monophyly of a clade containing *Blennioidei*, *Opistognathidae*, and *Gobiesocidae*. *Polycentridae* and *Nandidae*, with which *Blennioidei* is grouped in traditional taxonomies of *Acanthopterygii* are not closely related; Collins et al. 2015). Among *Embiotocidae*, *Grammatidae*, and *Gobiesocidae*, molecular phylogenetics has provided insight into the evolution of habitat partitioning by depth (Baldwin et al. 2018; Longo et al. 2018; Conway et al. 2020). Phylogenetic relationships among and within the lineages of *Blennioidei* have been inferred using Sanger-sequenced mtDNA and nuclear genes (Lin and Hastings 2013), and other molecular studies have focused on *Tripterygiidae* (Miller et al. 2014) and *Blenniidae* (Hundt et al. 2014; Wagner et al. 2021; Vecchioni et al. 2022). Molecular phylogenetic analyses agree in resolving the circumglobal tropical groups *Tripterygiidae* and *Blenniidae* as diverging earliest, followed by the temperate *Clinidae* and with the primarily Neotropical lineages *Labrisomidae*, *Calliclinus*, *Cryptotremi*,

*Chaenopsidae*, *Neoclini*, and *Dactyloscopidae* comprising the crown clade. Lin and Hastings (2013) resolve *Calliclinus* and the remainder of *Cryptotremi* as clades distinct from *Labrisomidae* and resolve *Neoclini* as separate from *Chaenopsidae*. The origin of *Blennioidei* is estimated at 60.3 Ma, with the Neotropical crown clade arising 37.6 Ma, when the Neotropics were becoming increasingly isolated from the Tethys-Indo-Pacific diversity hotspot (Lin and Hastings 2013). *Blenniidae*, the most species-rich blennioid lineage, is distributed worldwide, with most diversity in the tropics but also including significant radiations in temperate rocky intertidal regions as well as a small clade of freshwater species distributed throughout the islands and nearshore rivers of the Mediterranean coasts (Hundt et al. 2014; Wagner et al. 2021). The stem age of *Blenniiformes* is estimated as 96.2 Ma (95% credible interval 86.23–105.98 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Blenniiformes* are shown in Fig. 4.

### ***Carangiformes* (32 families, 1,107 species)**

*Centropomidae*\* (snooks), *Lactariidae*\* (false trevallies), *Latidae* (giant perches), *Polynemidae* (threadfins), *Sphyracidae*\* (barracudas).

***Carangoidei:*** *Carangidae* (jacks), *Coryphaenidae*\* (dolphinfishes), *Echeneidae* (remoras), *Istiophoridae*\* (marlin), *Leptobramidae*\* (beachsalmons), *Menidae*\* (moonfishes), *Nematistiidae*\* (roosterfishes), *Rachycentridae*\* (Cobia), *Toxotidae* (archerfishes), *Trachinotidae* (pompanos), *Xiphiidae*\* (swordfishes).

***Pleuronectoidei:*** *Achiridae* (American soles), *Achiropsettidae* (southern flounders), *Bothidae* (left-eye flounders), *Citharidae* (largescale flounders), *Cyclosettidae* (sand whiffs), *Cynoglossidae* (tonguefishes), *Oncopteridae*\* (Remo flounders), *Paralichthodidae*\* (peppered flounders), *Paralichthyidae* (sand flounders), *Pleuronectidae* (righteye flounders), *Poeciliopsettidae* (bigeye flounders), *Psettodidae*\* (spiny turbot), *Rhombosoleidae* (South Pacific flounders), *Samaridae* (crested flounders), *Scophthalmidae* (turbot), *Soleidae* (soles).

*Carangiformes* typically occupy marine environments and include strong pelagic swimmers as well as benthic flatfishes. Carangiform lineages range in

shape from fusiform to laterally compressed and the pelagic groups are often silvery, but the flatfishes are generally drably colored and have a remarkable ability to camouflage themselves against the substrate (Akkaynak et al. 2017). As far as is known, they are external spawners with pelagic eggs (Glass et al. 2023). Many of the lineages are species-depauperate, limited to one or a few species. The most species-rich clades in *Carangiformes* are three of the flatfish families, *Soleidae* (180 species), *Bothidae* (169 species), and *Cynoglossidae* (168 species), followed by *Carangidae* (152 species; Fricke et al. 2023; Near and Thacker 2024).

Phylogenies inferred from mitochondrial and nuclear sequences and genomic datasets are largely consistent in resolving three clades in *Carangiformes* (Harrington et al. 2016; Ribeiro et al. 2018; Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023). The first, with slight variations in the phylogenetic relationships among its constituent lineages, includes *Latidae*, *Centropomidae*, *Lactariidae* and *Sphyraenidae*. *Latidae* (distributed in the Indo-West Pacific and Africa) and *Centropomidae* (inhabiting the tropical Western Atlantic and Eastern Pacific) are large-bodied, with separate dorsal fins and a forked or rounded tail. *Lactariidae* (Indian and Western Pacific oceans) and *Sphyraenidae* (worldwide subtropical and tropical marine) are marine predators.

*Carangoidei* is the sister of a clade containing *Pleuronectoidei* and *Polynemidae* (Harrington et al. 2016; Ribeiro et al. 2018; Girard et al. 2020; Ghezelayagh et al. 2022; Glass et al. 2023). Species of *Carangoidei* are entirely marine except for the fresh and brackish water species of *Toxotidae*, and include several large predators, most notably species of *Coryphaenidae*, *Istiophoridae*, and *Xiphiidae*. *Carangidae* and *Trachinotidae* include a variety of strong-swimming pelagic fishes, ranging in shape from fusiform to highly laterally compressed. Most have two dorsal fins, slender caudal peduncles, and deeply forked caudal fins; many additionally have scutes on the lateral line and caudal peduncle (Smith-Vaniz 1999). *Scomberoides lysan* (*Trachinotidae*) is venomous, delivering the venom with spines in the dorsal and anal fins (Halsted et al. 1972; Smith and Wheeler 2006). The unusual species of *Toxotidae* inhabit the fresh and brackish waters of the Indo-Pacific region and catch prey by spitting streams of water at insects on overhanging vegetation (Allen 1978); the water jet

is generated by forcing water from the buccal cavity through a tube formed by the juxtaposition of several ridges and grooves elaborated from the bones and soft tissue of the oral cavity (Girard et al. 2022). *Leptobramidae* and *Toxotidae* resolve as a clade, and species of *Leptobrama* possess oral modifications similar to those in *Toxotidae* which they may use to push water onto the substrate and uncover buried prey (Girard et al. 2022).

*Echeneidae* are commensal, attaching to hosts such as sharks, turtles, whales, or larger fishes by means of a dorsal fin modified into an adherent disc (Friedman et al. 2013a). The commensalism is not permanent; the remora can attach or release the disk and is a capable swimmer but is usually attached to a host (O'Toole 2002; Friedman et al. 2013a). *Carangoidei* contains some of the largest and most spectacular pelagic fishes, the billfishes in *Xiphiidae* and *Istiophoridae* (Orrell et al. 2006). These migratory predators can reach body lengths of 3–5 M and have spear-like bills formed from fused extensions of the upper jaws (premaxillae). The bills are used for hunting by slashing through schools of smaller fish or squid and stunning or injuring them (Habegger et al. 2015). Billfishes are endothermic, but the endothermy is restricted to the eyes and brain and is accomplished with a thermogenic organ underneath the brain that is derived from external eye muscles in conjunction with a vascular countercurrent heat exchange system (Block et al. 1993; Block and Finnerty 1994; Dickson and Graham 2004; Wu et al. 2021).

The most species-rich lineage of *Carangiformes* is the clade that contains *Polynemidae* and *Pleuronectoidei*. Flatfishes are characterized by the remarkable larval transformation of eye migration from one side of the head to the other, resulting in cranial asymmetry and enabling them to rest sideways on the substrate while keeping both eyes exposed. The placement of *Polynemidae* as the sister taxon to *Pleuronectoidei* is a result resolved in molecular phylogenies (Harrington et al. 2016; Girard et al. 2020; Ghezelayagh et al. 2022), a phylogenetic hypothesis that is also supported by morphological characters (Girard et al. 2020). Flatfishes are also united by many morphological traits beyond the ontogenetic migration of one eye around the midline, including extension of the dorsal fin onto the head and the presence of the recessus orbitalis, a sac behind the eyeball that can be filled with fluid causing the eyeballs to protrude

above the surface of the head and above the substrate if the fish is buried (Chapleau 1993; Campbell et al. 2019). In contrast to the strong morphological evidence for flatfish monophyly, some molecular phylogenetic hypotheses resolve *Psettodidae* separately from the other flatfish lineages (Smith and Wheeler 2006; Li et al. 2011; Betancur-R et al. 2013; Campbell et al. 2013; Near et al. 2013; Lü et al. 2021). Others resolve *Psettodidae* as sister to all other flatfishes (Betancur-R and Orti 2014; Harrington et al. 2016; Betancur-R et al. 2017; Campbell et al. 2019; Girard et al. 2020; Evans et al. 2021; Duarte-Ribeiro et al. 2024), although in all molecular phylogenetic analyses the branch lengths connecting the internodes among flatfishes and their relatives are shallow.

The transformation from a symmetrical ancestor into asymmetric flatfishes was a rapid process that involved modular modifications of the skull, occurring near the K-Pg boundary at approximately 65.7 Ma and completing in no more than three million years (Friedman 2008; Harrington et al. 2016; Evans et al. 2021). Within *Carangoidei*, Frédéricich et al. (2016) compared body shape change with reef association and detected a higher rate of morphological change following transition from reef to non-reef habitats. Glass et al. (2023) identified a widespread pattern of sympatry between sister species pairs, with sympatric species exhibiting a greater difference in both body size and depth preference, regardless of their time of divergence. Allopatric species pairs could mostly be attributed to vicariance, either due to the rise of the Isthmus of Panama or to the barrier imposed by cold current systems off the coast of South Africa. The stem age of *Carangiformes* is estimated as 98.87 Ma (95% credible interval 87.37–110.69 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Carangiformes* are shown in Fig. 5.

### ***Synbranchiformes* (9 families, 414 species)**

***Anabantoidei:*** *Anabantidae* (climbing gouramis), *Channidae* (snakeheads), *Helostomatidae*\* (Kissing Gourami), *Nandidae* (Asian leaffishes), *Osphronemidae* (gouramis).

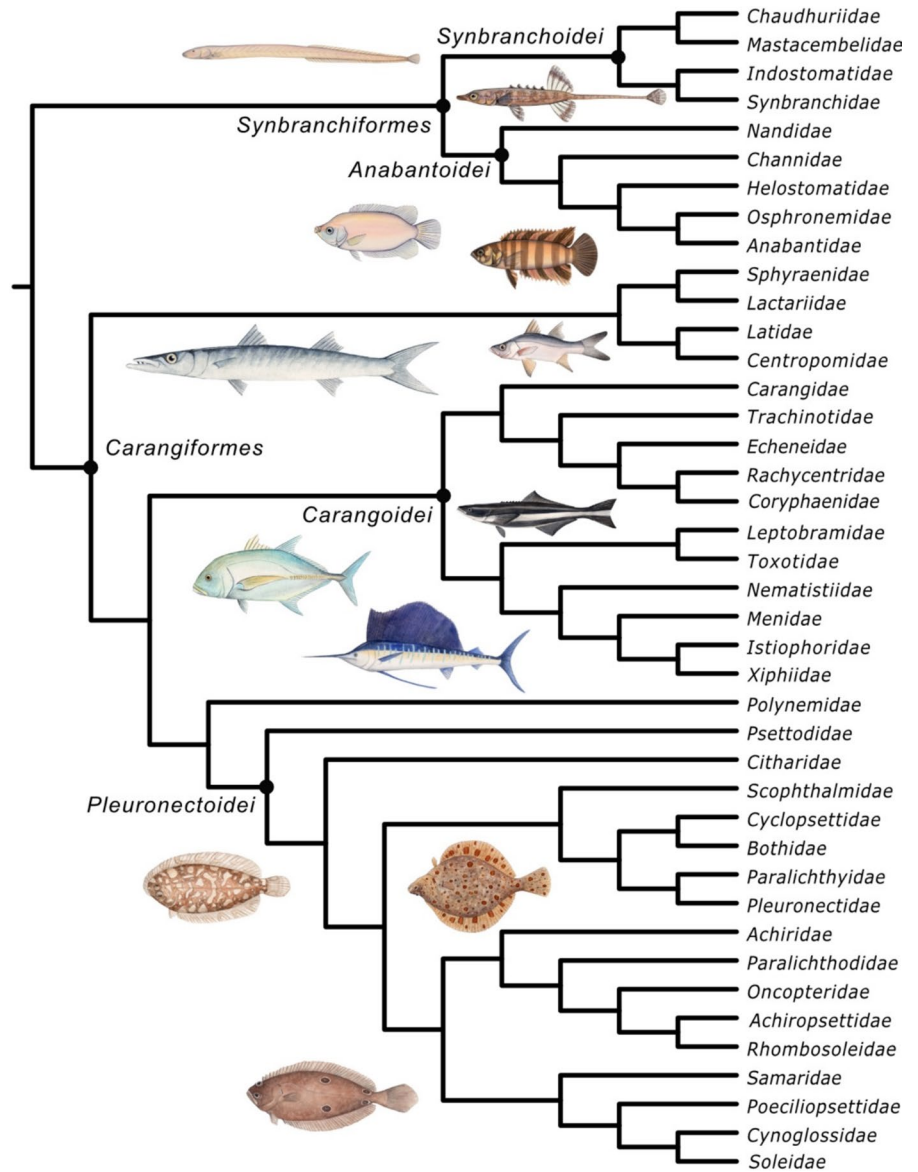
***Synbranchoidei:*** *Chaudhuriidae* (earthworm eels), *Indostomidae*\* (armored sticklebacks),

*Mastacembelidae* (freshwater spiny eels), *Synbranchidae* (swamp eels).

*Synbranchiformes* is the most geographically restricted of the acanthopterygian clades, distributed almost exclusively in freshwater habitats of Asia and Africa except for a few species of *Synbranchidae* in Mexico, Central and South America, and the Indo-Australian archipelago. All species of *Synbranchiformes* utilize freshwater habitats except for synbranchids and some channids which can tolerate brackish water. Notably, all species have vascularized pouches in the buccal cavity (suprabranchial or labyrinth organs) that enable them to absorb oxygen from air, a great advantage in that they can occupy stagnant, swampy habitats with low oxygen by gulping air at the surface. Some species of *Synbranchidae* and *Mastacembelidae* are capable of burrowing into mud and surviving periods out of water; they as well as species of *Channidae* can disperse over land. The most species-rich lineages of *Synbranchiformes* are *Osphronemidae* (135 species), *Channidae* (57 species), and *Mastacembelidae* (93 species; Fricke et al. 2023; Near and Thacker 2024).

The morphology of synbranchiform species varies greatly, from the elongate eel-like forms of *Synbranchidae*, *Mastacembelidae*, and *Chaudhuriidae* through to the brightly colored, long-finned species in *Osphronemidae*, popular in the aquarium trade and extensively bred in captivity. Species of *Nandidae* are laterally compressed and rhomboid. The unusual *Indostomus* is small (3–4 cm in length) and cylindrical, with an elongated snout and scutes on the body. In many respects *Indostomus* resembles a slender stickleback (*Gasterosteidae*) and their body armor has a similar ontogenetic pattern (Britz and Johnson 2002), but they are distantly related (Kawahara et al. 2008). A general commonality among all the disparate synbranchiforms is the presence of an elongate, single dorsal fin, usually originating far back on the body (in *Indostomus*, the separate spinous dorsal fin consists of five isolated spines with small membranes, each supported by a bony scute). The anal fin is also elongate, and in some *Osphronemidae* the first pelvic fin rays are extended and filamentous. The exception to that fin morphology is the eel-like *Synbranchidae*, in which both the dorsal and anal fins are reduced to ridges on the body, the caudal fin is tiny or absent, and the pectoral and pelvic fins are both absent in adults (pectorals are transitorily present in the larvae).

**Fig. 5** Phylogenetic relationships among the living lineages of *Synbranchiiformes* and *Carangiformes* (modified from Fig. 17 of Near and Thacker 2024)



Pelvic fins are also absent in *Mastacembelidae*, *Chaudhuriidae*, and some *Channidae* (Favorito et al. 2005; Rüber et al. 2006; Hastings et al. 2014).

Species of *Synbranchiiformes* usually engage in some form of egg guarding by the male involving mouthbrooding or the deposition of the eggs into bubble nests (*Osphronemidae*), plant or substrate nests (*Indostomidae*, *Chaudhuriidae*, *Mastacembelidae*, *Nandidae*), floating at the surface (*Channidae*), or in burrows (*Synbranchidae*); some species of *Synbranchus* are protogynous sequential hermaphrodites. *Helostomidae* and some *Anabantidae* are free

spawners; other *Anabantidae* are bubble nesters or mouthbrooders (Britz 1997; Rüber et al. 2004b, 2006; Favorito et al. 2005; Li et al. 2006; Britz et al. 2020). Some species of *Channa* attain large sizes and high fecundities, and that coupled with their ability to breathe air, survive out of water for extended periods, and locomote on land makes them highly invasive when transplanted (Courtenay and Williams 2004).

The historical biogeography of *Synbranchiiformes* is potentially tightly correlated to the movement of continents due to their nearly exclusive restriction to freshwater. Several lineages (*Osphronemidae*,

*Helostomatidae*, *Indostomidae*, and *Chaudhuriidae*) are restricted to Southern Asia, while the others (*Anabantidae*, *Channidae*, *Nandidae*, *Synbranchidae*, and *Mastacembelidae*) have a disjunct distribution that includes both South Asia and Central Africa. One possible explanation for this pattern is that those lineages originated in Africa prior to the breakup of eastern Gondwana 120–130 Ma and then some species were rifted northward on the Indian/Malagasy plate and delivered to southern Asia between 35 and 50 Ma, although no species of *Synbranchiformes* are distributed in Madagascar today. However, time-calibrated phylogenies that are not constrained by this biogeographic scenario estimate younger dates for the origin and diversification of synbranchiform lineages and infer a Southeastern Asian origin for the group, followed by dispersal into India and Africa (Li et al. 2006; Adamson et al. 2010; Rüber et al. 2020; Harrington et al. 2023). Paleontological evidence likewise rejects the Gondwanan vicariance scenario (Capobianco and Friedman 2019). Two genera of *Synbranchidae*, *Synbranchus* and *Ophisternon*, separately invaded Central America from Africa in the Miocene 12.7–23 Ma (Perdices et al. 2005). *Mastacembelidae* originated in Asia and migrated to Africa in the Miocene approximately 15.4 Ma, then radiated extensively throughout Central Africa including the Congo Basin and the Rift Valley Lakes during the Miocene (Day et al. 2017). Within the South Asian genera *Badis* and *Dario* (*Nandidae*), the phylogeny is consistent with vicariant speciation in several clades due to river drainage rearrangement caused by the uplift of the Tibetan Plateau in the late Oligocene to Miocene (19–23 Ma; Rüber et al. 2004a). The stem age of *Synbranchiformes* is estimated as 98.87 Ma (95% credible interval 87.37–110.69 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Synbranchiformes* are shown in Fig. 5.

### ***Eupercaria* (160 families and lineages, 7,073 species)**

#### ***Perciformes* (58 families and lineages, 3,200 species)**

*Acanthistiinae*\* (wirrahs), *Anthiidae* (fairly basslets), *Bembropidae* (duckbill flatheads), *Epinephelidae* (groupers), *Serranidae* (sea basses).

***Notothenoidei*:** *Aethotaxis* (Longfin Icedevil), *Bathydraconidae* (Antarctic dragonfishes), *Bovichtidae* (thornfishes), *Channichthyidae* (crocodile icefishes), *Dissostichus* (toothfishes), *Eleginopsidae*\* (Patagonian Blennie), *Gobionotothen* (goby rockcods), *Gvozdarus*, *Harpagiferidae* (spiny plunderfishes), *Nototheniidae* (cod icefishes), *Percophidae*\* (Brazilian Flathead), *Pleuragrammatinae*\* (Antarctic Silverfish), *Pseudaphritidae*\* (Congoli), *Trematominae* (notoperches).

***Percoidei*:** *Niponidae*\* (Ara Grouper), *Percidae* (perches and darters), *Trachinidae* (weeverfishes).

***Scorpaenoidei*:** *Anoplomatidae* (sablefishes), *Bembridgeae* (deepwater flatheads), *Gasterosteidae* (sticklebacks), *Platycephalidae* (flatheads), *Triglidae* (searobins).

***Cottoidea*:** *Agonidae* (poachers), *Cottidae* (sculpins), *Cyclopteridae* (lumpfishes), *Hexagrammidae* (greenlings), *Jordaniidae* (longfin sculpins), *Liparidae* (snailfishes), *Psychrolutidae* (marine sculpins), *Rhamphocottidae* (horsehead sculpins), *Scorpaenichthyidae*\* (Cabezón), *Trichodontidae* (sandfishes), *Zaniolepididae* (combfishes)

***Scorpaenoidea*:** *Congiopodidae* (pigfishes), *Hoplichthyidae*\* (spiny flatheads), *Neosebastidae* (gurnard scorpionfishes), *Normanichthyidae*\* (Mote Sculpin), *Plectrogeniidae* (stinger flatheads), *Scorpaenidae* (scorpionfishes), *Synanceiidae* (stonefishes)

***Zoarcoidea*:** *Anarhichadidae* (wolffishes), *Bathymasteridae* (ronquils), *Cebidichthyidae* (monkeyface pricklebacks), *Cryptacanthodidae*\* (wrymouths), *Eulophiidae* (spinous eelpouts), *Lumpenidae* (eel pricklebacks), *Neozoaridae* (largemouth kissing eelpouts), *Opisthocentridae* (rearspined fin pricklebacks), *Pholidae* (gunnels), *Ptilichthyidae*\* (Quillfish), *Stichaeidae* (pricklebacks), *Zaproridae*\* (Prowfish), *Zoaridae* (eelpouts)

Species of *Perciformes* are distributed globally in marine and freshwater environments, exhibiting significant presence in the nearshore marine areas of the Arctic and Antarctic as well as freshwater habitats across the Holarctic region. They include benthic and nektonic species, and body shapes are diverse, ranging from rhomboid to cylindrical and moderately elongate, with one or two dorsal fins and usually a forked or rounded tail (Hastings et al. 2014). Reproductive strategies include broadcast spawning, benthic deposition of eggs with parental care, and several instances of livebearing (Page et al. 1985; Yokoyama and Goto 2005; Hyde and Vetter 2007; Goto et al. 2014; La Mesa et al. 2020). *Perciformes* has had a long history as a catch-all taxon for lineages not morphologically distinct enough to be placed into other acanthopterygian groups (Dornburg and Near 2021; Near and Thacker 2024). Molecular phylogenies have been particularly effective at circumscribing *Perciformes* and resolving the relationships of the lineages within it (Smith and Wheeler 2004; Smith and Craig 2007; Smith and Busby 2014; Near et al. 2012b, 2015, 2018; Smith et al. 2018). The most species-rich lineages in this clade are *Liparidae* (448 species), *Scorpaenidae* (394 species), and *Zoarcidae* (314 species; Fricke et al. 2023; Near and Thacker 2024).

*Perciformes* includes several groups that encompass taxa traditionally placed in either *Perciformes* or *Scorpaeniformes*. *Percoidae* contains *Percidae*, a clade of 244 species distributed throughout the freshwater habitats in Eastern North America, Asia, and Europe, as well as its marine sister lineages *Trachinidae* and *Niponidae* (Near et al. 2013, 2015). The most species-rich genus of *Percidae* is *Etheostoma*, containing more than 160 species of small benthic fishes distributed primarily in the Eastern United States, with a complex history of speciation within and exchange among river drainages (Near et al. 2011; Near and Keck 2013; Kim et al. 2023). *Notothenoidei* is comprised of the radiation of icefishes, dragonfishes, and plunderfishes in circum-Antarctic waters and their sister lineages in Southern Hemisphere cold temperate habitats (Near et al. 2018). The ability of notothenioids to invade subzero polar waters is tied to the adaptation of antifreeze glycoproteins which bind to and encapsulate ice crystals in the blood, preventing their growth (Near et al. 2012a, 2015, 2018; Colombo et al. 2014).

*Scorpaenoidei* is most species-rich perciform subclade, with 2,208 species classified into *Scorpaenoidea*, *Cottoidea*, *Zoarcoidea*, *Gasterosteidae*, and three additional families (Ghezelayagh et al. 2022; Near and Thacker 2024). Most are marine, but the freshwater sculpin (*Cottidae*) radiations in Western North America and Eurasia are notable counterexamples (Smith and Wheeler 2004; Goto et al. 2014; Smith and Busby 2014). Species of *Sebastes* in the Eastern Pacific comprise a cold-temperate radiation of livebearers that cooccur across gradients of depth, temperature, and habitat (Hyde and Vetter 2007). *Zoarcoidea* species are marine, and many are small, elongate, and cryptic, sheltering on or in complex benthic habitats in cold temperate regions and the poles (Hotaling et al. 2021). Within *Scorpaenoidea*, many species bear spines on the head and opercles and in the fins, some of which are equipped with venom glands (Smith and Wheeler 2004, 2006).

The stem age of *Perciformes* is estimated as 93.73 Ma (95% credible interval 81.7–107.69 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Perciformes* are shown in Fig. 6.

### ***Centrarchiformes* (20 families, 304 species)**

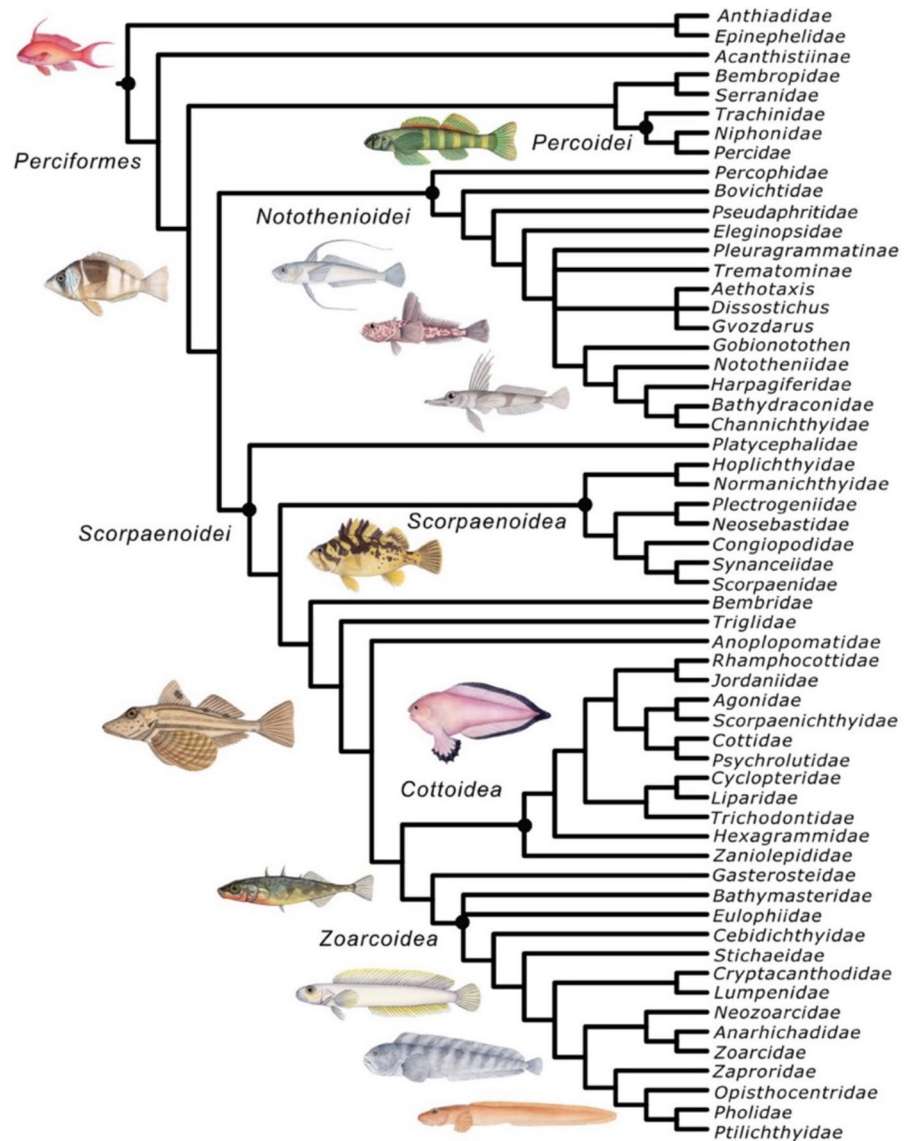
*Perkalates* (Australian basses).

***Centrarchoidei:*** \* *Aplodactylidae*\* (marblefishes), *Centrarchidae* (sunfishes and freshwater basses), *Cheilodactylidae*\* (fingerfins), *Chironemidae*\* (kelpfishes), *Cirrhitidae* (hawkfishes), *Enoplosidae*\* (Oldwife), *Latridae* (trumpeters), *Parascorpididae*\* (Jut-jaw), *Percichthyidae* (temperate basses), *Sinipercidae* (Chinese perches).

***Terapontoidei:*** \* *Caesioscorpididae*\* (Blow-hole Perch), *Dichistiidae*\* (galjoens), *Girellidae* (nibblers), *Kuhliidae*\* (flagtails), *Kyphosidae* (sea chubs), *Microcanthidae* (stripeys), *Oplegnathidae*\* (knifejaws), *Scorpididae* (halfmoons), *Terapontidae* (grunters).

*Centrarchiformes* comprises a clade of species distributed in nearshore marine habitats in the Atlantic, Pacific, and Indian Oceans, with freshwater lineages (*Centrarchidae*, *Percichthyidae*, *Sinipercidae*, *Terapontidae*) in North America, Australia, New Guinea, South America, and East Asia. Several groups (*Aplodactylidae*, *Caesioscorpididae*, *Cheilodactylidae*,

**Fig. 6** Relationships among the living lineages of *Perciformes* (modified from Fig. 18 of Near and Thacker 2024)



*Chironemidae*, *Enoplosidae*, *Latridae*, *Percalates*, *Percichthyidae*, *Terapontidae*) are known exclusively from the Southern Hemisphere, particularly in and around Australia. Others are restricted to temperate North America (*Centrarchidae*) or East Asia (*Siniperca*), with the remaining lineages (*Cirrhitidae*, *Dichistiidae*, *Girellidae*, *Kuhliidae*, *Kyphosidae*, *Microcanthidae*, *Oplegnathidae*, *Parascorpididae*, *Scorpididae*) distributed widely in temperate and tropical oceans (Burrige and Smolenski 2004; Davis et al. 2012; Knudsen and Clements 2013; Chen et al. 2014a; Arratia and Quezada-Romegialli 2019; Ludt et al. 2019).

The body of centrarchiform species is usually ovoid or disc-shaped, generally with a single dorsal fin (often with a notch between the spinous and rayed portions) and a forked or truncate tail. Most species of *Centrarchiformes* are predators of other fishes and invertebrates, but dietary diversity in the clade includes durophagous (e.g., *Oplegnathus*) and herbivorous species (e.g., *Aplodactylus*, *Kyphosidae*, *Hephaestus*, and *Scortum*) (Davis et al. 2016a, b; Maschette et al. 2020; Johnson and Clements 2022). Parental care through nest guarding is widespread in the freshwater lineages *Percichthyidae* and *Centrarchidae* (Growth 2004; Neff and Knapp 2009).

*Centrarchiformes* are economically important as many species are the targets of commercial and recreational fisheries (Long et al. 2015; Taylor et al. 2019). The most species-rich lineages in this clade are *Terapontidae* (62 species), *Centrarchidae* (47 species), and *Cirrhitidae* (35 species); most of the lineages contain 20 or fewer species (Fricke et al. 2023; Near and Thacker 2024).

*Centrarchiformes* were first resolved as a clade in molecular phylogenetic analyses in the first wave of studies with an inclusive taxon sampling of percomorph lineages that used mitochondrial and nuclear gene sequences (Near et al. 2012b, 2013; Betancur-R et al. 2013; Chen et al. 2014b; Sanciangco et al. 2016). There are three major lineages of *Centrarchiformes*: (1) *Percalates*, resolved as the sister lineage of all other *Centrarchiformes* (Fig. 18; Near et al. 2012b; Chen et al. 2014b; Lavoué et al. 2014; Ghezelayagh et al. 2022); (2) *Terapontoidei*, including *Girellidae*, *Scorpididae*, *Parascorpius typus*, *Dichistius*, *Microcanthidae*, *Caesiocorpius theagenes*, *Oplegnathus*, *Kyphosidae*, *Kuhlia*, and *Terapontidae* (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*, *Percichthyidae*, *Centrarchidae*, *Sinipercidae*, *Cirrhitidae*, *Latridae*, *Chironemus*, *Cheilodactylus*, and *Aplodactylus* (Li et al. 2010; Near et al. 2012b, 2013; Sanciangco et al. 2016; Betancur-R et al. 2017; Song et al. 2017; Ghezelayagh et al. 2022). The seven species of North American freshwater *Elassoma* (pygmy sunfishes) are classified in *Centrarchidae* based on molecular phylogenetic analyses (Near et al. 2012c; Chen et al. 2014a, b; Ghezelayagh et al. 2022).

The two largest radiations within *Centrarchiformes*, *Centrarchidae* and *Terapontidae*, occur in freshwater. *Centrarchidae* are widely distributed in the rivers of the Eastern United States, and freshwater *Terapontidae* (genera *Amniataba*, *Bidyanus*, *Hannia*, *Hephaestus*, *Lagusia*, *Leiopotherapon*, *Pingala*, *Scortum*, *Syncomistes*, and *Variichthys*) inhabit Australia, New Guinea, and parts of Southeast Asia, with the highest diversity in the Kimberly region of Northwestern Australia (Near et al. 2004, 2005; Shelley et al. 2019, 2020b; Near and Kim 2021). In both *Centrarchidae* and *Terapontidae*, the availability of time-calibrated phylogenies has enabled macroevolutionary studies investigating topics that include the

role of dietary specialization on phenotypic evolution and diversification (Collar et al. 2005, 2009; Davis et al. 2012, 2016a, b), the evolution of post-zygotic reproductive isolation (Bolnick and Near 2005; Bolnick et al. 2006, 2008), and the patterns of allopatric speciation among adjacent geographic regions (Sandel et al. 2014; Shelley et al. 2020c; Kim et al. 2022a). Species discovery and delimitation in *Centrarchiformes* remains an active area of research, particularly using molecular data (Shelley et al. 2020b; Kim et al. 2022a, b). The stem age of *Centrarchiformes* is estimated as 83.17 Ma (95% credible interval 75.25–92.76 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Centrarchiformes* are shown in Fig. 7.

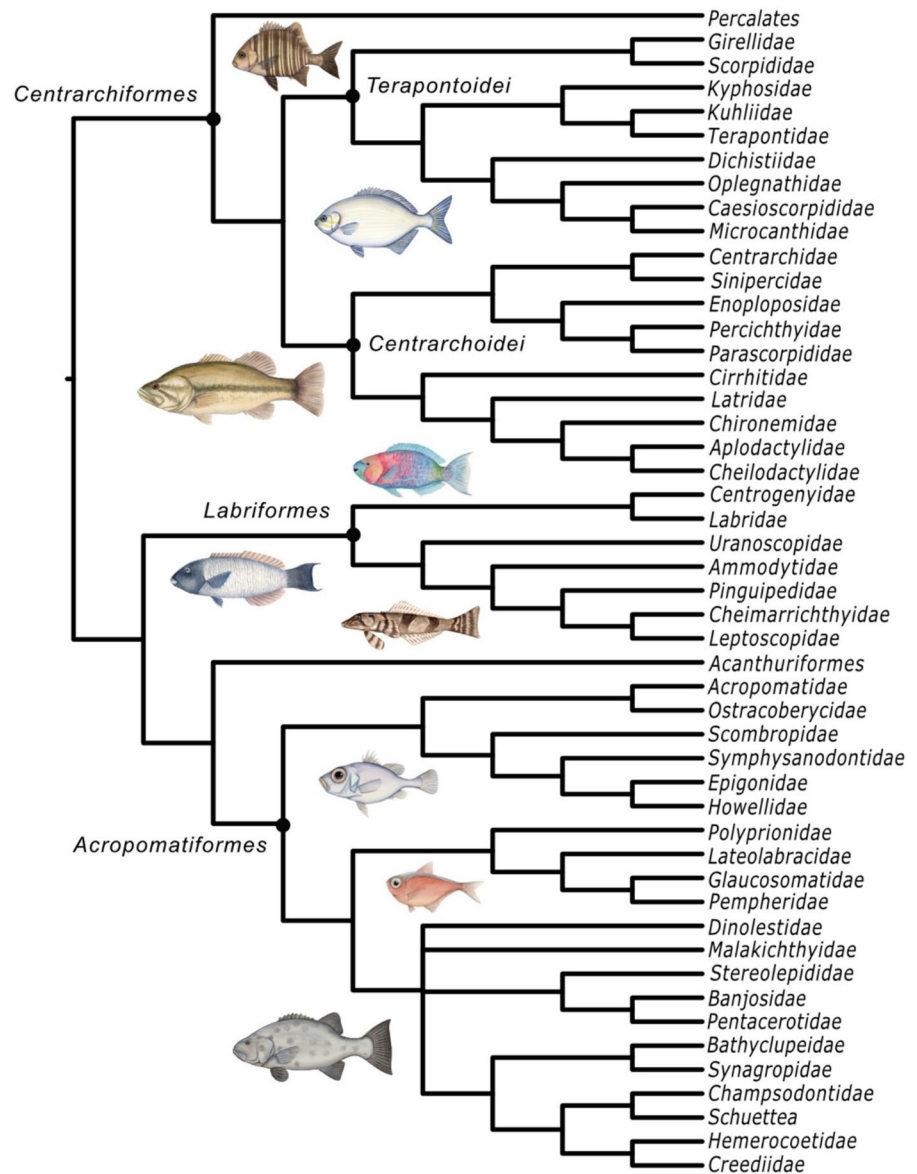
### ***Labriformes* (7 families, 887 species)**

*Ammodytidae* (sand lances), *Centrogenyidae*\* (False Scorpionfish), *Cheimarrichthyidae*\* (New Zealand Torrentfish), *Labridae* (wrasses and parrotfishes), *Leptoscopidae* (southern sandfishes), *Pinguipedidae* (sandperches), *Uranoscopidae* (stargazers).

*Labriformes* are exclusively marine, except for the amphidromous *Cheimarrichthys fosteri*. The clade includes many reef-dwelling species as well as several lineages that are benthic or burrow in sand. *Labriformes* comprises two clades, one containing *Labridae* as sister to *Centrogenyidae* and a second including *Ammodytidae*, *Cheimarrichthyidae*, *Leptoscopidae*, *Pinguipedidae*, and *Uranoscopidae*. *Labridae* range in shape from oblong to elongate and cylindrical, generally with either rounded or truncate caudal fins (Hastings et al. 2014). *Labridae* (680 species) is the most species-rich lineage, followed by *Pinguipedidae* (100 species) and *Uranoscopidae* (59 species; Fricke et al. 2023; Near and Thacker 2024).

*Labridae* includes some of the most brightly colored and charismatic reef fishes, including the fairy wrasses (*Cirrhilabrus*), flasher wrasses (*Paracheilinus*), rainbow wrasses (*Coris*), cleaner wrasses (*Labroides*), the parrotfish genera *Scarus* and *Sparisoma*, and the many species of *Halichoeres* and *Thalassoma* (Westneat and Alfaro 2005; Kazancioğlu et al. 2009; Tea et al. 2022). *Labridae* are characterized by the presence of a complex of oral and pharyngeal jaw specializations (pharyngognathy) resulting in a robust, mobile, and versatile feeding

**Fig. 7** Phylogenetic relationships among the living lineages of crown *Euperacaria*, focusing on *Centrarchiformes*, *Labriformes*, and *Acropomatiformes* (modified from Fig. 19 of Near and Thacker 2024)



apparatus that enables them to consume a wide variety of prey, including the fused oral teeth and pharyngeal mills with which parrotfishes grind coral and other hard substrates which they then excrete as sand (Westneat 1995; Mabuchi et al. 2007; Kazancioglu et al. 2009; Price et al. 2011; Wainwright et al. 2012). The labrid sister lineage *Centrogenyidae* shares some of the pharyngeal jaw modifications found in *Labridae* but it is benthic and has mottled coloration that resembles a scorpionfish, likely an adaptation for camouflage or possibly to mimic the venomous *Scorpaena* (Ghezelayagh et al. 2022). Most *Labridae*

and *Centrogenyidae* are less than 25 cm in length although some wrasse species may be much larger, including the Humphead Wrasse (*Cheilinus undulatus*) and the Green Humphead Parrotfish (*Bolbometopon muricatum*) in tropical Indo-Pacific waters, and the California Sheephead (*Semicossyphus pulcher*) in the temperate Eastern Pacific. Both *Labridae* and *Centrogenyidae* have single continuous dorsal fins with distinct spinous and rayed portions.

The sister lineage of the clade that includes *Labridae* and *Centrogenyidae* includes several groups whose species are benthic and often burrow into sand

substrates, plus the New Zealand endemic *Cheimarrichthyidae* which are amphidromous and inhabit fast-flowing streams (Scrimgeour and Eldon 1989). Species of *Uranoscopidae* and *Leptoscopidae* have dorsally placed eyes and bury themselves in sand. They are ambush predators and some species of *Uranoscopidae* have a lure modified from the buccal tissue that they use for prey attraction. Species of *Uranoscopidae* additionally bear paired venomous spines behind the opercles, and some species have electrogenic organs in their heads; both the spines and electric shocks are used for hunting and defense (Kishimoto 2001; Smith and Wheeler 2006). Species of *Leptoscopidae* inhabit the coastal waters of Australia and New Zealand and are also benthic ambush predators. Species of *Ammodytidae* are distributed worldwide but most are distributed in the cold temperate North Pacific and North Atlantic. They are also burrowers, with long slender bodies lacking swim bladders and pelvic fins, and species of *Ammodytes* spend part of the year dormant under the sand (Robards and Piatt 1999). Species of *Pinguipedidae* are benthic but do not burrow, they are active predators distributed worldwide in reef and sandy habitats. Species of *Cheimarrichthyidae* are known only from New Zealand and are benthic and specialized for life in fast-flowing streams. Species of *Leptoscopidae* and *Ammodytidae* have continuous dorsal fins; those in *Pinguipedidae* and *Uranoscopidae* have a distinct anterior spined portion, and *Cheimarrichthyidae* have the anterior dorsal spines each separate at the origin of the fin (McDowall 1973).

Within *Labridae*, most species are sequential protogynous hermaphrodites, but not all individuals are born female; some are primary males. Among the primary females, some will transition after attaining their adult sizes and the color morphs of these secondary males are different from those of primary males and females (Warner and Robertson 1978; Kazancioglu and Alonso 2010; Choat et al. 2012; Kuwamura et al. 2020). Generally, labrid species are broadcast spawners with various types of group spawning, but temperate species in *Centrolabrus*, *Labrus*, and *Symphysodus* engage in nest building and egg guarding by the male (Hanel et al. 2002). The reproductive strategies among *Uranoscopidae*, *Leptoscopidae*, and *Ammodytidae* are not as well known, but those that have been observed are benthic spawners with planktonic larvae (eggs are also planktonic in *Uranoscopus*;

Çoker et al. 2008) and no parental care (Robards and Piatt 1999; Han et al. 2012). *Pinguipedidae* are also benthic spawners and at least some species of *Parapercis* are protogynous hermaphrodites, with large males controlling a territory inhabited by a harem of females (Walker et al. 2007; Villanueva-Gomila et al. 2015). *Cheimarrichthyidae* are amphidromous, spawning in freshwater with larvae swept out to sea then returning to freshwater as juveniles (McDowall 1973; Scrimgeour and Eldon 1989). Many species of reef-dwelling *Labridae* engage in cleaning behaviors, obligately or facultatively, and the various types of cleaning strategy have evolved repeatedly within the group (Baliga and Law 2016). The stem age of *Labriiformes* is estimated as 81.03 Ma (95% credible interval 73.25–89.3 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Labriiformes* are shown in Fig. 7.

#### ***Acropomatiformes* (21 lineages, 306 species)**

*Acropomatidae* (lanternbellies), *Banjosidae*\* (banjofishes), *Bathyclupeidae* (deepsea herrings), *Champsodontidae*\* (gapers), *Creediidae* (sand burrowers), *Dinolestidae*\* (Long-finned Pike), *Epigonidae* (deepwater cardinalfishes), *Glaucosomatidae*\* (pearl perches), *Hemerocoetidae* (Indo-Pacific duckbills), *Howellidae* (oceanic basslets), *Lateolabracidae*\* (Asian seaperches), *Malakichthyidae* (temperate ocean-basses), *Ostracoberycidae*\* (shell-skin alfonosinos), *Pempheridae* (sweepers), *Pentacerotidae* (armorheads), *Polyprionidae*\* (wreckfishes), *Schuettea* (moonyfishes), *Scombropidae*\* (gnomefishes), *Stereolepididae*\* (giant sea basses), *Symphysanodontidae*\* (slopefishes), *Synagropidae* (splitfin ocean-basses).

*Acropomatiformes* is a recently identified group that includes 21 lineages, most of which contain only one or a few species (Davis et al. 2016a, b; Ghezelayagh et al. 2022; Smith et al. 2022). Species of *Acropomatiformes* inhabit nearshore and offshore marine habitats worldwide, frequently in deeper waters. They are generally schooling fishes; nearshore groups are often nocturnal (*Pempheridae*, *Glaucosomatidae*, *Malakichthyidae*, *Dinolestidae*) and several groups are bathypelagic or bathydemersal. Species of *Acropomatidae*, *Ostracoberycidae*, *Symphysanodontidae*, *Polyprionidae*, *Banjosidae*, *Pentacerotidae*,

*Bathyclupeidae*, *Synagropidae*, *Champsodontidae*, and *Malakichthyidae* occur from depths of roughly 200–500 M. Species of *Epigonidae* and *Howellidae* are the deepest-dwelling acropomatiforms and can be found below 1200 M (Smith et al. 2022). Most species are laterally compressed with an ovoid to rhomboid body, a forked tail, and one or two dorsal fins (Smith et al. 2022). Some attain very large sizes (*Polyprion* may be as large as 2 M), others are small and burrow in sand (*Creedidae*, *Hemerocoetidae*). The most species-rich lineages of *Acropomatiformes* are *Pempheridae* (85 species) and *Epigonidae* (48 species; Fricke et al. 2023; Near and Thacker 2024).

Reproductive patterns are known for only a few of the acropomatiform lineages and are characterized by pelagic spawning in seasonal aggregations (Koeda et al. 2012; Coulson et al. 2016; Allen et al. 2020). Given their similar ecologies, it is likely that most of the lineages are aggregate spawners, apart from the benthic *Creedidae* and *Hemerocoetidae*. *Stereolepis gigas*, the Giant Sea Bass known from the kelp forests of the Eastern Pacific, aggregates to spawn in summer and produces low-frequency booming sounds by compressing the swim bladder and drumming on it with its ribs (Allen et al. 2020). These sounds are used in aggressive interactions but may also be part of courting and spawning behaviors. Several species of *Pempheridae*, *Acropomatidae*, *Epigonidae*, and *Howellidae* are bioluminescent (Thacker and Roje 2009; Davis et al. 2016a, b; Ghedotti et al. 2018; Smith et al. 2022), with light organs derived from pockets of the gut that include elaborate epithelial folds, creating chambers that host symbiotic luminescent bacteria. The fishes take up luminescent bacteria from ocean water and the light they produce is transmitted ventrally through transparent musculature (Davis et al. 2016a, b; Ghedotti et al. 2018).

The phylogenetic relationships among groups within *Acropomatiformes* are still uncertain; several studies have included many of the acropomatiform lineages and some of the resolved relationships are consistent, but resolution among the deepest branches and nodes of the phylogeny are poorly supported (Near et al. 2013; Thacker et al. 2015; Betancur-R et al. 2017; Satoh 2018; Oh et al. 2021). Smith et al. (2022) placed the enigmatic genus *Hemilutjanus* within *Malakichthyidae* and provided evidence that the genus *Schuetta* is also part of *Acropomatiformes*, although with uncertain phylogenetic resolution.

The stem age of *Acropomatiformes* is estimated as 80.09 Ma (95% credible interval 73.1–88.58 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Acropomatiformes* are shown in Fig. 7.

### ***Acanthuriformes* (54 families, 2,376 species)**

*Callanthiidae* (splendid perches), *Caproidae* (boarfishes), *Cepolidae* (bandfishes), *Chaetodontidae* (butterflyfishes), *Dinopercidae* (cavebasses), *Drepaneidae*\* (sicklefishes), *Emmelichthyidae* (rovers), *Ephippidae* (spadefishes and batfishes), *Gerreidae* (mojarra), *Haemulidae* (grunts), *Leiognathidae* (ponyfishes), *Lethrinidae* (emperor snappers), *Lobotidae* (triple tails and tigerperches), *Lutjanidae* (snappers), *Malacanthidae* (tilefishes), *Monodactylidae* (moonies), *Moronidae* (temperate basses), *Nemipteridae* (threadfin breams and spinycheeks), *Pomacanthidae* (angelfishes), *Priacanthidae* (bigeyes), *Scatophagidae* (scats), *Sciaenidae* (croakers and drums), *Siganidae*\* (rabbitfishes), *Sillaginidae* (sillagos), *Sparidae* (porgys and seabreams).

***Acanthuroidei:*** *Acanthuridae* (surgeonfishes and unicornfishes), *Luvaridae*\* (Louvar), *Zanclidae*\* (Moorish Idol).

***Lophioidei:*** *Antennariidae* (Fibonacci frogfishes), *Caulophrynidae* (fanfins), *Centrophrynidae*\* (Prickly Seadevil), *Ceratiidae* (seadevils), *Chaunacidae* (sea toads), *Diceratiidae* (double spine seadevils), *Gigantactinidae* (whipnose seadevils), *Himantolophidae*\* (footballfishes), *Linophrynidae* (leftvent seadevils), *Lophichthyidae*\* (Boschma's Frogfish), *Lophiidae* (goosefishes), *Melanocetidae*\* (black seadevils), *Neoceratiidae*\* (Spiny Seadevil), *Ogcocephalidae* (batfishes), *Oneirodidae* (dreamers), *Thaumatichthyidae* (wolftrap seadevils).

***Tetraodontoidei:*** *Aracanthidae* (deepwater boxfishes), *Balistidae* (triggerfishes), *Diodontidae* (porcupinefishes and burrfishes), *Molidae* (ocean sunfishes), *Monacanthidae* (filefishes), *Ostraciidae* (boxfishes), *Tetraodontidae* (puffers), *Triacanthidae* (triplespines), *Triacanthodidae* (spikefishes), *Triodontidae*\* (Threetooth Puffer).

*Acanthuriformes* contains many of the larger-bodied shore and reef fishes including well-known food fish species of *Lutjanidae*, *Haemulidae*, *Sparidae*, and *Sciaenidae*, as well as *Tetraodontoidei* and its

sister clade *Lophioidei*. Their body shape is generally either laterally compressed, robust, and often oblong or rounded in profile with a single dorsal fin, or else globose, rectangular, or trapezoidal, as seen in *Tetraodontoidei* and *Lophioidei* (Hastings et al. 2014). The unusual shapes in *Tetraodontoidei* are complemented by the presence of thickened skin ornamented in many species with scales modified into plates or spines. Species of *Tetraodontidae* and *Diodontidae* can inflate their bodies by rapidly suctioning water into the stomach as a defense mechanism (Matsuura 2015b); in *Diodontidae*, this causes the strong spines covering the body to project outwards. *Acanthuriformes* also includes the reef fish groups *Acanthuridae*, *Chaetodontidae*, *Pomacanthidae*, and *Zanclidae*, as well as the viscerally bioluminescent, sexually dimorphic *Leiognathidae* (Sparks and Dunlap 2004; Chakrabarty et al. 2011) and venomous *Siganidae* (Smith and Wheeler 2006). All inhabit marine environments except for a few lineages in fresh and brackish water. The most species-rich lineages in *Acanthuriformes* are *Sciaenidae* (298 species), *Tetraodontidae* (193 species), and *Sparidae* (164 species; Fricke et al. 2023; Near and Thacker 2024).

Reproductive patterns among acanthuriform lineages, where documented, generally involve high fecundity and pelagic spawning in small to large aggregations, often with courtship behaviors and in a few lineages with subsequent parental care of the eggs. The spawning aggregations may involve thousands of individuals migrating to spawning grounds, occur in synchrony with lunar or seasonal cycles, and be specifically triggered to time of day by light levels (Colin and Clavijo 1988; Myrberg et al. 1988). Species of *Tetraodontoidei* also aggregate to spawn, particularly the larger pelagic species such as molas and sunfishes (Hellenbrecht et al. 2019). Species of *Tetraodontidae*, *Monacanthidae*, and *Balistidae* spawn in pairs or small harems on the substrate, in some cases depositing eggs in or on the sand, in others building and guarding complex radial sand nests (Kawase 2002; Matsuura 2015a; Kawase et al. 2017). Sequential hermaphroditism, generally protogynous or protandrous but sometimes bidirectional, is common among species of *Pomacanthidae*, *Nemipteridae*, *Lethrinidae*, *Sparidae*, and *Balistidae* (Kuwamura et al. 2020). Species of *Lophioidei* are all sexually dimorphic, with males much smaller than females (Pietsch 2009; Pietsch et al. 2013; Pietsch and Arnold

2020). Reproduction in *Lophioidei* ranges from free spawning onto the substrate or into the water column, to benthic egg guarding in a nest, and in a few frogfish species, brooding of the eggs in the pectoral fins, a pocket formed by curling the dorsal, caudal, and anal fins, or on the flanks of the female (Mori et al. 2022). Eggs are laid in a gelatinous mass (Pietsch and Arnold 2020). The deep sea anglerfishes are known for the extreme and unique system of miniaturized, parasitic males which attach to and fuse with the much larger females, acting as an external testis. This strategy is present in species of *Ceratiidae*, *Linophrynidae*, and *Neoceratiidae* (Pietsch 2009; Brownstein et al. 2024).

Phylogenies of *Acanthuriformes* have been inferred as part of larger molecular phylogenetic studies (Holcroft and Wiley 2008; Betancur-R et al. 2013; Hughes et al. 2018; Ghezelayagh et al. 2022) and they agree in resolving *Caproidae* as the sister lineage of a crown clade containing *Lophioidei* and *Tetraodontoidei*. The remaining acanthuriform lineages are resolved in a pectinate pattern with shallow internodes along the backbone of the phylogeny. Clades consistently resolved in molecular phylogenetic analyses with the densest taxon sampling include a clade containing *Acanthuridae*, *Luvaridae*, and *Zanclidae* (*Acanthuroidei*); the resolution of *Chaetodontidae* and *Leiognathidae* as sister taxa; and a clade containing *Nemipteridae*, *Lethrinidae*, and *Sparidae* (Betancur-R et al. 2013; Ghezelayagh et al. 2022). The phylogenetic resolution of *Gerreidae* is particularly controversial, with Ghezelayagh et al. (2022) placing it as the sister lineage to all other *Acanthuriformes*, however Betancur-R et al. (2013) and Hughes et al. (2018) resolved it outside of *Acanthuriformes*. The most detailed phylogenetic work has been in studies focusing on the relationships of *Acanthuridae*, *Chaetodontidae*, *Leiognathidae*, *Pomacanthidae*, *Lutjanidae*, *Haemulidae*, *Sciaenidae*, *Nemipteridae*, *Lethrinidae*, and *Sparidae*.

Time-calibrated phylogenetic relationships within the reef-associated *Acanthuridae*, *Chaetodontidae*, and *Pomacanthidae* estimate the origin of *Acanthuridae* at 54 Ma in the Eocene (Sorenson et al. 2013). Similarly, the colorful, disc shaped *Chaetodontidae* have an Eocene origin, with slightly different root age estimates (50–54 Ma) obtained in different studies (Fessler and Westneat 2007; Bellwood et al. 2009), followed by intrafamilial divergences throughout

the Miocene approximately 14–24 Ma and young endemic species in the Red and Arabian Seas arising with the invasion of deeper reef habitats (Cowman and Bellwood 2011; DiBattista et al. 2018). Relaxed molecular clock analyses of *Pomacanthidae* place the origin of the group in the Eocene (52 Ma in Gaither et al. 2014), with diversification among lineages spanning the Oligocene and Miocene. Biogeographic reconstructions indicate a Pacific origin for *Pomacanthidae*, with lineage diversification coinciding with the Miocene Terminal Tethyan Event and fragmentation of Indo-Pacific reef habitats as well as repeated independent invasions of the Atlantic and Eastern Pacific along different routes (Bellwood et al. 2004; Baraf et al. 2019). Species of *Pomacanthidae* as well as *Chaetodontidae*, *Acanthuridae*, *Balistidae* and *Tetraodontidae* hybridize in the Eastern Indian Ocean at both Christmas and Cocos-Keeling Islands, areas of secondary contact between fishes inhabiting the Indian and Pacific Oceans (Hobbs et al. 2009; Hobbs and Allen 2014; DiBattista et al. 2016). Pairs of species in *Acanthuriformes* dominate the hybrid combinations found in those areas, although some *Labridae* (*Labriformes*), *Pomacentridae* (*Blenniiformes*), and *Serranidae* (*Perciformes*) also hybridize there (Hobbs and Allen 2014).

Molecular phylogenetic hypotheses for *Sparidae*, *Lethrinidae*, and *Nemipteridae* have facilitated an untangling of long-standing taxonomic issues and identifying convergence among morphological characters (Chiba et al. 2009; Hung et al. 2017; Chen and Borsa 2020). Phylogenetic studies of *Lutjanidae*, *Haemulidae*, and *Sciaenidae* have also addressed taxonomic questions (Sanciangco et al. 2011; Lo et al. 2017; Veneza et al. 2019; da Silva et al. 2023) as well as inferring divergence times. Compared to other acanthuriform lineages, relatively old stem (~62 Ma) and crown (~54 Ma) ages are inferred for species of *Lutjanidae*, which occupy habitats ranging from estuaries, through shallow reef and near-reef habitats, to shelf habitats of 200 M depth or more (Frédérich and Santini 2017), and so are less tightly dependent on reef habitats than species of *Acanthuridae*, *Chaetodontidae*, or *Pomacanthidae*.

Relaxed molecular clock analyses estimate an origin of *Haemulidae* in the Eocene (55 to 42 Ma) followed by radiation of the relatively species-rich lineages in the Oligocene, 25 to 30 Ma (Tavera et al. 2018). Species of *Haemulidae* also occupy a variety

of habitats, including soft bottomed sand or mud as well as harder substrates including rocks and reef. The soft bottom habitat is ancestral for *Haemulidae*, with invasions of rocky and reef habitats occurring in three clades independently (Price et al. 2012). A time-calibrated molecular phylogeny of *Sciaenidae* reveals repeated transitions between marine, estuarine and freshwaters with an estimated crown age of 27.3 Ma (Oligocene) for the group, with divergences among major lineages taking place throughout the Miocene (Lo et al. 2015). *Sciaenidae* is inferred to have originated in the Eastern Pacific or Western Atlantic, followed by eastward expansion into the Eastern Atlantic and Indo-Pacific; the Indo-Pacific is the current area of greatest species diversity of sciaenids (Lo et al. 2015). *Haemulidae* and *Sciaenidae* are closely related and both produce sounds, although the mechanisms of sound generation differ. *Haemulidae* grunt by grinding their pharyngeal teeth (Tavera et al. 2018) and *Sciaenidae* croak or drum using vibration of muscles against the swim bladder, which functions as a resonance chamber (Lo et al. 2015).

The crown clade in *Acanthuriformes* consists of *Tetraodontoidei* and *Lophioidei*. This clade includes the globose *Tetraodontidae*, *Triodontidae*, and *Diodontidae*; the laterally compressed, rhomboid *Balistidae*, *Monacanthidae*, *Triacanthodidae*, *Triacanthidae*, and *Molidae*; the rectangular *Aracanidae* and *Ostraciidae*; the shallow benthic *Antennariidae*, *Lophichthyidae*, and *Ogocephalidae*; the deep water benthic *Lophiidae*; and twelve lineages of deep sea anglerfishes, mostly spherical to oblong, drably colored, with reduced eyes and weak ossification (Pietsch 2009; Hastings et al. 2014). All *Lophioidei* (except for *Neoceratias*) are equipped with a highly modified first dorsal spine used for attracting prey, placed on the midline near the eyes and composed of a line (illicium) and a terminal lure (esca). The escas of *Antennariidae*, *Lophichthyidae*, *Lophiidae*, and *Ogocephalidae* range in size from small knobs to enlarged frilly or worm-shaped structures; the escas of the deep sea anglerfishes also range from small to elaborate and are bioluminescent, hosting symbiotic bacteria (Pietsch 2009; Pietsch and Arnold 2020). Species of *Antennariidae* are ambush predators, covered with skin flaps and patterns that make them highly camouflaged on the substrate (Arnold and Pietsch 2012). They use their illicium to attract prey which they then consume with extremely

rapid suction (Pietsch and Arnold 2020). Relationships among lineages within *Lophioidei* have been inferred in comprehensive molecular phylogenies (Miya et al. 2010; Near et al. 2013; Betancur-R et al. 2017; Rabosky et al. 2018; Ghezelayagh et al. 2022; Hart et al. 2022), and those studies generally concur in recovering *Lophiidae* as sister to the remaining families, a close relationship between *Antennariidae* (encompassing the lineages *Brachionichthyidae*, *Tetrabrachiidae*, *Histiophrynidae*, *Rhycheridae*, and *Tathicarpidae* as used in Hart et al. 2022) and *Ogcocephalidae*, and *Chaunacidae* as sister to the deep sea anglerfish lineages.

Phylogenies of *Tetraodontoidei* mostly agree in recovering several clades: sister lineages of *Triacanthidae* and *Triacanthodidae*; *Diodontidae* and *Tetraodontidae*; *Balistidae* and *Monacanthidae*; and *Araucanidae* and *Ostraciidae*. Phylogenies differ on the resolutions among those clades, and in the placements of *Triodontidae* and *Molidae* (Alfaro et al. 2007; Near et al. 2013; Santini et al. 2013; Matsuura 2015b; Betancur-R et al. 2017; Arcila and Tyler 2017; Ghezelayagh et al. 2022; Troyer et al. 2022). The stem age of *Acanthuriformes* is estimated as 80.09 Ma (95% credible interval 73.1–88.58 Ma) based on Bayesian analysis of ultraconserved element sequence data (Ghezelayagh et al. 2022). Phylogenetic relationships among the living lineages of *Acanthuriformes* are shown in Fig. 8.

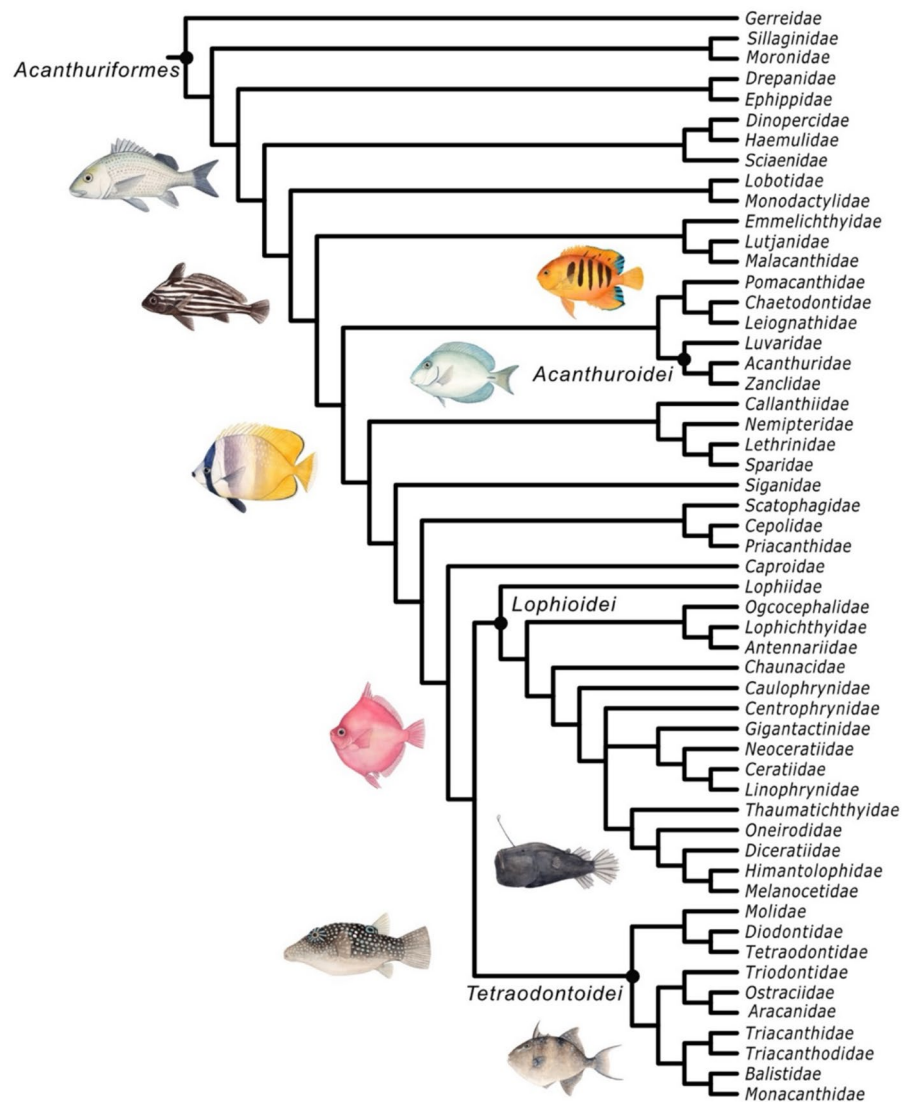
## Discussion

The phylogenetic pattern of acanthopterygian evolution is characterized by a mosaic distribution of notable traits with few broad trends. Features such as cutaneous and visceral bioluminescence, venom, specializations in the oral and pharyngeal jaws, complex mutualisms, muscular electrogenesis and thermogenesis, sound production, and various reproductive and parental care behaviors have arisen repeatedly throughout the entire radiation (Hanel et al. 2002; Little et al. 2010; Wainwright et al. 2012; Davis et al. 2016a, b; Smith et al. 2016). Acanthopterygian lineages have evolved in concert with their habitats and shifting continental landscapes, in particular the multiple transitions between shallow and deep seas, tropical and polar latitudes, marine and freshwater, and the long coevolution of fishes on reefs (Cowman

and Bellwood 2011, 2013a, 2013b; Brandl et al. 2018; Rabosky et al. 2018; Capobianco and Friedman 2019; Miller et al. 2022). Of the 16 acanthopterygian clades, five are exclusively marine (*Beryciformes*, *Trachichthyiformes*, *Scombriformes*, *Labriformes*, *Acropomatiformes*), five are primarily marine with a few freshwater lineages (*Ophidiiformes*, *Batrachoididae*, *Syngnathiformes*, *Carangiformes*, *Acanthuriformes*), five have significant representation in both marine and freshwater (*Gobiiformes*, *Atheriniformes*, *Blenniiformes*, *Perciformes*, and *Centrarchiformes*) and *Synbranchiformes* is unique in almost exclusively occupying freshwater habitats. *Synbranchiformes* is also the only acanthopterygian clade that does not have a worldwide distribution, inhabiting primarily Asia, Africa, Australia, and islands of the Indo-Pacific, with only a few lineages in the Neotropics. All acanthopterygian clades are found in tropical and temperate habitats, but in polar regions the primary representatives are several lineages of *Perciformes*. Arctic and Antarctic habitats each host a variety of *Cottoidea* and *Zoarcoidea*, and in Antarctic seas the primary acanthopterygian representatives are the icefishes, dragonfishes and plunderfishes in *Notothenioidei* (Near et al. 2012a; Rabosky et al. 2018).

Acanthopterygian clades have radiated globally throughout their history, successfully dispersing by means of nearly every potential aquatic pathway. Biogeographic analyses of acanthopterygian groups usually infer multiple invasion events into and out of newly occupied regions, with even sporadic long-distance dispersal events becoming likely over long timescales. The only biogeographic pattern that has been refuted for acanthopterygian clades is that of Gondwanan vicariance, potentially manifesting as sister group splits between freshwater lineages in South America and Africa or evolutionary links between Africa, Asia, and Australia due to Gondwanan breakup and northward rafting of the Indian subcontinent. Although that mechanism is likely responsible for distributions of older lineages such as *Lepidosireniiformes*, *Osteoglossiformes*, and certain *Ostariophysii*, the acanthopterygian lineages are simply too young (Friedman et al. 2013b; Capobianco and Friedman 2019; Adamson et al. 2010; Harrington et al. 2023). Ghezelayagh et al. (2022) dates the origin of *Acanthopterygii* at 145 Ma in the earliest Cretaceous, with the major acanthopterygian clades arising throughout the Cretaceous between 137 and 80 Ma. With all of

**Fig. 8** Phylogenetic relationships among the living lineages of *Acanthuriformes* (modified from Fig. 20 of Near and Thacker 2024)

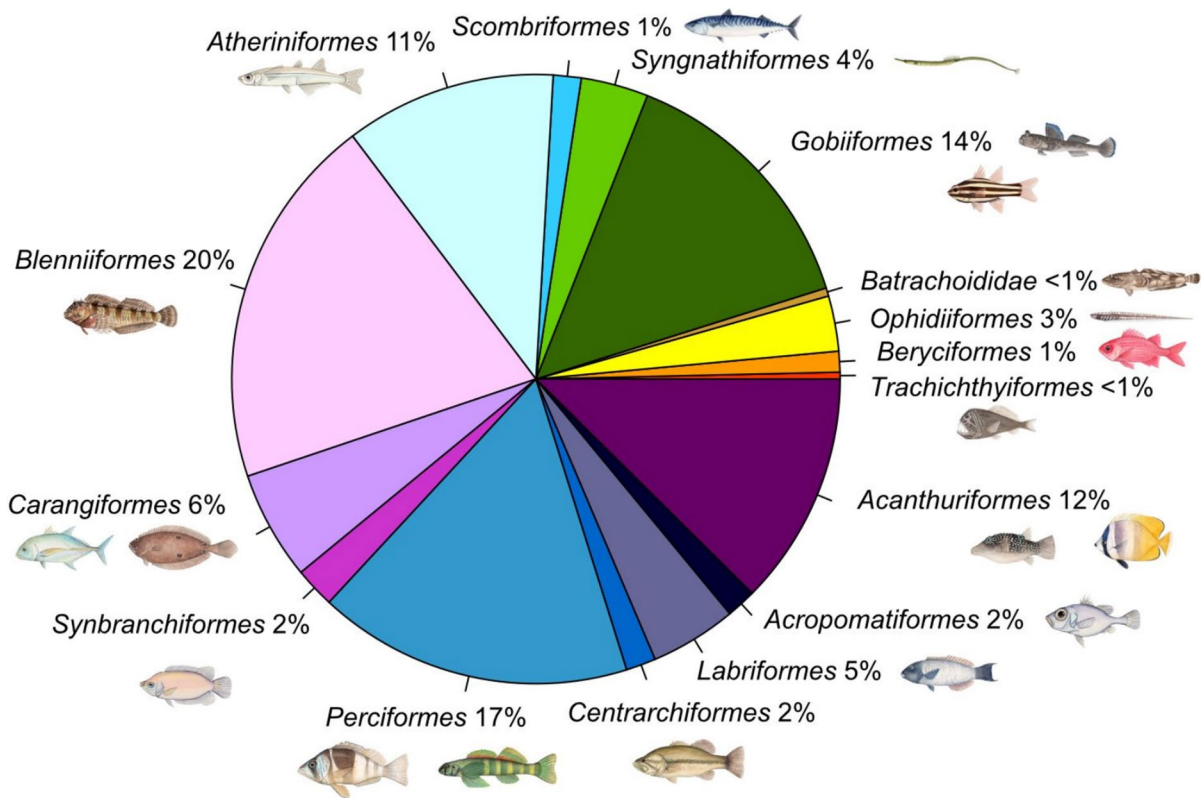


the major acanthopterygian clades established prior to the Cretaceous/Paleogene boundary, evolution within those clades would primarily be affected by Cenozoic events such as the Paleocene-Eocene Thermal Maximum (a period of global elevated temperatures and ocean acidification around 55 Ma), global cooling and collapse of the West Tethys coral reef hotspot (late Eocene/early Oligocene, approximately 33 Ma) and eastward movement of the center of coral reef diversity into the Coral Triangle, the Terminal Tethyan Event separating the Mediterranean/Atlantic from the Indian Ocean due to the collision of Africa with Eurasia (12–18 Ma), the closure of the Isthmus of Panama separating the Western Atlantic from

the Eastern Pacific (3.1 Ma), and the sea level fluctuations induced by glaciation cycles throughout the Pleistocene (Renema et al. 2008; Cowman and Bellwood 2011, 2013a, 2013b; Price et al. 2015; Thacker 2015, 2017; Arcila and Tyler 2017; Shelley et al. 2020c).

Species diversity among acanthopterygian clades varies widely. *Blenniiformes* (3,814 species) is the most species-rich, followed by *Perciformes* (3,200 species), *Gobiiformes* (2,740 species), *Acanthuriformes* (2,376 species) and *Atheriniformes* (2,126 species) (Fig. 9). The most species-depauperate lineages are *Trachichthyiformes* (71 species) and *Batrachoididae* (84 species), followed by *Beryciformes*

## Diversity of Acanthopterygian Clades



**Fig. 9** Percentage of total species diversity in each acanthopterygian clade

(213 species) and *Scombriformes* (287 species). No phylogenetic pattern in diversity is apparent; high and low species diversity clades are interspersed throughout the phylogeny.

The phylogenetic relationships of *Acanthopterygii* inferred based on molecular data accord in many respects with those derived from morphology (Lauder and Liem 1983; Johnson 1993; Johnson and Patterson 1993) but they include several notable differences. The reallocation of *Lophioidei* from *Paracanthopterygii* into crown group *Acanthuriformes* as sister to *Tetraodontoidei* is the most dramatic and yields a novel framework for evaluating the evolution of both body shape and depth preferences among anglerfishes and pufferfishes (Dornburg and Near 2021; Miller et al. 2022, 2023; Brownstein et al. 2024). Similarly, *Atheriniformes* has historically been placed outside *Percomorpha* but modern analyses resolve it as sister

to *Blenniiformes* (Lauder and Liem 1983). A long-held placement of tunas and billfishes as sisters was disconfirmed with the resolution of *Xiphiidae* and *Istiophoridae* in *Carangiformes*, prompting a reinterpretation of the evolution of endothermy (Orrell et al. 2006; Little et al. 2010). *Carangiformes* also contains *Pleuronectoidei*, the flatfishes, and the juxtaposition of these groups contextualizes the unique modifications of flatfish evolution (Harrington et al. 2016, 2021).

The molecular revolution in acanthopterygian phylogeny has provided detailed resolution of relationships and yielded a rich and comprehensive portrait of acanthopterygian evolution. Although some uncertainties remain such as the placements of *Ovalentaria* and the clade containing *Scombriformes* and *Syngnathiformes*, the interrelationships of clades within *Eupercaria*, and the resolution of lineages within

*Perciformes*, *Acanthuriformes*, *Scombriformes*, and *Belonoidei*, the overall pattern of acanthopterygian phylogeny is consistent and well-resolved (Near et al. 2012b, 2013; Betancur-R et al. 2013, 2017; Faircloth et al. 2013; Alfaro et al. 2018; Hughes et al. 2018; Rabosky et al. 2018; Dornburg and Near 2021; Ghezelayagh et al. 2022). In particular, the resolution of lineages previously assigned to *Perciformes* into nearly every other major acanthopterygian clade is a remarkable advance in the phylogenetics of vertebrates (Dornburg and Near 2021; Near and Thacker 2024). Understanding of the components and inter-relationships of large clades including *Acanthuriformes*, *Perciformes*, and *Blenniiformes*, as well as identification of previously unrecognized groups such as *Acropomatiformes*, is foundational for inferences of evolutionary processes and patterns across *Acanthopterygii*. With this clear structuring of acanthopterygian diversity, centuries of morphological descriptions may be reinterpreted in an evolutionary context as well as augmented with modern techniques that provide detailed resolution of anatomical structures such as CT scanning.

Future investigations into acanthopterygian evolution will rely on a consilience of data from paleontology, morphology, and molecular phylogenetics. With the relationships established by molecular phylogenies, calibrations and phylogenetic refinements provided by the inclusion of fossils, and phylogenetically informed techniques to infer patterns of biogeography, phenotypic trait evolution, and global biogeography, a comprehensive, detailed portrait of acanthopterygian fish evolution is developing (Thacker 2015; Rabosky et al. 2018; Ghezelayagh et al. 2022; Brownstein et al. 2024). However, molecular data are finite; as techniques that enable the near-complete sequencing of genomes become more available, the inference of molecular phylogeny may reach an inflection point beyond which no further resolution may be obtained. Molecular data are also susceptible to convergence in functionally critical genes as well as saturation, particularly over deep timescales (Duarte-Ribeiro et al. 2024). Even with extensive phylogenomic data, some areas of the acanthopterygian tree will likely remain poorly resolved, and some polytomies are likely accurate representations of rapid diversification. Potential solutions could include increase in the use of fossil taxa, both as cross-checks on the sequence of lineage appearance as well as direct inclusion of fossil

species in tip-dating analyses. Analysis of genome morphology (gene order, chromosomal configuration, and synteny patterns) may also hold promise in revealing evolutionary relationships over long timescales. Research into fish phylogeny and evolution is currently at a tipping point due to a convergence of centuries of morphological work with vast advances in molecular phylogenetics, analysis techniques, fossil discoveries and the extraction of new data from old fossils. It is from the integration of all these data types that a complete portrait of spiny-rayed fish evolution, distribution, and diversification will emerge.

**Acknowledgements** We thank Alex Dornburg for comments on an earlier draft of the manuscript, and Julie Johnson for the fish paintings used in the phylogeny figures. Comments from two anonymous reviewers were greatly helpful in improving the manuscript.

**Data availability** The authors declare that the data supporting the findings of this study are available within the paper.

#### Declarations

**Conflict of interest** The authors have no competing interests to declare that are relevant to the content of this article.

**Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

#### References

- Adamson EAS, Hurwood DA, Mather PB (2010) A reappraisal of the evolution of Asian snakehead fishes (Pisces: Channidae) using molecular data from multiple genes and fossil calibration. *Mol Phylogenet Evol* 56:707–171
- Adrian-Kalchauer I, Blomberg A, Larsson T et al (2020) The round goby genome provides insights into mechanisms that may facilitate biological invasions. *BMC Biol* 18:11

- Agorreta A, San Mauro D, Schlieven U et al (2013) Molecular phylogenetics of gobioides and phylogenetic placement of European gobies. *Mol Phylogenet Evol* 69:619–633
- Akkaynak D, Siemann LA, Barbosa A et al (2017) Changeable camouflage: How well can flounder resemble the colour and spatial scale of substrates in their natural habitats? *R Soc Open Sci* 4:160824
- Alfaro ME, Santini F, Brock CD (2007) Do reefs drive diversification in marine teleosts? Evidence from the pufferfishes and their allies (Order Tetraodontiformes). *Evolution* 61:2104–2126
- Alfaro ME, Santini F, Brock C et al (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *PNAS* 106:13410–13414
- Alfaro ME, Faircloth BC, Harrington RC et al (2018) Explosive diversification of marine fishes at the Cretaceous-Palaeogene boundary. *Nat Ecol Evol* 2:688–696
- Allen GR (1978) A review of the archerfishes (Family Toxotidae). *Rec West Aust Mus* 6:355–378
- Allen LG, Ladin ES, Rowell TJ (2020) Sound production and mechanism in the Giant Sea Bass, *Stereolepis gigas* (Polyprionidae). *Copeia* 108:809–814
- Amorim PF, Costa WJEM (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:e0199201
- Andrews JV, Schein JP, Friedman M (2023) An earliest Paleocene squirrelfish (Teleostei: Beryciformes: Holocentroidea) and its bearing on the timescale of holocentroid evolution. *J Syst Paleo* 21:2168571
- Arcila D, Tyler JC (2017) Mass extinction in tetraodontiform fishes linked to Palaeocene-Eocene thermal maximum. *Proc R Soc Lond B* 284:20171771
- Arcila D, Hughes LC, Melendez-Vazquez B et al (2021) Testing the utility of alternative metrics of branch support to address the ancient evolutionary radiation of tunas, stromateoids, and allies (Teleostei: Pelagiaria). *Syst Biol* 70:1123–1144
- Arnold RJ, Pietsch TW (2012) Evolutionary history of frogfishes (Teleostei: Lophiiformes: Antennariidae): a molecular approach. *Mol Phylogenet Evol* 62:117–129
- Arratia G, Quezada-Romegialli C (2019) The South American and Australian percichthyids and perciliids. What is new about them? *Neotrop Ichthyol* 17:e80102
- Awata S, Kimura MR, Sato N et al (2010) Breeding season, spawning time, and description of spawning behavior in the Japanese ornate dragonet, *Callionymus ornatipinnis*: a preliminary field study at the northern limit of its range. *Ichthyol Res* 57:16–23
- Baldwin CC, Tornabene L, Robertson DR et al (2018) More new deep-reef basslets (Teleostei, Grammatidae, *Lipogramma*), with updates on the eco-evolutionary relationships within the genus. *Zookeys* 729:129–161
- Baliga VB, Law CJ (2016) Cleaners among wrasses: phylogenetics and evolutionary patterns of cleaning behavior within Labridae. *Mol Phylogenet Evol* 94:424–435
- Baraf L, Pratchett MS, Cowman PF (2019) Ancestral biogeography and ecology of marine angelfishes (F: Pomacanthidae). *Mol Phylogenet Evol* 140:106596
- Bariche M, Kajajian A, Azzurro E (2013) Reproduction of the invasive bluespotted cornetfish *Fistularia commersonii* (Teleostei: Fistulariidae) in the Mediterranean Sea. *Mar Biol Res* 9:169–180
- Barth JMI, Damerou M, Matschiner M et al (2017) Genomic differentiation and demographic histories of Atlantic and Indo-Pacific yellowfin tuna (*Thunnus albacares*) populations. *Genome Biol Evol* 9:1084–1098
- Bellwood DR, van Herwerden L, Konow N (2004) Evolution and biogeography of marine angelfishes (Pisces: Pomacanthidae). *Mol Phylogenet Evol* 33:140–155
- Bellwood DR, Klanten S, Cowman PF et al (2009) Evolutionary history of the butterflyfishes (f: Chaetodontidae) and the rise of coral feeding fishes. *J Evol Biol* 23:335–349
- Berra TM, Gomelsky B, Thompson BA et al (2007) Reproductive anatomy, gonad development and spawning seasonality of nurseryfish, *Kurtus gulliveri* (Perciformes: Kurtidae). *Aust J Zool* 55:211–217
- Betancur-R R, Orti G (2014) Molecular evidence for the monophyly of flatfishes (Carangimorpharia: Pleuronectiformes). *Mol Phylogenet Evol* 73:18–22
- Betancur-R R, Broughton RE, Wiley EO et al (2013) The tree of life and a new classification of bony fishes. *PLOS Curr ToL* 18:5
- Betancur-R R, Wiley EO, Arratia G et al (2017) Phylogenetic classification of bony fishes. *BMC Evol Biol* 17:162
- Block BA, Finnerty JA (1994) Endothermy in fishes: a phylogenetic analysis of constraints, predispositions, and selection pressures. *Environ Biol Fish* 40:283–302
- Block BA, Finnerty JA, Stewart AFR et al (1993) Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* 260:210–214
- Bloom DR, Unmack PJ, Gosztonyi AE et al (2012) It's a family matter: molecular phylogenetics of Atheriniformes and the polyphyly of the surf silversides (Family: Notocheiridae). *Mol Phylogenet Evol* 62:1025–1030
- Bolnick DI, Near TJ (2005) Tempo of hybrid inviability in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* 59:1754–1767
- Bolnick DI, Near TJ, Wainwright PC (2006) Body size divergence promotes post-zygotic reproductive isolation in centrarchids. *Evol Ecol Res* 8:903–913
- Bolnick DI, Turelli M, Lopez-Fernandez H et al (2008) Accelerated mitochondrial evolution and “Darwin’s corollary”: asymmetric viability of reciprocal F-1 hybrids in centrarchid fishes. *Genetics* 178:1037–1048
- Bragança PHN, Amorim PF, Costa WJEM (2018) Pantandontidae (Teleostei: Cyprinodontiformes), the sister group to all other cyprinodontoid killifishes as inferred by molecular data. *Zoosys Evol* 94:137–145
- Brandl SJ, Goatley JHR, Bellwood DR et al (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs. *Bio Rev* 93:1846–1873
- Brandl SJ, Tornabene L, Goatley CHR et al (2019) Demographic dynamics of the smallest marine vertebrates fuel coral-reef ecosystem functioning. *Science* 364:1189–1192
- Britz R (1997) Egg surface structure and larval cement glands in nandid and badid fishes with remarks on phylogeny and biogeography. *AMNH Novit* 3195:1–7

- Britz R, Johnson GD (2002) “Paradox lost”: skeletal ontogeny of *Indostomus paradoxus* and its significance for the phylogenetic relationships of Indostomidae (Teleostei: Gasterosteiformes). *AMNH Novit* 3383:1–43
- Britz R, Dahanukar N, Anoope VK et al (2020) Aenigmachanidae, a new family of snakehead fishes (Teleostei: Channoidei) from subterranean waters of South India. *Nature Sci Rep* 10:16081
- Brownstein CD, Zapfe KL, Lott S et al (2024) Synergistic innovations enabled the radiation of anglerfishes in the deep open ocean. *Curr Biol* 34:2541–2550
- Burridge CP, Smolenski AJ (2004) Molecular phylogeny of the Cheilodactylidae and Latridae (Perciformes: Cirrhitidae) with notes on taxonomy and biogeography. *Mol Phylogenet Evol* 30:118–127
- Campanella D, Hughes LC, Unmack PJ et al (2015) Multi-locus fossil-calibrated phylogeny of Atheriniformes (Teleostei, Ovalentaria). *Mol Phylogenet Evol* 86:8–23
- Campbell MA, Chen W-J, López JA (2013) Are flatfishes (Pleuronectiformes) monophyletic? *Mol Phylogenet Evol* 69:664–673
- Campbell MA, Chanet B, Chen J-N et al (2019) Origins and relationships of the Pleuronectoidei: molecular and morphological analysis of living and fossil taxa. *Zoo Scr* 48:640–656
- Capobianco A, Friedman M (2019) Vicariance and dispersal in southern hemisphere freshwater fish clades: a palaeontological perspective. *Biol Rev* 94:662–699
- Chakrabarty P, Davis MP, Smith WL et al (2011) Evolution of the light organ system in ponyfishes (Teleostei: Leiognathidae). *J Morphol* 272:704–721
- Chapleau F (1993) Pleuronectiform relationships: a cladistic reassessment. *Bull Mar Sci* 52:516–540
- Chen W-J, Borsa P (2020) Diversity, phylogeny, and historical biogeography of large-eye seabreams (Teleostei: Lethrinidae). *Mol Phylogenet Evol* 151:106902
- Chen W-J, Lavoué S, Beheregaray LB et al (2014a) Historical biogeography of a new antitropical clade of temperate freshwater fishes. *J Biogeogr* 41:1806–1818
- Chen W-J, Santini F, Carnevale G et al (2014b) New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha). *Front Mar Sci* 1:53
- Chiba SN, Iwatsuki Y, Yoshino T et al (2009) Comprehensive phylogeny of the family Sparidae (Perciformes: Teleostei) inferred from mitochondrial gene analysis. *Gen Genet Syst* 84:153–170
- Choat JH, Klanten OS, Van Herwerden L et al (2012) Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). *Bio J Linn Soc* 107:529–557
- Çoker T, Leblebici S, Ozaydin S et al (2008) Determination of batch fecundity in *Uranoscopus scaber* Linnaeus, 1758 from the Aegean Sea, Turkey. *J Appl Ichthyol* 24:85–87
- Cole KS (1990) Patterns of gonad structure in hermaphroditic gobies (Teleostei: Gobiidae). *Environ Biol Fish* 28:125–142
- Colin PL, Clavijo IE (1988) Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico. *Bull Mar Sci* 43:249–279
- Collar DC, Near TJ, Wainwright PC (2005) Comparative analysis of morphological diversity: Does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution* 59:1783–1794
- Collar DC, O’Meara BC, Wainwright PC et al (2009) Piscivory limits diversification of feeding morphology in centrarchid fishes. *Evolution* 63:1557–1573
- Collar DC, Tremaine S, Harrington RC et al (2022) Mosaic adaptive peak shifts underlie body shape diversification in pelagarian fishes (Acanthomorpha: Percomorpha). *Bio J Linn Soc* 137:324–340
- Collins RA, Britz R, Rüber L (2015) Phylogenetic systematics of leaffishes (Teleostei: Polycentridae, Nandidae). *J Zoo Sys Evo Res* 53:259–272
- Colombo M, Damerau M, Hanel R et al (2014) Diversity and disparity through time in the adaptive radiation of Antarctic notothenioid fishes. *J Evo Bio* 28:376–394
- Conway KW, King CD, Summers AP et al (2020) Molecular phylogenetics of the clingfishes (Teleostei: Gobiocidae)—implications for classification. *Copeia* 108:886–906
- Cook BD, Adams M, Unmack PJ et al (2017) Phylogeography of the mouth-brooding freshwater fish *Glossamia aprion* (Apogonidae) in northern and eastern Australia: historical biogeography and allopatric speciation. *Bio J Linn Soc* 121:833–848
- Copus JM, Walsh CAJ, Hoban ML et al (2022) Phylogeography of mesophotic coral ecosystems: squirrelfish and soldierfish (Holocentriformes: Holocentridae). *Diversity* 14:691
- Coulson PG, Hall NG, Potter IC (2016) Biological characteristics of three co-occurring species of armorhead from different genera vary markedly from previous results for the Pentacerotidae. *J Fish Biol* 89:1393–1418
- Courtenay WR, Williams JD (2004) Snakeheads (Pisces, Channidae).—a biological synopsis and risk assessment, U.S. Geological Survey Circular. p. 1251
- Cowman PF, Bellwood DR (2011) Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. *J Evol Biol* 24:2543–2562
- Cowman PF, Bellwood DR (2013a) Vicariance across major marine biogeographic barriers: temporal concordance and the relative intensity of hard versus soft barriers. *Proc R Soc Lond B* 280:20131541
- Cowman PF, Bellwood DR (2013b) The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *J Biogeogr* 40:209–224
- Craig MT, Eble JA, Bowen BW et al (2007) High genetic connectivity across the Indian and Pacific oceans in the reef fish *Myripristis berndti* (Holocentridae). *Mar Ecol Prog Ser* 334:245–254
- da Silva TF, Sampaio I, Angulo A et al (2023) Species delimitation by DNA barcoding reveals undescribed diversity in Stelliferinae (Sciaenidae). *PLoS ONE* 18:e0296335
- Daane JM, Blum N, Lanni J et al (2021) Modulation of bioelectric cues in the evolution of flying fishes. *Curr Biol* 31:5052–5061.e8
- Dadzie S, Abou-Deedo F, Al-Shallal T (2008) Reproductive biology of the silver pomfret, *Pampus argenteus* (Euphrasen), in Kuwait waters. *J Appl Ichthyol* 16:247–253
- Davis AM, Unmack PJ, Pusey BJ et al (2012) Marine-freshwater transitions are associated with the evolution of dietary

- diversification in terapontid grunters (Teleostei: Terapontidae). *J Evo Bio* 25:1163–1179
- Davis AM, Unmack PJ, Vari RP et al (2016a) Herbivory promotes dental disparification and macroevolutionary dynamics in grunters (Teleostei: Terapontidae), a freshwater adaptive radiation. *Am Nat* 187:320–333
- Davis MP, Sparks JS, Smith WL (2016b) Repeated and widespread evolution of bioluminescence in marine fishes. *PLoS ONE* 11:e0155154
- Day JJ, Fages A, Brown KJ et al (2017) Multiple independent colonizations into the Congo Basin during the continental radiation of African *Mastacembelus* spiny eels. *J Biogeogr* 44:2308–2318
- de Queiroz K, Cantino P (2020) International code of phylogenetic nomenclature (PhyloCode). CRC Press, Boca Raton
- de Oliveira RF, Almada VC, Gil MF (1993) The reproductive behavior of the longspine snipefish, *Macrorhamphosus scolopax* (Synbranchiformes, Macrorhamphosidae). *Environ Biol Fish* 36:337–343
- de Souza GM, Monteiro-Neto C, da Costa MR et al (2021) Reproductive biology and recruitment of bluefish *Pomatomus saltatrix* (Perciformes: Pomatomidae) in the southwestern Atlantic. *Zoologia* 38:1–14
- Deef LEM (2021) First record of two squirrelfishes, *Sargocentron spinosissimum* and *Sargocentron tieerooides* (Actinopterygii, Beryciformes, Holocentridae) from the Egyptian Mediterranean coast. *Acta Ichthyol Pisc* 51:107–112
- DiBattista JD, Whitney J, Craig MT et al (2016) Surgeons and suture zones: hybridization among four surgeonfish species in the Indo-Pacific with variable evolutionary outcomes. *Mol Phylogenet Evol* 101:203–215
- DiBattista JD, Alfaro ME, Sorenson L et al (2018) Ice ages and butterflyfishes: phylogenomics elucidates the ecological and evolutionary history of reef fishes in an endemism hotspot. *Eco Evol* 8:10989–11008
- Dickson KA, Graham JB (2004) Evolution and consequences of endothermy in fishes. *Phys Biochem Zool* 77:998–1018
- Dornburg A, Near TJ (2021) The emerging phylogenetic perspective on the evolution of actinopterygian fishes. *Ann Rev Ecol Evol Syst* 52:427–452
- Dornburg A, Moore JA, Beaulieu JM et al (2014) The impact of shifts in marine biodiversity hotspots on patterns of range evolution: evidence from the Holocentridae (squirrelfishes and soldierfishes). *Evolution* 69:146–161
- Dornburg A, Townsend JP, Brooks W et al (2017) New insights on the sister lineage of percomorph fishes with an anchored hybrid enrichment dataset. *Mol Phylogenet Evol* 110:27–38
- Duarte-Ribeiro E, Rosas-Puchuri U, Friedman M et al (2024) Phylogenomic and comparative genomic analyses support a single evolutionary origin of flatfish asymmetry. *Nat Genet* 56:1069–1072
- Duchene D, Klanten SO, Munday PL et al (2013) Phylogenetic evidence for recent diversification of obligate coral-dwelling gobies compared with their host corals. *Mol Phylogenet Evol* 69:123–132
- Dyer BS, Chernoff B (1996) Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). *Zool J Linn Soc* 117:1–69
- Evans KM, Larouche O, Watson S-J et al (2021) Integration drives rapid phenotypic evolution in flatfishes. *PNAS* 118:e2101330118
- Faircloth BC, Sorenson L, Santini F et al (2013) A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). *PLoS ONE* 8:e65923
- Farrag MMS, AbouelFadl KY, Alabssawy AN et al (2018) Fishery biology of lessepsian immigrant squirrelfishes *Sargocentron rubrum* (Forsskål, 1775), Eastern Mediterranean Sea Egypt. *Egypt J Aquat Res* 44:307–313
- Favorito SE, Zanata AM, Assumpção MI (2005) A new *Synbranchus* (Teleostei: Synbranchiformes: Synbranchidae) from ilha de Marajó, Pará, Brazil, with notes on its reproductive biology and larval development. *Neotrop Ichthyol* 3:319–328
- Fessler JL, Westneat MW (2007) Molecular phylogenetics of butterflyfishes (Chaetodontidae): taxonomy and biogeography of a global coral reef fish family. *Mol Phylogenet Evol* 45:50–68
- Frédérich B, Santini F (2017) Macroevolutionary analysis of the tempo of diversification in snappers and fusiliers (Percomorpha: Lutjanidae). *Belg J Zoo* 147:17–35
- Frédérich B, Marrama G, Carnevale G et al (2016) Non-reef environments impact the diversification of extant jacks, remoras and allies (Carangoidei, Percomorpha). *Proc R Soc Lond B* 283:20161556
- Fricke R, Eschmeyer WN, Fong JD (2023) Eschmeyer's catalog of fishes: genera/species by family/subfamily; classification (17 March 2023). <https://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>. <https://www.calacademy.org/scientists/catalog-of-fishes-classification>
- Friedman M (2008) The evolutionary origin of flatfish asymmetry. *Nature* 454:209–212
- Friedman M, Johanson Z, Harrington RC et al (2013a) An early fossil remora (Echenoidea) reveals the evolutionary assembly of the adhesion disc. *Proc R Soc Lond B* 280:20131200
- Friedman M, Keck BP, Dornburg A et al (2013b) Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. *Proc R Soc Lond B* 280:20131733
- Friedman M, Feilich KL, Beckett HT et al (2019) A phylogenomic framework for pelagiarian fishes (Acanthomorpha: Percomorpha) highlights mosaic radiation in the open ocean. *Proc R Soc Lond B* 286:20191502
- Gaither MR, Schultz JK, Bellwood DR et al (2014) Evolution of pygmy angelfishes: recent divergences, introgression, and the usefulness of color in taxonomy. *Mol Phyl Evol* 74:38–47
- Galván-Quesada S, Doadrio I, Alda F et al (2016) Molecular phylogeny and biogeography of the amphidromous fish genus *Dormitator* Gill 1861 (Teleostei: Eleotridae). *PLoS ONE* 11:e0153538
- Ghedotti MJ, Davis MP (2013) Phylogeny, classification, and evolution of salinity tolerance of the North American Topminnows and killifishes, Family Fundulidae (Teleostei: Cyprinodontiformes). *Fieldiana* 7:1–65
- Ghedotti MJ, Gruber JN, Barton RW et al (2018) Morphology and evolution of bioluminescent organs in the

- glowbellies (Percomorpha: Acropomatidae) with comments on the taxonomy and phylogeny of Acropomatiformes. *J Morphol* 279:1640–1653
- Ghedotti MJ, DeKay HM, Maile AJ et al (2021) Anatomy and evolution of bioluminescent organs in the slimeheads (Teleostei: Trachichthyiformes). *J Morphol* 282:820–832
- Ghezelayagh A, Harrington RC, Burress ED et al (2022) Prolonged morphological expansion of spiny-rayed fishes following the end-Cretaceous. *Nat Ecol Evol* 6:1211–1220
- Giovannotti M, Cerioni PN, La Mesa M et al (2007) Molecular phylogeny of the three paedomorphic Mediterranean gobies (Perciformes: Gobiidae). *J Exp Zool B* 308:722–729
- Girard MG, Davis MP, Smith WL (2020) The phylogeny of carangiform fishes: morphological and genomic investigations of a new fish clade. *Copeia* 108:265–298
- Girard MG, Davis MP, Hui TH et al (2022) Phylogenetics of archerfishes (Toxotidae) and evolution of the toxotid shooting apparatus. *Integr Org Biol* 4:Obac013
- Glass JR, Harrington RC, Cowman PF et al (2023) Widespread sympatry in a species-rich clade of marine fishes (Carangidae). *Proc R Soc Lond B* 290:20230657
- Golani D, Ben-Tuvia A (1985) The biology of the Indo-Pacific squirrelfish, *Sargocentron rubrum* (Forsskål), a Suez Canal migrant to the eastern Mediterranean. *J Fish Biol* 27:249–258
- Goto A, Yokoyama R, Sideleva VG (2014) Evolutionary diversification in freshwater sculpins (Cottoidea): a review of two major adaptive radiations. *Environ Biol Fish* 98:307–335
- Greenfield DW, Winterbottom R, Collette BB (2008) Review of the toadfish genera (Teleostei: Batrachoididae). *Proc Calif Acad Sci Ser* 4(59):665–701
- Growns I (2004) A numerical classification of reproductive guilds of the freshwater fishes of south-eastern Australia and their application to river management. *Fish Manag Ecol* 11:369–377
- Habegger ML, Dean MN, Dunlop JWC et al (2015) Feeding in billfishes: inferring the role of the rostrum from a biomechanical standpoint. *J Exp Biol* 218:824–836
- Halsted BW, Danielson DD, Baldwin WJ et al (1972) Morphology of the venom apparatus of the leatherback fish *Scomberoides sanctipetri* (Cuvier). *Toxicon* 10:249–250
- Hamilton H, Saarman N, Short G et al (2017) Molecular phylogeny and patterns of diversification in syngnathid fishes. *Mol Phylogenet Evol* 107:388–403
- Hammer MP, Adams M, Thacker CE et al (2019) Comparison of genetic structure in co-occurring freshwater eleotrids (Actinopterygii: *Philypnodon*) reveals cryptic species, likely translocation and regional conservation hotspots. *Mol Phylogenet Evol* 139:106556
- Han Z, Yanagimoto T, Zhang Y et al (2012) Phylogeography study of *Ammodytes personatus* in northwestern Pacific: Pleistocene isolation, temperature and current conducted secondary contact. *PLoS ONE* 7:e37425
- Hanel R, Westneat MW, Sturmbauer C (2002) Phylogenetic relationships, evolution of broodcare behavior, and geographic speciation in the wrasse tribe Labrini. *J Mol Evol* 55:776–789
- Harper RD, Case JF (1999) Disruptive counterillumination and its anti-predatory value in the plainfin midshipman *Porichthys notatus*. *Mar Bio* 134:529–540
- Harrington RC, Faircloth BC, Eytan RI et al (2016) Phylogenomic analysis of carangimorph fishes reveals flatfish asymmetry arose in a blink of the evolutionary eye. *BMC Evol Biol* 16:224
- Harrington RC, Friedman M, Miya M et al (2021) Phylogenomic resolution of the monotypic and enigmatic *Amarsipus*, the Bagless Glassfish (Teleostei, Amarsipidae). *Zool Scr* 50:411–422
- Harrington RC, Kolmann M, Day JJ et al (2023) Dispersal sweepstakes: biotic interchange propelled air-breathing fishes across the globe. *J Biogeogr* 51:797–813
- Hart PB, Arnold RJ, Alda F et al (2022) Evolutionary relationships of anglerfishes (Lophiiformes) reconstructed using ultraconserved elements. *Mol Phylogenet Evol* 171:107459
- Hastings PA, Walker HJ Jr, Galland GR (2014) *Fishes: a guide to their diversity*. University of California Press, Oakland, California
- Hellenbrecht LM, Freese M, Pohlmann J-D et al (2019) Larval distribution of the ocean sunfishes *Ranzania laevis* and *Masturus lanceolatus* (Tetraodontiformes: Molidae) in the Sargasso Sea subtropical convergence zone. *J Plank Res* 41:595–608
- Herler J, Koblmüller S, Sturmbauer C (2009) Phylogenetic relationships of coral-associated gobies (Teleostei: Gobiidae) from the Red Sea based on mitochondrial DNA data. *Mar Bio* 156:725–739
- Hobbs J-PA, Allen GR (2014) Hybridisation among coral reef fishes at Christmas Island and the Cocos (Keeling) Islands. *Raffles Bull Zoo Supp* 30:220–226
- Hobbs J-PA, Frisch AJ, Allen GR et al (2009) Marine hybrid hotspot at Indo-Pacific biogeographic border. *Biol Lett* 5:258–261
- Holcroft N, Wiley EO (2008) Acanthuroid relationships revisited: a new nuclear gene-based analysis that incorporates tetraodontiform relatives. *Ichthyol Res* 55:274–283
- Hotaling S, Borowiec ML, Lins LSF et al (2021) The biogeographic history of eelpouts and related fishes: Linking phylogeny, environmental change, and patterns of dispersal in a globally distributed fish group. *Mol Phylogenet Evol* 162:107211
- Hrbek T, Seckinger J, Meyer A (2007) A phylogenetic and biogeographic perspective on the evolution of poeciliid fishes. *Mol Phylogenet Evol* 43:986–998
- Hughes LC, Ortí G, Huang Y et al (2018) Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *PNAS* 115:6249–6254
- Huie J, Thacker CE, Tornabene L (2020) Co-evolution of cleaning and feeding morphology in Caribbean and eastern Pacific gobies. *Evolution* 74:419–433
- Hundt PJ, Iglésias SP, Hoey AS et al (2014) A multilocus molecular phylogeny of combtooth blennies (Percomorpha: Blennioidei: Blenniidae): multiple invasions of intertidal habitats. *Mol Phylogenet Evol* 70:47–56
- Hung K-W, Russell BC, Chen W-J (2017) Molecular systematics of threadfin breams and relatives (Teleostei, Nemipteridae). *Zool Scr* 46:536–551

- Huyse T, Van Houdt J, Volckaert FAM (2004) Paleoclimatic history and vicariant speciation in the “sand goby” group (Gobiidae, Teleostei). *Mol Phylogenet Evol* 32:324–336
- Hyde JR, Vetter RD (2007) The origin, evolution, and diversification of rockfishes of the genus *Sebastes* (Cuvier). *Mol Phylogenet Evol* 44:790–811
- Iwata A, Hosoya S, Larson HK (2001) *Paedogobius kimurai*, a new genus and species of goby (Teleostei: Gobioidae: Gobiidae) from the west Pacific. *Rec Aust Mus* 53:103–112
- Johnson GD (1993) Percomorph phylogeny: progress and problems. *Bull Mar Sci* 52:3–28
- Johnson KS, Clements KD (2022) Histology and ultrastructure of the gastrointestinal tract in four temperate marine herbivorous fishes. *J Morphol* 283:16–34
- Johnson GD, Patterson C (1993) Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bull Mar Sci* 52:554–626
- Johnson GD, Paxton JR, Sutton TT et al (2009) Deep-sea mystery solved: astonishing larval transformations and extreme sexual dimorphism unite three fish families. *Biol Lett* 5:235–239
- Juan-Jordá MJ, Mosaquiera I, Friere J et al (2013) The conservation and management of tunas and their relatives: setting life history research priorities. *PLoS ONE* 8:e70405
- Karplus I, Thompson AR (2011) The partnership between gobioid fishes and burrowing alpheid shrimps. In: Patzner RA, van Tassell JL, Kovačić M, Kapoor BG (eds) *The biology of gobies*. CRC Press, Jersey and Enfield, New Hampshire, pp 559–607
- Kautt AF, Kratochwil CF, Nater A et al (2020) Contrasting signatures of genomic divergence during sympatric speciation. *Nature* 588:106–111
- Kawahara R, Miya M, Mabuchi K et al (2008) Interrelationships of the 11 gasterosteiform families (sticklebacks, pipefishes, and their relatives): a new perspective based on whole mitogenome sequences from 75 higher teleosts. *Mol Phylogenet Evol* 46:224–236
- Kawase H (2002) Simplicity and diversity in the reproductive ecology of triggerfish (Balistidae) and filefish (Monacanthidae). *Fish Sci* 68(I):119–122
- Kawase H, Mizuuchi R, Shin H et al (2017) Discovery of an earliest-stage “mystery circle” and development of the structure constructed by pufferfish *Torquigener albomaculosus* (Pisces: Tetraodontidae). *Fishes* 2:14
- Kazancıoğlu E, Alonzo SH (2010) A comparative analysis of sex change in Labridae supports the size advantage hypothesis. *Evolution* 64:2254–2264
- Kazancıoğlu E, Near TJ, Hanel R et al (2009) Influence of feeding functional morphology and sexual selection on diversification rate of parrotfishes (Scaridae). *Proc R Soc Lond B* 276:3439–3446
- Kim D, Bauer BH, Near TJ (2022a) Introgression and species delimitation in the Longear Sunfish *Lepomis megalotis* (Teleostei: Percomorpha: Centrarchidae). *Syst Biol* 71:273–285
- Kim D, Taylor AT, Near TJ (2022b) Phylogenomics and species delimitation of the economically important Black Basses (*Micropterus*). *Nat Sci Res* 12:9113
- Kim D, Stokes MF, Ebersole S et al (2023) Erosional exhumation of carbonate rock facilitates dispersal-mediated allopatric speciation in freshwater fishes. *Evolution* 77:2442–2455
- Kishimoto H (2001) Uranoscopidae. Stargazers. In: Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol 6, Bony fishes part 4 (Labridae to Latimeriidae), estuarine crocodiles*. FAO, Rome, pp. 3519–3531
- Knudsen SW, Clements KD (2013) Revision of the fish family Kyphosidae (Teleostei: Perciformes). *Zootaxa* 3751:1–101
- Knudsen SW, Clements KD (2016) World-wide species distributions in the family Kyphosidae (Teleostei: Perciformes). *Mol Phyl Evol* 101:252–266
- Knudsen SW, Choat JH, Clements KD (2019) The herbivorous fish family Kyphosidae (Teleostei: Perciformes) represents a recent radiation from higher latitudes. *J Biogeogr* 46:2067–2080
- Koeda K, Ishihara T, Tachihara K (2012) The reproductive biology of *Pempheris schwenkii* (Pempheridae) on Okinawa Island, southwestern Japan. *Zool Stud* 51:1086–1093
- Kon T, Yoshino T (2002) Diversity and evolution of life histories of gobioid fishes from the viewpoint of heterochrony. *Mar Freshw Res* 53:377–402
- Kon T, Yoshino T, Mukai T et al (2007) DNA sequences identify numerous cryptic species of the vertebrate: a lesson from the gobioid fish *Schindleria*. *Mol Phylogenet Evol* 44:53–62
- Kuwamura T, Sunobe T, Sakai Y et al (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. *Ichthyol Res* 67:341–360
- La Mesa M (2012) Planktonic and paedomorphic gobioids. In: Patzner RA, van Tassell JL, Kovačić M, Kapoor BG (eds) *The biology of gobies*. CRC Press, Jersey and Enfield, New Hampshire, pp 465–491
- La Mesa M, Llompарт F, Riginella E et al (2020) Parental care and reproductive strategies in notothenioid fishes. *Fish Fish* 22:356–376
- Lauder GV, Liem KL (1983) The evolution and interrelationships of the actinopterygian fishes. *Bull MCZ Harv* 150:95–197
- Lavoué S, Nakayama K, Jerry DR et al (2014) Mitogenomic phylogeny of the Percichthyidae and Centrarchiformes (Percomorpha): comparison with recent nuclear gene-based studies and simultaneous analysis. *Gene* 549:46–57
- Li X, Musicasinthorn P, Kumazawa Y (2006) Molecular phylogenetic analyses of snakeheads (Perciformes: Channidae) using mitochondrial DNA sequences. *Ichthyol Res* 53:148–159
- Li C, Ortí G, Zhao JL (2010) The phylogenetic placement of siniperid fishes (“Perciformes”) revealed by 11 nuclear loci. *Mol Phylogenet Evol* 56:1096–1104
- Li C, Betancur-R R, Smith WL et al (2011) Monophyly and interrelationships of Snook and Barramundi (Centropomidae sensu Greenwood) and five new markers for fish phylogenetics. *Mol Phylogenet Evol* 60:463–471
- Li C, Olave M, Hou Y et al (2021) Genome sequences reveal global dispersal routes and suggest convergent genetic adaptations in seahorse evolution. *Nat Comm* 12:1094

- Lin H-C, Hastings PA (2013) Phylogeny and biogeography of a shallow water fish clade Blenniiformes. *BMC Evol Biol* 13:210
- Little AG, Lougheed SC, Moyes CD (2010) Evolutionary affinity of billfishes (Xiphiidae and Istiophoridae) and flatfishes (Pleuronectiformes): Independent and trans-subordinal origins of endothermy in teleost fishes. *Mol Phylogenet Evol* 56:897–904
- Lo P-C, Liu S-H, Chao NL et al (2015) A multi-gene dataset reveals a tropical New World origin and early Miocene diversification of croakers (Perciformes: Sciaenidae). *Mol Phylogenet Evol* 88:132–143
- Lo P-C, Liu S-H, Nor SAM et al (2017) Molecular exploration of hidden diversity in the Indo-West Pacific sciaenid clade. *PLoS ONE* 12:e0176623
- Long JM, Allen MS, Porak WF et al (2015) A historical perspective of Black Bass management in the United States. *Am Fish Soc Symp* 82:99–122
- Longo SJ, Faircloth BC, Meyer A et al (2017) Phylogenomic analysis of a rapid radiation of misfit fishes (Syngnathiformes) using ultraconserved elements. *Mol Phylogenet Evol* 113:33–48
- Longo GC, Bernardi G, Lea RN (2018) Taxonomic revisions within Embiotocidae (Teleostei: Perciformes) based on molecular phylogenetics. *Zootaxa* 4482:591–596
- Lopes-Ferreira M, Ramos AD, Martins IA et al (2014) Clinical manifestations and experimental studies on the spine extract of the toadfish *Porichthys porosissimus*. *Toxicon* 86:28–39
- Lovejoy NR, Iranpour M, Collette BB (2004) Phylogeny and jaw ontogeny of Beloniform fishes. *Intgr Comp Biol* 44:366–377
- Lü Z, Gong L, Ren Y et al (2021) Large-scale sequencing of flatfish genomes provides insights into the polyphyletic origin of their specialized body plan. *Nat Genet* 53:742–751
- Ludt WB, Burrige CP, Chakrabarty P (2019) A taxonomic revision of Cheilodactylidae and Latridae (Centrarchiformes: Cirrhitidae) using morphological and genomic characters. *Zootaxa* 4585:121–141
- Mabuchi K, Miya M, Azuma Y et al (2007) Independent evolution of the specialized pharyngeal jaw apparatus in cichlid and labrid fishes. *BMC Evol Biol* 7:10
- Mace PM, Fenaughty JM, Coburn RP et al (1990) Growth and productivity of orange roughy (*Hoplostethus atlanticus*) of the north Chatham Rise. *NZ J Mar Fresh Res* 24:105–119
- Maina JN, Wood CM, Hogstrand C et al (1998) Structure and function of the axillary organ of the Gulf Toadfish, *Opsanus beta* (goode and bean). *Comp Biochem Physiol* 119:17–26
- Majtánová Z, Dedukh D, Choleva L et al (2021) Uniparental genome elimination in Australian carp gudgeons. *Genome Biol Evol* 13:eva03
- Malavasi S, Collatuzzo S, Torricelli P (2008) Interspecific variation of acoustic signals in Mediterranean gobies (Perciformes: Gobiidae): comparative analysis and evolutionary outlook. *Bio J Linn Soc* 93:763–778
- Martin KLM, Swiderski DL (2001) Beach spawning in fishes: phylogenetic tests of hypotheses. *Am Zool* 41:526–537
- Martin CH, Turner BJ (2018) Long distance dispersal over land by fishes: extremely rare ecological events become probable over millennial timescales. *Proc R Soc Lond B* 285(2017):2436
- Martin CH, Wainwright PC (2011) Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of *Cyprinodon* pupfish. *Evolution* 65:2197–2212
- Maschette D, Fromont J, Platell ME et al (2020) Characteristics and implications of spongivory in the Knifejaw *Oplegnathus woodwardi* (Waite) in temperate mesophotic waters. *J Sea Res* 157:101847
- Matsuura K (2015a) A new pufferfish of the genus *Torquigener* that builds “mystery circles” on sandy bottoms in the Ruykyu Islands, Japan (Actinopterygii: Tetraodontiformes: Tetraodontidae). *Ichthyol Res* 62:207–212
- Matsuura K (2015b) Taxonomy and systematics of tetraodontiform fishes: a review focusing primarily on progress in the period from 1980 to 2014. *Ichthyol Res* 62:72–113
- Maxfield JM, Van Tassell JL, St Mary CM et al (2012) Extreme gender flexibility: using a phylogenetic framework to infer the evolution of variation in sex allocation, phylogeography, and speciation in a genus of bidirectional sex changing fishes (*Lythrypnus*, Gobiidae). *Mol Phylogenet Evol* 64:416–427
- McDowall RM (1973) Relationships and taxonomy of the New Zealand torrent fish, *Cheimarrichthys fosteri* Haast (Pisces: Mugiloididae). *J R Soc NZ* 3:199–217
- McGee MD, Borstein SR, Meier JI et al (2020) The ecological and genomic basis of explosive adaptive radiation. *Nature* 586:75–79
- Meier JI, Marques DA, Mwaiko S et al (2017) Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nature Commun* 8:14363
- Mennesson MI, Bonillo C, Feunteun E et al (2018) Phylogeography of *Eleotris fusca* (Teleostei: Gobiidae: Eleotridae) in the Indo-Pacific area reveals a cryptic species in the Indian Ocean. *Conserv Genet* 19:1025–1038
- Miller EC, Lin H-C, Hastings PA (2014) Improved resolution and a novel phylogeny for the Neotropical triplefin blennies (Teleostei: Tripterygiidae). *Mol Phylogenet Evol* 96:70–78
- Miller EC, Martinez CM, Friedman ST et al (2022) Alternating regimes of shallow and deep-sea diversification explain a species-richness paradox in marine fishes. *PNAS* 119:e2123544119
- Miller EC, Faucher R, Hart PB et al (2023) Phylogenomics reveals the deep ocean as an accelerator for evolutionary diversification in anglerfishes. *bioRxiv* 1331:15
- Miya M, Takahashi M, Endo H et al (2003) Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Mol Phylogenet Evol* 26:121–138
- Miya M, Satoh TP, Nishida M (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. *Biol J Linn Soc* 85:289–306
- Miya M, Pietsch TW, Orr JW et al (2010) Evolutionary history of anglerfishes (Teleostei: Lophiiformes): a mitogenomic perspective. *BMC Evol Biol* 10:58

- Miya M, Friedman M, Satoh TP et al (2013) Evolutionary origin of the Scombridae (Tunas and Mackerels): members of a Paleogene adaptive radiation with 14 other fish families. *PLoS ONE* 8:e73535
- Møller PR, Knudsen SW, Schwarzhanz W et al (2016) A new classification of viviparous brotulas (Bythitidae)—with family status for Dinematchthyidae—based on molecular, morphological and fossil data. *Mol Phylogenet Evol* 100:391–408
- Moore JA, Paxton, JR (1999a) Trachichthyidae. Slimeheads (roughies). In: Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae)*. FAO, Rome, pp. 2215–2217
- Moore JA, Paxton, JR (1999b) Berycidae. Alfonsinos. In: Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae)*. FAO, Rome, pp. 2218–2224
- Mori T, Murai R, Ito T et al (2022) Reproduction of marblemouth frogfish *Lophiocharon lithinostomus* (Lophiiformes, Antennariidae) and the evolution of parental care among frogfishes. *Arpha Prepr.* <https://doi.org/10.3897/arphapreprints.e84895>
- Mossop KD, Adams M, Unmack PJ et al (2015) Dispersal in the desert: ephemeral water drives connectivity and phylogeography of an arid-adapted fish. *J Biogeogr* 42:2374–2388
- Myrberg AA Jr, Montgomery WL, Fishelson L (1988) The reproductive behavior of *Acanthurus nigrofuscus* (Forsk.) and other surgeonfishes (Fam. Acanthuridae) off Eilat, Israel (Gulf of Aqaba, Red Sea). *Ethology* 79:31–61
- Near TJ, Keck BP (2013) Free from mitochondrial DNA: nuclear genes and the inference of species trees among closely related darter lineages (Teleostei: Percidae: Etheostomatinae). *Mol Phylogenet Evol* 66:868–876
- Near TJ, Kim D (2021) Phylogeny and time scale of diversification in the fossil-rich sunfishes and black basses (Teleostei: Percomorpha: Centrarchidae). *Mol Phylogenet Evol* 161:107156
- Near TJ, Thacker CE (2024) Phylogenetic classification of living and fossil ray-finned fishes (*Actinopterygii*). *Bull Peabody Mus Nat Hist* 65:3–302
- Near TJ, Bolnick DI, Wainwright PC (2004) Investigating phylogenetic relationships of sunfishes and black basses (*Actinopterygii*: Centrarchidae) using DNA sequences from mitochondrial and nuclear genes. *Mol Phylogenet Evol* 32:344–357
- Near TJ, Bolnick DI, Wainwright PC (2005) Fossil calibrations and molecular divergence time estimates in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* 59:1768–1782
- Near TJ, Bossu CM, Bradburd GS et al (2011) Phylogeny and temporal diversification of darters (Percidae: Etheostomatinae). *Syst Biol* 60:565–595
- Near TJ, Dornburg A, Kuhn KL et al (2012a) Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. *PNAS* 109:3434–3439
- Near TJ, Eytan RI, Dornburg A et al (2012b) Resolution of ray-finned fish phylogeny and timing of diversification. *PNAS* 109:13698–13703
- Near TJ, Sandel M, Kuhn KL et al (2012c) Nuclear gene-inferred phylogenies resolve the relationships of the enigmatic Pygmy sunfishes, *Elassoma* (Teleostei: Percomorpha). *Mol Phylogenet Evol* 63:388–395
- Near TJ, Dornburg A, Eytan RI et al (2013) Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *PNAS* 110:12738–12743
- Near TJ, Dornburg A, Harrington RC et al (2015) Identification of the notothenioid sister lineage illuminates the biogeographic history of an Antarctic adaptive radiation. *BMC Evol Biol* 15:109
- Near TJ, MacGuigan DJ, Parker E et al (2018) Phylogenetic analysis of Antarctic notothenioids illuminates the utility of RADseq for resolving Cenozoic adaptive radiations. *Mol Phylogenet Evol* 129:268–279
- Neff BD, Knapp R (2009) Alternative reproductive tactics in the Centrarchidae. In: Cooke SJ, Philipp DP (eds) *Centrarchid fishes: diversity, biology, and conservation*. Blackwell Science, London, pp 90–104
- Neilson ME, Stepien CA (2009) Escape from the Ponto-Caspian: evolution and biogeography of an endemic goby species flock (Benthophilinae: Gobiidae: Teleostei). *Mol Phylogenet Evol* 52:84–102
- O'Toole B (2002) Phylogeny of the species of the superfamily Echeneoidea (Perciformes: Carangoidei: Echeidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeiid hitchhiking and behaviour. *Can J Zool* 80:596–623
- Oh D-J, Lee J-C, Ham Y-M et al (2021) The mitochondrial genome of *Stereolepis doederleini* (Pempheeriformes: Polyprionidae) and mitogenomic phylogeny of Pempheeriformes. *Genet Mol Biol* 44:e20200166
- Orrell TM, Collette BB, Johnson GD (2006) Molecular data support separate scombroid and xiphoid clades. *Bull Mar Sci* 79:505–519
- Page LM, Smith PW, Burr BM et al (1985) Evolution of reproductive behaviors in percoid fishes. III *Nat Hist Surv Bull* 33:275–295
- Parenti LR (1981) A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei: Atherinomorpha). *Bull Am Mus Nat Hist* 168:335–557
- Pavlov DA, Emel'yanova NG, Thuan LTB et al (2011) Reproduction and initial development of manybar goatfish *Parupeneus multifasciatus* (Mullidae). *J Ichthyol* 51:604–617
- Paxton JR, Johnson GD (1999) Anomalopidae. Flashlight fishes. In: Carpenter KE, Niem V (eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae)*. FAO, Rome, pp. 2212–2213
- Paxton JR (1999a) Anoplogastridae. Fangtooths. In: Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae)*. FAO, Rome, p 2210
- Paxton JR (1999b) Diretmidae. Spinyfins. In: Carpenter KE, Niem V (eds.) *FAO species identification guide*

- for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae). FAO, Rome, p 2211
- Paxton JR (1999c) Monocentrididae. Pineapple fishes. In: Carpenter KE, Niem V (eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae). FAO, Rome, p 2214
- Perdices A, Doadrio I, Bermingham E (2005) Evolutionary history of the synbranchid eels (Teleostei: Synbranchidae) in Central America and the Caribbean Islands inferred from their molecular phylogeny. *Mol Phylogenet Evol* 37:460–473
- Pietsch TW (2009) Oceanic anglerfishes: extraordinary diversity in the deep sea. University of California Press, Berkeley, California
- Pietsch TW, Arnold RJ (2020) Frogfishes: biodiversity, zoogeography, and behavioral ecology. Johns Hopkins University Press, Baltimore, Maryland
- Pietsch TW, Ross SW, Caruso JH et al (2013) In-situ observations of deep-sea goosefish *Sladenia shafersi* Caruso and Bulis (Lophiiformes: Lophiidae), with evidence of extreme sexual dimorphism. *Copeia* 2013:660–665
- Piñeros VJ, Beltrán-López RB, Baldwin CC et al (2019) Diversification of the genus *Apogon* (Lacepède, 1801) (Apogonidae: Perciformes) in the tropical eastern Pacific. *Mol Phylogenet Evol* 132:232–242
- Pohl M, Milvertz FC, Meyer A et al (2015) Multigene phylogeny of cyprinodontiform fishes suggests continental radiations and a rogue taxon position of *Pantodon*. *Vert Zool* 65:37–44
- Polgar G, Zane L, Babbucci M et al (2014) Phylogeography and demographic history of two widespread Indo-Pacific mudskippers (Gobiidae: *Periophthalmus*). *Mol Phylogenet Evol* 73:161–176
- Price SA, Holtzman AR, Near TJ et al (2011) Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecol Lett* 14:462–469
- Price SA, Tavera JJ, Near TJ et al (2012) Elevated rates of morphological and functional diversification in reef-dwelling haemulid fishes. *Evolution* 67:417–428
- Price SA, Claverie T, Near TJ et al (2015) Phylogenetic insights into the history and diversification of fishes on reefs. *Coral Reefs* 34:997–1009
- Rabosky DL, Chang J, Title PO et al (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* 559:392–395
- Renema W, Bellwood DR, Braga JC et al (2008) Hopping hotspots: global shifts in marine biodiversity. *Science* 321:654–657
- Reznick DN, Furness AI, Meredith RW et al (2017) The origin and biogeographic diversification of fishes in the family Poeciliidae. *PLoS ONE* 12:e017546
- Ribeiro E, Davis AM, Rivero-Vega RA et al (2018) Post-cretaceous bursts of evolution along the benthic-pelagic axis in marine fishes. *Proc R Soc Lond B* 285:20182010
- Rice AN, Bass AH (2009) Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: insights into the diversity of the Batrachoididae. *J Exp Bio* 212:1377–1391
- Robards MD, Piatt JF (1999) Biology of the genus *Ammodytes*, the sand lances. In: Robards MD, Wilson MF, Armstrong RH et al (eds) Sand lance: a review of biology and predator relations and annotated bibliography. US Dep Agric Forest Serv, Seattle, pp 1–16
- Robitzch V, Molina-Valdivia V, Solano-Iguaran JJ et al (2021) Year-round high abundances of the world's smallest marine vertebrate (*Schindleria*) in the Red Sea and worldwide associations with lunar phases. *Nat Sci Res* 11:14261
- Rodríguez-Machado S, Elías DJ, McMahan CD et al (2024) Disentangling historical relationships within Poeciliidae (Teleostei: Cyprinodontiformes) using ultraconserved elements. *Mol Phyl Evol* 190:107965
- Ronco F, Matschiner M, Böhne A et al (2021) Drivers and dynamics of a massive adaptive radiation in cichlid fishes. *Nature* 589:76–81
- Rüber L, Van Tassell JL, Zardoya R (2003) Rapid speciation and ecological divergence in the american seven-spined gobies (Gobiidae: Gobiomatini) inferred from a molecular phylogeny. *Evolution* 57:1584–1598
- Rüber L, Britz R, Kullander O et al (2004a) Evolutionary and biogeographic patterns of the Badidae (Teleostei: Perciformes) inferred from mitochondrial and nuclear sequence data. *Mol Phylogenet Evol* 32:1010–1022
- Rüber L, Britz R, Tan HH et al (2004b) Evolution of mouthbrooding and life history correlates in the fighting fish genus *Betta*. *Evolution* 58:799–813
- Rüber L, Britz R, Zardoya R (2006) Molecular phylogenetics and evolutionary diversification of labyrinth fishes (Perciformes: Anabantoidae). *Syst Bio* 55:374–397
- Rüber L, Tan HH, Britz R (2020) Snakehead (Teleostei: Channidae) diversity and the Eastern Himalaya biodiversity hotspot. *J Zool Syst Evol Res* 58:256–286
- Sanciango MD, Rocha LA, Carpenter KE (2011) A molecular phylogeny of the Grunts (Perciformes: Haemulidae) inferred using mitochondrial and nuclear genes. *Zootaxa* 2966:37–50
- Sanciango MD, Carpenter KE, Betancur-R R (2016) Phylogenetic placement of enigmatic percomorph families (Teleostei: Percomorphaceae). *Mol Phylogenet Evol* 94:565–576
- Sandel M, Rohde FC, Harris PM (2014) Interspecific relationships and the evolution of sexual dimorphism in pygmy sunfishes (Centrarchidae: *Elassoma*). *Mol Phylogenet Evol* 77:166–176
- Santaquiteria A, Siqueira AC, Duarte-Ribero E et al (2021) Phylogenomics and historical biogeography of seahorses, dragonets, goatfishes, and allies (Teleostei: Syngnatharia): assessing factors driving uncertainty in biogeographic inferences. *Syst Biol* 70:1145–1162
- Santini F, Harmon LJ, Carnevale G et al (2009) Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evo Bio* 9:164
- Santini F, Sorenson L, Alfaro ME (2013) A new phylogeny of tetraodontiform fishes (Tetraodontiformes, Acanthomorpha) based on 22 loci. *Mol Phylogenet Evol* 69:177–187
- Satoh TP (2018) Complete mitochondrial genome sequence of *Glaucosoma buergeri* (Pempheferiformes:

- Glucosomatidae) with implications based on the phylogenetic position. *Mt DNA* 3:107–109
- Schwarzahns W, Møller PR (2007) Review of the Dinematchthyini (Teleostei: Bythitidae) of the Indo-West Pacific. Part III. *Beaglichthys*, *Brosmolus*, *Monothrix* and eight new genera with description of 20 new species. *R Mus Art Galleries NT* 23:29–110
- Schwarzahns W, Møller PR (2011) New Dinematchthyini (Teleostei: Bythitidae) from the Indo-West Pacific with description of a new genus and 5 new species. *R Mus Art Galleries NT* 27:161–177
- Schwarzahns W, Møller PR (2021) Revision of the ‘dragonhead’ cusk eels of the genus *Porogadus* (Teleostei: Ophiidiidae), with description of eight new species and one new genus. *Zootaxa* 5029:1–96
- Schwarzahns W, Møller PR, Nielsen JG (2005) Review of the Dinematchthyini (Teleostei: Bythitidae) of the Indo-West Pacific. Part I. *Diancistrus* and two new genera with 26 new species. *R Mus Art Galleries NT* 21:73–163
- Scrimgeour GJ, Eldon GA (1989) Aspects of the reproductive biology of torrentfish, *Cheimarrichthys fosteri*, in two braided rivers of Canterbury, New Zealand. *NZ J Mar Freshw Res* 23:19–25
- Setiamarga DHE, Miya M, Yamanoue Y et al (2008) Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes, silversides, and their relatives): the first evidence based on whole mitogenome sequences. *Mol Phylogenet Evol* 49:598–605
- Shelley JJ, Unmack PJ, Dempster T et al (2019) The Kimberley, north-western Australia, as a cradle of evolution and endemic biodiversity: an example using grunters (Terapontidae). *J Biogeogr* 46:2420–2432
- Shelley JJ, David BO, Thacker CE et al (2020a) Phylogeography of the Cran’s bully *Gobiomorphus basalis* (Gobiiformes: Eleotridae) and an analysis of species boundaries within the New Zealand radiation of *Gobiomorphus*. *Bio J Linn Soc* 130:365–381
- Shelley JJ, Delaval A, Le Feuvre MC et al (2020b) Revision of the genus *Hannia* (Teleostei, Terapontidae), with description of a new species, *Hannia wintoni*, from the Kimberley, Western Australia. *Zootaxa* 4869(4):5
- Shelley JJ, Swearer SE, Dempster T et al (2020c) Plio-Pleistocene sea-level changes drive speciation of freshwater fishes in north-western Australia. *J Biogeogr* 47:1727–1738
- Smith WL, Busby MS (2014) Phylogeny and taxonomy of sculpins, sandfishes, and snailfishes (Perciformes: Cottoidei) with comments on the phylogenetic significance of their early-life-history specializations. *Mol Phylogenet Evol* 79:332–352
- Smith WL, Craig MT (2007) Casting the percomorph net widely: the importance of broad taxonomic sampling in the search for the placement of serranid and percid fishes. *Copeia* 2007:35–55
- Smith WL, Wheeler WC (2004) Polyphyly of the mail-cheeked fishes (Teleostei: Scorpaeniformes): evidence from mitochondrial and nuclear sequence data. *Mol Phylogenet Evol* 32:627–646
- Smith WL, Wheeler WC (2006) Venom evolution widespread in fishes: a phylogenetic road map for the bioprospecting of piscine venoms. *J Hered* 97:206–217
- Smith WL, Stern JH, Girard MG et al (2016) Evolution of venomous cartilaginous and ray-finned fishes. *Intgr Comp Biol* 56:950–961
- Smith WL, Elizabeth E, Clara R (2018) Phylogeny and taxonomy of flatheads, scorpionfishes, sea robins, and stonefishes (Percomorpha: Scorpaeniformes) and the evolution of the lachrymal saber. *Copeia* 106:94–119
- Smith WL, Ghedotti MJ, Dominguez-Dominguez O et al (2022) Investigations into the ancestry of the Grape-eye Seabass (*Hemilutjanus macrophthalmos*) reveal novel limits and relationships for the Acropomatiformes (Teleostei: Percomorpha). *Neotrop Ichthyol* 20:e210160
- Smith-Vaniz WF (1999) Carangidae. Jacks and scads (also trevallies, queenfishes, runners, amberjacks, pilotfishes, pampanos, etc.). In: Carpenter KE, Niem V (eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific vol. 4, Bony fishes part 2 (Mugilidae to Carangidae)*. *FAO, Rome*, pp 2659–2756
- Song S, Zhao J, Li C (2017) Species delimitation and phylogenetic reconstruction of the sinipercids (Perciformes: Sinipercidae) based on target enrichment of thousands of nuclear coding sequences. *Mol Phylogenet Evol* 111:44–55
- Sorenson L, Santini F, Carnevale G et al (2013) A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. *Mol Phylogenet Evol* 68:150–160
- Sparks JS, Dunlap PV (2004) A clade of non-sexually dimorphic ponyfishes (Teleostei: Perciformes: Leiognathidae): Phylogeny, taxonomy, and description of a new species. *AMNH Novit* 3459:1–21
- Stiassny M (1981) Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika. *Bull Br Mus Nat Hist Zool Ser* 40:67–101
- Stiller J, Short G, Hamilton H et al (2022) Phylogenomic analysis of Syngnathidae reveals novel relationships, origins of endemic diversity and variable diversification rates. *BMC Biol* 20:75
- Svardal H, Quah FX, Malinsky M et al (2020) Ancestral hybridization facilitated species diversification in the Lake Malawi cichlid fish adaptive radiation. *Mol Biol Evol* 37:1100–1113
- Tavera J, Acero PA, Wainwright PC (2018) Multilocus phylogeny, divergence times, and a major role for the benthic-pelagic axis in the diversification of grunts (Haemulidae). *Mol Phylogenet Evol* 121:212–223
- Taylor MS, Hellberg ME (2005) Marine radiations at small geographic scales: speciation in neotropical reef gobies (*Elacatinus*). *Evolution* 59:374–385
- Taylor AT, Long JM, Tringali MD et al (2019) Conservation of black bass diversity: an emerging management paradigm. *Fisheries* 44:20–36
- Tea Y-K, Xu X, DiBattista JD et al (2022) Phylogenomic analysis of concatenated ultraconserved elements reveals the recent evolutionary radiation of the fairy wrasses (Teleostei: Labridae: *Cirrhilabrus*). *Syst Biol* 71:1–12
- Thacker CE (2009) Phylogeny of Gobioidae and placement within Acanthomorpha, with a new classification and

- investigation of diversification and character evolution. *Copeia* 2009:93–104
- Thacker CE (2013) Phylogenetic placement of the European sand gobies in Gobionellidae and characterization of gobionellid lineages (Gobiiformes: Gobioidei). *Zootaxa* 3619:369–382
- Thacker CE (2015) Biogeography of goby lineages (Gobiiformes: Gobioidei): origin, invasions, and extinction throughout the Cenozoic. *J Biogeol* 42:1615–1625
- Thacker CE (2017) Patterns of divergence in fish species separated by the Isthmus of Panama. *BMC Evol Biol* 17:111
- Thacker CE, Gkenas C (2019) Morphometric convergence among European sand gobies in freshwater (Gobiiformes: Gobionellidae). *Ecol Evol* 9:8087–8103
- Thacker CE, Grier H (2005) Unusual gonad structure in the paedomorphic teleost *Schindleria praematura* (Teleostei: Gobioidei): a comparison with other gobioid fishes. *J Fish Biol* 66:378–391
- Thacker CE, Roje DM (2009) Phylogeny of cardinalfishes (Teleostei: Gobiiformes: Apogonidae) and the evolution of visceral bioluminescence. *Mol Phylogenet Evol* 52:735–745
- Thacker CE, Roje DM (2011) Phylogeny of Gobiidae and identification of gobiid lineages. *Syst Biodivers* 9:329–347
- Thacker CE, Unmack PJ, Matsui L et al (2007) Comparative phylogeography of five sympatric *Hypseleotris* species (Teleostei: Eleotridae) in south-eastern Australia reveals a complex pattern of drainage basin exchanges with little congruence across species. *J Biogeogr* 34:1518–1533
- Thacker CE, Unmack PJ, L. Matsui L, et al (2008) Phylogeography of *Philypnodon* species (Teleostei: Eleotridae) across south-eastern Australia: testing patterns of connectivity across drainage divides and among coastal rivers. *Bio J Linn Soc* 95:175–192
- Thacker CE, Thompson AR, Roje DM (2011) Phylogeny and evolution of Indo-Pacific shrimp-associated gobies (Gobiiformes: Gobiidae). *Mol Phylogenet Evol* 59:168–176
- Thacker CE, Satoh TP, Katayama E et al (2015) Molecular phylogeny of Percomorpha resolves *Trichonotus* as the sister lineage to Gobioidei (Teleostei: Gobiiformes) and confirms the polyphyly of Trachinoidei. *Mol Phylogenet Evol* 93:172–179
- Thacker CE, Gkenas C, Triantafyllidis A et al (2019) Phylogeny, systematics, and biogeography of the European sand gobies (Gobiiformes: Gobionellidae). *Zool J Linn Soc* 185:212–225
- Thacker CE, Shelley JJ, McCraney WT et al (2022) Phylogeny, diversification, and biogeography of a hemiclinal hybrid system of native Australian freshwater fishes (Gobiiformes: Gobioidei: Eleotridae: *Hypseleotris*). *BMC Ecol Evol* 22:22
- Thacker CE, McCraney WT, Harrington RC et al (2023) Diversification of the sleepers (Gobiiformes: Gobioidei: Eleotridae) and evolution of the root gobioid families. *Mol Phylogenet Evol* 186:107841
- Thiesen TC, Bowen BW, Lanier W et al (2008) High connectivity on a global scale in the pelagic wahoo, *Acanthocybium solandri* (tuna family Scombridae). *Mol Ecol* 17:4233–4247
- Thines M, Aoki T, Cross PW et al (2020) Setting scientific names at all taxonomic ranks in italics facilitates their quick recognition in scientific papers. *IMA Fungus* 11:25
- Thompson AR, Adam TC, Hultgren KM et al (2013) Ecology and evolution affect network structure in an intimate marine mutualism. *Am Nat* 182:E58–E72
- Tornabene L, Ahmadi GN, Berumen ML et al (2013) Evolution of microhabitat association and morphology in a diverse group of cryptobenthic coral reef fishes (Teleostei: Gobiidae; *Eviota*). *Mol Phylogenet Evol* 66:391–400
- Tornabene L, Valdez S, Erdmann M et al (2015) Support for a ‘center of origin’ in the coral triangle: cryptic diversity, recent speciation, and local endemism in a diverse lineage of reef fishes (Gobiidae: *Eviota*). *Mol Phylogenet Evol* 82:200–210
- Tornabene L, Van Tassell JL, Robertson DR et al (2016) Repeated invasions into the twilight zone: evolutionary origins of a novel assemblage of fishes from deep Caribbean reefs. *Mol Ecol* 25:3662–3682
- Troyer EM, Betancur-R R, Hughes LC et al (2022) The impact of paleoclimatic changes on body size evolution in marine fishes. *PNAS* 119:e2122486119
- Unmack PJ, Adams M, Bylemans J et al (2019) Perspectives on the clonal persistence of presumed ‘ghost’ genomes in unisexual or allopolyploid taxa arising via hybridization. *Nat Sci Rep* 9:4730
- Uribe MC, Grier HJ, Mejia-Roa V (2014) Comparative testicular structure and spermatogenesis in bony fishes. *Spermatogenesis* 4:3
- Vanhove MPM, Economou AN, Zogaris S et al (2012) Phylogenetics and biogeography of the Balkan ‘sand gobies’ (Teleostei: Gobiidae): vulnerable species in need of taxonomic revision. *Biol J Linn Soc* 105:73–91
- Vecchioni L, Ching AC, Marrone F et al (2022) Multi-locus phylogenetic analyses of the *Almadablennius* clade reveals inconsistencies with the present taxonomy of blennioid fishes. *Diversity* 14:53
- Veneza I, da Silva R, da Silva D et al (2019) Multiloci analyses suggest synonymy among *Rhomboplites*, *Ocyurus* and *Lutjanus* and reveal the phylogenetic position of *Lutjanus alexandrei* (Lutjanidae: Perciformes). *Neotrop Ichthyol* 17:e180109
- Villanueva-Gomila GL, Macchi GJ, Ehrlich MD et al (2015) The reproductive biology of *Pinguipes brasiliensis* Cuvier, 1829 (Osteichthys: Pinguipedidae) in temperate rocky reefs of Argentina. *Neotrop Ichthyol* 13:733–744
- Wagner M, Zogaris S, Berrebi P et al (2021) Diversity and biogeography of Mediterranean freshwater blennies (Blenniidae, *Salaria*). *Divers Distrib* 27:1832–1847
- Wainwright PC, Smith WL, Price SA et al (2012) The evolution of pharyngognath: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Syst Biol* 61:1001–1027
- Walker SPW, Ryen CA, McCormick MI (2007) Rapid larval growth predisposes sex change and sexual size dimorphism in a protogynous hermaphrodite, *Paraperceis snyderi* Jordan & Starks 1905. *J Fish Biol* 71:1347–1357
- Warner RR, Robertson DR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, I: the wrasses (Labridae). *Smith Cont Zool* 254:1–27

- Watson W, Walker HJ (2004) The world's smallest vertebrate, *Schindleria brevipinguis*, a new paedomorphic species in the family Schindleriidae (Perciformes: Gobioidae). *Rec Aust Mus* 56:129–142
- Watson W (1996a) Anoplogastridae: fangtooths. In: Moser HG (ed.) The early stages of fishes in the California Current Region. California cooperative oceanic fisheries investigations (CalCOFI) Atlas No. 33. Allen Press, Lawrence, Kansas, pp. 683–685
- Watson W (1996b) Diretmidae: spinyfins. In: Moser HG (ed.) The early stages of fishes in the California Current Region. California Cooperative Oceanic Fisheries Investigations (CalCOFI) Atlas No. 33. Allen Press, Lawrence, Kansas, pp. 679–681
- Westneat MW (1995) Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst Biol* 44:361–383
- Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol Phylogenet Evol* 36:370–390
- Wilson AB, Orr JW (2011) The evolutionary origins of Syngnathidae: pipefishes and seahorses. *J Fish Biol* 78:1603–1623
- Wong M-K, Chen W-J (2024) Exploring the phylogeny and depth evolution of cusk eels and their relatives (Ophidiiformes: Ophidioidae). *Mol Phylogenet Evol* 199:108164
- Wu B, Chenguang F, Zhu C et al (2021) The genomes of two billfishes provide insights into the evolution of endothermy in teleosts. *Mol Biol Evol* 38:2413–2427
- Yagishita N, Kobayashi T, Nakabo T (2002) Review of monophyly of the Kyphosidae (sensu Nelson, 1994), inferred from the mitochondrial ND2 gene. *Ichthyol Res* 49:103–108
- Yagishita N, Miya M, Yamanoue Y et al (2009) Mitogenomic evaluation of the unique facial nerve pattern as a phylogenetic marker within the perciform fishes (Teleostei: Percomorpha). *Mol Phylogenet Evol* 53:258–266
- Yokoyama R, Goto A (2005) Evolutionary history of freshwater sculpins, genus *Cottus* (Teleostei: Cottidae) and related taxa, as inferred from mitochondrial DNA phylogeny. *Mol Phylogenet Evol* 36:654–658
- You X, Bian C, Zan Q et al (2014) Mudskipper genomes provide insights into the terrestrial adaptation of amphibious fishes. *Nat Commun* 5:5594
- Zhang R, Wang X, Wan S et al (2020) A new species of *Pegasus* (Syngnathiformes: Pegasidae) from the South China Sea. *Zootaxa* 4894:521–534

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.