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The evolutionary relationships of marine hatchetfishes (Stomiiformes: Sternoptychidae) based on genomic and morphological data

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Abstract

The dragonfishes and allies (Stomiiformes) are among the most species rich and ecologically important clades of deep-sea fishes. Within the Stomiiformes, the marine hatchetfishes (Sternoptychidae) are the second largest family with 10 genera and 79 species. Sternoptychids are well known for their highly reflective bodies and bioluminescent photophores that are hypothesized to aid camouflage and allow communication with conspecifics in the deep sea. While sternoptychids in *Argyropelecus*, *Polyipnus*, and *Sternoptyx* have anteriorly deep and posteriorly shallow bodies that resemble a hatchet or an ax in lateral view, the seven other sternoptychid genera have a more uniform, slender body; these differences have been used to separate these clades into two subfamilies. Despite their ecological importance and captivating life history, the phylogeny of this group has not been studied as extensively as other deep-sea fish groups. To date, phylogenetic studies have primarily used morphological characters to examine sternoptychid evolutionary relationships, and, perhaps surprisingly, prior molecular studies with sufficient genus-level sampling have never recovered the family as monophyletic. Herein, we investigate the evolutionary relationships of the Sternoptychidae using 415 mitochondrial and nuclear loci (including ultraconserved elements [UCEs]) and 149 morphological characters. We present the results of concatenated and species-tree molecular analyses and combined phylogenetic analysis. Based on these results, we provide a revised monophyletic classification that recognizes a monophyletic Sternoptychidae without any subfamilies because our results recovered a paraphyletic Sternoptychinae and a polyphyletic Maurolicinae. Specifically, our combined analyses revealed that the slender-bodied species in *Maurolicus* were nested within the traditionally recognized deeper-bodied sternoptychines (*Argyropelecus*, *Polyipnus*, and *Sternoptyx*). This four-genus clade was found sister to a slender-bodied clade composed of *Araiophos, Argyripnus, Danaphos, Sonoda, Thorophos,* and *Valenciennellus*. Unlike previous molecular analyses, all genera that included more than one species in our analyses were recovered as monophyletic. Our revised sternoptychid phylogeny provides a comprehensive framework for subsequent researchers interested in exploring evolutionary scenarios for the marine hatchetfishes.

Key words: Systematics, Genomics, Taxonomy, Deep-sea

Introduction

The Stomiiformes (dragonfishes and allies) are a clade of marine fishes with 464 described species found worldwide in pelagic deep-sea habitats at depths typically ranging from 200–1,500 m (Ahlstrom *et al.* 1984; Fricke *et al.* 2025). These deep-sea fishes live in an environment that changes with depth in the ocean: sunlight decreases, eventually disappears completely; pressure increases linearly; and temperature generally cools, with a steep thermocline between 100 and 1,000 m (Helfman *et al.* 2009; Haddock *et al.* 2010). Many stomiiforms have adaptations to this midwater habitat, ranging from enlarged fangs, abundant teeth, elongate bodies, and bioluminescent lures and photophores (Nelson *et al.* 2016; Alves Gomes *et al.* 2024). Researchers have hypothesized that bioluminescence in these and other midwater fishes plays a crucial role in predator-prey interactions, camouflage, and species-specific communication (Harvey 1952; and Moring 1978; Haddock *et al.* 2010; Widder 2010). Understanding how these adaptations arose and vary necessitates a clear understanding of the phylogeny of the group.

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Smith *et al.* (2024) revised the classification of the Stomiiformes based on a phylogenetic analysis of morphological and genome-scale molecular data. Their revisions recognized three monophyletic families: Gonostomatidae (bristlemouths and portholefishes), Sternoptychidae (marine hatchetfishes), and Stomiidae (dragonfishes and lightfishes). The revised Gonostomatidae and Stomiidae contain predominantly elongate and dark-bodied fishes, while the sternoptychids are generally less elongate and characterized by more reflective (silver) bodies. Sternoptychids have traditionally been classified phylogenetically based on body shape and internal anatomy, with the Maurolicinae (seven genera and 34 species) being more elongated and the Sternoptychinae (three genera and 45 species) being more deep-bodied and ax-shaped (Weitzman 1974). All marine hatchetfishes have ventrally directed photophores, and the increased body depth seen in the sternoptychines has been hypothesized to allow for the emission of lateral light as the photophores are situated high on each side of their bodies allowing the light to be reflected laterally as well as ventrally (Baird 1971; Baird and Eckardt 1972; Weitzman 1974; Davis *et al.* 2014, 2016). As in other bioluminescent pelagic fishes, hatchetfish photophores have been hypothesized to help with counterillumination and communication (Mensinger and Case 1990; Randall and Farrell 1997; Priede 2017) and their patterns have been shown to be species specific (Harold, 1994).

Despite the important role that sternoptychids play in their midwater habitat and general interest in their biological specializations for thriving in the deep sea (e.g., Kinzer and Schulz 1988; Eduardo *et al.* 2020), there has not been a comprehensive molecular or combined analysis of the relationships within the family. Using morphological data, Weitzman (1974) was the first to recognize the taxonomic composition of the modern Sternoptychidae. Several previous studies had hypothesized that some genera within the modern Sternoptychidae were more closely allied to taxa in the Gonostomatidae or Stomiidae (Brauer 1906, 1908; Regan 1923; Norman 1930; Schultz 1938, 1961; Grey 1959, 1960; Weitzman 1967; Baird 1971; Baird and Eckardt 1972). Baird (1971) and Baird and Eckardt (1972) studied the systematics and zoogeography of three genera of sternoptychines (*Argyropelecus, Polyipnus*, and *Sternoptyx*) by examining 41 anatomical characters with a Wagner parsimony-based approach. They hypothesized that *Polyipnus* was sister to a clade composed of *Argyropelecus* and *Sternoptyx* to the exclusion of all other sternoptychids. Weitzman (1974) conducted a more comprehensive study that suggested that this Sternoptychinae was monophyletic while the Maurolicinae (*Araiophos*, *Argyripnus*, *Danaphos*, *Maurolicus*, *Sonoda*, *Thorophos,* and *Valenciennellus*; Figure 1) *sensu* Parin and Kobyliansky (1996) was paraphyletic relative to the Sternoptychinae. Although Weitzman's (1974) work pre-dated computer-aided phylogenetic approaches, he identified traits that he inferred as "primitive" for the stem lineages of a paraphyletic Maurolicinae, followed by "advanced" synapomorphies for the deeper-bodied Sternoptychinae. He summarized these features with a genus-level phylogeny that was fully resolved other than an ambiguous placement of *Maurolicus* near the base of the Sternoptychidae (Figure 1). Next, Ahlstrom (1974) discussed the evolution of stomiiform fishes based on larval and adult anatomical characters. He identified differences in the formation and types of photophores found in these fishes as well as characters associated with their metamorphosis from larval to adult forms. Within the modern Sternoptychidae, Ahlstrom (1974) identified two distinct groups based on specializations of photophore development that were consistent with Weitzman's (1974) Maurolicinae (Ahlstrom Group C) and Sternoptychinae (Ahlstrom Group D). Later, Harold and Weitzman (1996) revisited the phylogeny of the group and explicitly coded 150 morphological characters for three outgroups and 11 sternoptychid taxa (some at the genus and some at the species level). They presented two trees that differed by one step in their parsimony analyses that largely corroborated the results in Weitzman (1974; Figure 1). Harold and Weitzman (1996) resolved *Araiophos* and *Thorophos* as a grade leading up to all other sternoptychids (Figure 1) rather than sister taxa (Weitzman 1974; Figure 1). Their most parsimonious tree recovered *Maurolicus* sister to a clade composed of *Danaphos* and *Valencienellus*, and their nearly optimal tree recovered *Maurolicus* sister to all sternoptychids excluding *Araiophos* and *Thorophos*; together, these placements are reminiscent of Weitzman's partially ambiguous placement of *Maurolicus* (Figure 1). In addition to these intergeneric studies, Harold (1993, 1994) also provided species-level morphological phylogenies for *Argyropelecus* and *Polyipnus*. Given the extensive published anatomical research on this family and the periodic reappraisal of features by subsequent researchers, the Sternoptychidae is currently one of the best studied families of deep-sea fishes from a morphology-based phylogenetic perspective.

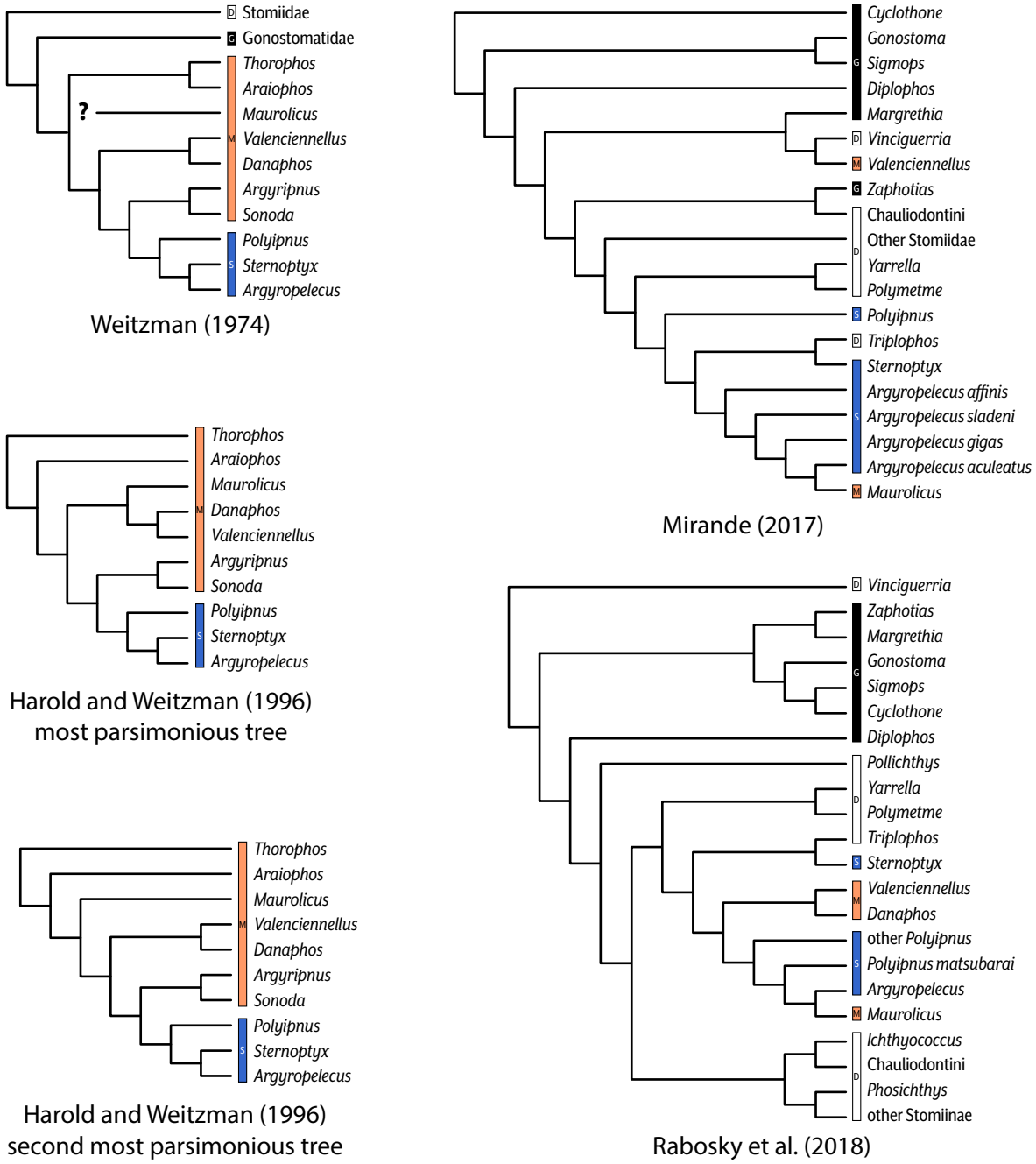

FIGURE 1. Hypotheses of relationships among the Stomiiformes based on previously published studies. Black (G), blue (S), orange (M), and white (D) rectangles represent the Gonostomatidae, Sternoptychinae, Maurolicinae, and Stomiidae, respectively. Note that these figures use the currently recognized classification (e.g., use of *Zaphotias* instead of *Bonapartia* and separate recognition of *Gonostoma* and *Sigmops*) rather than the classification used in the original studies.

In contrast to the extensive morphological phylogenetic studies of the Sternoptychidae, there have been no family-level molecular phylogenies of the marine hatchetfishes. The few studies looking at the phylogeny of sternoptychids using DNA sequence data have either focused on specific genera (Miya and Nishida 1998; Rees *et al.* 2020) or have examined relationships across the Actinopterygii or Stomiiformes. Among actinopterygian studies that have included four or more sternoptychid genera (Mirande 2017; Rabosky *et al.* 2018), neither study recovered a monophyletic Maurolicinae, Sternoptychinae, or Sternoptychidae (Figure 1). Mirande (2017; Figure 1) showed that the maurolicine *Maurolicus* was nested within the sternoptychine genus *Argyropelecus*. Further, he found that *Valenciennellus* was more closely related to the gonostomatid *Margrethia* and the stomiid *Vinciguerria* near the

base of the stomiiforms while the stomiid *Triplophos* was nested within the Sternoptychidae, sister to *Sternoptyx.* Next, Rabosky *et al.* (2018) recovered more conventional relationships, but still recovered *Triplophos* sister to *Sternoptyx*, a polyphyletic Maurolicinae and Sternoptychinae, and a paraphyletic *Polyipnus* with *Argyropelecus* and *Maurlolicus* nested within it (Figure 1). Given the discordance between molecular and morphological studies and the corresponding implied taxonomy where the marine hatchetfishes and its subfamilies and occasionally genera are not recovered as monophyletic with molecular data, a comprehensive study of the sternoptychids that combines existing morphological and molecular data with new genomic data is needed to resolve sternoptychid relationships.

Herein, we present the results of a simultaneous analysis combining existing morphological characters, new and existing Sanger-based sequence data, and new genome-scale ultraconserved-element (UCE) sequence data. Earlier studies have shown that combining these classes of data produces robust phylogenetic hypotheses, even when key taxa are available only as morphological data (e.g., Martin *et al.* 2018; Girard *et al.* 2020; Maile *et al.* 2025). These data were combined and analyzed to produce a species-rich phylogeny of the Sternoptychidae. The 149 variable morphological features (Harold and Weitzman 1996) were combined with 415 mitochondrial and nuclear loci for all ten sternoptychid genera, 48 sternoptychid terminals, and ten outgroups (including *Triplophos* that was consistently recovered within the Sternoptychidae in previous molecular studies; Figure 1). Given the different results between molecular and morphological phylogenies, the objectives of this study are to use morphological features and DNA sequence data to 1) hypothesize the relationships among stomiiforms; 2) test the monophyly of the Maurolicinae, Sternoptychinae, and Sternoptychidae; 3) resolve relationships among the sternoptychid genera and provide the morphological evidence for higher-level relationships within the family; and 4) make taxonomic changes, as needed, to produce a classification for the Sternoptychidae based upon monophyletic groups.

Materials and Methods

Taxonomic sampling. All analyses were rooted with the argentiniform *Argentina silus* (Ascanius) and included nine additional outgroups (one osmerid, four gonostomatids, and four stomiids; Supplemental Table 1). These outgroups were chosen based on the results of previous large-scale analyses that recovered the Osmeriformes sister to the Stomiiformes with the Argentiniformes more distantly related (e.g., Near *et al.* 2012; Smith *et al.* 2016; Hughes *et al.* 2018). Our least inclusive, species-tree dataset included ten outgroups and ten sternoptychids classified in five genera: *Argyropelecus*, *Maurolicus*, *Polyipnus*, *Sternoptyx*, and *Valenciennellus* (Supplemental Table 1). Our concatenated molecular dataset included ten outgroups and 43 sternoptychids classified in seven genera: *Argyripnus*, *Argyropelecus*, *Danaphos*, *Maurolicus*, *Polyipnus*, *Sternoptyx*, and *Valenciennellus* (Supplemental Table 1). This concatenated molecular dataset included 39 known species of sternoptychids and four additional sternoptychids that could not be identified to the species level or are potentially undescribed species. In addition to the two molecular datasets, we combined the concatenated molecular dataset with a morphological dataset (Harold and Weitzman 1996) for a combined dataset that added *Araiophos*, *Sonoda,* and two species of *Thorophos* as well morphological data for all included sternoptychids and five (of ten) outgroups (*Diplophos*, *Margrethia*, *Sigmops*, *Triplophos*, and *Zaphotias*). The combined analysis included all ten sternoptychid genera and nearly two-thirds of sternoptychid species (Supplemental Table 1). The family-level classification follows Smith *et al.* (2024), and all genus- and species-level taxonomy follows Fricke *et al.* (2024). All collection and institutional codes follow Sabaj (2020).

Morphological data. The morphological dataset used in this study included 149 characters coded and described by Harold and Weitzman (1996). Their character 67 was removed because it was invariant in our dataset (which cannot be used with the M+ASC likelihood model), so characters 67 to 149 in our study represent their characters 68 to 150 (Supplemental Table 2). The morphological matrix is available as Supplemental Table 3.

DNA extraction. Fish tissues were preserved in 70–95% ethanol or stored cryogenically prior to the extraction of DNA. Tissue samples used in these analyses were housed in the following collections: AMNH, CSIRO, FMNH, KU, and SIO. Nucleotide extractions were conducted using muscle tissue or fin clips with either a DNeasy Tissue Extraction Kit (Qiagen) or the Maxwell® RSC Whole Blood DNA Kit (Promega) following the manufacturers' extraction protocols (with the replacement of the blood DNA kit's lysis buffer with Promega's tissue lysis buffer). For Sanger sequence data, polymerase chain reaction (PCR) was used to amplify seven gene fragments (COI, ENC1, MYH6, RAG1, SH3PX3, TBR1, and ZIC1). Sanger molecular protocols for extracting, amplifying, cleaning, and sequencing these markers followed Davis *et al.* (2016). High-throughput extraction and quantification protocols

followed Smith *et al.* (2022). Quantified samples were sent to Arbor Biosciences (Ann Arbor, MI) for library preparation (e.g., DNA shearing, size selection, cleanup), target capture (using the 500 UCE actinopterygian loci probe set; Faircloth *et al.* [2013]), enrichment, sequencing using an Illumina HiSeq 2500 or NovaSeq 6000, and demultiplexing of samples.

DNA sequence data. New Sanger sequence data for COI, ENC1, MYH6, RAG1, SH3PX3, TBR1, and ZIC1 were built and edited in Geneious v8.1.8 (Kearse *et al.* 2012). These edited Sanger sequences were combined with previously published data for 12S, 16S, COI, ENC1, MYH6, PLAGL2, RAG1, SH3PX3, TBR1, and ZIC1 from the following published studies: Miya and Nishida (1998, 2000); Ilves and Taylor (2009); Davis (2010); Near *et al.* (2012, 2013); Chen *et al.* (2013, 2014); Grande *et al.* (2013); Davis *et al.* (2014, 2016); Sparks *et al.* (2014); Poulsen (2015); Rees *et al.* (2017, 2020); Vourey *et al.* (2017); Arrondo *et al.* (2020); Teramura *et al.* (2022); Smith *et al.* (2024). Additionally, unpublished DNA sequence data that were publicly available were downloaded from BOLD (Ratnasingham *et al.* (2024) or GenBank (Supplemental Table 1). Finally, high-throughput sequence data were queried for fragments homologous with these Sanger data; specifically, the cleaned reads from Arbor Biosciences were compared to existing sequences of close taxonomic allies using the "map to reference" function in Geneious Prime 2022.2.2 (Kearse *et al.* 2012) set to low-sensitivity with three iterations. The sources of all new and existing molecular data can be found in Supplemental Table 1. The DNA sequence data for these loci were aligned individually with MAFFT 7.130b (Katoh and Standley 2013) using default settings. The resulting alignment of this Sanger dataset was 6,580 base pairs (bps), which was 48.6% complete at the locus level and 45.7% complete at the base-pair level. Novel Sanger sequences were submitted to GenBank and assigned accession numbers PX508944-PX508950 and PX511749-PX511761.

Uce amplification, sequencing and assembly, and molecular dataset construction. New high-throughput DNA sequence data were collected by Arbor Biosciences using genomic extractions using the 500 UCE actinopterygian loci probe set (Faircloth *et al.* 2013). We processed the raw FASTQ files from Arbor Biosciences using the PHYLUCE 1.71 (Faircloth 2016) workflow to retrieve UCE and flanking regions from newly sequenced specimens. All genome-scale bioinformatic methods follow Smith *et al.* (2022). The new cleaned sequencing reads were submitted to GenBank and have been assigned SRA accession numbers SRA35738855 – SRA35738861. We assembled cleaned reads, assembled contigs for the UCE loci, aligned (with MAFFT), and concatenated the sequences present for ≥ 75% of taxa using the PHYLUCE pipeline. The resulting 75% complete UCE matrix was based on 406 UCEs or 217,246 aligned bps that were present for the 20 species that had UCE data. Across all UCE loci, median sequence fragment length was 1,066 bps, with a range of 117–3,019 bps. The UCE and flanking region sequences were then partitioned using the sliding-window site characteristics—entropy method (SWSC-EN; Tagliacollo and Lanfear 2018) to split each UCE locus into left and right flanking regions and the ultraconserved core (i.e., center segment) by rate of evolution. The final concatenated molecular matrix was based on 406 UCE loci and ten Sanger loci and included 223,826 aligned base pairs for 54 taxa.

Combined dataset. In addition to the concatenated molecular dataset, we also combined this matrix with 149 morphological characters from the sternoptychid dataset of Harold and Weitzman (1996 [less character 67 because it was invariant among included taxa]). Outgroup taxa that were not coded in Harold and Weitzman (1996) were coded as unknown in this dataset.

Phylogenetic analysis. The concatenated molecular and combined datasets were analyzed using maximum likelihood using IQ-Tree v2.2.2.6 (Lanfear *et al.* 2012; Chernomor *et al.* 2016; Minh *et al.* 2020). The submitted concatenated molecular dataset was partitioned into the left, central, and right UCE segments identified by SWSC-EN as well as the combined 12S and 16S fragments and the three independent codon positions for each of the eight protein-coding fragments. IQ-Tree determined the best-fitting nucleotide substitution model for each molecular partition in the first run of the analysis, and this was input directly in subsequent molecular and combined analyses. These 1,237 partitions from the concatenated molecular dataset were combined with a morphological dataset that used an MK+ASC model (Lewis 2001) of evolution for the combined analysis. For each dataset, 20 independent analyses were conducted and the tree with the optimal likelihood score was recognized. Additionally, 300 traditional bootstraps (-bo) were conducted in IQ-Tree. For bootstrap support, we recognize three levels: ≥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 strongly supported node or clade. In addition to the concatenated molecular analyses above, each of the 406 UCEs, seven nuclear genes, and one combined mitochondrial locus were analyzed individually using RAxML v 8.2 (Stamatakis 2014) using a GTRGAMMA substitution model for

the 20 taxa that have UCE data. The best likelihood result from five independent analyses for each of these 414 loci were retained and for subsequent analysis in ASTRALv 5.7.7 (Zhang *et al.* 2018) to infer a species tree from the individual gene trees (referred to as the "species-tree analysis" below). Finally, we examined and analyzed the datasets (ancestral-state reconstructions) in Mesquite v3.5 (Maddison and Maddison 2018) using parsimony and maximum likelihood.

Results

The analysis of the concatenated molecular dataset resulted in a single optimal tree (Figure 2) with a likelihood score of —1173087.087. Forty-five of 51 possible nodes (88%) were supported with bootstrap values >50%. Additionally, 37 of 51 nodes (73%) were moderately well supported, and 17 of 51 nodes (33%) were well supported (Figure 2). The analysis of the combined morphological and molecular dataset resulted in a single optimal tree (Figure 3) with a likelihood score of —1175003.170. In the combined analysis, 47 of 57 nodes (82%) were supported with a bootstrap value >50%. Additionally, 39 of 57 nodes (68%) were moderately well supported, and 27 of 57 nodes (47%) were well supported (Figure 3). Finally, the species-tree analysis had a final normalized quartet score of 0.61455 with all 18 nodes being moderately well supported and 15 of 18 nodes being well supported (Supplemental Figure 1). All three analyses were completely congruent with each other for the included taxa, so the Discussion will focus on the most taxon-rich combined analysis (Figure 3).

The results of both maximum-likelihood analyses and the species-tree analysis supported the monophyly of the order Stomiiformes and the families Gonostomatidae, Sternoptychidae, and Stomiidae with Sternoptychidae and Stomiidae resolved as sister taxa (Figures 2–3, Supplemental Figure 1). Every genus represented by multiple species was recovered as monophyletic in all three analyses (Figures 2–3, Supplemental Figure 1). Neither the Maurolicinae nor the Sternoptychinae were recovered as monophyletic in any analyses (Figures 2–3, Supplemental Figure 1). In all analyses, *Maurolicus* was nested within the Sternoptychinae. With the exception of *Maurolicus*, the Maurolicinae was otherwise consistently resolved as a clade (Figures 2–3, Supplemental Figure 1). In all analyses, *Argyropelecus* was resolved sister to *Sternoptyx* (Figures 2–3, Supplemental Figure 1). These two genera were consistently recovered sister to *Maurolicus*, and all three of these genera were recovered as the sister group to *Polyipnus* (Figures 2–3, Supplemental Figure 1). The sister group to the clade of these four genera was the remainder of the Sternoptychidae in all three analyses, but the taxon sampling for this shallower-bodied clade varied across all three analyses while the relationships among the included taxa were identical (Figures 2–3, Supplemental Figure 1). As such, we will describe the relationships for the combined analysis (Figure 3) and Figure 2 and Supplemental Figure 1 should be examined for the hypothesized intergeneric relationships in the more taxon-limited, exclusively DNA-based, analyses. In the combined analysis, this shallower-bodied clade was composed of three pairs of sister taxa. *Argyripnus* was recovered sister to *Sonoda*, and this clade was recovered sister to a clade composed of *Danaphos* and *Valenciennellus*. As a clade, these four genera were then recovered sister to a clade composed of *Araiophos* and *Thorophos.* Given these results, we will continue to recognize all currently valid marine hatchetfish genera (Fricke *et al.* 2024). We no longer recognize the sternoptychid subfamilies Maurolicinae and Sternoptychinae because they were not recovered as monophyletic. We also do not recognize the sternoptychid tribe Sternoptychini (Baird, 1986) which had the same taxonomic composition as Sternoptychinae. We have elected not to describe or recognize any new or existing sternoptychid subfamilies because the support values for the two major clades are among the least supported nodes in the phylogeny (Figure 3). This lack of support for the major clades is primarily due to the inclusion of several morphology-only taxa (*Araiophos*, *Sonoda*, and *Thorophos*) in the shallower-bodied clade that, in the absence of molecular data, includes *Maurolicus* (Harold and Weitzman 1996). Further evidence of this explanation for the low support is that the molecular-only analysis recovered both clades as reciprocally monophyletic with moderate support (87%; Figure 2).

Our combined phylogeny recovered a monophyletic Sternoptychidae (Figure 3), which is consistent with the hypotheses of Weitzman (1974) and Harold and Weitzman (1996), but is contradicted by the findings of all previous molecular phylogenies that recovered a non-monophyletic Sternoptychidae (e.g., Mirande 2017; Rabosky *et al.* 2018; Figure 1). Our revised intergeneric phylogeny is somewhat congruent with Weitzman (1974) and Harold and Weitzman's (1996) morphological hypothesis, particularly regarding the following sister-group relationships: *Argyripnus*+*Sonoda, Argyropelecus*+*Sternoptyx*, and *Danaphos*+*Valencienellus*. Beyond these sister-group pairings,

the results are more similar to Weitzman (1974). Given the topological changes, many of the synapomorphies for the various genera and the higher-level sternoptychid clades are altered relative to Harold and Weitzman (1996) and are presented in Figure 4.

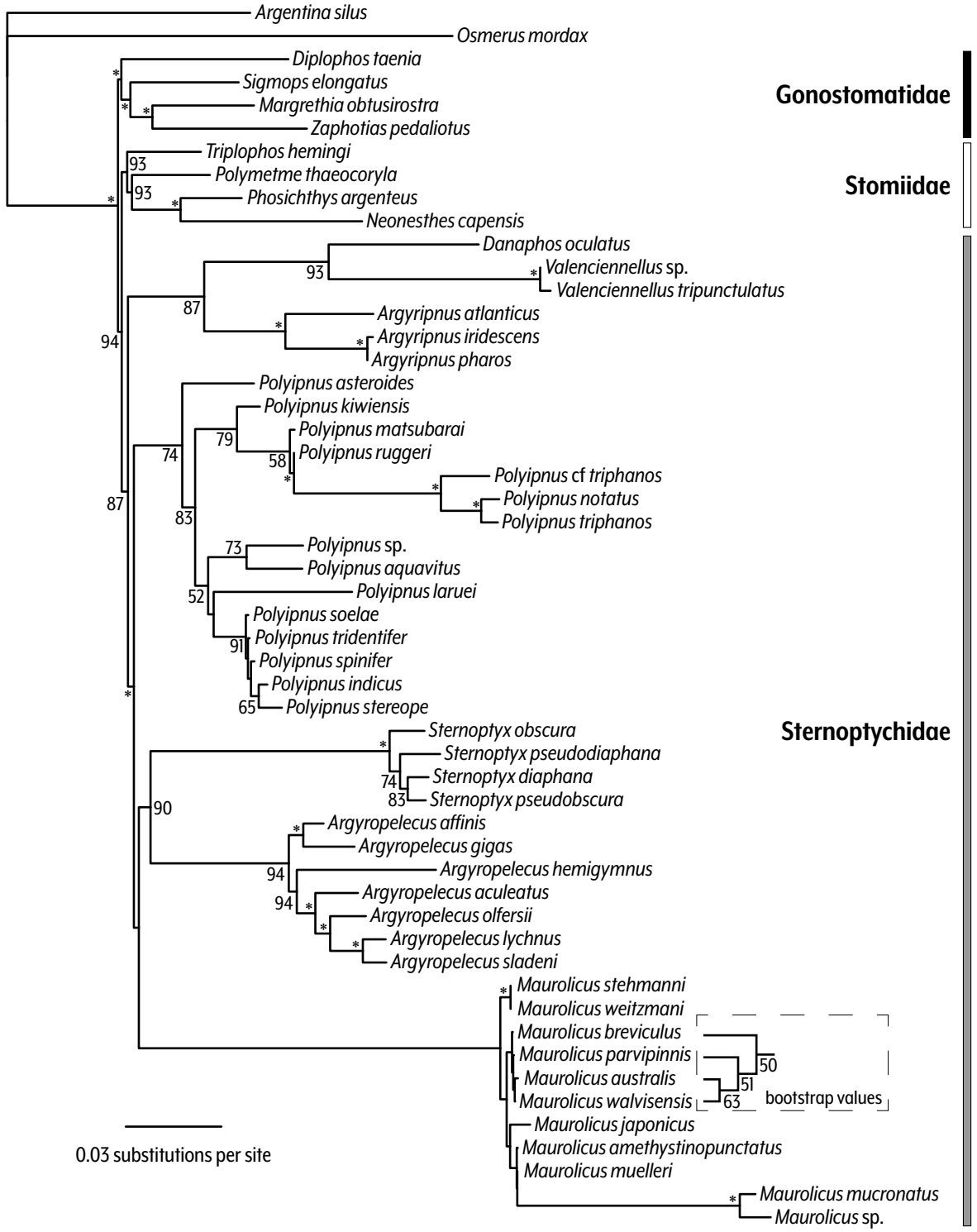

FIGURE 2. Maximum-likelihood relationships of the Sternoptychidae based on molecular data (ultraconserved elements and mitochondrial and nuclear coding fragments). Numbers at nodes indicate bootstrap support values and bootstrap values ≥95 are listed as an asterisk. Nodes with no number had less than 50 bootstrap support.

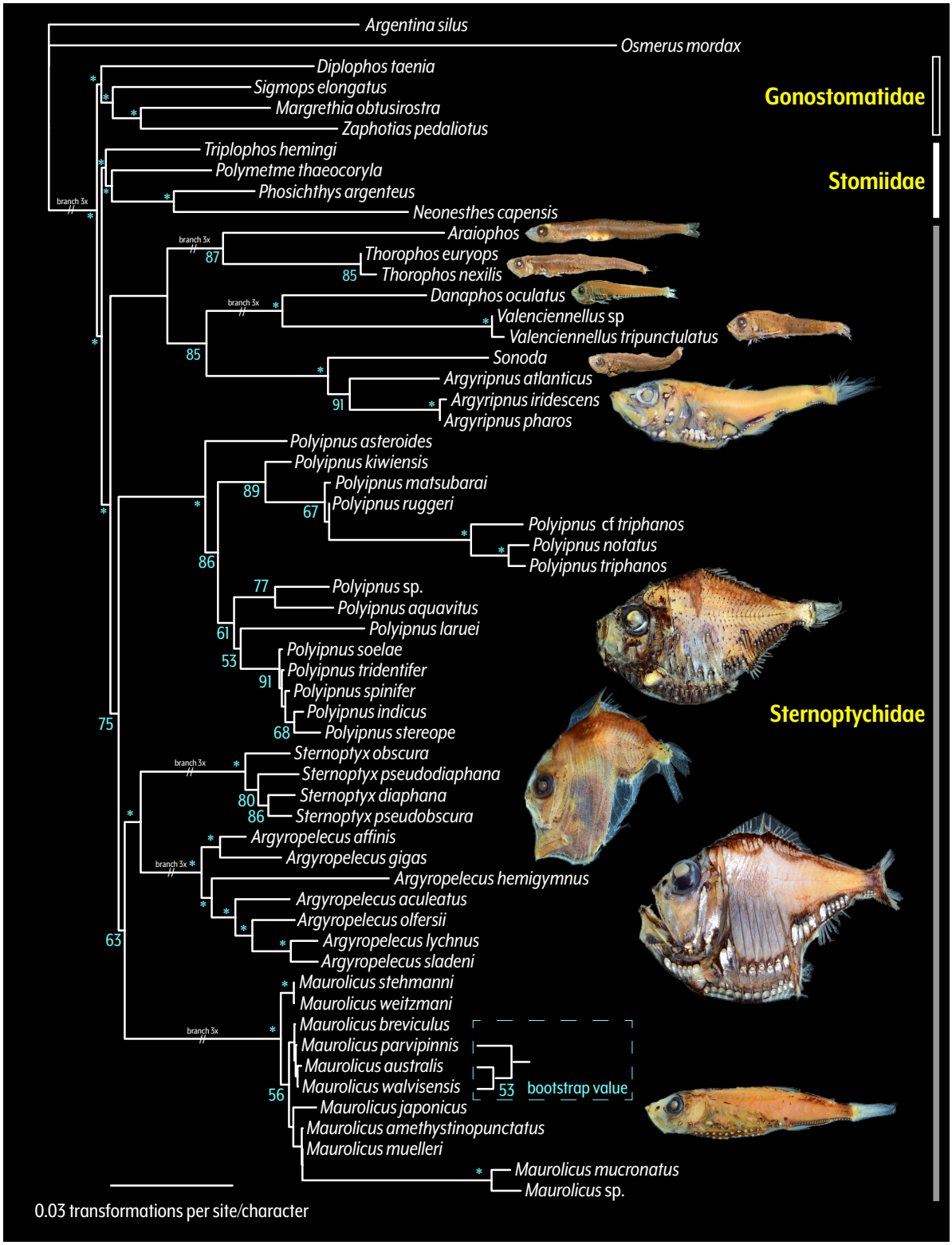

FIGURE 3. Maximum-likelihood combined relationships of the Sternoptychidae based on ultraconserved elements, mitochondrial and nuclear coding fragments, and morphological features. Numbers at nodes indicate bootstrap support values and bootstrap values ≥95 are listed as an asterisk. Nodes with no number had less than 50 bootstrap support. Images of representative species from each sternoptychid genus are: *Araiophos eastropas* Ahlstrom & Moser USNM 203240; *Thorophos nexilis* (Myers) USNM 151400; *Argyripnus brocki* Struhsaker USNM 207657; *Sonoda paucilampa* Grey USNM 196967; *Danaphos oculatus* (Garman) USNM 438499; *Valenciennellus tripunctulatus* (Esmark) USNM 203267; *Maurolicus muelleri* (Gmelin) USNM 202396; *Polyipnus asteroides* Schultz USNM 298936; *Argyropelecus aculeatus* Valenciennes USNM 247619; *Sternoptyx diaphana* Hermann USNM 192850.

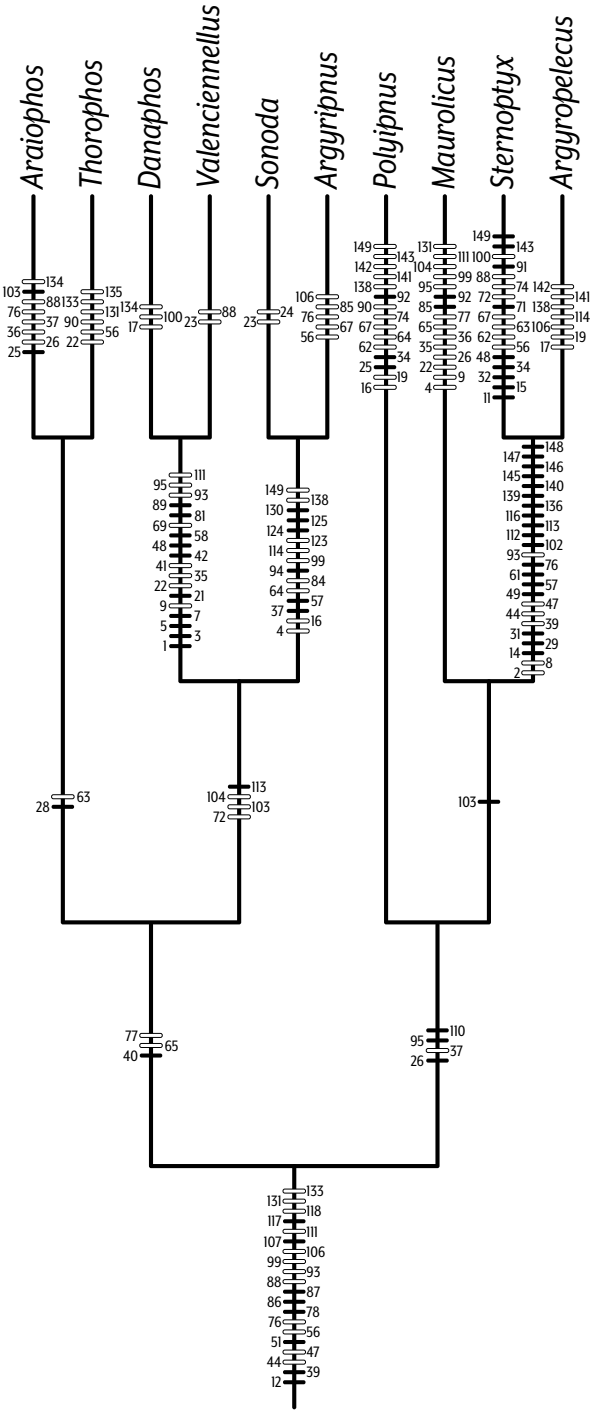

FIGURE 4. Genus-level topology based on the combined result optimizing the unambiguous transformations of the 149 morphological features from Harold and Weitzman (1996) using parsimony. Note: their character 67 was removed, so all characters beginning with number 67 are one number fewer than their reported character numbers. Full or black bars represent unique unreversed synapomorphies and hollow or outlined bars represent homoplastic synapomorphies. See Supplemental Table 2 for character (linked via numbers in figure) and character-state descriptions.

Discussion

There were four primary goals of this study that combined morphological data from Harold and Weitzman (1996) with new and existing DNA sequence data to produce the first robust molecular or combined analysis of sternoptychid relationships. Our broadest goal was to test the monophyly of the Stomiiformes and the limits and relationships of its families proposed by Smith *et al.* (2024). Our second goal was to test the limits of the Sternoptychidae and its subfamilies given that molecular studies of the Stomiiformes with sufficient genus-level sampling have failed to recover these clades as monophyletic (Figure 1; Mirande 2017; Rabosky *et al.* 2018). Our third goal was to resolve the intrarelationships of marine hatchetfishes and provide morphological evidence for these relationships using a dataset that was densely sampled with molecular and morphological data. Finally, we will make the necessary taxonomic changes dictated by our results to produce a classification for the Sternoptychidae based upon monophyletic groups.

Stomiiform monophyly and intrarelationships. Essentially all explicit analyses that have investigated stomiiform monophyly have recovered the order as monophyletic (e.g., Weitzman 1974; Fink 1984; Betancur-R. *et al.* 2013; Kenaley *et al.* 2014; Davis *et al.* 2016; Mirande 2017; Rabosky *et al.* 2018; Smith *et al.* 2024). While this study did not extensively test stomiiform monophyly, all three of our analyses recovered a monophyletic order with strong bootstrap support (Figures 2–3; Supplemental Figure 1). None of the morphological features coded by Harold and Weitzman (1996) united the Stomiiformes, as their dataset only included gonostomatids, sternoptychids, and stomiids. Fink and Weitzman (1982) identified eight diagnostic characters of the Stomiiformes, encompassing features from their light-organ system, jaws, cranial ligaments, gill arches, hyoid arches, and gas bladder. Given the consistent finding of a monophyletic Stomiiformes, these features should still be treated as synapomorphies for the order.

In contrast to the consistent recovery of a monophyletic Stomiiformes, the limits of the order's families and their interrelationships have varied tremendously (Figure 1). Smith *et al.* (2024) reviewed the historical treatment of the stomiiform families, so we will focus on the explicit higher-level relationships of stomiiforms with sufficient sampling of sternoptychids. Weitzman (1974) placed his Gonostomatidae sister to the Sternoptychidae; together, these families were sister to his Photichthya (i.e., the modern Stomiidae less *Triplophos*, which he included in his Gonostomatidae). Fink (1984) recovered Sternoptychidae sister to the modern Stomiidae, and this was recovered sister to the Gonostomatidae less *Diplophos.* Further, Fink (1984) placed *Diplophos* sister to all other stomiiforms. Harold (1998) recovered the Sternoptychidae sister to the Gonostomatidae (less *Diplophos* and *Manducus*) with the modern Stomiidae sister to these two clades. Then, he placed a clade composed of *Diplophos* and *Manducus* sister to all other stomiiforms. Next, Mirande (2017) recovered a clade composed of the sternoptychines with *Maurolicus* and *Triplophos* nested within it (Figure 1). This predominantly sternoptychid clade was nested within a grade that included most other stomiids and *Zaphotias*. This clade was sister to a clade composed of representatives of all three families. Finally, there was a grade of gonostomatids at the base of the order (Figure 1). Rabosky *et al.* (2018) recovered *Vinciguerria* sister to all other stomiiforms (Figure 1). Moving up the tree, the next two branches included all gonostomatids (Figure 1). Finally, the Sternoptychidae (with *Triplophos* nested within it) was nested within the remainder of the Stomiidae (Figure 1). All of these previous studies hypothesized different relationships among the core stomiiform taxa with *Diplophos* and *Triplophos* being the most variably placed genera.

Our results were in contrast to most previous studies (Figure 1) and consistent with the findings of Smith *et al.* (2024) who recovered a monophyletic Gonostomatidae (including *Diplophos*), a monophyletic Stomiidae (including *Triplophos*), and a monophyletic Sternoptychidae with the Sternoptychidae sister to the Stomiidae with moderate to strong support (Figures 2–3; Supplemental Figure 1). Given the changes in sister-group relationships relative to Harold and Weitzman (1996), the characters supporting the monophyly of the Sternoptychidae have changed with Harold and Weitzman (1996) reporting 22 synapomorphies for the clade. In this study, we recovered 20 synapomorphies supporting the monophyly of the family (Figure 4), so morphological character support has decreased with the altered phylogenetic result. Further, our results were consistent with Smith *et al.* (2024) who included a largely independent morphological dataset and vastly different taxonomic sampling.

Sternoptychidae. Both previous morphological phylogenetic analyses of sternoptychids have recovered the family Sternoptychidae and subfamily Sternoptychinae as monophyletic (Weitzman 1974; Harold and Weitzman 1996; Figure 1). Previous molecular studies have failed to recover the Sternoptychidae as monophyletic (Mirande 2017; Rabosky *et al.* 2018). Our molecular analyses (Figure 2; Supplemental Figure 1) and combined analysis

(Figure 3) recovered the family as monophyletic. Given that our results are consistent with the traditional familial limits, we continue to recognize the Sternoptychidae as previously circumscribed (i.e., Weitzman 1974; Harold and Weitzman 1993; Smith *et al.* 2024; Fricke *et al.* 2025) with 79 species and 10 genera (Fricke *et al.* 2025). This family was supported by 20 characters (Figure 4): parietals separated by the supraoccipital (character 12: state 1); mesopterygoid long (39: 1); quadrate dorsally articulates with the ectopterygoid and/or mesopterygoid plus metapterygoid (44: 1); mandible coronoid platform present (47: 1); infraorbital series reduced to four or fewer bones (51: 1); interopercle much longer than subopercle (56: 1); anterior ceratohyal shape not greatly constricted (76: 2); branchiostegal rays ten or fewer (78: 1); ventral ethmoid absent (86: 1); myodome bone absent (87: 1); lateral ethmoid small to moderate in size (88: 1); ethmoid cornu moderately to well developed (93: 1); epipleurals absent (99: 1); parhypural fused to preural centrum 1 and/or hypural 1 (106: 1); hypurals 1 and 2 fused (107: 1); sagitta crista superior absent (111: 1); photophores development via budding (117: 1); adipose fin with long-based shape (118: 1); SO photophores absent (131: 1); posterior infraorbital bones absent (133: 1). Our results do not support the monophyly of the two sternoptychid subfamilies (Maurolicinae and Sternoptychinae); this is not surprising given that no previous study had found the two subfamilies as reciprocally monophyletic (Figure 1).

While previous studies have failed to recover a monophyletic Maurolicinae and Sternoptychinae (Weitzman 1974; Harold and Weitzman 1996; Mirande 2017; Rabosky *et al.* 2018), our dataset provides the first opportunity to rigorously test the monophyly of both subfamilies with molecular data, and that hypothesis of monophyly is rejected because *Maurolicus* was resolved as sister to the clade composed of *Argyropelecus* and *Sternoptyx* rather than a member of the Maurolicinae. Given the lack of support for these two subfamilies and the result that *Argyropelecus*, *Maurolicus*, and *Sternoptyx* form a clade relative to other sternoptychids, and include the type genera for all available marine hatchetfish family-level names, we do not recognize any supergeneric names between genus and family.

Relationships among members of the Sternoptychidae. Our combined analysis recovered two clades within the Sternoptychidae: one composed of exclusively slender-bodied genera (*Araiophos*, *Argyripnus*, *Danaphos*, *Sonoda*, *Thorophos*, and *Valenciennellus*) and another composed of predominantly deeper-bodied genera (*Argyropelecus*, *Maurolicus*, *Polyipnus*, and *Sternoptyx*). Despite the lack of support for the traditional subfamilies (Maurolicinae and Sternoptychinae), these two major clades of sternoptychids are supported with morphological support despite non-compelling bootstrap support (44% or 75%). The clade of more slender forms composed of *Araiophos*, *Argyripnus*, *Danaphos*, *Sonoda*, *Thorophos*, and *Valenciennellus* was supported by three morphological characters (mesopterygoid fenestra present [40: 1]; palatopremaxillary ligament continuous [65: 1]; anterior ceratohyal is larger [77: 1]) and a bootstrap support of 44%. The predominantly deeper-bodied clade composed of *Argyropelecus*, *Maurolicus*, *Polyipnus*, and *Sternoptyx* was supported by four morphological characters (posttemporal fossa reduced and specialized [26: 3]; palatine posterior head lost [37: 1]; ethmoid cartilage broad and modified [95: 2]; sagittal post-caudal trough absent [110: 1]) and a bootstrap support of 75%. For the remaining smaller-scale relationships, interested parties should examine Appendices 1–2 and Figure 4 for morphological support.

Within the clade of exclusively slender-bodied forms, *Argyripnus* and *Sonoda* formed a clade supported by 15 characters (Figure 4) and with a bootstrap support of 100% (Figure 3). This same clade was presented in Weitzman (1974) and Harold and Weitzman (1996). The sister group of this clade was composed of species in *Danaphos* and *Valenciennellus*, which was supported by 18 characters (Figure 4) and a bootstrap support of 100% (Figure 3). This same clade was resolved in Weitzman (1974) and Harold and Weitzman (1996). This four-genus clade was supported by four characters (Figure 4) and a bootstrap support of 85%. The last remaining clade in the more slender-bodied clade was composed of *Araiophos* and *Thorophos*, and it was supported by two morphological characters (Figure 4), a bootstrap support of 87%, and was recovered by Weitzman (1974).

In contrast to the shallow-bodied clade, the predominantly deeper-bodied clade (*Argyropelecus*, *Maurolicus*, *Polyipnus*, and *Sternoptyx*) has generally more morphologically distinct and species-rich genera with four of the five genera with the most diagnostic features (Figure 4). *Argyropelecus* was recovered sister to *Sternoptyx* with 24 characters (Figure 4) and a bootstrap support of 100% (Figure 3). This clade was recovered in Baird and Eckardt (1972), Weitzman (1974), and Harold and Weitzman (1996). The sister group to this clade was *Maurolicus*, and this was supported by one morphological character (Figure 4) and a bootstrap support of 63% (Figure 3). No previous analyses recovered this clade (Figure 1). Neither morphological nor molecular data support the traditional subfamilial classification (Figures 1–3). Our hypothesis and classification is based on the first combined analysis of the Sternoptychidae with sufficient molecular and morphological data to assess the limits. Bootstrap support for several nodes in our phylogeny are not compelling (Figure 3), but when morphology-only taxa are removed

or species-tree methods are applied, the relationships are not disrupted and show increased support. The current hypothesis of relationships among sternoptychid genera is the best current hypothesis, and, if corroborated, we believe that a subfamilial designation for the two recovered clades would be warranted. With the current morphological and bootstrap support combined with the lack of molecular data for some genera, we felt such a change was premature.

While the species-level relationships within the larger genera of sternoptychids were not the focus of this study, the dense sampling of marine hatchetfishes allows for commentary relative to other focused studies of *Argyropelecus*, *Maurolicus*, and *Polyipnus*. Relationships within *Argyropelecus* were among the most strongly supported in our phylogeny, with both the genus and all internal nodes receiving high support (Figure 3). Although our dataset did not include the morphological variation described by Harold (1993), our inferred relationships differed from his only in the placement of *A. hemigymnus*. We recovered *A. hemigymnus* as sister to a clade composed of *A. aculeatus*, *A. lychnus*, *A. olfersii*, and *A. sladeni*, rather than to *A. aculeatus* alone, indicating strong congruence between our molecular results and the existing morphological hypothesis.

Our relationships within *Maurolicus* (Figure 3) were among the least supported in our phylogeny with the genus and two additional clades being well supported. Our results largely corroborated the findings of Rees *et al.* (2017, 2020), including the separation of *M. mucronatus* and an unidentified species on a long branch separate from most congeners. The weak support and short branch lengths within the genus further support the conclusions of Rees *et al.* (2017, 2020) that *Maurolicus* may contain fewer valid species than currently recognized (Parin & Kobyliansky, 1996; Fricke *et al.*, 2025).

Relationships within the species-rich genus *Polyipnus* varied in support, ranging from moderate to strong across different nodes (Figure 3). As with *Argyropelecus*, we did not include the existing morphological data for the genus (Harold 1994) in our analysis that was focusing on higher levels. While our taxon sampling relative to Harold (1994) was not identical, our relationships largely corroborated the findings of Harold (1994). In contrast to Harold (1994), we recovered *Polyipnus asteroides* Schultz sister to all other species in the genus. The remaining members of Harold's (1994) *P. asteroides* species group were nested within the *P. meteori* species group. The included members of the *P. spinosus* species group were recovered as monophyletic and sister to the included members of the *P. omphus* species group. This was sister to clade composed of the *P. asteroides* and *P. meteori* species group, so our molecular phylogeny (Figure 3) largely corroborated the species groups recognized by the morphological phylogeny of Harold (1994). As with *Argyropelecus*, the congruence between our results and prior morphological studies suggests that relationships within *Polyipnus* are relatively well resolved.

Support for prior morphological hypotheses. The results of our combined analyses are clear—Weitzman's (1974) inexplicit hypothesis regarding the limits and relationships of hatchetfishes are largely corroborated. Our results also broadly corroborate the relationships proposed by Harold (1993, 1994) and Harold and Weitzman (1996). All four sister-group pairs proposed by Weitzman (1974) were recovered in our combined hypothesis, with support values ranging from 87% to 100% (*Araiophos* and *Thorophos*, *Argyripnus* and *Sonoda*, *Argyropelecus* and *Sternoptyx*, and *Danaphos* and *Valenciennellus*; Figures 1–3; Supplemental Figure 1). The differences between Weitzman's hypothesis and our own (e.g., the placement of *Maurolicus*, grouping of *Argyripnus*, *Danaphos*, *Sonoda*, and *Valenciennellus*, and the monophyly of the slender-bodied hatchetfishes excluding *Maurolicus*) correspond to the poorest supported higher-level nodes in our combined phylogeny, with support values ranging from 44% to 85% (Figure 3) and only one to four diagnostic morphological characters (Figure 4). While our hypothesis is best supported by the available data, it remains possible that additional elements of Weitzman's hypothesis may yet be supported.

Evolution of body depth. Our results with a paraphyletic Sternoptychinae indicate that body-depth has transitioned at least twice within the Sternoptychidae. Recent studies have demonstrated the body-shape variation among deep-sea fishes vary interestingly along evolutionary or ecological trajectories (Martinez *et al.* 2021, Martin *et al.* 2022, Maile *et al.* 2025) Either the ancestor of *Argyropelecus* and *Sternoptyx* and the ancestor of *Polyipnus* independently evolved the deep-bodied hatchetfish shape or the ancestor of *Argyropelecus*, *Maurolicus*, *Polyipnus*, and *Sternoptyx* evolved a deeper body and *Maurolicus* reverted to a shallower body (Figure 3). May (2019) noted that outside of *Argyropelcus*, *Polyipnus*, and *Sternoptyx,* that *Argyripnus* and *Maurolicus* possess bodies with less compression than the other hatchetfishes, so the more moderate body depth in *Maurolicus* does not particularly support either evolutionary scenario more. Additional research is required to resolve this ambiguity.

The reason that body-depth evolution is intriguing in this clade is due to the hypothesis that the increased

body depth of "sternoptychines" allowed for the emission of lateral light as the photophores are situated high on each side of their bodies (Baird 1971; Baird and Eckardt 1972; Weitzman 1974; Davis *et al.* 2016). This is particularly relevant in the species-rich genus *Polyipnus* (43% of described marine hatchetfishes) in which Harold (1994) clearly demonstrated that the lateral light organs had species-specific locations. The presence of species-specific bioluminescent systems (particularly when sexually dimorphic) has been tied to increased diversification (Chakrabarty *et al.* 2011; Davis *et al.* 2014; Ellis and Oakley 2016). Interestingly, the shallow bodied *Maurolicus* is the second most species-rich sternoptychid genus with 15 species (19% of described marine hatchetfishes, but see Rees *et al.* [2017, 2020] and above for possibility that species are in need of synonymy). This genus has the common name of "pearlsides" because the light organs looking like a string of pearls along the ventrolateral margin of the fish. Despite the presence of these clearly visible lateral photophores, they are notoriously invariant with Parin and Kobyliansky (1996: 186) noting that species in this genus "unlike most other luminescent fishes … have almost the same pattern and number of photophores." Given this lack of morphological variation in the photophores, these light organs would need behavioral (e.g., flashing duration or pattern) or color differentiation to have species-specific bioluminescent signaling, which contrasts with the deep-bodied marine hatchetfish species. Additional ecological or physiological work is needed to explore the possibility that variation in lighting is playing a role in the diversification in *Maurolicus*, specifically, sternoptychids, generally. It is likely that other aspects of their biology are aiding speciation in this midwater clade (see Wainwright and Longo [2017] for a discussion of potentially relevant specializations).

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References

Ahlstrom, E.H. (1974) The diverse patterns of metamorphosis in gonostomatid fishes - an aid to classification. *In*: Blaxter, J.H.S. (Ed.), *The Early Life History of Fish*. Springer-Verlag, Berlin, pp. 659–674. https://doi.org/10.1007/978-3-642-65852-5_52

Ahlstrom, E.H., Richards, W.J. & Weitzman, S.H. (1984) Families Gonostomatidae, Sternoptychidae, and associated stomiiform groups: development and relationships. *In*: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall Jr., A.W. & Richardson, S.L. (Eds.), *Ontogeny and Systematics of Fishes*. *American Society of Ichthyologists and Herpetologists, Special Publication No. 1*. American Society of Ichthyologists and Herpetologists, Lawrence, Kansas, pp. 184–198.

Alves Gomes, A.A., Sidlauskas, B.L., Machado, F.A., Caires, R.A. & de Melo, M.R.S. (2024) Body-shape evolution among the dragonfishes and their allies (Teleostei: *Stomiiformes*). *Ichthyology & Herpetology*, 112 (3), 473–488. https://doi.org/10.1643/i2023068

Arrondo, N.V., Gomes-Dos-Santos, A., Román Marcote, E., Pérez, M., Froufe, E. & Castro, L.F.C. (2020) A new gene order in the mitochondrial genome of the deep-sea diaphanous hatchet fish *Sternoptyx diaphana* Hermann, 1781 (Stomiiformes: Sternoptychidae). *Mitochondrial DNA*, Part B, 5 (3), 2850–2852. https://doi.org/10.1080/23802359.2020.1790325

Baird, R.C. (1971) Systematics, distribution, and zoogeography of the marine hatchetfish (Family Sternoptychidae). *Bulletin of the Museum of Comparative Zoology*, 142 (1), 1–128.

Baird, R.C. & Eckardt, M.J. (1972) Divergence and relationship in deep-sea hatchetfishes (Sternoptychidae). *Systematic Zoology*, 21 (1), 80–90.

https://doi.org/10.2307/2412260
Baird, R.C. (1986) Tribe Sternoptychini. *In*: Smith, M.M. & Heemstra, P.C. (Eds.), *Smith's Sea Fishes*. Macmillan South Africa, Johannesburg, pp. 255–259.
Betancur-R., R., Broughton, R.E., Wiley, E.O., Carpenter, K., López, J.A., Li, C., Holcroft, N.I., Arcila, D., Sanciangco, M., Cureton, II, J.C., Zhang, F., Buser, T., Campbell, M.A., Ballesteros, J.A., Roa-Varon, A., Willis, S., Borden, W.C., Rowley, T., Reneau, P.C., Hough, D.J., Lu, G., Grande, T., Arratia, G. & Ortí, G. (2013) The tree of life and a new classification of bony fishes. *PLoS Currents Tree of Life*, 5, ecurrents.tol.53ba26640df0ccaee75bb165c8c26288. https://doi.org/10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288
Brauer, A. (1906) Die Tiefsee-Fische. I. Systematischer Teil. *In*: Chun, C. (Ed.), *Wissenschaftl. Ergebnisse der deutschen Tiefsee-Expedition "Valdivia," 1898–99. Jena.1898–1899. Vol. 15*. Verlag von Gustav Fescher, Jena, pp. 1–432.
Brauer, A. (1908) Die Tiefsee-Fische. II. Systematischer Teil. *In*: Chun, C. (Ed,), *Wissenschaftl. Ergebnisse der deutschen Tiefsee-Expedition "Valdivia," 1898–99. Jena.1898–1899. Vol. 15*. Verlag von Gustav Fescher, Jena, pp. 1–266.
Chakrabarty, P., Davis, M.P., Smith, W.L., Baldwin, Z.H. & Sparks, J.S. (2011) Is sexual selection driving diversification of the bioluminescent ponyfishes (Teleostei: Leiognathidae)? *Molecular Ecology*, 20, 2818–2834. https://doi.org/10.1111/j.1365-294X.2011.05112.x
Chen, W.-J., Lavoué, S. & Mayden, R.L. (2013) Evolutionary origin and early biogeography of otophysan fishes (Ostariophysi: Teleostei). *Evolution*, 67 (8), 2218–2239. https://doi.org/10.1111/evo.12104
Chen, W.-J., Santini, F., Carnevale, G., Chen, J.-N., Liu, S.-H., Lavoué, S. & Mayden, R.L. (2014) New insights on early evolution of spiny-rayed fishes (Teleostei: Acanthomorpha). *Frontiers in Marine Science*, 1 (53), 1–17. https://doi.org/10.3389/fmars.2014.00053
Chernomor, O., von Haeseler, A. & Minh, B.Q. (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Systematic Biology*, 65 (6), 997–1008. https://doi.org/10.1093/sysbio/syw037
Davis, M.P. (2010) Evolutionary relationships of the Aulopiformes (Euteleostei: Cyclosquamata): a molecular and total evidence approach. *In*: Nelson, J.S., Schultze, H.-P. & Wilson, M.V.H. (Eds.), *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. F. Pfeil, München, pp. 431–470.
Davis, M.P., Holcroft, N.I., Wiley, E.O., Sparks, J.S. & Smith, W.L. (2014) Species-specific bioluminescence facilitates speciation in the deep-sea. *Marine Biology*, 161, 1139–1148. https://doi.org/10.1007/s00227-014-2406-x
Davis, M.P., Sparks, J.S. & Smith, W.L. (2016) Repeated and widespread evolution of bioluminescence in marine fishes. *PLoS ONE*, 11 (6), 1–11. https://doi.org/10.1371/journal.pone.0155154
Eduardo, N.L., Bertrand, A., Mincarone, M.M., Santos, L.V., Frédou, T., Assunção, R.V., Silva, A., Ménard, F., Schwamborn, R. & Le Loc'h, Lucena-Frédou, F. (2020) Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Progress in Oceanography*, 187, 122389. https://doi.org/10.1016/j.pocean.2020.102389
Ellis, E.A. & Oakley, T.H. (2016) High rates of species accumulation in animals with bioluminescent courtship displays. *Current Biology*, 26 (14), 1916–1921. https://doi.org/10.1016/j.cub.2016.05.043
Faircloth, B.C. (2016) PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics*, 32 (5), 786–788. https://doi.org/10.1093/bioinformatics/btv646
Faircloth, B.C., Sorenson, L., Santini, F. & Alfaro, M.E. (2013) A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). *PLoS ONE*, 8, e65923. https://doi.org/10.1371/journal.pone.0065923
Fink, W.L. (1984) Stomiiformes: relationships. *In*: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, Jr., A.W. & Richardson, S.L. (Eds.), *Ontogeny and Systematics of Fishes*. *American Society of Ichthyologists and Herpetologists Special Publication No. 1*. American Society of Ichthyologists and Herpetologists, Lawrence, Kansas, pp. 181–184.
Fink, W.L. & Weitzman, S.H. (1982) Relationships of the stomiiform fishes (Teleostei), with a description of *Diplophos*. *Bulletin of the Museum of Comparative Zoology*, 150 (2), 31–93.
Fricke, R., Eschmeyer, W.N. & van der Laan, R. (2025) Eschmeyer's Catalog of Fishes: genera, species, references. Available from: https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed June 2025)
Girard, M.G., Davis, M.P. & Smith, W.L. (2020) The phylogeny of carangiform fishes: morphological and genomic investigations of a new fish clade. *Copeia*, 108 (2), 265–298. https://doi.org/10.1643/ci-19-320
Grande, T., Borden, W.C. & Smith, W.L. (2013) Limits and relationships of Paracanthopterygii: a molecular framework for evaluating past morphological hypotheses. *In*: Arratia, G., Schultze, H.-P. & Wilson, M.V.H. (Eds.), *Mesozoic Fishes 5–Global Diversity and Evolution*. Verlag Dr. Friedrich Pfeil, München, pp. 385–418.
Grey, M. (1959) Three new genera and one new species of the family Gonostomatidae. *Bulletin of the Museum of Comparative Zoology*, 121, 167–184.

Grey, M. (1960) A preliminary review of the family Gonostomatidae, with a key to the genera and the description of a new species from the tropical Pacific. *Bulletin of the Museum of Comparative Zoology*, 122, 57–125.
Haddock, S.H.D., Moline, M.A. & Case, J.F. (2010) Bioluminescence in the sea. *Annual Review of Marine Science*, 2, 443–493.
https://doi.org/10.1146/annurev-marine-120308-081028
Harold, A.S. (1993) Phylogenetic relationships of the sternoptychid *Argyropelecus* (Teleostei: Stomiiformes). *Copeia*, 1993 (1), 123–133.
https://doi.org/10.2307/1446303
Harold, A.S. (1994) A taxonomic revision of the sternoptychid genus *Polyipnus* (Teleostei: Stomiiformes), with an analysis of phylogenetic relationships. *Bulletin of Marine Science*, 54 (2), 428–534.
Harold, A.S. (1998) Phylogenetic relationships of the Gonostomatidae (Teleostei: Stomiiformes). *Bulletin of Marine Science*, 62 (3), 715–741.
Harold, A.S. & Weitzman, S.H. (1996) Interrelationships of stomiiform fishes. *In*: Stiassny, M.L.J., Parenti, L.R. & Johnson, G.D. (Eds.), *Interrelationship of Fishes. 2nd Edition*. Academic Press, San Diego, pp. 333–353.
https://doi.org/10.1016/B978-012670950-6/50014-X
Harvey, E.N. (1952) *Bioluminescence*. Academic Press Inc., New York, New York, 649 pp.
Helfman, G.S., Collette, B.B., Facey, D.E. & Bowen, B.W. (2009) *The Diversity of Fishes: Biology, Evolution, and Ecology, 2nd Edition*. Wiley-Blackwell, Hoboken, New Jersey, 720 pp.
Herring, P.J. & Morin, J.G. (1978) Bioluminescence in fishes. *In*: Herring, P.J. (Ed.), *Bioluminescence in Action*. Academic Press, London, pp. 273–329.
Hughes, L.C., Ortí, G., Huang, Y., Sun, Y., Baldwin, C.C., Thompson, A.W., Arcila, D., Betancur-R, R., Li, C., Becker, L., Bellora, N., Zhao, X., Li, X., Wang, M., Fang, C., Xie, B., Zhoug, Z., Huang, H., Chen, S., Venkatesh, B. & Shi, Q. (2018) Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proceedings of the National Academy of Sciences of the United States of America*, 115 (24), 6249–6254.
https://doi.org/10.1073/pnas.1719358115
Ilves, K.L. & Taylor, E.B. (2009) Molecular resolution of the systematics of a problematic group of fishes (Teleostei: Osmeridae) and evidence for morphological homoplasy. *Molecular Phylogenetics and Evolution*, 50, 163–178.
https://doi.org/10.1016/j.ympev.2008.10.021
Katoh, K. & Standley, D.M. (2013) MAFFT multiple-sequence-alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30 (4), 772–780.
https://doi.org/10.1093/molbev/mst010
Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, 28 (12), 1647–1649.
https://doi.org/10.1093/bioinformatics/bts199
Kenaley, C.P., DeVaney, S.C. & Fjeran, T.T. (2014) The complex evolutionary history of seeing red: molecular phylogeny and the evolution of an adaptive visual system in deep-sea dragonfishes (Stomiiformes: Stomiidae). *Evolution*, 68 (4), 996–1013.
https://doi.org/10.1111/evo.12322
Kinzer, J. & Schulz, K. (1988) Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic II. Sternoptychidae. *Marine Biology*, 99 (2), 261–269.
https://doi.org/10.1007/BF00391989
Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29 (6), 1695–1701.
https://doi.org/10.1093/molbev/mss020
Lewis, P.O. (2001) A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50 (6), 913–925.
https://doi.org/10.1080/106351501753462876
Maddison, W.P. & Maddison, D.R. (2018) Mesquite: a modular system for evolutionary analysis. Version. 3.8.1 Available from: https://mesquiteproject.org (accessed May 2025)
Maile, A.J., Smith, W.L. & Davis, M.P. (2025) A total-evidence phylogenetic approach to understanding the evolution, depth transitions, and body-shape changes in the anglerfishes and allies (Acanthuriformes: Lophioidei). *PLoS ONE*, 20 (5), e0322369.
https://doi.org/10.1371/journal.pone.0322369
Martin, R.P., Davis, M.P. & Smith, W.L. (2022) The impact of evolutionary trade-offs among bioluminescent organs and body shape in the deep sea: a case study on lanternfishes. *Deep-sea Research I*, 184, 103769.
https://doi.org/10.1016/j.dsr.2022.103769
Martin, R.P., Olson, E.E., Girard, M.G., Smith, W.L. & Davis, M.P. (2018) Light in the darkness: new perspectives on lanternfish relationships and classification using genomic and morphological data. *Molecular Phylogenetics and Evolution*, 121, 71–85.
https://doi.org/10.1016/j.ympev.2017.12.029

Martinez, C.M., Friedman, S.T., Corn, K.A., Larouche, O., Price, S.A. & Wainwight, P.C. (2021) The deep sea is a hot spot of fish body shape evolution. *Ecology Letters*, 24 (9), 1788–1799.
https://doi.org/10.1111/ele.13785

May, Z.A. (2019) *Evolutionary relationships and evolution of body shape of the deep-sea hatchetfishes (Stomiiformes: Sternoptychidae)*. M.S. Thesis, St. Cloud State University, St. Cloud, Minnesota, 76 pp.

Mensinger, A.F. & Case, J.F. (1990) Luminescent properties of deep sea fish. *Journal of Experimental Marine Biology and Ecology*, 144 (1), 1–15.
https://doi.org/10.1016/0022-0981(90)90015-5

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., von Haeseler, A. & Lanfear, R. (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution*, 37 (5), 1530–1534.
https://doi.org/10.1093/molbev/msaa015

Mirande, J.M. (2017) Combined phylogeny of ray-finned fishes (Actinopterygii) and the use of morphological characters in large-scale analyses. *Cladistics*, 33 (4), 333–350.
https://doi.org/10.1111/cla.12171

Miya, M. & Nishida, M. (1998) Molecular phylogeny and evolution of the deep-sea fish genus *Sternoptyx*. *Molecular Phylogenetics and Evolution*, 10 (1), 11–22.
https://doi.org/10.1006/mpev.1997.0479

Miya, M. & Nishida, M. (2000) Molecular systematics of the deep-sea fish genus *Gonostoma* (Stomiiformes: Gonostomatidae): two paraphyletic clades and resurrection of *Sigmops*. *Copeia*, 2000 (2), 378–389.
https://doi.org/10.1643/0045-8511(2000)000[0378:MSOTDS]2.0.CO;2

Near, T.J., Dornburg, A., Eytan, R.I., Keck, B.P., Smith, W.L., Kuhn, K.L., Moore, J.A., Price, S.A., Burbrink, F.T., Friedman, M. & Wainwright, P.C. (2013) Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings of the National Academy of Sciences of the United States of America*, 110 (31), 12738–12743.
https://doi.org/10.1073/pnas.1304661110

Near, T.J., Eytan, R.I., Dornburg, A., Kuhn, K.L., Moore, J.A., Davis, M.P., Wainwright, P.C., Friedman, M. & Smith, W.L. (2012) Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America*, 109 (34), 13698–13703.
https://doi.org/10.1073/pnas.1206625109

Nelson, J.S., Grande, T.C. & Wilson, M.V.H. (2016) *Fishes of the World. 5th edition*. John Wiley & Sons, Hoboken, New Jersey, 752 pp.

Norman, J.R. (1930) Oceanic fishes and flatfishes collected in 1925–1927. *Discovery Reports*, 2, 261–369.

Parin, N.V. & Kobyliansky, S.G. (1996) Diagnoses and distribution of fifteen species recognized in genu *Maurolicus* Cocco (Sternoptychidae, Stomiiformes) with a key to their Identification. *Cybium*, 20 (2), 185–195.

Poulsen, J.Y. (2015) A new species of pencil smelt *Nansenia boreacrassicauda* (Microstomatidae, Argentiniformes) from the North Atlantic Ocean. *Zootaxa*, 4020 (3), 517–532.
https://doi.org/10.11646/zootaxa.4020.3.6

Priede, I.G. (2017) *Deep-Sea Fishes: Biology, Diversity, Ecology and Fisheries*. Cambridge University Press, Cambridge, 492 pp.
https://doi.org/10.1017/9781316018330

Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T.J., Coll, M. & Alfaro, M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395.
https://doi.org/10.1038/s41586-018-0273-1

Randall, D.J. & Farrell, A.P. (1997) *Deep-sea Fishes*. Academic Press, San Diego, 388 pp.

Ratnasingham, S., Wei, C., Chan, D., Agda, J., Agda, J., Ballesteros-Mejia, L., Ait Boutou, H., El Bastami, Z.M., Ma, E., Manjunath, R., Rea, D., Ho, C., Telfer, A., McKeowan, J., Rahulan, M., Steinke, C., Dorsheimer, J., Milton, M. & Hebert, P.D.N. (2024) BOLD v4: A centralized bioinformatics platform for DNA-based biodiversity data. *In*: *DNA Barcoding: Methods and Protocols*. Springer US, New York, New York, pp. 403–441.
https://doi.org/10.1007/978-1-0716-3581-0_26

Rees, D.J., Byrkjedal, I. & Sutton, T.T. (2017) Pruning the pearlsides: reconciling morphology and molecules in mesopelagic fishes (*Maurolicus*; Sternoptychidae). *Deep-Sea Research, Part II: Topical Studies in Oceanography*, 137, 246–257.
https://doi.org/10.1016/j.dsr2.2016.04.024

Rees, D.J., Poulsen, J.Y., Sutton, T.T., Costa, P.A.S. & Landaeta, M.F. (2020) Global phylogeography suggests extensive eucosmopolitanism in mesopelagic fishes (*Maurolicus*; Sternoptychidae). *Scientific Reports*, 10, 20544.
https://doi.org/10.1038/s41598-020-77528-7

Regan, C.T. (1923) LXIX.—The classification of the stomiatoid fishes. *Annals and Magazine of Natural History*, Series 9, 11, 612–614.
https://doi.org/10.1080/00222932308632899

Sabaj, M.H. (2020) Codes for natural history collections in ichthyology and herpetology. *Copeia*, 108 (3), 593–669.
https://doi.org/10.1643/ASIHCODONS2020

Schultz, L.P. (1938) Review of the fishes of the genera *Polyipnus* and *Argyropelecus* (Family Sternoptychidae), with descriptions

of three new species. *Proceedings of the United States National Museum*, 86 (3047), 135–155.
https://doi.org/10.5479/si.00963801.86-3047.135
Schultz, L.P. (1961) Revision of the marine silver hatchetfishes (family Sternoptychidae). *Proceedings of the United States National Museum*, 112 (3449), 587–649.
https://doi.org/10.5479/si.00963801.112-3449.587
Smith, W.L., Ghedotti, M.J., Domínguez-Domínguez, O., McMahan, C.D., Espinoza, E., Martin, R.P., Girard, M.G. & Davis, M.P. (2022) Investigations into the ancestry of the Grape-eye Seabass (*Hemilutjanus macrophthalmos*) reveal novel limits and relationships for the Acropomatiformes (Teleostei: Percomorpha). *Neotropical Ichthyology*, 20 (3), e210160.
https://doi.org/10.1590/1982-0224-2021-0160
Smith, W.L., Girard, M.G., Walker, Jr., H.J. & Davis, M.P. (2024) The phylogeny of bristlemouths, lightfishes, and portholefishes with a revised family-level classification of the dragonfishes (Teleostei: Stomiiformes). *National Oceanic and Atmospheric Administration Professional Papers National Marine Fisheries Service*, 24 (13), 167–184.
https://doi.org/10.7755/PP.24.13
Smith, W.L., Stern, J.H., Girard, M.G. & Davis, M.P. (2016) Evolution of venomous cartilaginous and ray-finned fishes. *Integrative and Comparative Biology*, 56 (5), 950–961.
https://doi.org/10.1093/icb/icw070
Sparks, J.S., Schelly, R.C., Smith, W.L., Davis, M.P., Tchernov, D., Pieribone, V.A. & Gruber, D.F. (2014) The covert world of fish biofluorescence: a phylogenetically widespread and phenotypically variable phenomenon. *PLoS ONE*, 9 (1), e83259.
https://doi.org/10.1371/journal.pone.0083259
Stamatakis, A. (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30 (9), 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033
Tagliacollo, V.A. & Lanfear, R. (2018) Estimating improved partitioning schemes for ultraconserved elements. *Molecular Biology and Evolution*, 35 (7), 1798–1811.
https://doi.org/10.1093/molbev/msy069
Teramura, A., Koeda, K., Matsuo, A., Sato, M.P., Senou, H., Ho, H.-C., Suyama, Y., Kikuchi, K. & Hirase, S. (2022) Assessing the effectiveness of DNA barcoding for exploring hidden genetic diversity in deep-sea fishes. *Marine Ecology Progress Series*, 701, 83–98.
https://doi.org/10.3354/meps14193
Vourey, E., Dupoux, C. & Harold, A.S. (2017) A new species of *Polyipnus* (Stomiiformes: Sternoptychidae) from the western South Pacific. *Zootaxa*, 4263 (3), 567–577.
https://doi.org/10.11646/zootaxa.4263.3.8
Wainwright, P.C. & Longo, S.J. (2017) Functional innovations and the conquest of the oceans by acanthomorph fishes. *Current Biology*, 27 (11), PR550–PR557.
https://doi.org/10.1016/j.cub.2017.03.044
Weitzman, S.H. (1967) The origin of stomiatoid fishes with comments on the classification of salmoniform fishes. *Copeia*, 1967 (3), 507–540.
https://doi.org/10.2307/1442231
Weitzman, S.H. (1974) Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families. *Bulletin of the American Museum of Natural History*, 153 (3), 329–478.
Widder, E.A. (2010) Bioluminescence in the ocean: origins of biological, chemical, and ecological diversity. *Science*, 328 (5979), 704–708.
https://doi.org/10.1126/science.1174269
Zhang, C., Rabiee, M., Sayyari, E. & Mirarab, S. (2018) ASTRAL-III: polynomial time species tree reconstruction from partially resolved gene trees. *BMC Bioinformatics*, 19 (Supplement 6), 153.
https://doi.org/10.1186/s12859-018-2129-y

Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

SUPPLEMENTAL TABLE 1. Morphology presence, voucher, and GenBank SRA and nucleotide accession numbers for existing and previously published sequences.

SUPPLEMENTAL TABLE 2. Characters taken without modification directly from Harold and Weitzman (1996) except that character 67, which was removed. Reproduced here to aid with the use of these features given the necessary renumbering caused by removal of character 67.

SUPPLEMENTAL TABLE 3. Matrix of morphological characters analyzed in the current study. Species were coded by Harold and Weitzman (1996) generally at the genus-level, so only a single genus will be included below if invariant. All terminals in each genus were coded identically, even if the species was not examined by Harold and Weitzman (1996).

SUPPLEMENTAL FIGURE 1. Species-tree relationships of the Sternoptychidae based on molecular data (ultraconserved elements and mitochondrial and nuclear coding fragments) for the 20 taxa with ultraconserved element data. Numbers at nodes indicate bootstrap support values and bootstrap values ≥95 are listed as an asterisk. Nodes with no number had less than 50 bootstrap support.