Abstract—The Stomiiformes are among the most abundant and ecologically important groups of deep-sea fishes. Despite this importance, our understanding of their evolutionary history is limited. Morphological work advanced our understanding of stomiiform relationships, but subsequent analyses using DNA sequence data have suggested alternative hypotheses and consistently questioned the monophyly of some or all stomiiform families. To assess the limits and relationships of the Stomiiformes and its currently recognized families (Gonostomatidae, Phosichthyidae, Sternoptychidae, and Stomiidae), we conducted a simultaneous analysis of 88 morphological characters and 409 mitochondrial and nuclear loci to resolve the relationships within this order. Here we present our results and a monophyletic classification that recognizes 3 families (Gonostomatidae, Sternoptychidae, and Stomiidae). This taxonomy places the Phosichthyidae into the synonymy of the Stomiidae and transfers *Triplophos* from the Gonostomatidae to the Stomiidae. These changes to the Stomiidae result in the family now being one of the 10 largest families of fishes and the largest deep-sea or open-ocean family of fishes (344 species). This revised phylogeny of the Stomiiformes based on the combination of anatomical and genomic data will allow subsequent researchers to explore phylogenetic scenarios for the Stomiiformes in a comprehensive framework.

The phylogeny of bristlemouths, lightfishes, and portholefishes with a revised family-level classification of the dragonfishes (Teleostei: Stomiiformes)

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Introduction

The Stomiiformes are a diverse order of pelagic, deep-water marine fishes found worldwide where they are often a dominant and ecologically important component of the deep scattering layer (Ahlstrom et al., 1984; Moser and Watson, 1996). The order includes approximately 455 species that are classified among 4 families and 52 genera (Fricke et al., 2023). These species exhibit remarkable variation in body shape, ranging from the ax-shaped members of the Sternoptychidae (marine hatchetfishes) to the snake-like members of the Stomiidae (dragonfishes). In addition to these 2 quintessential deep-sea fish families, the Stomiiformes also include the Gonostomatidae (bristlemouths) and Phosichthyidae (lightfishes). These 2 lesser-studied families lack a bioluminescent chin barbel and are generally elongate and darkly pigmented (Grey, 1964; Fink, 1985; Harold and Weitzman, 1996; Harold, 1998). Although the Gonostomatidae and Phosichthyidae have received less attention than their stomiiform allies, they remain critical to the ocean environment and pelagic food web because of their sheer abundance (Sutton et al., 2010). Because of the importance and abundance of gonostomatids and phosichthyids, it is critical that their relationships to other stomiiforms are resolved, so that ecological and evolutionary scenarios can be studied in a phylogenetic framework.

Despite their abundance and importance in the deep sea, the limits and relationships of the Stomiiformes generally, and the Gonostomatidae and Phosichthyidae in particular, remain unsettled (e.g., Fink, 1984; Harold and Weitzman, 1996; Rabosky et al., 2018) (Fig. 1). These stomiiform groups have been the focus of several groundbreaking, morphological phylogenetic studies (Weitzman, 1974; Fink, 1985; Harold and Weitzman, 1996), but they have rarely been the focus of molecular studies (but see Miya and Nishida, 1996, 2000). The explicit morphological studies (Harold and Weitzman, 1996; Harold, 1998) have resulted in phylogenetic hypotheses that frequently separate *Diplophos* Günther, 1873, *Manducus* Goode and Bean, 1896, and *Triplophos* Brauer, 1902 from the Gonostomatidae and resolve the Phosichthyidae as a grade leading toward a

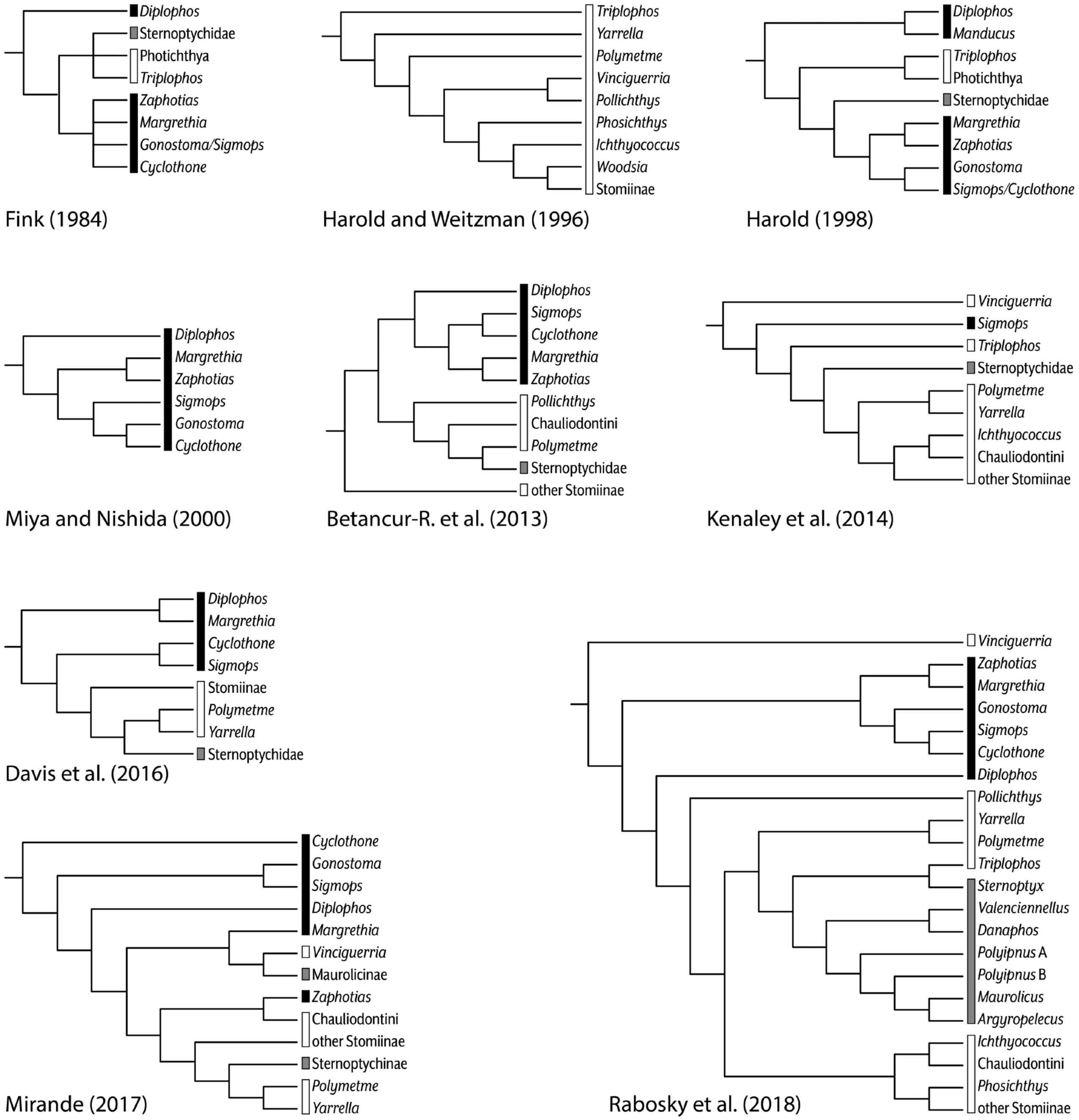

Figure 1

Hypotheses of relationships among the Stomiiformes based on previously published studies. Black, gray, and white rectangles represent the Gonostomatidae, Sternoptychidae, and Stomiidae, respectively, in our revised classification. Note that these figures use the currently recognized classification (e.g., use of *Zaphotias* instead of *Bonapartia* and recognition of *Gonostoma* and *Sigmops*) rather than the classification used in the original studies.

crown-group Stomiidae (Fig. 1). Despite these results, the classification of the Stomiiformes has not been substantially altered to reflect these findings, and it is almost certain that the family-level taxonomy of stomiiforms needs revision.

In contrast to morphological studies, most molecular studies have not focused on either the Gonostomatidae or Phosichthyidae. Instead, representatives of these families have been included among larger studies looking at the Stomiidae (Kenaley et al., 2014) (Fig. 1) or the Actinopterygii (Betancur-R. et al., 2013; Davis et al., 2016; Mirande, 2017; Rabosky et al., 2018) (Fig. 1). The results of the molecular phylogenetic studies of the Stomiiformes, Gonostomatidae, and Phosichthyidae share many similarities with the morphological studies and suggest that the Gonostomatidae is para- or polyphyletic (Davis et al., 2016; Mirande, 2017) (Fig. 1) and that the Phosichthyidae is either para- or polyphyletic (Betancur-R. et al., 2013; Kenaley et al., 2014; Mirande, 2017; Rabosky et al., 2018) (Fig. 1). Finally, some of these studies have suggested that either the Stomiidae is polyphyletic (Betancur-R. et al., 2013; Kenaley et al., 2014) or that all 4 stomiiform families are para- or polyphyletic (Mirande, 2017; Rabosky et al., 2018). These conflicting hypotheses highlight the need for a study of the Gonostomatidae and Phosichthyidae using molecular data.

Given the fairly consistent result that the Gonostomatidae and Phosichthyidae are not monophyletic using morphological, molecular, or a combination of these data (Fig. 1), it is clear that a comprehensive study across the Stomiiformes that combines existing morphological and molecular data with new data is needed to resolve their relationships. In particular, a study including all gonostomatid and phosichthyid genera is needed to resolve the limits and relationships of these deep-sea fish families.

Using the wealth of available evidence as well as newly collected morphological and molecular data, we present the results of a simultaneous analysis of morphological characters, Sanger-based sequence data, and genome-scale ultraconserved-element sequence data. Previous studies have shown that the combination of these data produce robust phylogenetic hypotheses at the ordinal level (e.g., Martin et al., 2018; Girard et al., 2020). These data were combined and analyzed to resolve the family-level phylogeny of the Stomiiformes and the genus-level relationships of the Gonostomatidae. The morphological features used by Harold and Weitzman (1996), Harold (1998), or described and coded anew were combined with molecular data from Sanger and high-throughput sequencing in all gonostomatid and phosichthyid genera, all stomiiform families, and relevant outgroups. The objectives of this study are to use adult and larval morphological features and DNA sequence characters to 1) hypothesize the intrarelationships of the Stomiiformes; 2) test the monophyly of the Gonostomatidae, Phosichthyidae, Sternoptychidae, and Stomiidae; 3) resolve relationships among the gonostomatid and phosichthyid genera; and 4) make family-level taxonomic changes, as needed, to provide a monophyletic family-level classification of the Stomiiformes.

Materials and methods

Classification and taxon sampling

All order-, family-, genus-, and species-level taxonomy follows Fricke et al. (2023) unless modified in this study. All analyses were rooted with the Atlantic argentine (*Argentina silus*) (Ascanius, 1775) (Argentinidae) and included 35 or 38 species from all stomiiform families and either one or 2 outgroup families. Supplementary Table 1 notes the taxa used in each dataset. Morphology was coded for *Argentina silus* (root) and 34 ingroup species from all stomiiform families and 24 genera. Molecular data were collected for *Argentina silus* and rainbow smelt (*Osmerus mordax*) (Mitchill, 1814) (Osmeridae) as outgroups and included 33 ingroup species from all 4 previously recognized stomiiform families and 21 genera. Combined, these 2 datasets included *Argentina silus*, *O. mordax*, and 36 ingroup species from all 4 previously recognized stomiiform families and 24 genera, including all gonostomatid and phosichthyid genera. All collection and institutional codes follow Sabaj (2020).

Morphological data

A morphological data matrix was built from multiple sources. The matrix focused on the work of Harold and Weitzman (1996) and Harold (1998). Additional character states and characters were coded from information presented in Ahlstrom et al. (1984), Moser (1996), Richards (2006), Fahay (2007), and Okiyama (2014). Further, osteological characters for *Argentina silus* were coded from KUI 28114. Larval character states for *Phosichthys* Hutton, 1872 were coded from photographs provided by Dr. Gretchen Grammer. We present the morphological characters and character states as a matrix (Table 1) and describe them in Supplementary Table 2. Although we have attributed the morphological data to lightorgan snaggletooth (*Astronesthes gemmifer* Goode and Bean, 1896), Pacific viperfish (*Chauliodus macouni* Bean, 1890), and Mueller's pearlside (*Maurolicus muelleri*) (Gmelin, 1789), to combine with DNA sequence data, these 3 species were coded morphologically from a mix of species in their respective genera for more complete anatomical coverage for the terminals. In total, the *morphological matrix* was composed of 35 taxa and 88 characters and analyzed using the Mk model of character evolution (Lewis, 2001).

Table 1

Matrix of morphological characters (characters 1–88) used to analyze the phylogeny of the Stomiiformes. Data for the matrix were pulled from the literature, museum specimens, and photographs. The character and character-state reconstructions (0, 1, 2, 3, and 4) are listed in Supplementary Table 2. The first line in the "Characters" column represents the tens place digits, and the second line represents the ones. A question mark (?) represents a missing character, and a dash (-) represents an inapplicable character. All species of *Cyclothone* have the exact character distribution for every analyzed species. The data for the lightorgan snaggletooth (*Astronesthes gemmifer*), Pacific viperfish (*Chauliodus macouni*), and Mueller's pearlside (*Maurolicus muelleri*) were based on multiple species in their respective genera. The coding for *Cyclothone* was used for all included species in the morphological and combined analyses.

Characters	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–88
Argentina silus	00--00?00-	---0?1-011	0000-?0000	?000?00000	000?0000??	0?0000?000	?00?0?0?00	0??0?1??00	10000000
Maurolicus muelleri	2100010002	-010001010	0010100000	0001-00000	00000010?0	2010110000	0000000000	0000000000	00000000
Sternoptyx pseudobscura	20--0-0002	-010001010	0010100000	0001-00000	00000010?1	2010110000	0000000000	0000000000	00000000
Valenciennellus tripunctulatus	2100010002	-010001010	0010100000	0001-00000	00000010?1	2010110000	0000000000	0000000000	00000000
Triplophos hemingi	20--010000	0000000000	0010100000	00101011-1	00010000?0	0011020000	0000000011	0000000010	010?????
Yarrella blackfordi	20--010001	-000000000	0110100000	00001011-0	000?0010?0	0011020010	0000100011	0000010010	01000000
Polymetme thaeocoryla	20--010001	-000001010	0110101000	0000100000	00000010?0	0010020000	0000100011	0000010000	00000000
Pollichthys mauli	20--010001	-100001010	1110101100	0000100011	00000010?0	0010020000	0000000011	0001010000	00000000
Vinciguerria nimbaria	20--010001	-100001010	1110101100	0000100011	00000010?0	0010120010	0000000010	0001010000	00000000
Ichthyococcus ovatus	20--010001	-100001010	1110101010	00001011-0	00100111?0	4010020000	1100010000	1000010000	00111110
Phosichthys argenteus	20--010001	-100101010	1110101000	0000100000	01110010?0	001002-001	0100001000	1000010000	0010?010
Woodsia meyerwaardeni	20--010001	-100101010	1110101010	0000110000	11100010?0	0010020001	0100001000	1000010000	00111110
Astronesthes gemmifer	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	00111010
Borostomias antarcticus	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	00111010
Chauliodus macouni	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	00110010
Heterophotus ophistoma	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	00111010
Malacosteus niger	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	001?????
Neonesthes capensis	20--010001	-100101010	1010101010	0000110000	11110011?0	3010020001	0100001000	1000010000	00110011
Diplophos taenia	10--000000	0001000000	0000-00000	0010000000	00010000?0	1100000100	0000020000	0000000000	01000001
Diplophos rebainsi	10--000000	0101000000	0000-00000	0010000000	00010000?0	1110000100	0000000000	0000000000	01000001
Manducus maderensis	10--000000	0001000000	0000-00000	0000000000	0001000000	1100000100	0000000000	0000000000	01000001
Margrethia obtusirostra	2101010000	0110011110	0010210001	1100100010	0000000000	1010001000	1010010100	0000000101	00000000
Zaphotias pedaliotus	2101010010	0110011110	0010210001	1100100010	0000000000	?010000000	1000010100	0000000101	01000000
Sigmops bathyphilus	2110111100	1010011011	0010210001	0100101000	0000110010	0010100000	1001010100	0110001100	10000000
Sigmops elongatus	2110111100	1010011010	0011210001	0100100000	0000100010	1010000000	1001010100	0110000100	00000000
Sigmops gracilis	2110111100	1010011011	0011210001	0100100000	0000110010	1010000000	1001010100	0110100100	11000000
Sigmops longipinnis	2110111100	1010011010	0011210001	0100100000	0000110010	0010000000	1001010100	0110100100	10000000
Gonostoma atlanticum	2110111100	1010011010	0011210001	0100100000	0000100000	1010000000	1001010100	0110000100	01000000
Gonostoma denudatum	2110111100	1010011010	0011210001	0100100000	0000100000	1010000000	1001010100	0110000100	00000000
Cyclothone spp.	2120211100	1000011011	0010110001	01001011-1	0000110011	?010100000	1001010100	0110121100	11000000

DNA sequence data

Tissue extraction and Sanger sequencing techniques followed Davis et al. (2016). New Sanger sequence data for mitochondrial cytochrome *c* oxidase subunit 1 (COI) and nuclear ectodermal-neural cortex 1 (ENC1), myosin heavy chain 6 (MYH6), recombination activating gene 1 (RAG1), and Zic family member 1 (ZIC1), were built and edited in Geneious, vers. 8.1.8 (Kearse et al., 2012). These edited Sanger sequences were combined with previously published data for 12S ribosomal RNA gene, 16S ribosomal RNA gene, COI, ENC1, MYH6, RAG1, and ZIC1 from the following: Miya and Nishida (1996, 1999, 2000), López et al. (2004), Ilves and Taylor (2009), Davis (2010), Near et al. (2012, 2013), Betancur-R. et al. (2013), Grande et al. (2013), Chen et al. (2014), Davis et al. (2014, 2016), Poulsen (2015), Kenchington et al. (2017), and Waap et al. (2017). Additionally, unpublished data that are publicly available were taken from GenBank (National Institutes of Health, available from https://www.ncbi.nlm.nih.gov/genbank/) (Suppl. Table 1). Finally, high-throughput sequence data were queried for fragments homologous with these Sanger data following the procedure in Smith et al. (2022). The sources of all Sanger data can be found in Supplementary Table 1. The 7 Sanger loci were aligned individually with MAFFT, vers. 7.130b (Katoh and Standley, 2013) using default settings. The resulting alignment of this matrix was 5206 base pairs (bp), which was 66.5% complete at the locus level and 61.8% complete at the base-pair level. Novel sequences were submitted to GenBank and assigned accession numbers (PQ305927–PQ305930, PQ309621–PQ309634).

High-throughput tissue extraction and quantification protocols followed Smith et al. (2022). Quantified high-throughput samples were sent to Arbor Biosciences (Ann Arbor, MI) for library preparation (e.g., DNA shearing, size selection, cleanup), target capture (using the 500 ultraconserved elements (UCE) actinopterygian loci probe set; Faircloth et al., 2013), enrichment, sequencing using an Illumina HiSeq 2500 (San Diego, CA) or NovaSeq 6000 (Illumina), and demultiplexing of samples. We processed the raw FASTQ files from Arbor Biosciences using the Phyluce 1.71 (Faircloth, 2016) workflow to retrieve UCE and flanking regions. All genome-scale bioinformatic methods follow Smith et al. (2022). The cleaned sequencing reads were submitted to GenBank and have been assigned BioProject PRJNA1159332 and sequence read archive, or SRA, accession numbers: SAMN43572806– SAMN43572825). We assembled cleaned reads, assembled contigs for the UCE loci, aligned, and concatenated the sequences present for ≥75% of taxa. The resulting 75% complete UCE matrix was based on 402 UCEs or 196,625 aligned base pairs that were present for the 20 species with UCE data; this UCE matrix was 93.6% complete at the locus level. Across all UCE loci, median sequence fragment length was 1060 bp, with a range of 379–1448 bp (Suppl. Table 3). The UCE and flanking region sequences were then partitioned using the sliding-window site characteristics–entropy method (Tagliacollo and Lanfear, 2018) to split each UCE locus into left and right flanking regions and the ultraconserved core by rate of evolution.

The final concatenated *molecular matrix* was based on 402 UCE loci and 7 Sanger loci and included 201,831 aligned base pairs (42,083 parsimony-informative characters) for 35 taxa. The resulting left, core, and right UCE segments were then used as input, along with the independent 12S and 16S loci and the 3 independent codon positions for each of the 5 protein-coding Sanger genes, to PartitionFinder, vers. 2.1.1 (Lanfear et al., 2014, 2017; Stamatakis, 2014) to find the best-fitting nucleotide substitution model for each molecular data partition. PartitionFinder selected among models using Akaike information criterion with an adjustment for small sample size and the rclusterf search method with the setting *-raxml* (Lanfear et al., 2014). PartitionFinder designated 967 subsets and models for these regions. A list of the subsets, partitions, and models is presented in Supplementary Table 4.

Combined dataset

In addition to independent morphological and molecular datasets, we also combined the morphological and molecular matrices for simultaneous study. This *combined matrix* included 38 species, all gonostomatid and phosichthyid genera, and 201,919 characters, of which 42,171 were parsimony informative. For this dataset, the 967 subsets from the molecular matrix were combined with an independent morphological matrix partition that used an Mk model of character evolution.

Phylogenetic analyses

The morphological, molecular, and combined datasets were analyzed using IQ-Tree v2.1.1 (Chernomor et al., 2016; Minh et al., 2020). Each analysis consisted of a minimum of 20 independent runs of the software using the datasets and partition strategies noted above, *Argentina silus* as the root, and the default behavior. Support for the phylogenies for each matrix was assessed using IQ-Tree (-bo), and the results from 200 ultrafast bootstrap replicates were summarized using majority-rule consensus trees. We recognize 3 levels of nodal support: ≥50% bootstrap support represents a supported node or clade, ≥70% bootstrap support represents a moderately well-supported node or clade, and ≥95% bootstrap support represents a well-supported or strongly supported node or clade. In addition to phylogenetic reconstructions, we examined and analyzed the datasets (ancestralstate reconstructions) in Mesquite, vers. 3.5 (Maddison and Maddison, 2018) using parsimony and maximum likelihood.

Results

The analysis of the morphological matrix or *morphological analysis* resulted in a single optimal tree (Fig. 2A) with a likelihood score of −922.094. Eight nodes (of the 29 possible nodes [because all *Cyclothone* Goode and Bean, 1883 were coded identically]; 27.6%) were well supported, 11 nodes (37.9%) were moderately supported or better, and 21 nodes (72.4%) were supported or better. The analysis of the molecular matrix or *molecular analysis* resulted in a single optimal tree (Fig. 2B) with a likelihood score of −1121603.482. Twenty-four nodes (of 33 possible nodes; 72.7%) were well supported, 26 nodes (78.8%) were moderately supported or better, and 30 nodes (90.9%) were supported or better. The simultaneous analysis of the molecular and morphological data *combined analysis* resulted in a single optimal tree (Fig. 3) with a likelihood score of −1122830.977. Nineteen nodes (of 36 nodes; 52.8%) were well supported, 27 nodes (75.0%) were moderately supported or better, and 31 nodes (86.1%) were supported or better.

Stomiiform familial interrelationships

Overall, the relationships hypothesized in the 3 phylogenies (Figs. 2 and 3) agree more than they disagree, but, importantly, none of the phylogenies were consistent with the taxonomy in Fricke et al. (2023) or other prevailing classifications (Betancur-R. et al., 2013; Davis et al., 2016; Nelson et al., 2016; Mirande, 2017; Rabosky et al., 2018). All analyses recovered the Phosichthyidae, Stomiidae, and *Triplophos* together as a clade. The molecular and combined analyses recovered the Phosichthyidae, Sternoptychidae, Stomiidae, and *Triplophos* together as a clade; whereas the morphological analysis recovered the Sternoptychidae and the core Gonostomatidae (all gonostomatid genera except *Diplophos*, *Manducus*, and *Triplophos*) as a clade. The molecular and combined analyses recovered the Gonostomatidae (less *Triplophos*) sister to all other stomiiforms. In contrast, the morphological analysis recovered a clade of both species of *Diplophos* and *Manducus* at the base of the Stomiiformes.

Stomiiform family intrarelationships

All analyses recovered a polyphyletic Gonostomatidae (Figs. 2 and 3). The molecular and combined analyses recovered Gonostomatidae less *Triplophos* as a clade (Figs. 2B and 3). In contrast, the morphological analysis resulted in a clade composed of *Cyclothone*, *Gonostoma* Rafinesque, 1810, *Margrethia* Jespersen and Tåning, 1919, *Sigmops* Gill, 1883, and *Zaphotias* Goode and Bean in Jordan and Evermann, 1898, an independent lineage of *Diplophos*+*Manducus*, and a separate *Triplophos* (Fig. 2A). The separation of *Triplophos* from the remainder of the Gonostomatidae and its resolution among the phosichthyids is consistent with previous morphological studies (Harold and Weitzman, 1996; Harold, 1998) (Fig. 1). The morphological analysis, like previous morphological analyses, separated *Diplophos*, *Manducus*, and *Triplophos* from the remainder of the gonostomatids (Fink, 1984; Harold, 1998) (Figs. 1 and 2A).

All analyses recovered the phosichthyids as a paraphyletic grade relative to the Stomiidae that was nested within it and with *Triplophos* either nested among the grade (Fig. 2A) or sister to the Phosichthyidae+Stomiidae (Figs. 2B and 3). Non-monophyly of the Phosichthyidae relative to the Stomiidae was substantive but expected based on Fink (1985) and Harold and Weitzman (1996) (Fig. 1).

All analyses recovered a monophyletic Sternoptychidae (Figs. 2 and 3) as was found in earlier morphological studies (Weitzman, 1974; Fink, 1984; Harold, 1998) (Fig. 1) and some molecular studies (Betancur-R. et al., 2013; Kenaley et al., 2014; Davis et al., 2016) (Fig. 1). The large studies of Mirande (2017) and Rabosky et al. (2018) recovered the Sternoptychidae as para- or polyphyletic (Fig. 1).

All 3 of our hypotheses (Figs. 2 and 3) recovered a monophyletic Stomiidae. A monophyletic Stomiidae that includes *Chauliodus* Bloch and Schneider, 1801 and other stomiids is consistent with the results of Harold and Weitzman (1996) and Davis et al. (2016), but it contradicts the results of Betancur-R. et al. (2013), Kenaley et al. (2014), Mirande (2017), and Rabosky et al. (2018), who all recovered *Chauliodus* more closely related to other clades in the Stomiiformes than to the remainder of the Stomiidae (Fig. 1).

Interrelationships of gonostomatid and phosichthyid genera

Among the gonostomatids, all analyses recovered a clade composed of *Cyclothone*, *Gonostoma*, and *Sigmops*. Of these, the morphological analysis recovered *Cyclothone* as a crown clade with species of *Sigmops* and *Gonostoma* as sequential grades (Fig. 2A). The molecular and combined analyses recovered all 3 genera as reciprocally monophyletic with *Cyclothone* and *Gonostoma* as sister genera with *Sigmops* sister to the other 2 genera (Figs. 2B and 3). All 3 of our analyses (Figs. 2 and 3) recovered a clade of *Margrethia* and *Zaphotias* sister to the clade composed of *Cyclothone*, *Gonostoma*, and *Sigmops*. With the exception of Mirande (2017), all previous explicit analyses essentially supported this (Fig. 1). Finally, the molecular analysis had *Diplophos* sister to all other

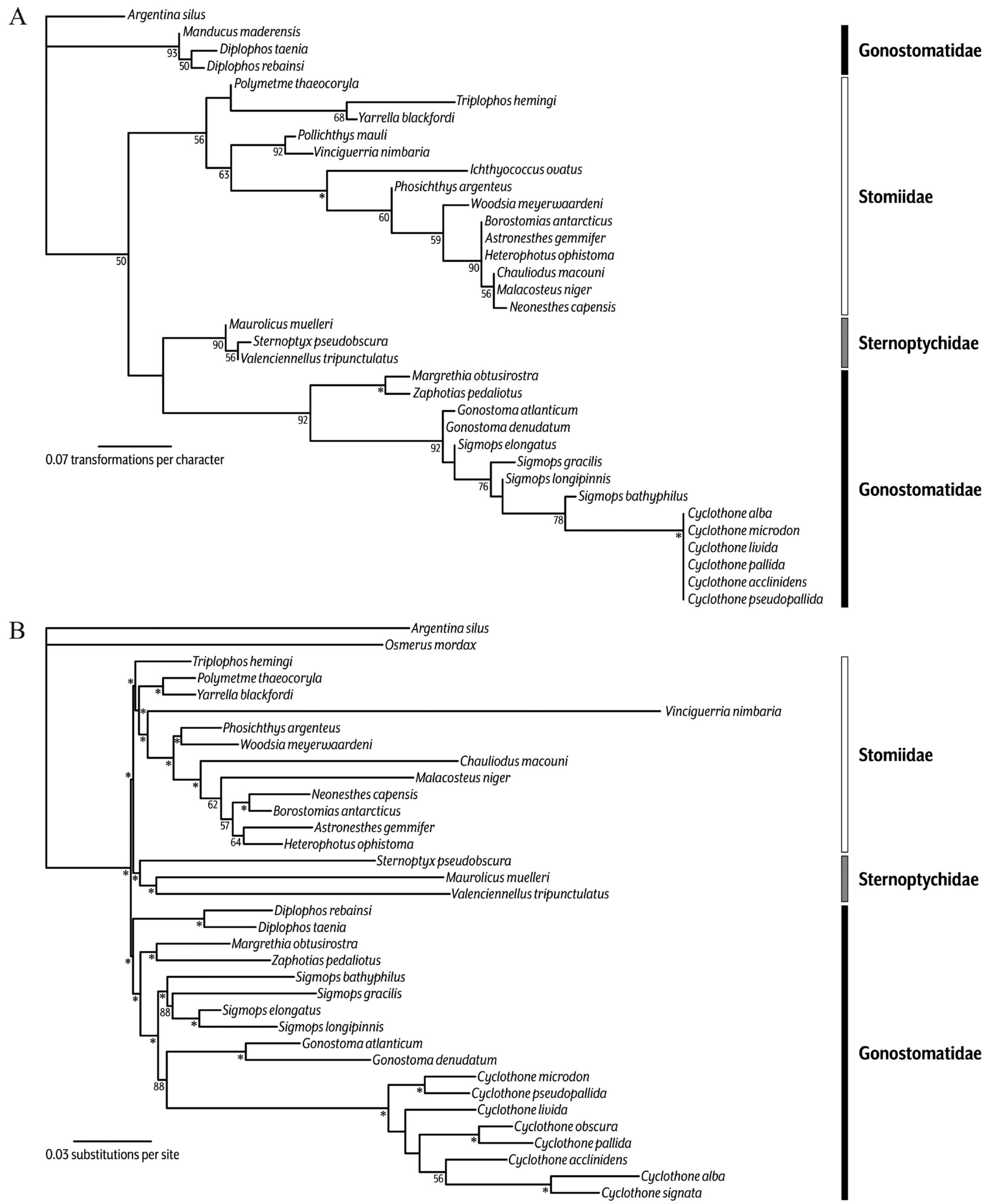

Figure 2

Optimal cladograms representing relationships of the Stomiiformes and outgroups resulting from the likelihood analysis of (**A**) the morphological dataset for 35 taxa and 88 characters and (**B**) the molecular dataset for 35 taxa and 201,831 characters. Bootstrap support for each node with ≥50% is noted on each node, and nodes with ≥95% bootstrap support are identified with an asterisk. Black, gray, and white rectangles represent the Gonostomatidae, Sternoptychidae, and Stomiidae, respectively, in our revised classification.

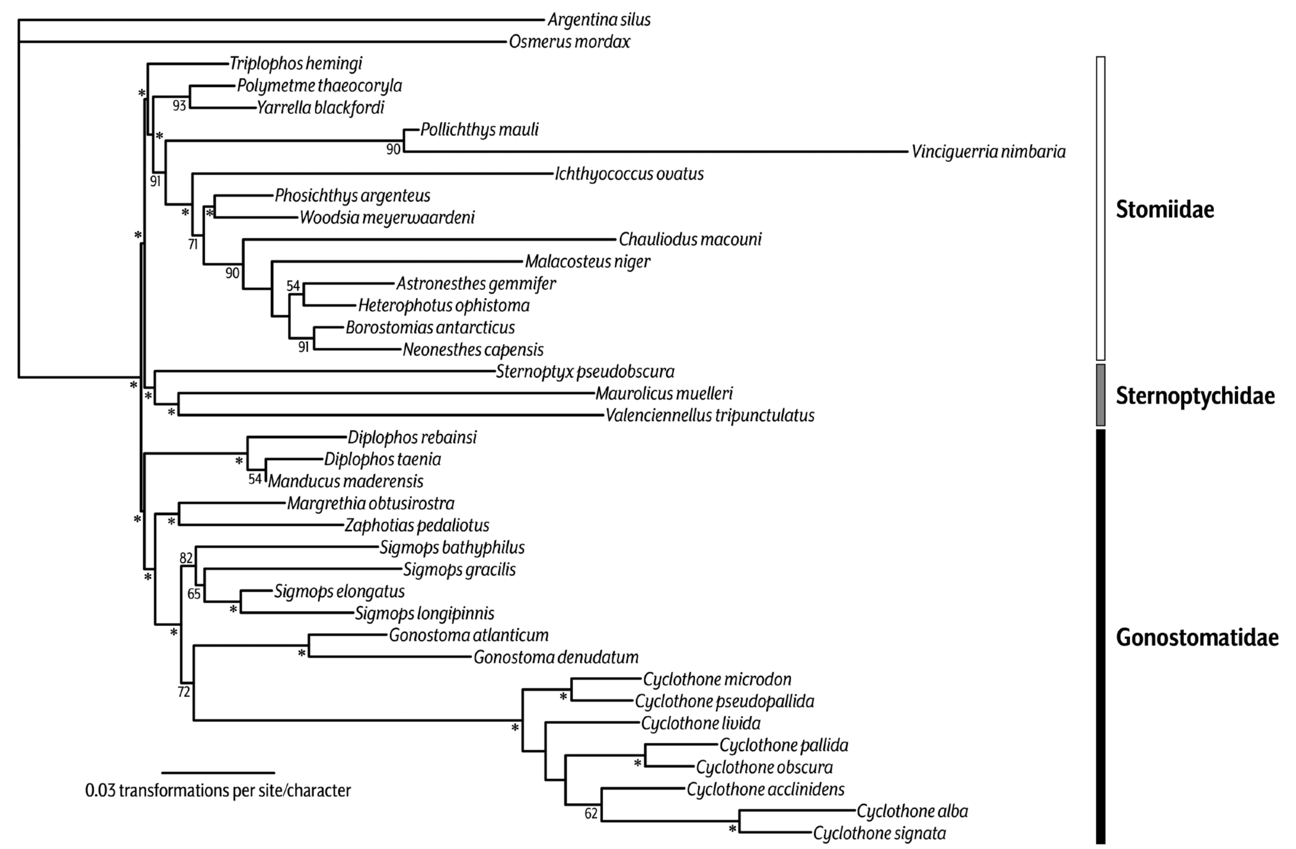

Figure 3

Optimal cladogram representing relationships of the Stomiiformes and outgroups resulting from the likelihood analysis of the combined dataset for 38 taxa and 201,919 characters. Bootstrap support for each node with ≥50% is noted on each node, and nodes with ≥95% bootstrap support are identified with an asterisk. Black, gray, and white rectangles represent the Gonostomatidae, Sternoptychidae, and Stomiidae, respectively, in our revised classification.

non-*Triplophos* gonostomatids (Fig. 2B), the combined analysis had the clade of *Diplophos* and *Manducus* sister to all other gonostomatids (Fig. 3), and the morphological analysis had a clade of *Diplophos* and *Manducus* sister to all other stomiiforms (Fig. 2A).

The molecular and combined analyses recovered a clade composed of *Phosichthys* and *Woodsia* Grey, 1959 sister to the Stomiidae (Figs. 2B and 3), a pairing first suggested by Fink (1985:52). The morphological analysis recovered *Woodsia* sister to the Stomiidae with *Phosichthys* as the subsequent sister group to the Stomiidae+*Woodsia* (Fig. 2A). The morphological (Fig. 2A) and combined analyses (Fig. 3) recovered *Ichthyococcus* Bonaparte, 1840 sister to *Phosichthys, Woodsia,* and the Stomiidae (*Ichthyococcus* was not included in the molecular analysis). All 3 analyses recovered *Pollichthys* Grey, 1959 (if included) and *Vinciguerria* Jordan and Evermann in Goode and Bean, 1896 as the subsequent sister group (Figs. 2 and 3). The morphological analysis (Fig. 2A) recovered a clade of *Polymetme* McCulloch, 1926 and *Triplophos*+*Yarrella* Goode and Bean, 1896 as the earliest diverging lineage among the Phosichthyidae+Stomiidae+*Triplophos*. Finally, the molecular and combined analyses recovered *Polymetme* and *Yarrella* as a clade sister to all other phosichthyids and stomiids (Figs. 2B and C), and these analyses recovered *Triplophos* sister to the Phosichthyidae+Stomiidae.

Stomiiform taxonomic changes

Considering the non-monophyly of half of the stomiiform families, the strongly supported results in our combined analysis (Figs. 3 and 4), and the similarity of our combined results to earlier morphological analyses despite the addition of genome-scale DNA sequence data (Fink, 1985; Harold and Weitzman, 1996), we recommend changes to the classification of stomiiform fishes. These changes are necessary given the recovery of *Triplo-*

phos at the base of the Phosichthyidae+Stomiidae clade and the rampant non-monophyly of the Phosichthyidae (Figs. 3 and 4). A monophyletic taxonomy of the Stomiiformes requires either recognition of one large Stomiidae that includes all phosichthyids, stomiids, and *Triplophos* (*sensu* Nelson, 2006) or breaking the clade into many small families with 1–4 genera each. Recognizing many families would highlight the clade's diversity, but a monophyletic taxonomy would require the recognition of 5 to 13 families (depending on treatment of the current stomiid subfamilies). These changes would be highly disruptive to stomiiform taxonomy, which has been remarkably stable for half a century.

Our proposed taxonomic changes are to place the Phosichthyidae into the synonymy of the Stomiidae, to reduce the diversity of gonostomatids (by excluding *Triplophos*), and to expand the Stomiidae (to include *Ichthyococcus*, *Phosichthys*, *Pollichthys*, *Polymetme*, *Triplophos*, *Vinciguerria*, *Woodsia*, and *Yarrella*). Further, the Stomiidae (*sensu* Fink, 1985) or stomiids with barbels would now be referred to as the Stomiinae. This revised classification (unless otherwise noted) will be used for the remainder of this paper and is used in the figures to highlight the revised families with black (Gonostomatidae), gray (Sternoptychidae), or white (Stomiidae) bars in Figures 1–3. When relevant in the Discussion and Conclusions, we will refer to the former Phosichthyidae by placing the family name in quotes as was done by Fink (1985) and Harold and Weitzman (1996).

We are recommending these taxonomic changes because we believe that they will maintain the recent taxonomic stability within the Stomiiformes while also recognizing exclusively monophyletic families. Further, the expansion of the Stomiidae to include these 8 additional genera is more consistent with the spirit of the changes made by Weitzman (1974) and Fink (1985), who tended to emphasize similarities more than differences by combining smaller families into larger families rather than recognizing large numbers of families. Following Fink's (1985) lead and based on our combined analysis, we believe that grouping the phosichthyids, stomiids, and *Triplophos* together into an expanded Stomiidae would result in a stable monophyletic taxonomy for the Stomiiformes, Gonostomatidae, and Stomiidae.

Brief description of the larva of *Phosichthys*

The imaged specimens of the silver lightfish (*Phosichthys argenteus*) Hutton, 1872 were initially identified through DNA COI barcoding, and the imaged larvae themselves were consistent with the counts of *Phosichthys argenteus* and physiognomy of most larval early diverging stomiids. From these digital photos, we generated a mostly complete composite illustration (*Phosichthys* in Figure 4 and Supplementary Figure 1) that is representative of the imaged specimens (based on digital photos of a number of postflexion specimens ranging from approximately 9–20 mm standard length). None of the digital photos included specimens with a completely undamaged head, pectoral fin, or gut. These digital photos were insufficient to provide a complete description and illustration of a larva of *Phosichthys*, but they did allow us to conclusively code all but one of the larval characters for this species and provide a tentative illustration.

Clearly, larval *Phosichthys* look similar to their close allies in *Ichthyococcus* and *Woodsia* and some stomiines (Fig. 4). This larva is distinguished by being more elongate and similar in dimensions to *Diplophos*. Larval *Phosichthys* and *Diplophos* can be distinguished from each other by the dorsal and ventral pigment pattern in *Diplophos* versus the lateral pigment pattern in *Phosichthys* where each larva has patches of melanophores every 3 to 5 (modally 4) myomeres. We have included these larval differences, character coding of *Phosichthys* (Table 1), and a draft illustration (Fig. 4, Suppl. Fig. 1) to help subsequent researchers identify and, ideally, describe the morphology of a larval series of *Phosichthys*.

Discussion

This study was designed primarily to investigate the phylogeny and taxonomy of the Stomiiformes, Gonostomatidae, and Phosichthyidae. Given our taxonomic focus on the Gonostomatidae and Phosichthyidae, only 3 and 6 representatives of the species-rich Sternoptychidae and Stomiinae, respectively, were included in our analyses. We hope that our updated phylogenetic framework and representative larval illustrations will help researchers identify, document, and illustrate more larvae. Given the morphological variation in adult stomiiforms, a comprehensive understanding of larval stomiiforms will serve as the basis of future phylogenetic comparisons across the less differentiated yet often highly specialized larvae.

Stomiiformes

Recognizing the consistent earlier finding of a monophyletic Stomiiformes (e.g., Rosen, 1973; Betancur-R. et al., 2013; Davis et al., 2016; Mirande, 2017; Rabosky et al., 2018), this study did not extensively test stomiiform monophyly. Our molecular and combined analyses recovered a monophyletic Stomiiformes with strong bootstrap support with 2 or fewer outgroups (Figs. 2B and 3). The previous morphological analyses (Harold and Weitzman, 1996; Harold, 1998) included a single outgroup, so our analyses could not resolve any stomiiform synapomorphies since we built our morphological dataset from these studies. Fink and Weitzman (1982) proposed 8 diagnostic characters for the Stomiiformes that

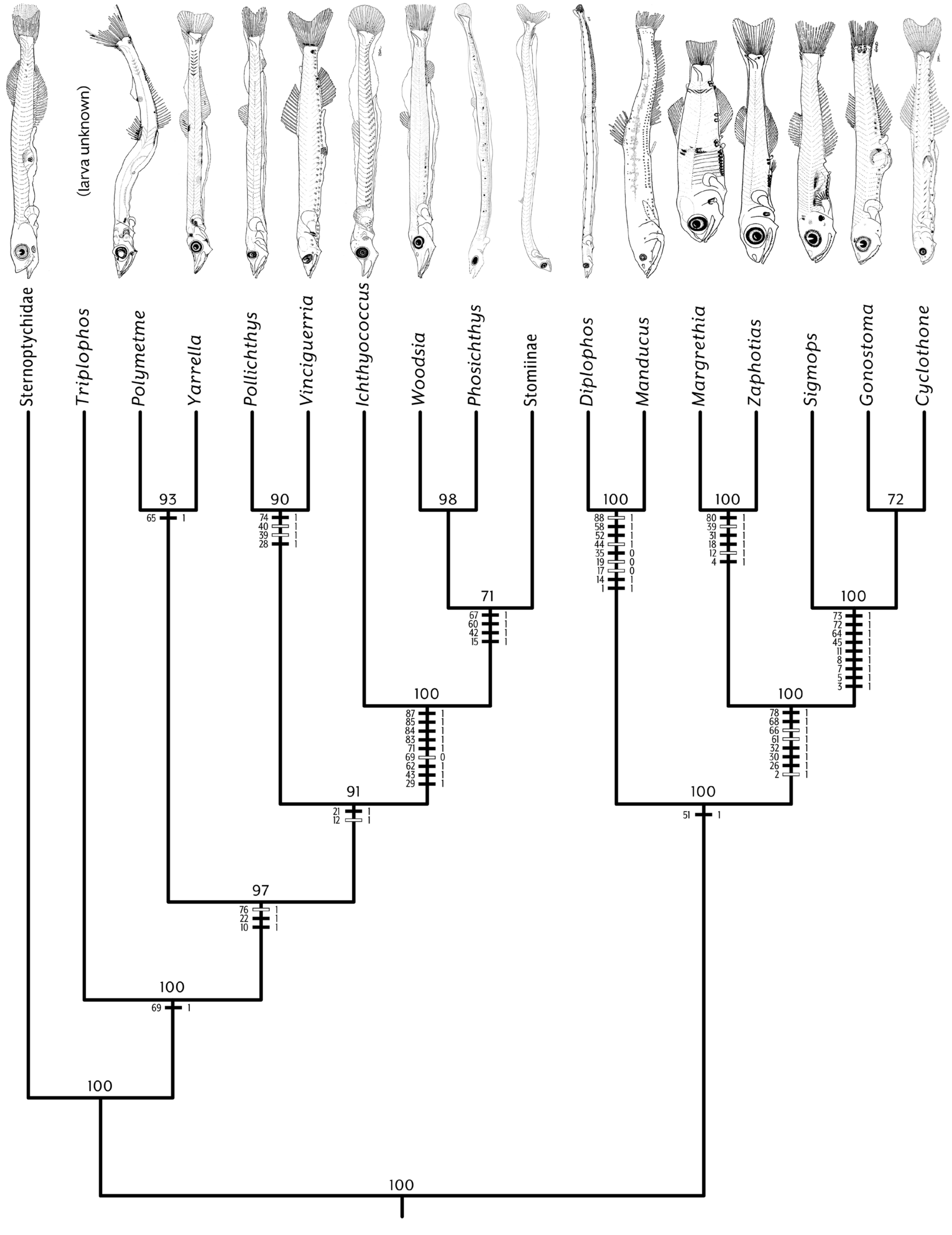

Figure 4

See caption next page

Figure 4

Reduced phylogeny representing the relationships among the Stomiiformes resulting from the combined analysis of 38 taxa and 201,919 characters. Bootstrap supports are noted on each node. Parsimony reconstructions of morphological features are optimized for each clade with character number (left) and character state (right) of black boxes representing non-homoplastic transformations or white boxes representing homoplastic transformations. Representative drawings of known stomiiform larvae are illustrated for comparative purposes. The Sternoptychidae is represented by the eastropac lightfish (*Araiophos eastropas*) (Ahlstrom and Moser, 1969; used with permission of the American Society of Ichthyologists and Herpetologists [PASIH]). *Polymetme* is represented by *Polymetme elongata* (Fukui and Kuroda, 2005). *Yarrella* is represented by the rendezvous lightfish (*Y. blackfordi*) (Ahlstrom et al., 1984; PASIH). *Pollichthys* is represented by the stareye lightfish (*Pollichthys mauli*) (Ahlstrom et al., 1984; PASIH). *Vinciguerria* is represented by the Panama lightfish (*V. lucetia*) (Ahlstrom and Counts, 1958). *Ichthyococcus* is represented by the bulldog lightfish (*I. irregularis*) (Watson, 1996a). *Woodsia* is represented by the bigeye lightfish (*W. nonsuchae*) (Watson, 1996a). *Phosichthys* is represented by the silver lightfish (*Phosichthys argenteus* (new illustration). The Stomiinae is represented by the Pacific viperfish (*Chauliodus macouni*) (Kawaguchi and Moser, 1984; PASIH). *Diplophos* is represented by the warmseas portholefish (*D. taenia*) (Watson, 1996b). *Manducus* is represented by the Atlantic manducus (*Manducus maderensis*) (Jespersen and Tåning, 1919). *Margrethia* is represented by the bighead lightfish (*Margrethia obtusirostra*) (Ahlstrom et al., 1984; PASIH). *Zaphotias* is represented by the longray lightfish (*Z. pedaliotus*) (Ahlstrom et al., 1984; PASIH). *Sigmops* is represented by the elongate lightfish (*S. elongatus*) (Ahlstrom et al., 1984; PASIH). *Gonostoma* is represented by the cosmopolitan bristlemouth (*G. atlanticum*) (Ahlstrom et al., 1984; PASIH). *Cyclothone* is represented by the benttooth bristlemouth (*Cyclothone acclinidens*) (Watson, 1996b).

included features of the photophores, teeth, jaw muscles, cranial ligaments, dorsal gill arches, branchiostegal rays, and gas bladder.

Stomiiform familial interrelationships

Weitzman (1967, 1974) provided a detailed historical account of the Stomiiformes. Historically, the Gonostomatidae had been a much more species-rich family than we recognize herein. An early monographic study of the Gonostomatidae (Norman, 1930) included not only our gonostomatids, but also *Triplophos*, "phosichthyids," and several sternoptychids for a total of 15 of the 52 currently recognized stomiiform genera. Grey (1964) had similar familial limits, but her Gonostomatidae included 22 of the 52 currently recognized stomiiform genera given additional material and the new diversity that was described between 1930 and 1964.

For most of the 20th century, researchers essentially classified the Stomiiformes into 3 groups even though they recognized many families: hatchetfishes with deeper bodies (our Sternoptychinae; 3 genera and 61 species), dragonfishes with barbels (our Stomiinae; 27 genera and 319 species), and bristlemouths (our Gonostomatidae; the remaining 22 genera and 75 species). Weitzman (1974) split this historically larger Gonostomatidae into the Maurolicinae (which he moved to the Sternoptychidae), the "phosichthyids" (which he allied with our Stomiinae in his Photichthya), and a more restricted Gonostomatidae. Subsequently, Fink (1984, 1985) placed the Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, and Melanostomiatidae into the synonymy of the Stomiidae. These changes to the limits of the Gonostomatidae, "Phosichthyidae," Sternoptychidae, and Stomiidae have been largely followed in later fish classifications (e.g., Nelson et al., 2016; Fricke et al., 2023). Further, Fink (1984) and Harold (1998) separated *Diplophos* or *Diplophos*, *Manducus*, and *Triplophos* from the other gonostomatids.

After revising the major clades of the Stomiiformes, Weitzman (1974) provided the first phylogenetic hypothesis for the order where he grouped the Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, Melanostomiatidae, and our Stomiinae (his Stomiatidae) into the Stomiatoidea and depicted this grouping sister to the "Phosichthyidae" (his Photichthyidae). Together, this Photichthya was hypothesized to be the sister group to the Gonostomata, which was composed of the sister-group pairing of Gonostomatidae and Sternoptychidae. Fink (1984, 1985) (Fig. 1) provided a revised phylogeny of the Stomiiformes and our Stomiinae (his Stomiidae that then included the Astronesthidae, Chauliodontidae, Idiacanthidae, Malacosteidae, and Melanostomiatidae). His phylogenetic hypothesis differed most significantly from Weitzman (1974) by grouping *Triplophos*, the Sternoptychidae, and the Photichthya together to the exclusion of the remaining gonostomatids. Harold (1998) (Fig. 1) supported some of Fink's (1985) results (e.g., treatment of *Diplophos* [and *Manducus*] as the earliest diverging lineage in the Stomiiformes), but he also returned to Weitzman's (1974) grouping of the Gonostomatidae (less *Diplophos*, *Manducus*, and *Triplophos*) and Sternoptychidae.

Molecular and combined analyses (Fig. 1) have recovered numerous families as non-monophyletic and have had vastly different hypothesized relationships compared to the morphological studies. For example, Betancur-R. et al. (2013) (Fig. 1) recovered most stomiines sister to all other stomiiforms and recovered a grade of "phosichthyids" and Chauliodontini leading up to a crown-group Sternoptychidae. Kenaley et al. (2014) (Fig. 1) recovered a clade of the Stomiidae (less *Triplophos* and *Vinciguerria*) sister to the Sternoptychidae. Later studies (Davis et al., 2016; Mirande, 2017; Rabosky et al., 2018) (Fig. 1) continued to have some unexpected relationships rendering families non-monophyletic, but the general pattern of a sister-group relationship between the Stomiidae and Sternoptychidae relative to Gonostomatidae was typical. In contrast, we find a polyphyletic "gonostomatids" with a first clade sister to all other stomiiforms and a second clade sister to the Sternoptychidae (Fig. 2A). As we brought all the gonostomatid and phosichthyid genera together with extensive morphological and molecular data, we recovered a strongly supported phylogeny that was more consistent with both the earlier morphological phylogenies (e.g., monophyly of Photichthya) and with the general trends of the molecular hypotheses (e.g., Sternoptychidae sister to Stomiidae) without any significant unexpected results (Figs. 1 and 4).

Gonostomatidae

The revised and smaller Gonostomatidae included herein is a modestly sized teleostean family (7 genera and 52 species) that is found worldwide in bathy- and mesopelagic zones, often in great abundance (Moser and Watson, 1996; Sutton et al., 2010). As noted above, Weitzman (1974) dramatically restricted the limits of the Gonostomatidae, which had historically been a much more species-rich family. Weitzman's changes to the limits of the Gonostomatidae have been largely followed in subsequent classifications (e.g., Nelson et al., 2016; Fricke et al., 2023). Later work by Fink (1984) and Harold (1998) separated *Diplophos* or *Diplophos*, *Manducus*, and *Triplophos* from the other gonostomatids. Although these authors did not make explicit taxonomic recommendations, some authors have partially followed the phylogenetic results from these 2 studies by classifying *Diplophos*, *Manducus*, and *Triplophos* into an independent Diplophidae (e.g., Nelson, 2006; Betancur-R. et al., 2013). However, neither of these classifications was fully compatible with the explicit phylogenetic hypotheses of Harold and Weitzman (1996), Harold (1998), previous molecular studies, or the current combined analysis (Figs. 1, 3, and 4) because *Diplophos*, *Manducus*, and *Triplophos* have never been resolved as a clade or grouped to the exclusion of all other stomiiforms.

The Gonostomatidae recognized in this study differs in its composition relative to all previous taxonomies (e.g., Grey, 1964; Weitzman, 1974; Harold and Weitzman, 1996; Harold, 1998; Nelson, 2006; Betancur-R. et al., 2013; Nelson et al., 2016; Fricke et al., 2023). Relative to Fricke et al. (2023), our Gonostomatidae differs only by the treatment of *Triplophos* as a member of the Stomiidae. Our mildly more restricted Gonostomatidae that has morphological and molecular support also differs in composition from previous implied classifications based on morphological features (e.g., Fink and Weitzman, 1982; Fink, 1984; Harold and Weitzman, 1996; Harold, 1998) by its inclusion of *Diplophos* and *Manducus*, in the Gonostomatidae rather than as a distinct clade. We could have chosen to recognize a Diplophidae composed of *Diplophos* and *Manducus* and a Gonostomatidae composed of *Cyclothone*, *Gonostoma*, *Margrethia*, *Sigmops*, and *Zaphotias*. Both taxonomies would be based on exclusively monophyletic groups. Certainly, there are more morphological features diagnosing each of these 2 clades than for the clade as a whole (Fig. 4). However, and as noted above for expanding the limits of the Stomiidae, we have chosen to embrace similarity and tradition over differences or anatomical changes between sister clades, particularly given that our Gonostomatidae was well supported in our molecular and combined analyses. This combined analysis also included explicit morphological support (Fig. 4) with the family being diagnosed by an elongate parapophysis on the first vertebra that is continuous with Baudelot's ligament (reversed in 2 species of *Sigmops*).

The gonostomatid relationships hypothesized in our combined analysis largely corroborate previous hypotheses (Fig. 1). With morphological data, Fink (1984) placed *Diplophos* near the base of the Stomiiformes. Harold (1998) placed *Diplophos* and *Manducus* near the base of the Stomiiformes. Fink (1984) left relationships among *Cyclothone, Gonostoma*, *Margrethia*, *Sigmops*, and *Zaphotias* unresolved, while Harold (1998) hypothesized 2 major clades within the 5 remaining genera: one composed of *Margrethia* and *Zaphotias* and one composed of *Cyclothone*, *Gonostoma*, and *Sigmops*.

Molecular analyses have largely recovered similar groupings of these major clades (Miya and Nishida, 2000; Betancur-R. et al., 2013; Davis et al., 2016; Rabosky et al., 2018) (Fig. 1), although (Mirande, 2017) had an alternative hypothesis with a polyphyletic Gonostomatidae (Fig. 1). Across all these studies (except Mirande, 2017), the single consistent grouping is the monophyly of *Cyclothone*, *Gonostoma*, *Margrethia*, *Sigmops*, and *Zaphotias*. We note that our combined analysis recovered *Manducus* within *Diplophos*. This is a result of the lack of molecular data for *Manducus* and variation in the anatomy among the species in *Diplophos*; we do not recommend placing *Manducus* in the synonymy of *Diplophos*.

Sternoptychidae

The Sternoptychidae is a large family (10 genera and 99 species) that includes both the deeper-bodied Sternoptychinae and the more elongate Maurolicinae. Unlike the other stomiiform family-level clades, the limits and relationships of the Sternoptychidae have been fairly stable. Historically, 2 sternoptychid clades (Sternoptychinae and Maurolicinae) were often recognized, but not necessarily grouped together or classified in the same family (Norman, 1930; Schultz, 1961; Grey, 1964). Following Weitzman (1974), a larger Sternoptychidae that combined these clades into a monophyletic Sternoptychidae has been recovered fairly consistently (Fink, 1984; Harold, 1994, 1998; Betancur-R. et al., 2013; Davis et al., 2016; Fig. 1); however, Mirande (2017) and Rabosky et al. (2018) recovered sternoptychids as para- or polyphyletic. The limits of the Sternoptychidae recognized in the combined analysis of this study are identical to all major phylogenetic studies and summary works (Nelson, 2006; Betancur-R. et al., 2013; Davis et al., 2016; Nelson et al., 2016; Fricke et al., 2023). Our combined analysis recovered the 3 included genera as a clade, and this clade was supported by 4 characters: 1) the presence of alpha photophores, 2) the loss of the basihyal, 3) the parapophyses on vertebrae 1 and 2 being subequal and short, and 4) hypurals 3 and 4 fused into a plate (Table 1, Suppl. Table 2).

Given our limited assessment of the family's monophyly and intrarelationships and the lack of incorporation of the overwhelming majority of Harold and Weitzman's (1996) sternoptychid morphological data, the phylogeny of the Sternoptychidae should be examined more completely with the combination of genome-scale and focused morphological data as was done for the Gonostomatidae, "Photichthyidae," and *Triplophos* relative to the Sternoptychidae and Stomiinae in this study.

Stomiidae

Our revised and expanded Stomiidae is now a very large family (35 genera and 344 species) that includes the Stomiinae, "Phosichthyidae," and *Triplophos*. With the genera we added to the family, this revised Stomiidae is decidedly the largest family of deep-sea vertebrates, the third largest family of predominantly marine fishes, and the ninth largest family of fishes (Fricke et al., 2023). The monophyly of our species-rich Stomiidae was both hypothesized and supported by Fink (1984), Harold and Weitzman (1996), and Harold (1998) (Fig. 1). Despite being a result in these earlier morphological phylogenetic analyses (Fig. 1), the monophyletic classification of the Stomiiformes provided herein had not been previously suggested because earlier authors viewed their results as preliminary. We understand the trepidation of these authors to place the "Phosichthyidae" and *Triplophos* into the synonymy of the Stomiidae without a more detailed examination given that the "Phosichthyidae" were never the focus of their morphological character discovery in the relevant studies. In this study, the earlier morphological data were combined and expanded along with the addition of a genome-scale molecular dataset to explicitly examine "phosichthyid" limits and relationships. Our combined results (Figs. 3 and 4) largely corroborate earlier authors' initial morphological conclusions at both broad- and fine-scale levels, which provides sufficient evidence to alter stomiiform family-level classification. As such, we propose a monophyletic stomiiform taxonomy that recognizes just 3 families and corroborates earlier morphological results of Fink (1984), Harold and Weitzman (1996), and Harold (1998). This expanded Stomiidae is strongly supported in our combined analysis (Figs. 3 and 4) and is diagnosed by the presence of the anterior palatomaxillary ligament being looped over the dorsal surface of the lateral process of the rostrodermethmoid. This character was discussed extensively by Fink and Weitzman (1982), providing additional evidence for the monophyly of this subset of stomiids as well, although it is reversed in *Ichthyococcus*, *Phosichthys*, *Woodsia*, and the Stomiinae (Fig. 4).

Although our revised Stomiidae had been resolved as a clade in earlier phylogenetic analyses, it was not formally recognized. In contrast, the Photichthya ("Phosichthyidae" and Stomiinae [previous Stomiidae]) and the Stomiinae (previous Stomiidae) have been recognized in earlier phylogenetic studies (e.g., Weitzman, 1974; Fink and Weitzman, 1982; Fink, 1984, 1985; Harold and Weitzman, 1996; Harold, 1998). As we only included 6 stomiines, we have little to contribute to studies of the generic interrelationships of the Stomiinae other than to say that we recovered *Chauliodus* sister to other stomiines in contrast to Betancur-R. et al. (2013), Kenaley et al. (2014), Mirande (2017), and Rabosky et al. (2018) who did not recover a monophyletic Stomiinae. Our stomiine sampling follows Harold and Weitzman (1996) by emphasizing early diverging lineages. With regard to the "phosichthyids" (*sensu* Nelson, 2006), our hypothesized relationships are similar to the most comprehensive earlier analysis (Harold and Weitzman, 1996) (Figs. 1 and 4). Our combined analysis recovered a clade composed of *Phosichthys* and *Woodsia* sister to the Stomiinae. These relationships were suggested by Fink (1985) and differed mildly from Harold and Weitzman (1996) who recovered *Woodsia* sister to the Stomiinae, *Ichthyococcus* sister to the Stomiinae+*Woodsia*, and *Phosichthys* sister to the Stomiinae+*Ichthyococcus*+*Woodsia*. The remaining relationships among "phosichthyids" in the combined results relative to the morphological results of Harold and Weitzman (1996) were identical except for the placement of *Polymetme* sister to *Yarrella* in the combined analysis, rather than *Polymetme* and *Yarrella* as subsequent sister groups to the clade composed of *Ichthyococcus*, *Phosichthys*, *Pollichthys*, *Polymetme*, *Vinciguerria*, *Woodsia*, and the Stomiinae in Harold and Weitzman (1996) (Figs. 1 and 4). Importantly, there are 27 genera in the Stomiinae, and we only included 6 of them. Fink (1985) analyzed the relationships among 26 stomiine genera (all currently recognized genera except *Eupogonesthes*) using 323 characters that we did not incorporate. Given our limited assessment of this species-rich subfamily's monophyly and intrarelationships and the lack of incorporation of Fink's (1985) characters, the phylogeny of the Stomiinae should be examined more completely with the combination of genome-scale and focused morphological data as was done for the Gonostomatidae, "Photichthyidae," and *Triplophos* relative to the Sternoptychidae and Stomiinae in this study.

Role of larval features in understanding the systematics and evolution of the Stomiiformes

Moser (1981:90) noted that "marine teleost larvae have evolved an enormous array of morphological specializations, such that it seems we are looking at a distinct evolutionary domain quite separate from that of the adults." As emphasized by Moser, the early life history stages of fishes where pelagic and demersal organisms are briefly interacting together in the upper epipelagic provide many opportunities for natural selection to impact the evolutionary history of fishes, generally, and the Stomiiformes, specifically. As evidenced by the many contributions in the "Ahlstrom Symposium" and focused research articles (e.g., Moser et al., 1984; Tyler et al., 1989; Smith and Busby, 2014), larval fishes were and remain an incredibly valuable and often untapped resource for phylogenetic characters because of the unique selective pressures at this early life history stage.

Across the Stomiiformes, we see larvae with variation that could be coded, such as differential timing of fin development, differences in body length at flexion, and changes in fin position between adults and larvae, but we also see dramatic specializations that include trailing guts, stalked eyes, and rudder-like finfolds (Ahlstrom et al., 1984; Kawaguchi and Moser, 1984). Despite all this larval variation, we were only able to include 5 larval characters in this analysis (characters 84–88) (Fig. 4, Table 1, Suppl. Table 2). Although these 5 included characters do support multiple nodes in the phylogeny of the Stomiiformes (e.g., monophyly of the *Diplophos+Manducus* and grouping of *Ichthyococcus*, *Phosichthys*, *Woodsia*, and the Stomiinae), we had hoped to include more larval characters, but the variation that is known was either restricted to stomiines or sternoptychids (not our focus) or simply could not be informatively coded because the larval specimens (particularly larval series) were not sufficiently available or described.

It is our hope that drawing attention to this group through the representative larval drawings and the revised phylogeny and classification will stimulate researchers to identify and study these larvae in collections or in the field. Focused effort to identify and describe marine larvae will facilitate scientists exploring the relationships of the Stomiiformes (or any marine fish group) as well as provide additional context for understanding the ecology and evolutionary history of both the adult and larval stages of fishes.

Conclusions

Following the development of phylogenetic methods, ichthyologists made tremendous advances in our understanding of fish relationships through the analysis of anatomical variation (Weitzman, 1974; Fink, 1985; Nelson, 2006). Since the end of the 20th century, DNA sequence data have played a progressively larger role in studies of the phylogenetic relationships of fishes. For many clades, conflicting relationships between morphological or molecular studies remain (Fig. 1). While there are concerns about how best to combine morphological and molecular data, it is clear that studies that explicitly combine both classes of data (e.g., Smith and Busby, 2014; Martin et al., 2018; Girard et al., 2020) or that explicitly test hypotheses with data from the alternative datatype (e.g., Grande et al., 2013; Gill and Leis, 2019) help bridge the gap between datatypes and allow systematic ichthyology to move toward a more holistic and comprehensive assessment of fish phylogeny. Our combination of morphological and molecular data allowed us to include most previous data and every genus of the Gonostomatidae and "Phosichthyidae" as well as the enigmatic *Triplophos* and representative sampling of the Sternoptychidae and Stomiinae. Using our revised phylogeny, we presented a revised classification that recognizes 3 monophyletic families (Gonostomatidae, Sternoptychidae, and Stomiidae). This taxonomy placed the "Phosichthyidae" into the synonymy of the Stomiidae and transferred *Triplophos* from the Gonostomatidae to the Stomiidae. This revised phylogeny and classification of the Stomiiformes based on the combination of anatomical and genomic data will now allow researchers to explore phylogenetic scenarios for this order in a comprehensive framework.

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