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Dragons of the deep (Stomiiformes: Stomiidae): Evolutionary relationships and taxonomy of the barbeled dragonfishes (Stomiinae) and viperfishes (Chauliodontinae)

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Abstract

The stomiiforms are a diverse radiation of ray-finned fishes found in pelagic deep-sea environments, with taxa encompassing the barbeled dragonfishes including more than 350 species placed in the family Stomiidae. Barbeled dragonfishes are a diverse lineage of stomiiforms with most taxa and nearly all stomiines having a bioluminescent chin barbel that is hypothesized to be used for conspecific communication and prey attraction. Prior studies on the evolutionary relationships of the stomiids have produced conflicting hypotheses regarding the monophyly of the order's families and subfamilies and the interrelationships among genera. In this study, we investigate the evolutionary relationships among the stomiids and present a novel hypothesis of evolutionary relationships for the family based on data from ultraconserved elements (UCEs), protein-coding gene fragments, and morphology. Our combined dataset includes 29 of the 35 currently recognized stomiid genera *sensu* Smith *et al.* (2024) with taxonomic representatives from all previously recognized stomiid subfamilies and tribes. Our resulting evolutionary hypotheses conflict with the current classification of the family, rendering several currently recognized clades as para- or polyphyletic. These findings necessitate a revised classification that reflects monophyletic groups. Herein, we present a revised classification of the Stomiidae that recognizes the distinct tribal lineages of the barbeled dragonfishes.

Key words: Phylogenomics, Evolution, Deep sea, Taxonomy

Introduction

Background. Dragonfishes and their allies (Stomiiformes) comprise the largest radiation of pelagic marine fishes, with ~464 species distributed across 52 genera (Fricke *et al.* 2025). The Stomiiformes are predominantly distributed in deep-sea habitats worldwide (Harold and Weitzman 1996) and are a major component of mesopelagic and bathypelagic food webs (e.g., Sutton and Hopkins 1996; Drazen and Sutton 2017). Variation in the shape and presence of bioluminescent structures of stomiiform fishes have been used to distinguish taxa across and within the three families (Smith *et al.* 2024) of dragonfishes and their allies: Gonostomatidae (bristlemouths), Sternoptychidae (hatchetfishes), and Stomiidae (dragonfishes).

The barbeled dragonfishes (Figures 1–3) include taxa within the subfamily Stomiinae *sensu* Smith *et al.* (2024) and represent a monophyletic group within the expanded Stomiidae (dragonfishes) *sensu* Smith *et al.* (2024) that also included the traditional phosichthyids (lightfishes) and *Triplophos hemingi* (McArdle). The barbeled dragonfishes are predatory open-ocean fishes that are a species-rich lineage of stomiiforms with 27 genera and 352 species (Fricke *et al.* 2025). All taxa within the Stomiinae *sensu* Smith *et al.* (2024), except eight of nine species of *Chauliodus* and loose-jaw dragonfishes *Malacosteus* and *Photostomias*, possess an unpaired, bioluminescent chin barbel that is often species-specific in morphology that extends from the urohyal (Fink 1984, 1985). These barbels typically have a range of distal structures and bioluminescent tissue and do not house bioluminescent bacteria

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(Jørgensen and Munk 1979; Fink 1984, 1985; Davis *et al.* 2014, 2016). It has been hypothesized that the species-specific and sexually dimorphic bioluminescent barbels of barbeled dragonfishes are used for prey attraction and conspecific communication, which may be associated with rapid diversification in this lineage in deep-sea pelagic habitats (e.g., Davis *et al.* 2014, 2016). The anatomy and morphology of dragonfish barbels varies greatly among the different species ranging from simple and elongate tubes to complex structures with bulbs, branching networks, and/or filaments (Regan and Trewavas 1929, 1930; Morrow 1964b; Fink 1985).

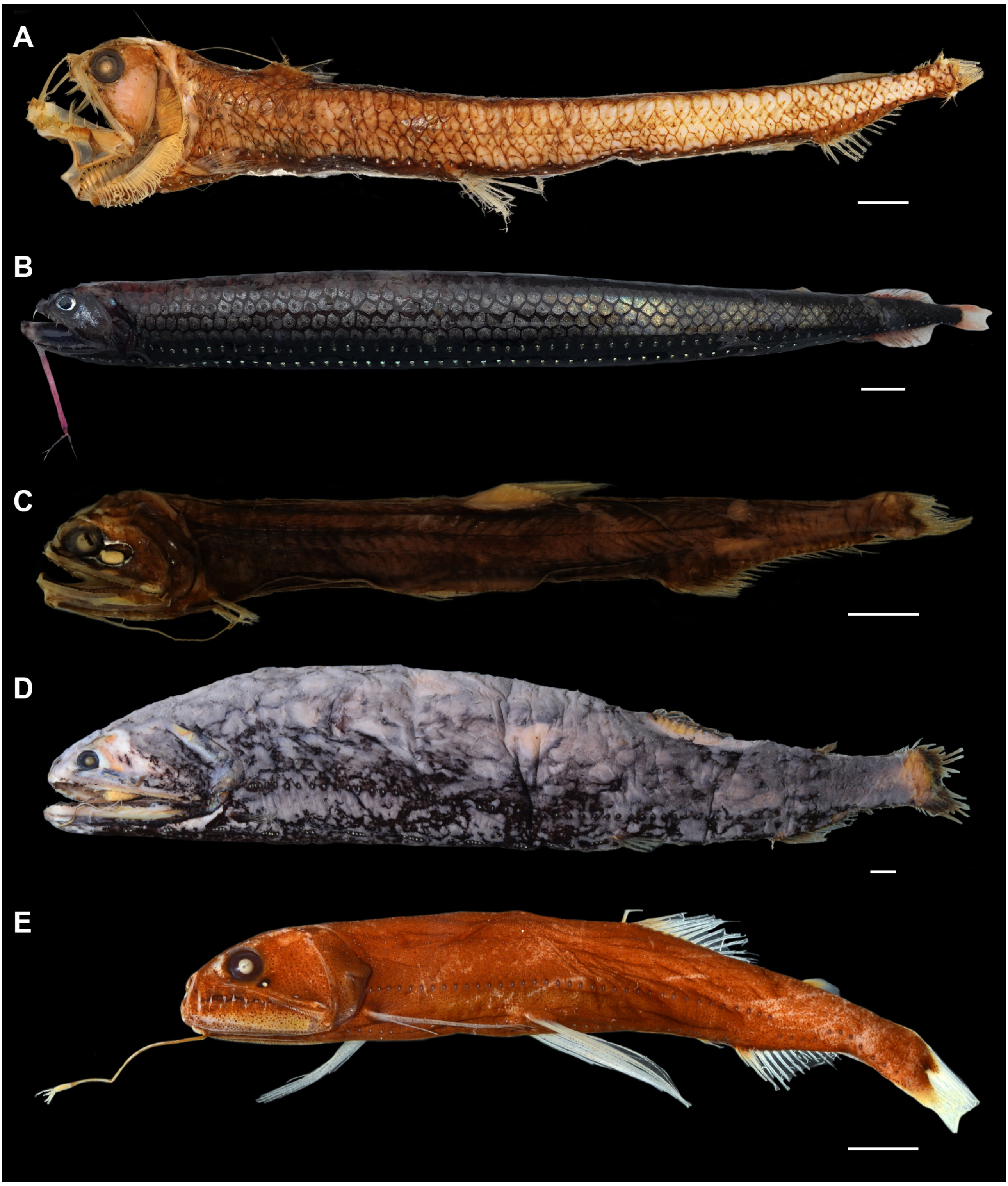

FIGURE 1. Representative images of dragonfish genera including (A) *Chauliodus* (FMNH 88244); (B) *Stomias* (SCSU uncat.); (C) *Neonesthes* (FMNH 49649); (D) *Heterophotus* (USNM uncat.); (E) *Astronesthes* (USNM 214466). Scale bar = 1 cm. Images taken by M.P. Davis, E.S. DeArmon, and/or W.L. Smith.

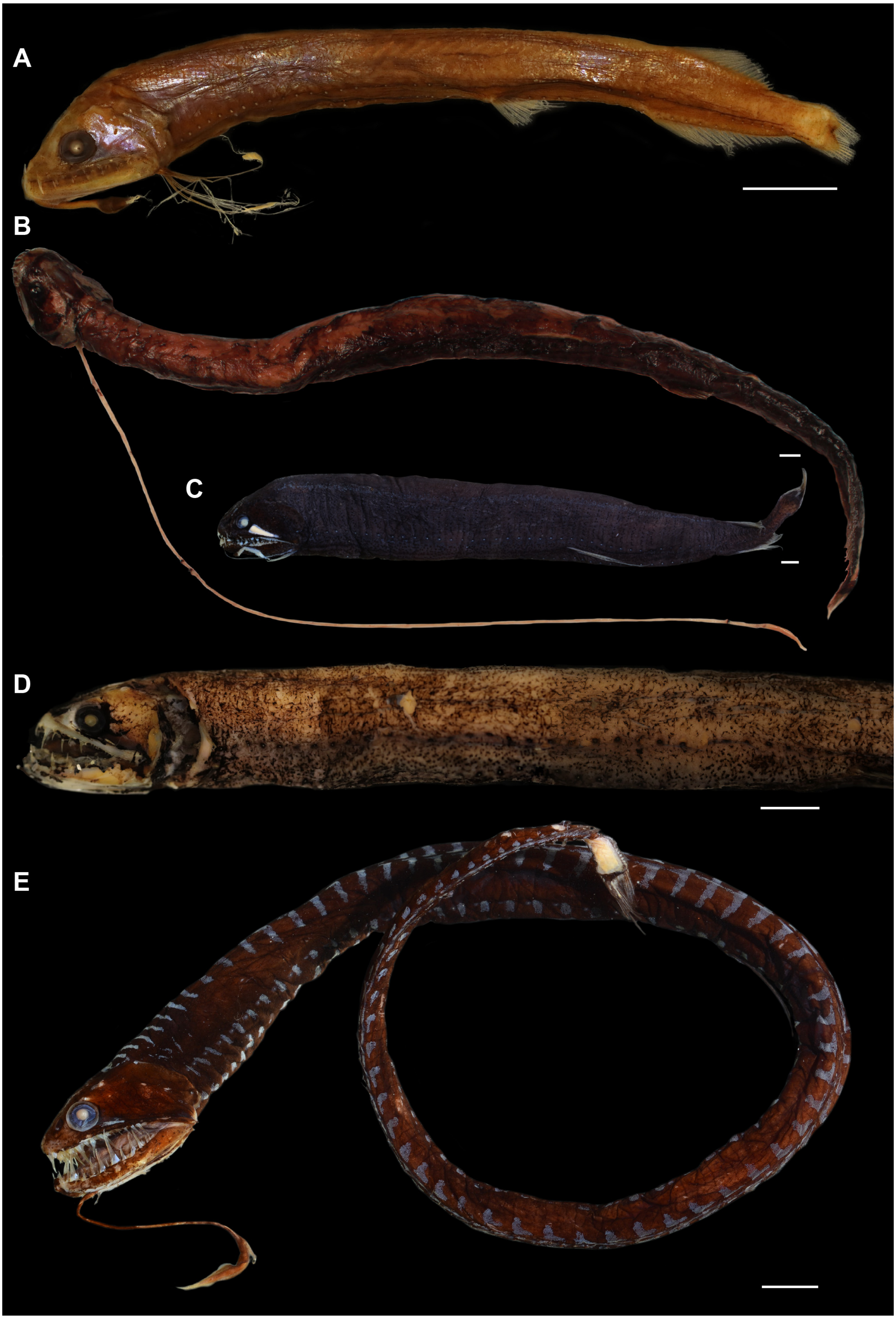

FIGURE 2. Representative images of barbeled dragonfish genera including (A) *Chirostomias* (FMNH 49737); (B) *Leptostomias* (USNM 234478); (C) *Echiostoma* (USNM 409549); (D) *Photonectes* (FMNH 117803); (E) *Idiacanthus* (USNM 206722). Scale bar = 1 cm. Images taken by M.P. Davis, E.S. DeArmon, and/or W.L. Smith.

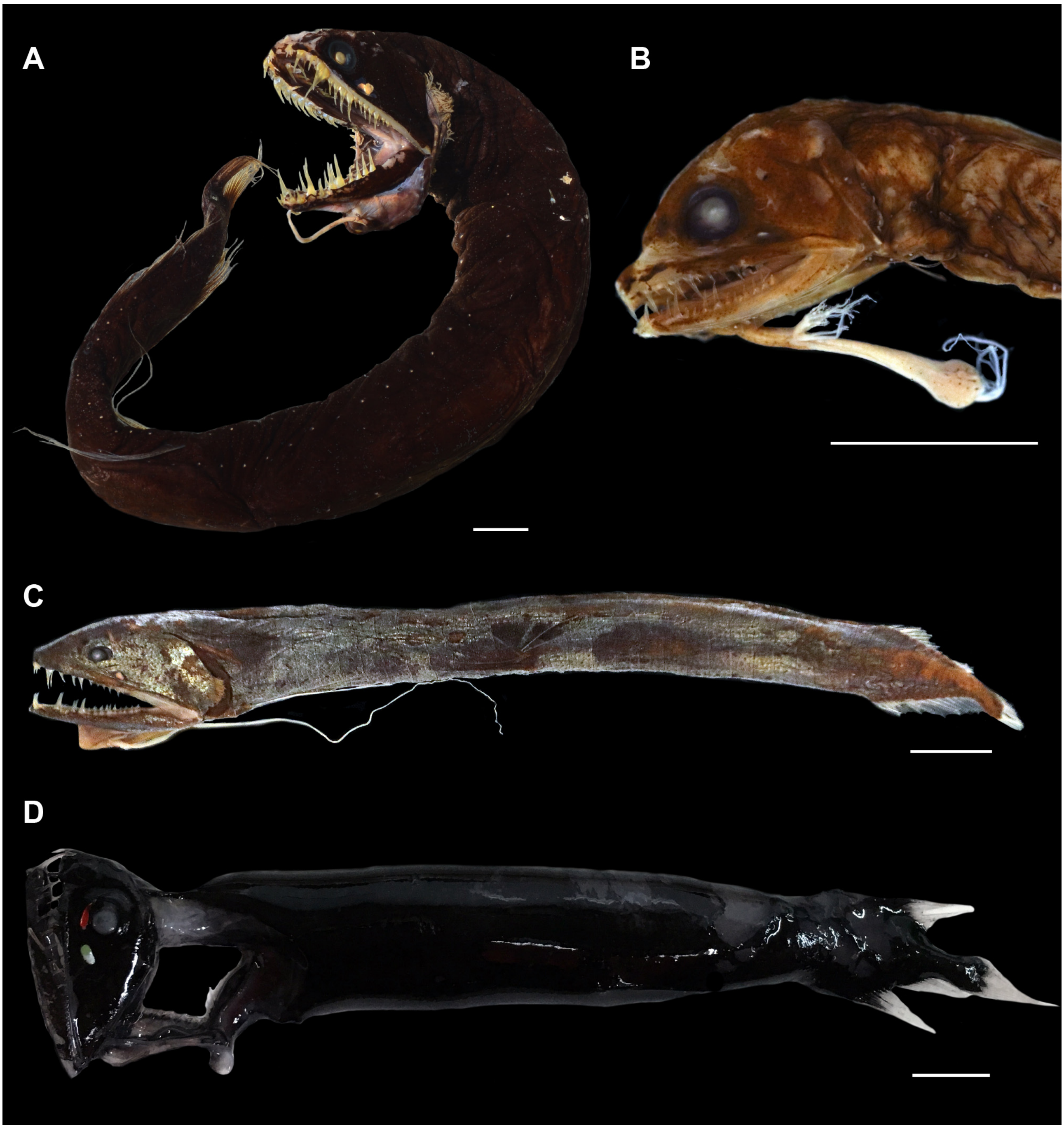

FIGURE 3. Representative images of barbeled dragonfish genera including (A) *Melanostomias* (USNM 25673); (B) *Eustomias* (FMNH 49859); (C) *Bathophilus* (FMNH 49736); (D) *Photostomias* (SCSU uncat.). Scale bar = 1 cm. Images taken by M.P. Davis, E.S. DeArmon, and/or W.L. Smith.

Classification. Herein we follow the Linnaean classification of Smith *et al.* (2024) in recognizing three families within the Stomiiformes, including an expanded Stomiidae (dragonfishes) that includes taxa previously associated with the Phosichthyidae and *Triplophos*. For a detailed discussion on the history of classification of fishes in the Stomiiformes broadly, refer to Weitzman (1974), Fink (1985), and Smith *et al.* (2024). The focus of this work is to investigate the relationships among the taxa previously attributed to the Stomiinae *sensu* Smith *et al.* (2024) or Stomiidae *sensu* Fink (1985). Prior to Fink (1985), several studies classified these dragonfish taxa in six families (e.g., Morrow 1964b; Greenwood *et al.* 1966; Weitzman 1974), including the Astronesthidae (snaggletooths), Chauliodontidae (viperfishes), Idiacanthidae (black dragonfishes), Malacosteidae (loosejaw dragonfishes), Melanostomiidae (deep-sea dragonfishes), and Stomiidae (scaly dragonfishes). Weitzman (1974) considered these six families as constituting the superfamily Stomiatoidea, within an infraorder Photichthya that also included the superfamily Photichthyoidea. Weitzman (1974) noted that the recognition of these six families within the Stomiatoidea required further investigation and would likely need to be revised over time. The inferred relationships and taxonomic composition of these six families later varied based on morphological (Weitzman 1974; Fink 1985), molecular (Betancur-R. *et al.* 2013; Davis *et al.* 2014; Kenaley *et al.* 2014; Rabosky *et al.* 2018), and total-evidence (Mirande 2017; Smith *et al.* 2024) studies as shown in Figures 4 and 5.

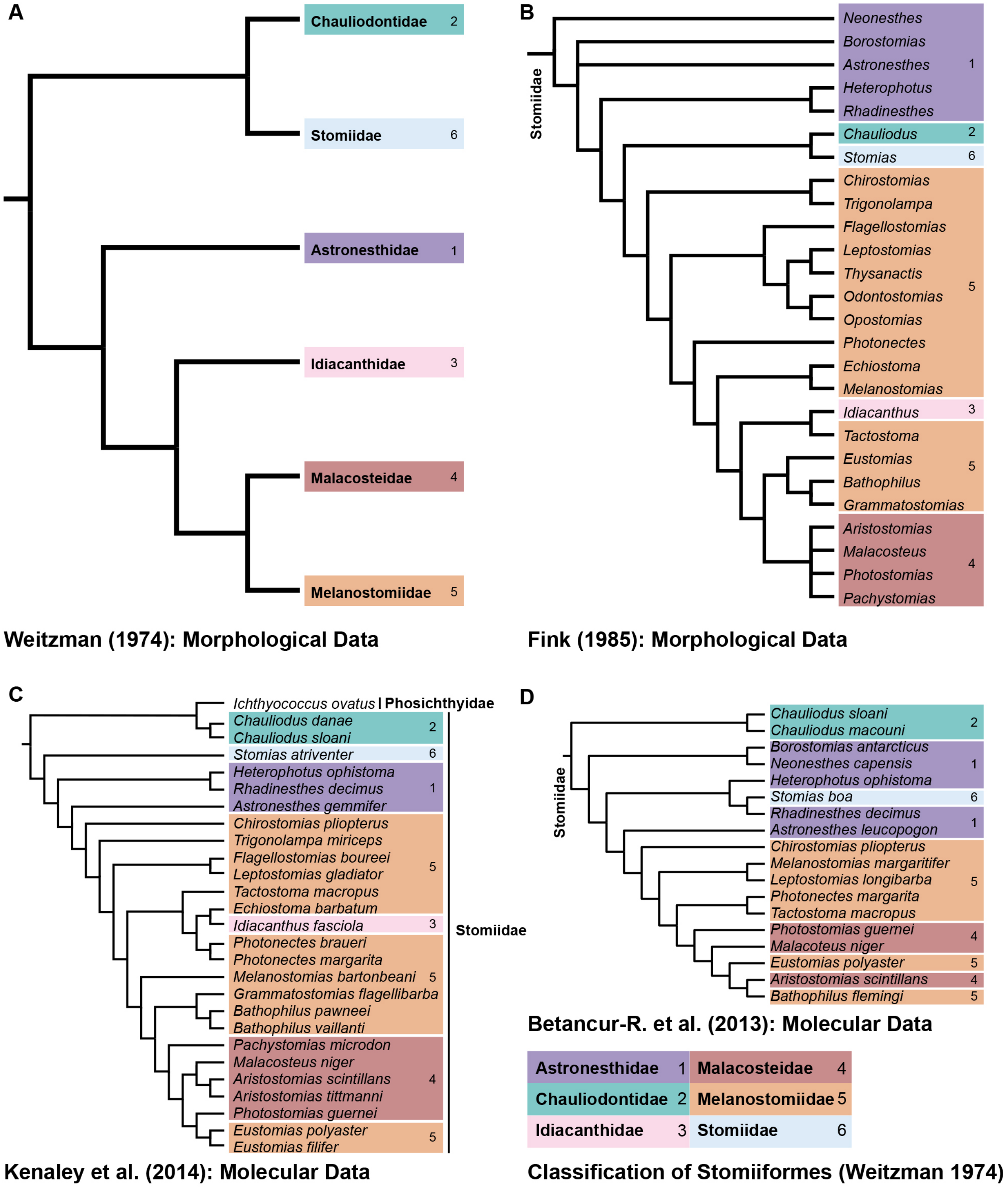

FIGURE 4. Previous hypotheses of relationships of barbeled dragonfish taxa, including the morphological studies of (A) Weitzman (1974) and (B) Fink (1985), and the molecular gene-fragment studies of (C) Kenaley *et al.* (2014) and (D) Betancur-R. *et al.* (2013). Taxa are highlighted by the six families of barbeled dragonfishes recognized by Weitzman (1974).

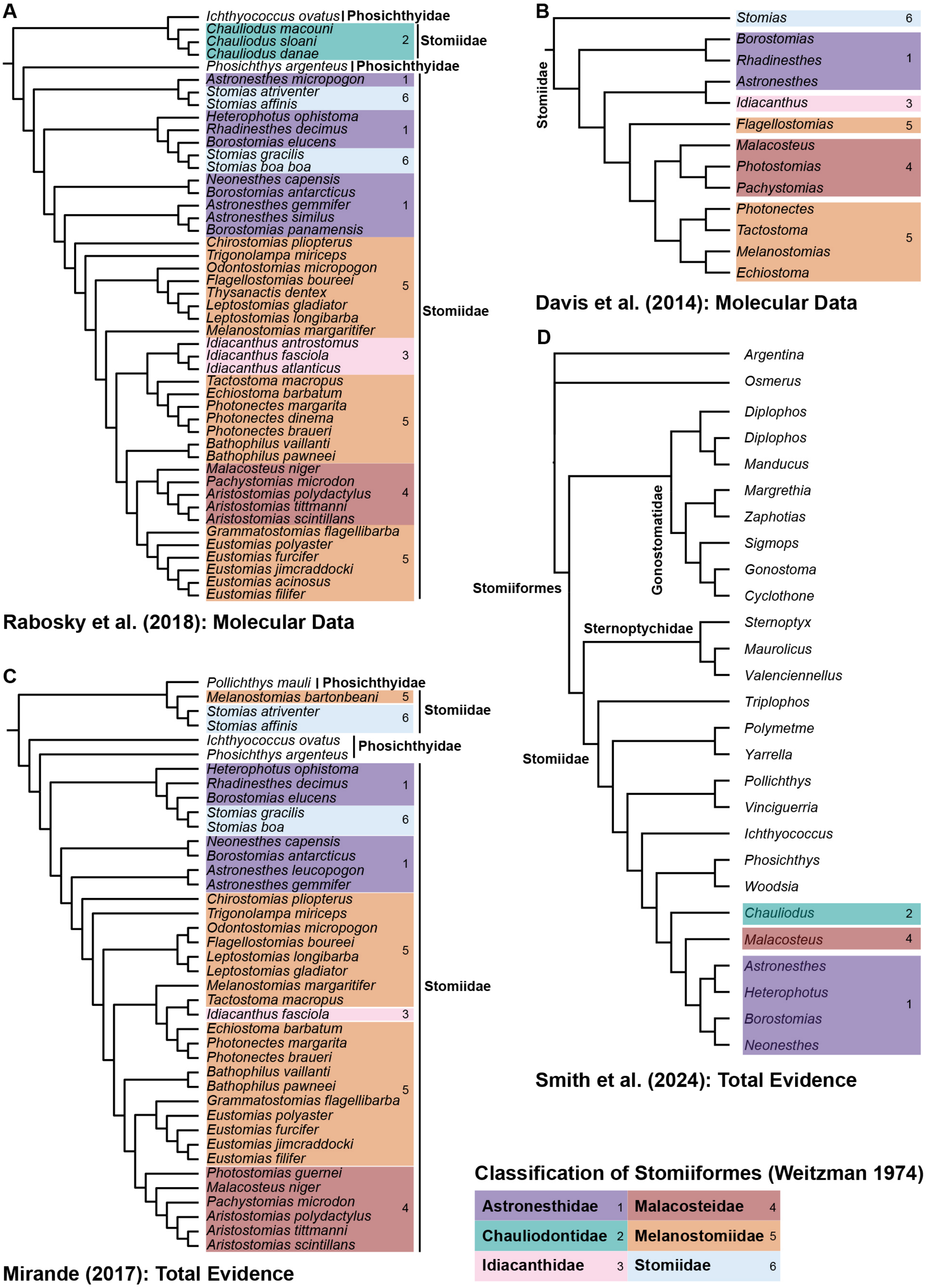

FIGURE 5. Previous hypotheses of relationships of barbeled dragonfish taxa, including the molecular gene-fragment studies of (A) Rabosky *et al.* (2018) and (B) Davis *et al.* (2014) with the total-evidence study of (C) Mirande 2017 and the ultraconserved elements, gene fragments, and morphological analysis of (D) Smith *et al.* (2024). Taxa are highlighted by the six families of barbeled dragonfishes as recognized by Weitzman (1974).

Fink (1985) investigated the evolutionary relationships among taxa in the Stomiatoidea of Weitzman (1974) with morphological data and inferred that many of the previously recognized families of dragonfishes were not monophyletic (Figure 4B). Many of these families were also initially described with no clear diagnoses to establish the limits and taxonomic composition of the families. For this reason, Fink (1985) recognized all taxa placed in Weitzman's (1974) Stomiatoidea into the single family Stomiidae. Going forward, many works (e.g., Nelson 2006; Kenaley *et al.* 2014; Nelson *et al.* 2016) would continue to recognize subfamilies within the Stomiidae *sensu* Fink (1985) based on the previous six stomiatoid families despite the recognition that many of these groupings (e.g., Melanostomiinae) were demonstrably not monophyletic in phylogenetic analyses (Figures 4 and 5). A revised classification of the clades within the Stomiinae *sensu* Smith *et al.* (2024) is needed to create a more stable classification that reflects the distinct evolutionary lineages informed by explicit phylogenetic analyses that includes molecular and morphological data.

Evolutionary Relationships. The monophyly of barbeled dragonfish taxa within the Stomiatoidea was first established by Weitzman (1974), with additional work by Fink and Weitzman (1982) further corroborating the clade (Figure 4A). Fink's (1985) phylogeny of his revised Stomiidae included 323 morphological characters with a single outgroup representing several traditional phosichthyid taxa (e.g., *Polymetme*). While the use of a single operational taxonomic unit that was based of multiple outgroups limited his ability to test the monophyly of the Stomiidae, Fink (1985) provided the most comprehensive investigation into the evolutionary relationships among barbeled dragonfish genera (Figure 4B). The monophyly of the proposed six families stomiatoids was not tested by Weitzman (1974; Figure 4A), but he hypothesized that the viperfishes (Chauliodontidae, *Chauliodus*), in which only one of nine species has a small chin barbel, were sister to his Stomiidae (in his study restricted to only *Stomias*). Fink (1985) also inferred a sister-group relationship between *Chauliodus* and *Stomias*, and he identified them along with a paraphyletic Astronesthidae *sensu* Weitzman (1974) as the stem barbeled dragonfish lineages in his Stomiidae (Figure 4B). The family Melanostomiidae *sensu* Weitzman (1974) was also inferred to be paraphyletic by Fink (1985), but he did recover the loosejaw dragonfishes (Malacosteidae *sensu* Weitzman, 1974) as monophyletic. Ultimately, Fink (1985) proposed a single family Stomiidae constituting all the lineages previously included in Weitzman's (1974) superfamily Stomiatoidea.

Subsequent studies focused on investigating the evolutionary relationships among the barbeled dragonfishes (Stomiidae *sensu* Fink, 1985) using molecular data with varying levels of taxonomic sampling within the family (Figure 4C and 4D, Figure 5). Kenaley *et al.* (2014) inferred a phylogeny of the barbeled dragonfishes (Figure 2C) using protein-coding gene fragments (ENC1, RAG1, MYH6, and rod opsin) that rendered the Stomiidae *sensu* Fink (1985) as paraphyletic (Figure 4C) with the genus *Chauliodus* as the sister group to *Ichthyococcus* (treated in the Phosichthyidae at the time). The families Astronesthidae and Melanostomiidae *sensu* Weitzman (1974) were also not inferred as monophyletic (Figure 4B and 4C) in Kenaley *et al.* (2014), which was also found by Fink (1985). An interesting result from Kenaley *et al.* (2014), relative to most studies, is that they inferred the loosejaw dragonfishes (Malacosteidae *sensu* Weitzman, 1974) as paraphyletic with *Eustomias* nested in the clade (Figure 4C). Betancur-R. *et al.* (2013) also did not infer the clade composed of only the loosejaw dragonfishes (Figure 4D).

Rabosky *et al.*'s (2018) meta-analysis of 27 gene fragments across ray-finned fishes (Figure 5A), recovered *Ichthyococcus* (lightfish) as the sister group to the viperfish *Chauliodus*, a relationship previously found by Kenaley *et al.* (2014). Rabosky *et al.* (2018) additionally inferred *Phosichthys* as the sister group to the remaining stomiid taxa *sensu* Fink (1985). Rabosky *et al.* (2018) also did not recover the Astronesthidae, Melanostomiidae, or Stomiidae as monophyletic *sensu* Weitzman (1974). Mirande (2017) used a total-evidence approach and was one of a few studies (Rabosky *et al.* 2018) that did not recover *Stomias* or the Stomiidae *sensu* Fink, 1985 as monophyletic (Figure 5C). Davis *et al.* (2014), using two nuclear genes (RAG1 and ZIC1) and one mitochondrial gene (COI), recognized the family Stomiidae *sensu* Fink (1985) as monophyletic (Figure 5B) and recovered the loosejaw dragonfishes (Malacosteidae *sensu* Weitzman, 1974) as monophyletic. Davis *et al.* (2014) also found the Astronesthidae and Melanostomiidae *sensu* Weitzman (1974) to not be monophyletic (Figure 5B).

Smith *et al.* (2024) incorporated a total-evidence approach including genome-scale ultraconserved element data, protein-coding fragments, and morphology to explore the evolutionary relationships broadly among stomiiform fishes (Figure 5D). Smith *et al.* (2024) expanded the taxonomic limits of the Stomiidae (dragonfishes) to include *Triplophos* and taxa within the traditional Phosichthyidae (Figure 5D). The phosichthyids were previously hypothesized to have a close evolutionary affinity to barbeled dragonfish taxa (Weitzman 1974) or with similar limits to Harold and Weitzman (1996). The revision by Smith *et al.* (2024) to the Stomiidae (dragonfishes) more accurately reflects the evolutionary relationships inferred from both morphological and molecular datasets (Figures

4–5) and provides stability for the family-level classification of the Stomiiformes going forward. The taxonomic sampling for the Stomiinae *sensu* Smith *et al.* (2024) was limited and the character data from Fink (1985) were not included in their broader analysis. Although the Stomiidae *sensu* Fink (1985) was inferred to be monophyletic and treated as the Stomiinae (barbeled dragonfishes) within the more broadly defined Stomiidae (dragonfishes), further work was clearly needed to clarify the evolutionary relationships among barbeled dragonfishes to develop a revised classification of this species-rich clade.

To date, no study has investigated the evolutionary relationships of the barbeled dragonfishes broadly with genome-scale data. In this study, we incorporate ultraconserved elements (UCEs; Faircloth *et al.* 2012), which are highly conserved regions of the nuclear genome that have been used to infer the evolutionary relationships of animal lineages including mammals, birds, and squamates (e.g., Crawford *et al.* 2012; Faircloth *et al.* 2012, 2013; McCormack *et al.* 2013) to explore the evolutionary relationships among the barbeled dragonfishes. Ultraconserved elements have also been used to reconstruct the evolutionary relationships among various lineages of fishes such as the Acanthomorpha (Ghezelayagh *et al.* 2022), Acropomatiformes (Smith *et al.* 2022), Carangiformes (Harrington *et al.* 2016; Girard *et al.* 2020), Lophioidei (Maile *et al.* 2025), Myctophiformes (Martin *et al.* 2018), and Syngnathiformes (Longo *et al.* 2017).

The evolutionary relationships among barbeled dragonfishes are broadly incongruent when comparing morphological, molecular, and combined studies. In this study, we seek to resolve the evolutionary relationships among dragonfishes with a genome-scale approach in combination with additional molecular data and previously published morphological data (Fink 1985; Schnell and Johnson 2017) toward a goal of producing a revised classification of the lineage that reflects updated evolutionary relationships using a combination of data.

Materials and Methods

Taxonomic Sampling. The genus *Osmerus* was included as the root and as a representative of the order Osmeriformes, which is often inferred as the sister group to the Stomiiformes (e.g., Near *et al.* 2012; Davis *et al.* 2016; Smith *et al.* 2016). Additional outgroups outside of the Stomiidae (dragonfishes) included five (Figures 6–7) genera from the families Gonostomatidae and Sternoptychidae. The newly collected UCE data include representatives from 22 of 27 barbeled dragonfish (Stomiinae *sensu* Smith *et al.* 2024) genera, with the total-evidence analysis including 51 species representing 26 of 27 verified genera (Supplemental Table 1), with only the genus *Eupogonesthes* missing from the total-evidence analyses. There is also one monotypic genus of barbeled dragonfishes, *Bathysphaera intacta*, that was described by Beebe (1932) as a six-foot long member of the group based on a visual account from dives in a bathysphere that was not included in this study. Since the initial observation by Beebe (1932), this species has never been collected or further verified to exist and is not included in this study. The total-evidence analysis also included additional previously published protein-coding gene fragments from GenBank (Supplemental Table 1). All collection and institutional codes follow Sabaj (2020).

DNA Extraction. Prior to the extraction of DNA sequenced for UCE loci, muscle or fin clips were preserved in either 95% ethanol or RNA*later* Stabilization Solution (Thermo Fisher Scientific, Waltham, MA). Either a DNeasy Tissue Extraction Kit (Qiagen, Germantown, MD) or a Maxwell RSC Blood DNA Kit and Instrument (Promega, Madison, WI) was used to extract DNA from tissue samples following manufacturers' extraction protocols (except for the replacement of the Blood DNA Kit's lysis buffer with Promega's tissue lysis buffer). For Qiagen DNeasy Kit extractions only, the first and second elution from a Qiagen filter were combined and dried to a volume of 102 µL using a Savant DNA120 SpeedVac Concentrator (Thermo Fisher Scientific). For Maxwell RSC extractions only, extractions were eluted into a volume of 102 µL. Two µL of the raw DNA extracts were quantified using a Qubit Fluorometer 2.0 (Thermo Fisher Scientific) using the dsDNA BR Assay Kit (Thermo Fisher Scientific). When insufficient DNA was collected, multiple samples from the same specimen were extracted, combined, dried, and quantified again using the same methods stated above. Final quantified samples (100 µL in volume) were sent to Arbor Biosciences (Ann Arbor, MI) for library preparation (e.g., DNA shearing, size selection, cleanup), target capture, enrichment, sequencing on an Illumina HiSeq 2500 (Illumina, San Diego, CA), and demultiplexing. Target capture for UCE loci used the 500 UCE actinopterygian-loci probe set (Faircloth *et al.* 2013).

UCE Amplification, Sequencing, and Assembly. Raw FASTQ files received from Arbor Biosciences were cleaned of indices and adapters using illumiprocessor and Trimmomatic and then assembled into contigs using

SPAdes within PHYLUCE 1.71 (Faircloth 2016). PHYLUCE 1.71 was used to create a database of UCE loci by taxon and then to construct FASTA files of the UCE data. The extracted UCE data were aligned with MAFFT 7.130b (Katoh and Standley 2013) with a data matrix that included only contigs found in at least 65% of the included taxa. For the 30 taxa that were sampled for UCEs, a total of 420 aligned UCE fragments were concatenated for a total length of 250,457 bp. Novel cleaned sequencing reads to this study were submitted to GenBank and have been assigned BioProject accession number PRJNA1338071 with SRA accession numbers SRR35742187–SRR 35742207 (Supplemental Table 1).

Protein-coding Gene Sequences. To increase the taxonomic sampling of barbeled dragonfishes, previously published gene-fragment data from GenBank were collected and concatenated with the UCE dataset (Supplemental Table 1). Sequences taken from GenBank include the following ten nuclear gene fragments: ENC1, GLYT, MYH6, PLAGL2, PTR, RAG1, SH3PX3, SREB2, TBR1, and ZIC1 and one mitochondrial gene fragment: COI. GenBank accession numbers for previously published gene fragments are listed in Supplemental Table 1. Nuclear and mitochondrial gene fragments were aligned with MAFFT 7.130b for each individual fragment using default settings. Following alignment, each additional gene fragment was concatenated with the UCE dataset. The addition of the protein-coding gene fragments increased the taxonomic sampling to 60 species with a combined molecular dataset of 259,807 bp.

Morphological Data. The morphological dataset used in this study as part of the total-evidence analysis included 323 characters coded and described by Fink (1985) as corrected by Schnell and Johnson (2017) with the matrix presented in Supplemental Table 2. For the total-evidence analysis, the morphological data were concatenated with the ultraconserved elements and the protein-coding gene fragments for a dataset that included 61 terminals and a total dataset of 260,130 characters.

Phylogenetic Analysis. The UCE data alone included 30 taxa and were partitioned to find the best model of molecular evolution using an entropy-based method (Sliding-Window Site Characteristics-Entropy Method, SWSC-EN; Tagliacollo and Lanfear 2018). Each species-specific UCE locus is split into regions of left flanking, right flanking, and ultra-conserved core by rate of evolution. These UCE segments become the output for PartitionFinder v2.1.1 (Lanfear *et al.* 2014, 2017; Stamatakis 2014) where the best-fitting nucleotide substitution model for each data partition is found. PartitionFinder2 uses selected models from AICc and the recluster search method (Lanfear *et al.* 2014) to assign models of molecular evolution. We additionally used PartitionFinder 2 to identify the best-fitting models of molecular evolution for the combined UCE and gene-fragment dataset that included a total of 60 taxa. In the combined dataset, the UCE data were partitioned based on the entropy-based method into segments and the protein-coding gene fragments were partitioned by gene and codon position. PartitionFinder2 identified 1,193 subsets for the UCE dataset and 1,233 subsets for the combined molecular dataset with associated models. These 1,233 partitions from the concatenated molecular dataset were combined with the morphological dataset that used an MK+ASC model (Lewis 2001) for the total-evidence analysis. The UCE dataset and the total-evidence datasets were analyzed using a maximum-likelihood approach with IQ-Tree v2.2.2.6 (Lanfear *et al.* 2012; Chernomor *et al.* 2016; Minh *et al.* 2020). The phylogenetic analyses included 20 independent replicates with the topology representing the maximum likelihood of those 20 replicates presented herein as the optimal hypothesis for the UCE dataset (Figure 6) and the total-evidence dataset (Figure 7). Traditional bootstrap replicates (-bo) were also conducted 100 times for both datasets, with bootstrap support values for nodes indicated on Figures 6 and 7.

Character Evolution for Diagnostic Characters. Morphological synapomorphies were identified through ancestral character-state reconstruction of the 323 anatomical characters from Fink's (1985) data matrix. For this study, *Polymetme theaocoryla* was assigned the outgroup codings from Fink (1985), as *Polymetme* was included in his material examined and "phosichthyid" taxa served as the functional outgroups for comparison in that study. Other outgroups in this study were coded as missing for morphological characters as they were not explicitly examined in Fink (1985). The software package Mesquite v4.01 (Maddison and Maddison 2025) was used to infer character evolution with a maximum-parsimony approach to identify synapomorphies and unique character combinations for diagnoses of higher-level taxonomic names.

Results

Evolutionary Relationships of Barbeled Dragonfishes. Both the UCE and total-evidence analysis support the monophyly of the stomiiform families Gonostomatidae, Sternoptychidae, and Stomiidae (Figures 6 and 7) as presented in Smith *et al.* (2024). Smith *et al.* (2024) recovered *Triplophos* as the stem stomiid lineage, followed by "phosichthyid" taxa. Our analysis did not include *Triplophos*, and the stem stomiid lineages were "phosichthyid" taxa (Figures 6 and 7). In general, traditional bootstrap support was strong for most nodes in both analyses (Figures 6 and 7). Both analyses (UCE and total-evidence) recovered the same overall clades and relationships among clades for barbeled dragonfishes, so the discussion here will be restricted to the total-evidence analyses that included additional genera. Within the Stomiidae *sensu* Smith *et al.* (2024), the subfamily Stomiinae *sensu* Smith *et al.* (2024) was inferred to be monophyletic with the stem lineage being *Chauliodus* (viperfishes, family Chauliodontidae *sensu* Weitzman, 1974) as seen in Figures 6 and 7. All but one species of viperfishes (*Chauliodus*) lack a bioluminescent chin barbel, as do all of the stem stomiid taxa that were previously classified in the Gonostomatidae (*Triplophos*) or Phosichthyidae. Herein we refer to *Chauliodus* as belonging to the subfamily Chauliodontinae (viperfishes) and as the sister group to a broad clade discussed next that includes the other five stomiid families from Weitzman (1974) that constitute a revised Stomiinae that we recommend have the common name barbeled dragonfishes. We recommend the common name dragonfishes for the Stomiidae sensu Smith *et al.* (2024) as a whole.

The barbeled dragonfishes form a clade, with *Stomias* (scaly dragonfishes, Stomiidae *sensu* Weitzman, 1974) as the stem lineage (Figures 6 and 7). The next three clades in sequence include a grade of taxa associated with the Astronesthidae *sensu* Weitzman (1974), which was not found to be monophyletic in our analyses (Figures 6 and 7). The first clade includes *Borostomias* + *Neonesthes*, the second clade includes *Heterophotus* + *Rhadinesthes*, and the third clade includes *Astronesthes* (Figures 6 and 7). Next, we have a series of clades that form a grade belonging to the family Melanostomiidae *sensu* Weitzman (1974) as observed in Figures 6 and 7. The first clade in this grade includes *Chirostomias* + *Trigonolampa* (Figures 6 and 7). The second clade in this grade includes *Flagellostomias* as the sister group to a clade that includes *Odontostomias* + *Opostomias* sister to a clade that includes *Leptostomias* + *Thysanactis* (Figures 6 and 7). The third clade within the barbeled dragonfishes (Figures 6 and 7) includes *Photonectes* as the sister group to a clade that includes *Echiostoma* sister to a clade including *Idiacanthus* + *Tactostoma* (Idiacanthidae *sensu* Weitzman 1974). The fourth clade in this grade (Figures 6 and 7) includes species of *Melanostomias* and the fifth clade in this grade includes *Bathophilus* + *Grammatostomias*. The final clade in this grade (Figures 6 and 7) includes *Eustomias* as the sister group to a monophyletic Malacosteidae (loosejaw dragonfishes) *sensu* Weitzman (1974).

Revised Classification of the Stomiinae *sensu* Smith *et al.* (2024). The UCE and total-evidence analyses resulted in phylogenies that were largely congruent with each other (Figures 6 and 7). One consistent thread with the hypothesized evolutionary relationships from this work and those of prior studies (Figures 4 and 5) is the need to revisit and revise the former subclades within the Stomiidae *sensu* Fink (1985) that are currently treated as subfamilies in many classifications (e.g., Kenaley *et al.* 2014; Nelson *et al.* 2016). This is necessary because many of these subfamilies (e.g., Astronesthinae and Melanostomiinae) are found to be paraphyletic in this study (Figures 6 and 7). Smith *et al.* (2024) recently expanded the taxonomic composition of the family Stomiidae as well but commented that their limited taxonomic sampling of their Stomiinae (Stomiidae *sensu* Fink 1985) made classification within their Stomiinae premature. Herein we propose a revised classification of dragonfishes that reflects monophyletic lineages with clear diagnoses. For a discussion on the taxonomic account of the expanded Stomiidae refer to Smith *et al.* (2024)

Within the Stomiinae *sensu* Smith *et al.* (2024) we recognize *Chauliodus* (viperfish) as the sole genus in the subfamily Chauliodontinae and the sister group to a revised subfamily Stomiinae that includes the barbeled dragonfishes (Figures 6 and 7). Within the revised Stomiinae, we recognize the tribe Stomiini, which is restricted to the genus *Stomias*. The polyphyletic Astronesthidae *sensu* Weitzman (1974) is herein recognized as three monophyletic tribes, Astronesthini (*Astronesthes* and *Eupogonesthes* [based on Parin and Borodulina 2003]), Borostomiini (*Borostomias* and *Neonesthes*), and Rhadinesthini (*Heterophotus* and *Rhadinesthes*). The polyphyletic family Melanostomiidae *sensu* Weitzman (1974) is recognized herein as eight tribes including, Bathophilini (*Bathophilus* + *Grammatostomias*), Chirostomiini (*Chirostomias*), Echiostomini (*Echiostoma*), Eustomiini (*Eustomias*), Leptostomiini (*Flagellostomias*, *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*), Melanostomiini (*Melanostomias*), Photonectini (*Photonectes*), and Trigonolampini (*Trigonolampa*). The family Idiacanthidae *sensu* Weitzman (1974) is recognized as Idiacanthini which includes *Idiacanthus* and is expanded here to include *Tactostoma*, originally included in the polyphyletic Melanostomiidae *sensu* Weitzman (1974). The family Malacosteidae *sensu* Weitzman (1974) is recognized herein as Malacosteini (*Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*). The revised classification of stomiid subfamilies and tribes will be discussed going forward herein while discussing the evolutionary relationships among the barbeled dragonfishes, and are illustrated on Figures 6–8. Diagnostic features below were inferred to be unambiguous synapomorphies at nodes in the total-evidence analysis based on the morphological characters (Supplemental Table 2) with character descriptions from Fink (1985). Taxonomic accounts are presented in phylogenetic sequence based on the total-evidence analysis (Figures 7 and 8).

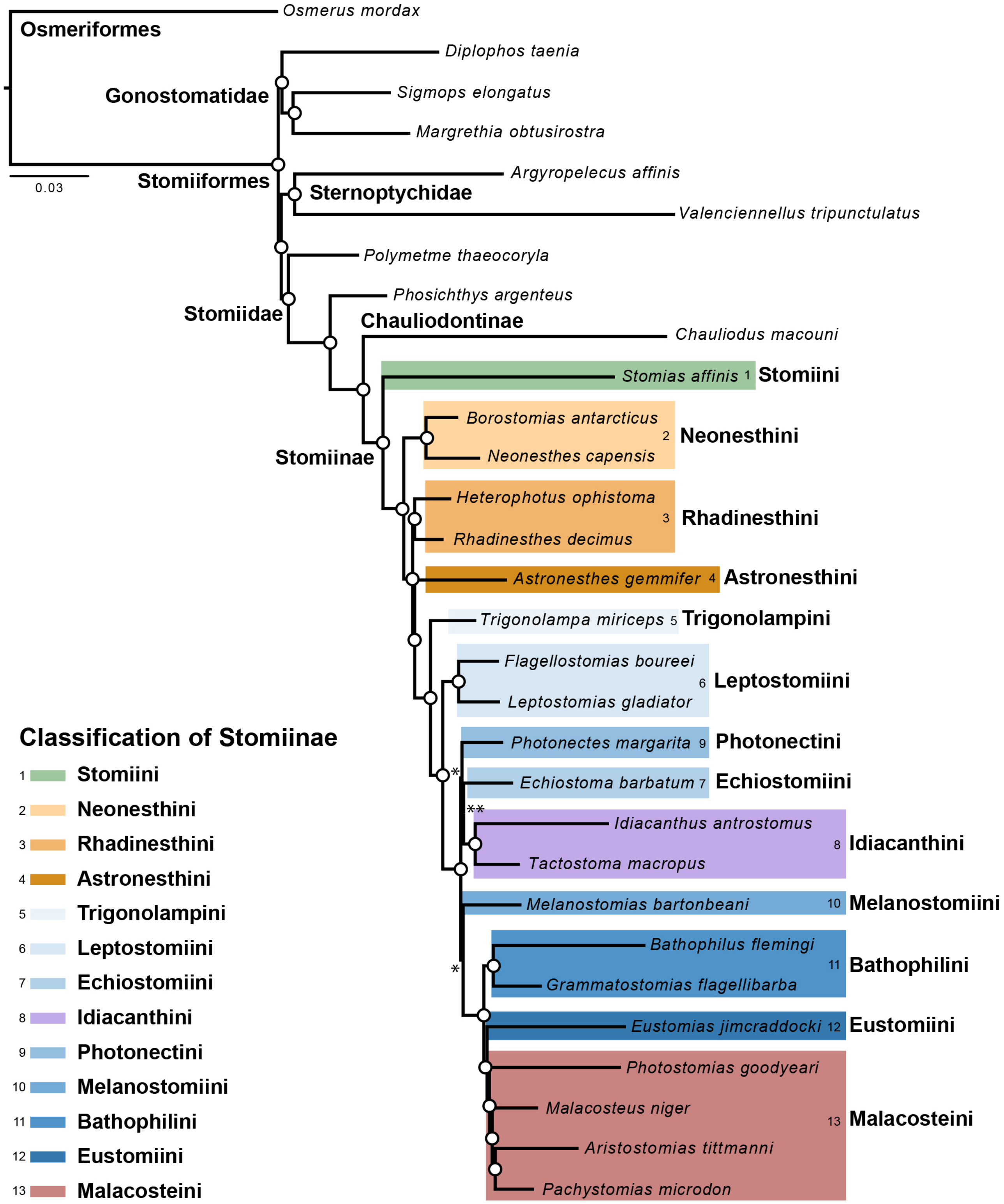

FIGURE 6. Maximum-likelihood molecular relationships of the barbeled dragonfishes based on ultraconserved elements. White circles at nodes indicate bootstrap support values ≥95. A single asterisk at node indicates a bootstrap value between 75 and 94. A double asterisk at node indicates a bootstrap value between 50 and 74.

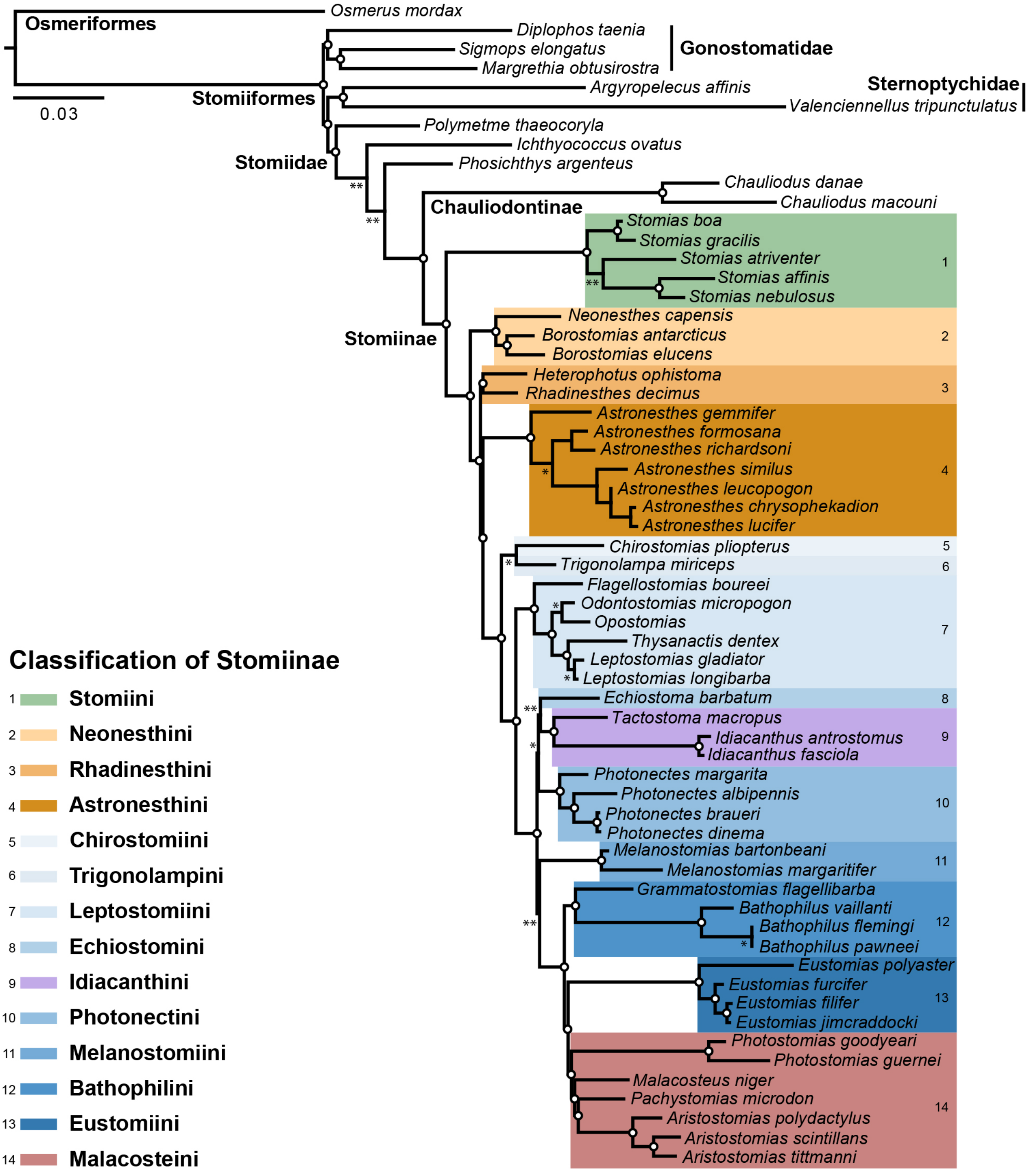

FIGURE 7. Maximum-likelihood total-evidence relationships of the barbeled dragonfishes based on ultraconserved elements, mitochondrial and nuclear coding fragments, and morphological data (Fink 1985). White circles at nodes indicate bootstrap support values ≥95. A single asterisk at node indicates a bootstrap value between 75 and 94. A double asterisk at node indicates a bootstrap value between 50 and 74.

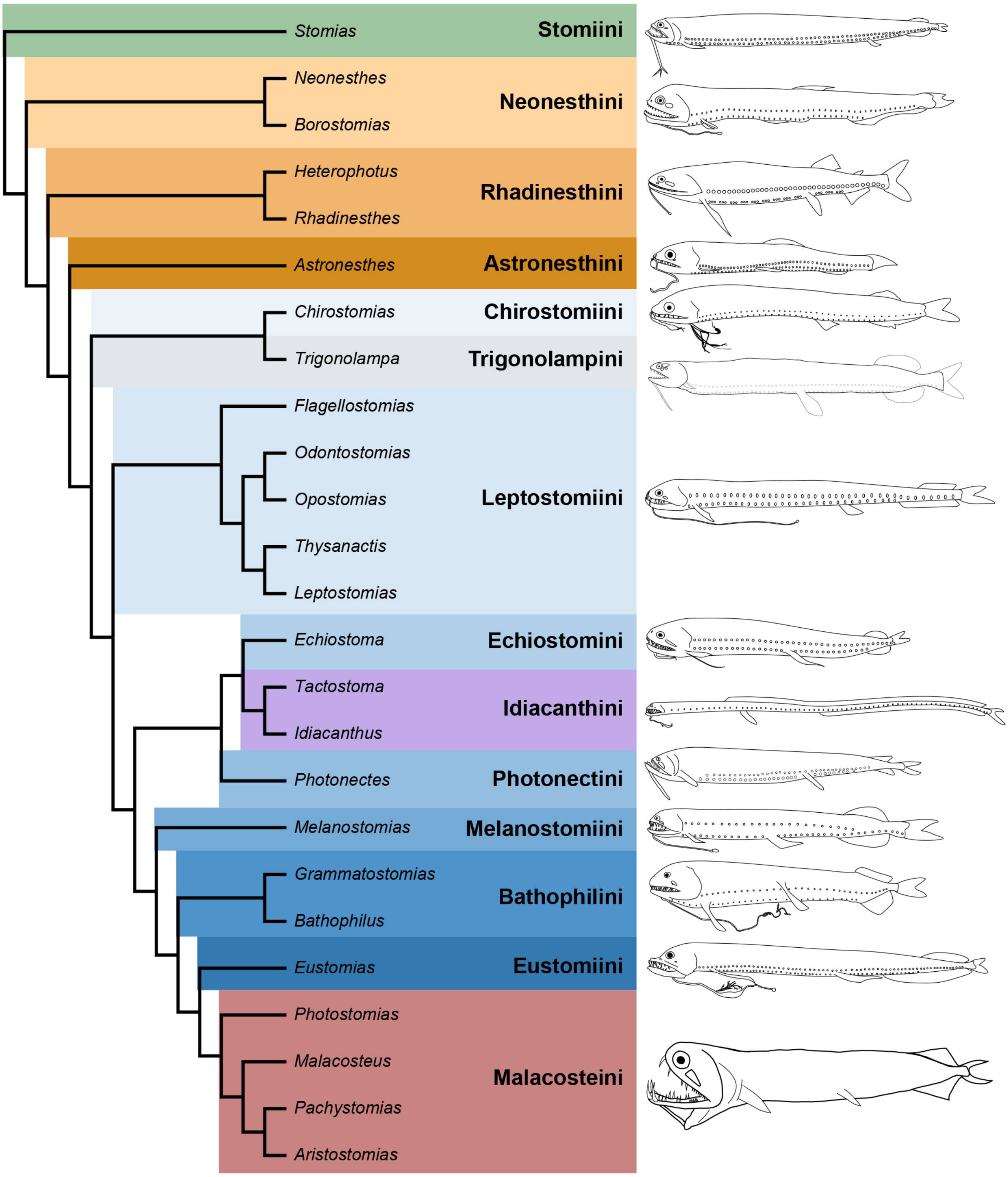

FIGURE 8. Phylogenetic tree highlighting the revised classification of the Stomiinae based on the taxonomic accounts provided herein and the results of the total-evidence hypothesis of evolutionary relationships.

Taxonomic Accounts

Subfamily Chauliodontinae Bonaparte, 1845

Type genus.—*Chauliodus* Bloch and Schneider, 1801
Genera included.—*Chauliodus*

Diagnosis. The Chauliodontinae is diagnosed by the following unambiguous synapomorphies: there is a ligament between the subopercle and the posterior borders of both the interhyal and the posterior ceratohyal along the joint between the two bones (Character 66, State 1), hypobranchial 2 is less than half the length of hypobranchial 1 (Character 135, State 1), the dorsal fin lies well anterior to the midbody (Character 217, State 1), the distal cartilages of all the dorsal-fin proximal pterygiophores are fused together. (Character 224, State 1), and the posttemporal is a thin disc of bone lying just anterior to the dorsal tip of the supracleithrum (Character 232, State 1).

Subfamily Stomiinae Bleeker, 1859

Type genus.—*Stomias* Cuvier, 1816
Genera included.—*Aristostomias*, *Astronesthes*, *Bathophilus*, *Borostomias*, *Chirostomias*, *Echiostoma*, *Eupogonesthes*, *Eustomias*, *Flagellostomias*, *Grammatostomias*, *Heterophotus*, *Idiacanthus*, *Leptostomias*, *Malacosteus*, *Melanostomias*, *Neonesthes*, *Odontostomias*, *Opostomias*, *Pachystomias*, *Photonectes*, *Photostomias*, *Rhadinesthes*, *Stomias*, *Tactostoma*, *Thysanactis*, and *Trigonolampa*

Diagnosis. The Stomiinae is diagnosed by a combination of the following characters: presence of a mental bioluminescent chin barbel (Character 320, state 1; lost in *Malacosteus* and *Photostomias*), possession of the *rector communis* muscle extending anteriorly to attach at least as far forward as the anterior of the second hypobranchial (Character 180, state 1; lost in *Astronesthes*), and the presence of more than three pelvic-fin radials (Character 293, state 1; lost in *Aristomias*, *Bathophilus*, *Flagellostomias*, and *Photostomias*).

Tribe Stomiini Bleeker, 1859

Type genus.—*Stomias* Cuvier, 1816
Genus included.—*Stomias*

Diagnosis. The Stomiini is diagnosed by the following unambiguous synapomorphies: the maxillae closely approach each other at the midline, anterior to the ethmoid region (Character 38, state 1), the interhyal is posteroventrally elongate and has a large ventral cartilaginous tip (Character 72, state 1), the posterior ceratohyal has a dorsally directed bony process which serves as the attachment site for the ceratohyal-retroarticular ligament (Character 101, state 1), the cartilage-tipped posterior ramus of the posterior ceratohyal is elongate and in many species is equal in length to the main body of the bone (Character 102, state 1), the A_2 portion of the *adductor mandibulae* has its origin on the sphenotic spine anteriorly and is joined along its anterodorsal border by a raphe to the *levator arcus palatini*. (Character 190, state 1), the anterior supraneural is proximally greatly expanded in an anteroposterior plane. (Character 197, state 1), Baudelot's ligament (Ligament 2) is looped just proximal to its attachment on the supracleithrum and the sheath-like supracleithrum—cleithrum ligament (Ligament 3) passes through the loop. (Character 282, state 1), possession of 4 or 5 pelvic-fin rays (Character 306, state 1).

Tribe Neonesthini Fowler, 1934

Type genus.—*Neonesthes* Regan and Trewavas, 1929
Genera included.—*Borostomias* and *Neonesthes*

Diagnosis. The Neonesthini is diagnosed by a unique combination of characters: absence of regularly and closely set teeth posteriorly on the ventral border of the maxilla which are about equal in length, or which become sequentially enlarged posteriorly (Character 39, State 0; also lost in the Rhadinesthini), absence of a blood vessel which passes through the hypohyal element that penetrates the lateral face of the element in the ventral hypohyal (Character 87, State 0; also lost in the Astronesthini), absence of a ligament between the basihyal and the hypohyal that attaches on the anterior half of the hypohyal element (Character 90, State 0; also lost in the Astronesthini), and presence of fusion between the distal cartilages of over half of the proximal pterygiophores of the dorsal fin (Character 223, State 1; also in the Chauliodontinae and Rhadinesthini).

Tribe Astronesthini Günther, 1864

Type genus.—*Astronesthes* Richardson, 1845
Genera included.—*Astronesthes* and *Eupogonesthes*

Diagnosis. The Astronesthini is diagnosed by the following unambiguous synapomorphies: the blood vessel which passes through the hypohyal element exits the dorsal hypohyal on the lateral face of the bone, then reenters the lateral face in the ventral hypohyal (Character 88, State 1), and the prezygapophyses of some of the anterior 10–20 neural arches are enlarged, closely approximate each other dorsally, and extend anteriorly over the neural tube as a bony hood (Character 199, State 1). It is important to note that Fink (1985) and our analysis did not formally include *Eupogonesthes* as it was described subsequently by Parin and Borodulina (1993) and compared to and placed sister to *Astronesthes* by Parin and Borodulina (2003) in an independent analysis of these two genera. Similarities noted by Parin and Borodulina (1993, 2003) that unite these two genera include a compact body, enlarged eyes, a vertical descending branch of the suspensorium, and large photophores.

Tribe Rhadinesthini DeArmon, Smith, and Davis, new tribe

ZooBank: LSID urn:lsid:zoobank.org:act:C252183E-DD1E-44A4-B0D6-9ADA2F94AC62

Type genus.—*Rhadinesthes* Regan and Trewavas, 1929
Genera included.—*Heterophotus* and *Rhadinesthes*

Diagnosis. The Rhadinesthini is diagnosed by the following unambiguous synapomorphies: the preopercle is very narrow at the symplectic-hyomandibular joint, so that the joint between the interhyal and the suspensorium is visible from lateral view (Character 57, State 1), and the dorsal tip of the cleithrum is an elongated, slender spine (Character 235, State 1).

Tribe Chirostomiini DeArmon, Smith, and Davis, new tribe

ZooBank: LSID urn:lsid:zoobank.org:act:79DBFA56-83C0-478E-B6D7-0EA2BF7A100D

Type genus.—*Chirostomias* Regan and Trewavas, 1930
Genus included.—*Chirostomias*

Diagnosis. The Chirostomiini is diagnosed by the following unambiguous synapomorphies: the urohyal anteriorly has a pair of ventral processes longer than the anterior margin of the basihyal element (Character 83, State 1), the anterior tips of the first and second hypobranchials are bifurcated, articulating dorsally and ventrally with the basibranchial cartilage (Character 134, State 1), the cleithrum is bifurcated anteroventrally, with the primary axis of the girdle curving medially and terminating in a long, tapering posteroventral ramus, and a ventrally oriented lateral wing extends posteriorly from the lateral ramus (Character 238, State 1), the coracoid is a more or less disc-shaped ossification lying ventral to the mesocoracoid and articulating fully with the ventral termination of that bone (Character 251, State 1).

Tribe Trigonolampini DeArmon, Smith, and Davis, new tribe

ZooBank: LSID urn:lsid:zoobank.org:act:24887D9C-18E0-48EF-995B-7E4D628075C7

Type genus.—*Trigonolampa* Regan and Trewavas, 1930
Genus included.—*Trigonolampa*

Diagnosis. The Trigonolampini is diagnosed by the following unambiguous synapomorphies: the third hypobranchials are fused to the third basibranchial (Character 136, State 1), the portion of the *adductor mandibulae* inserting on the PO photophore forms the posterior muscular border of the orbit and has its origin on the sphenotic and pterotic bones (Character 188, State 1), there is a large, multipartite superficial light organ behind the eye, extending posteriorly almost to the far edge of the operculum (Character 315, State 1).

Tribe Leptostomiini DeArmon, Smith, and Davis, new tribe

ZooBank: LSID urn:lsid:zoobank.org:act:583C390C-A8C0-40F6-97CC-BB47AA282570

Type genus.—*Leptostomias* Gilbert, 1905
Genera included.—*Flagellostomias*, *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis*

Diagnosis. The Leptostomiini is diagnosed by the following unambiguous synapomorphies: the ventrolateral process of the lateral ethmoid is anteriorly elongate and the ventral border is approximately one fifth of the length of the ventral border of neurocranium (Character 10, State 1), the second large tooth from the symphysis of the dentary projects into the mouth at about a 60 degree angle (Character 44, State 1), the opercular process of the hyomandibula is elongate and projects well posterior to the body of the hyomandibula, as does the dorsal ramus of the preopercle, leaving a large triangular space dorsally between the two bones (Character 56, State 1), the interopercle has a characteristic shape, with a distinct triangular anterior process and an elongate slender posterodorsal process, the front border of which is aligned with the front border of the ventral portion of the bone (Character 59, State 1), and the flanges for muscle attachment on the dorsal halves of the more lateral fin rays form slender, pointed processes which project from near the proximal termination of the ray (Character 274, State 1).

Tribe Echiostomini DeArmon, Smith, and Davis, new tribe

ZooBank: LSID urn:lsid:zoobank.org:act:2F381116-C7A9-4917-98D0-F7B1EC9D30C7

Type genus.—*Echiostoma* Lowe, 1843
Genus included.—*Echiostoma*

Diagnosis. The Echiostomini is diagnosed by the following unambiguous synapomorphies: the rugosities on the frontal sensory canals are large and pointed, and there are similar rugosities present on the ridges of the antorbital (Character 26, State 1), and the preopercle has spinous lateral extensions ventrally, and the supramaxilla and antorbital are spinous or rugose (Character 58, State 1).

Tribe Idiacanthini Gill, 1893

Type genus.—*Idiacanthus* Peters, 1877
Genera included.—*Idiacanthus* and *Tactostoma*

Diagnosis. The Idiacanthini is diagnosed by the following unambiguous synapomorphies: the ventral border of the palatine arch is dorsally arched from lateral view (Character 49, State 1), the basihyal is reduced to a thin, cylindrical element no broader distally than proximally and there is no ligament between its distal tip and the hypohyal element (Character 77, State 1), the dorsal portion of the *geniohyoideus* has both a tendinous and muscular insertion on the dentary (Character 170, State 1), and the dorsal section of the medial division of the *adductor mandibulae* has its origin anterior or anteromedial to the insertion of the *levator arcus palatini* (Character 189, State 1).

Tribe Photonectini Jordan and Evermann, 1896

Type genus.—*Photonectes* Günther, 1887
Genus included.—*Photonectes*

Diagnosis. The Photonectini is diagnosed by the following unambiguous synapomorphies: the process of the anguloarticular posterior to the articulation with the quadrate is elongate, almost equal to the length of the anterodorsal border of the quadrate (Character 46, State 1), the anterodorsal section of the hypohyal element is elongate and the corner forms a highly acute angle (Character 100, State 1), and there is dense fibrocartilage lying between the anteromedial tip of the coracoscapular plate and the cleithrum (Character 244, State 1).

Tribe Melanostomiini Parr, 1927

Type genus.—*Melanostomias* Brauer, 1902
Genus included.—*Melanostomias*

Diagnosis. The Melanostomiini is diagnosed by a unique combination of characters: presence of a small and conical bone in a pocket on the ventrolateral surface of the ethmoid cartilage (Character 9, State 1; also present in *Echiostoma*), the distal cartilage tips of the lateral ethmoid and the supraethmoid are fused together, leaving a rounded opening medial to the lateral margin of the ethmoid cartilage (Character 11, State 1; also present in the Leptostomiini), there is an elongate groove in the lateral ethmoid and pterosphenoid bones associated with the exit of the supraorbital nerve trunk from the orbital region (Character 14, State 1; also present in *Echiostoma*), the posterior process of the pterotic is robust and projects posterodorsally (Character 24, State 1; also present in *Echiostoma*), rugosities are present on the dorsal ridges of the frontal sensory canals (Character 25, State 1; also present in *Echiostoma* and *Trigonolampa*), the fourth basibranchial is approximately square from dorsal aspect (Character 129, State 1; also present in *Echiostoma*), the first and second hypobranchials have a rounded anterior tip (Character 133, State 1; also present in *Eustomias*, *Idiacanthus*, and *Malacosteus*), the *levator externus* of the third epibranchial is absent (Character 176, State 1; also present in *Echiostoma* and *Leptostomias*), the extrascapular borders are rugose or spiny (Character 230, State 1; also present in *Echiostoma* and *Trigonolampa*), the supracleithrum-cleithrum ligament (Ligament 3) is proximally adherent to almost the entire anteromedial surface of the supracleithrum (Character 281, State 1; also present in *Echiostoma*).

Tribe Bathophilini Fowler, 1936

Type genus.—*Bathophilus* Giglioli, 1882
Genera included.—*Bathophilus* and *Grammatostomias*

Diagnosis. The Bathophilini is diagnosed by the following unambiguous synapomorphies: the anterior part of the ethmoid, in the region of the supraethmoid and vomer, particularly the anteromedian ethmoid process, is produced ventrally with the anteromedian ethmoid process having a narrow concavity from dorsal view (Character 8, State 1), the hypohyal element is deepest (dorsoventrally) posterior to the mid-length of the element (Character 97, State 1), there are three branchiostegal rays articulating with the posterior ceratohyal ossification (Character 164, State 1), and the lateral wing of the cleithrum is laterally extended, somewhat thickened, and enlarged relative to the main body of the cleithrum anterior to the main curvature; the anterior termination of the main axis is somewhat to greatly foreshortened (Character 236, State 1).

Tribe Eustomiini Fowler, 1925

Type genus.—*Eustomias* Vaillant, 1884
Genus included.—*Eustomias*

Diagnosis. The Eustomiini is diagnosed by the following unambiguous synapomorphies: the ectopterygoid and palatine are largely separate from the quadrate, metapterygoid, and other bones of the jaw suspensory apparatus, the only attachment being by a thick ligament between the posterior tip of the ectopterygoid and the ventral, articular process of the quadrate. The ectopterygoid and palatine instead form a unit which is bound along the anterior three-fourths of its length to the posterior face of the maxilla. In addition, the anterior head of the palatine is large, with both the bony and cartilage portions projecting well dorsal to the margin of the maxilla (Character 52, State 1), the interopercle has an elongate dorsal ramus, along which runs the interopercle-opercle ligament; in many species there is also a ventral ramus associated with the interoperculo-mandibular ligament (Character 60, State 1), the notochord is greatly curved and there is a reduction of vertebral centra and hypertrophy of the neural arches (Character 192, State 1), the medial pterygiophore cartilage of the dorsal and anal fins is separate from that of the proximal pterygiophore, and is fused instead to that of the distal pterygiophore, and there is only one ossification on the resulting compound element (Character 221, State 1), the supracleithrum is absent (Character 234, State 1), and the coracoscapular plates are fused to each other anteriorly (Character 243, State 1).

Tribe Malacosteini Gill, 1890

Type genus.—*Malacosteus* Ayres, 1848
Genera included.—*Aristomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*

Diagnosis. The Malacosteini is diagnosed by the following unambiguous synapomorphies: the parasphenoid terminates posteriorly well anterior to the posteroventral margin of the basioccipital (Character 18, State 1), the sphenotic spine extends posterior to the mid-length of the prootic and the anterior margin of the facet for the hyomandibula (Character 22, State 1), the cartilage of the posterior process of the exoccipital projects anterodorsal to the posterodorsal bony border of the process (Character 30, State 1), the cartilage of the palatine arch is interrupted between the posterior margin of the palatine and the rest of the suspensorium, and the palatine itself terminates posteriorly in a bony point (Character 47, State 1), the anterodorsal region of the hypohyal element projects anterolaterally (Character 98, State 1), and the suborbital photophore is ventral or posteroventral to the eye (Character 310, State 1).

Discussion

This study is the first to use genome-scale data (ultraconserved elements) to broadly investigate the evolutionary relationships of the barbeled dragonfishes (Stomiinae). Our total-evidence approach has produced a comprehensive phylogeny of the barbeled dragonfishes that was critical for the development of the classification presented herein that reflects their evolutionary history and diverse ecology and anatomy. Herein we propose splitting the taxa composing the subfamily Stomiinae *sensu* Smith *et al.* (2024) into two subfamilies, the Chauliodontinae (viperfishes) and the Stomiinae (barbeled dragonfishes), which are sister groups to each other with the barbeled dragonfishes (Stomiinae) representing a species rich lineage of Stomiidae (dragonfishes) *sensu* Smith *et al.* (2024).

Within the Stomiidae, previous studies have not agreed on the phylogenetic position of *Chauliodus* (viperfishes) with a sister-group relationship to *Ichthyococcus* (lightfish) proposed in some DNA-based studies (e.g., Kenaley *et al.* 2014; Rabosky *et al.* 2018) and a sister-group relationship to *Stomias* (scaly dragonfishes) proposed with morphological data (Weitzman 1974; Fink 1985) as seen in Figures 4 and 5. Smith *et al.* (2024) investigated the relationships of the stomiiforms with the goals a monophyletic family-level classification for the order and resolution of the limits and relationships of the Gonostomatidae and the previously recognized Diplophidae and Phosichthyidae. In that study, they inferred that *Chauliodus* was sister to a clade including all five included representatives of our revised Stomiinae. We identified the same phylogenetic position for our Chauliodontinae here and greatly expanded the taxonomic sampling within the Stomiinae (Figures 6 and 7) in all analyses (UCE, all molecular, total-evidence). Overall, the Chauliodontinae includes the nine species of viperfishes (*Chauliodus*) that have fascinating dentition where their anterior dentary teeth extend above their upper jaw (Tchernavin 1953). Along with their fanged teeth, members of *Chauliodus* possess an elongated dorsal fin ray that is bioluminescent and hypothesized to attract prey (Clarke 1982; Gartner *et al.* 1997; Butler *et al.* 2001; Greven *et al.* 2009). Most species of *Chauliodus* do not have a mental bioluminescent chin barbel, but *Chauliodus minimus* has a small bulbous chin barbel and lacks the more typical elongate dorsal-fin ray (Parin and Novikova 1974).

The revised barbeled dragonfishes (Stomiinae) have been inferred to be monophyletic in most prior phylogenetic studies (Figures 4 and 5) that included several representatives, however, there have been some exceptions. Mirande (2017) recognized the Stomiinae as polyphyletic with some of its genera also inferred to be para- or polyphyletic (e.g., *Melanostomias* and *Stomias*; Figure 5C). In this study, we inferred the barbeled dragonfishes as monophyletic, with the Stomiini (*Stomias*) as the stem lineage, which is consistent with hypotheses using molecular data by Davis *et al.* (2014) and Kenaley *et al.* (2014). We included five species of *Stomias* in the molecular-only and the total-evidence analysis (Figure 7), with the monophyly of *Stomias* strongly supported. Prior morphological hypotheses (e.g., Weitzman 1974; Fink 1985; Harold and Weitzman 1996) often inferred a clade composed of *Chauliodus* and *Stomias* (Figure 4) with both genera having species with distinct hexagonal patterns on their scaled bodies (Morrow

1964; Gibbs 1969). Molecular studies such as Betancur-R. *et al.* (2013) found *Stomias* nested in a clade of rhadinesthin taxa (Figure 4D), with Mirande (2017) and Rabosky *et al.* (2018) inferring that *Stomias* was polyphyletic. We find that the monophyly of the Stomiini (scaly dragonfishes) was highly supported (Figure 7) and the tribe is diagnosed by eight unambiguous morphological synapomorphies presented herein.

While the stem stomiine lineage, Stomiini, has well defined hexagonal scales, as do species in *Chauliodus* (Schnell and Johnson 2012), all other stomiine species the remaining 13 stomiine tribes are scaleless (Supplemental Table 2). In phylogenetic sequence, the next three smallest early diverging stomiine tribes included taxa that were previously recognized in the Astronesthidae *sensu* Weitzman (1974), including the Astronesthini, Neonesthini, and Rhadinesthini. The Neonesthini consists of two genera, *Borostomias* and *Neonesthes*, with these genera inferred as a clade in all analyses (Figure 6 and 7). A sister-group relationship between these taxa has also been previously recovered by Betancur-R. *et al.* (2013). Mirande (2017) and Rabosky *et al.* (2018) inferred a polyphyletic *Borostomias*; however, the monophyly of that genus was strongly supported in our study (Figure 7). Fink (1985) resolved *Neonesthes* as the sister taxon to all other stomiids, and, in our study, the Neonesthini is the stem lineage of scaleless dragonfishes.

The remaining taxa from the Astronesthidae *sensu* Weitzman (1974) include the Rhadinesthini, which consists of *Heterophotus* and *Rhadinesthes*, and the Astronesthini which includes *Astronesthes* and *Eupogonesthes*. A clade composed of the rhadinesthin taxa has previously been hypothesized with morphological (Fink 1985) and molecular data (Kenaley *et al.* 2013). First described by Regan and Trewavas (1930) from the Danish Dana Expedition, both *Heterophotus* and *Rhadinesthes* are monotypic genera that lack fangs and ceratohyal teeth (Gibbs 1964a). The Astronesthini includes the genus *Astronesthes* with 49 species of snaggletooth dragonfishes and the monotypic *Eupogonesthes*. Parin and Borodulina (1993, 2003) hypothesized a close relationship between *Astronesthes* and *Eupogonesthes* based on morphological features. Rabosky *et al.* (2018) recovered a polyphyletic *Astronesthes*, but in our molecular-only and total-evidence analyses, the Astronesthini (represented by seven species of *Astronesthes*) was strongly supported as monophyletic (Figure 7). Evidence of sexual dimorphism has been recorded in a few species of *Astronesthes* associated with differences in chin barbel size as well as the size of postorbital photophores (Gibbs 1969; Goodyear and Gibbs 1969; Herring 2007).

Our phylogenetic analyses inferred a polyphyletic Melanostomiidae *sensu* Weitzman (1974) and we recognize the taxa associated with this assemblage in eight tribes including the Bathophilini, Chirostomiini, Eustomiini, Leptostomiini, Melanostomiini, Opostomiini, Photonectini, and Trigonolampini. These tribes will be discussed in order of phylogenetic sequence among this nearly grade-like assemblage leading toward the Malacosteini. The total-evidence analysis inferred a sister-group relationship between the monotypic tribes Chirostomiini (*Chirostomias*) and Trigonolampini (*Trigonolampa*) with moderate bootstrap support (75, Figure 7). Fink (1985), with morphological data alone, also recovered a sister-group relationship between *Chirostomias* and *Trigonolampa*. In contrast, the UCE data combined with the other protein-coding gene fragments recovered these two tribes as a grade (not shown) similar to the molecular data studies of Kenaley *et al.* (2013, Figure 4C) and Rabosky *et al.* (2018, Figure 5A). First described by Regan and Trewavas (1930) from the Danish Dana Exploration, these two monotypic genera have unique anatomical structures including the possession of a tripartite orbital light organ in *Trigonolampa* (Morrow and Gibbs 1964) that is not observed in any other barbeled dragonfish.

In this study, we infer the Leptostomiini as a clade across all analyses (UCE, all molecular data, total-evidence), with the total-evidence analysis indicating this tribe includes *Flagellostomias*, *Leptostomias*, *Odontostomias*, *Opostomias*, and *Thysanactis* while the molecular analyses had fewer genera, but always recovered the included taxa as a clade (Figures 6–8). This clade was also recovered by Fink (1985) with morphological data (Figure 4B) and the same taxonomic composition. Kenaley *et al.* (2014) resolved *Flagellostomias* sister to *Leptostomias*, while *Odontostomias*, *Opostomias*, and *Thysanactis* were not included in their study (Figure 4C). This clade was also recovered in the DNA-based study of Rabosky *et al.* (2018) and the total-evidence study of Mirande (2017), as seen in Figure 5.

The Idiacanthini (black dragonfishes) includes *Idiacanthus* and *Tactostoma* which were inferred to be sister groups in all analyses (Figures 6 and 7). A close relationship between these genera has been hypothesized before, with this clade being resolved with morphological work (Fink 1985) and total-evidence approaches (Mirande 2017). There is evidence of significant sexual dimorphism in *Idiacanthus*, with males completely lacking a chin barbel and teeth (Gibbs 1964b) and females possessing a bioluminescent barbel that has a leaf-like tip appendage that is unique to this genus within the Stomiinae (Marshall 1954; Nafpaktitis *et al.* 1977; Herring 2007). In all analyses

(Figures 6–8), the Idiacanthini was inferred to be the sister group to the monotypic Echiostomini, with *Echiostoma barbatum* known to possess a yellow lens in its eyes that is hypothesized to be used for hunting pelagic organisms that exhibit bioluminescent camouflage for countershading (Muntz 1976; Somiya 1978). The clade comprising the Idiacanthini and the Echiostomini was found to be the sister group to the Photonectini (*Photonectes*) in all analyses (Figures 6–8). A clade including taxa from the Echiostomini, Idiacanthini, and Photonectini has previously been inferred in molecular (Kenaley *et al.* 2014, Figure 4C; Rabosky *et al.* 2018, Figure 5A) and total-evidence studies (Mirande 2017, Figure 5C), but with different relationships among the genera in these tribes than recovered in our study (Figures 6–8).

The Melanostomiini is restricted to only two species of *Melanostomias* in our analyses and consistently resolved as monophyletic (all molecular, total-evidence) with strong bootstrap values (Figure 7). Some species of *Melanostomias* have sexual dimorphism with females possessing a filamentous structure on the bioluminescent barbel whereas this structure is absent in males (Herring, 2007). The Melanostomiini was inferred to be the sister group to a clade including the Borostomiini, Eustomiini, and Malacosteini in all analyses in our study. This phylogenetic placement within the Stomiinae is similar to the molecular study of Kenaley *et al.* (2014), but broadly incongruent with all other prior works (Figures 4–5), with Fink (1985) hypothesizing a sister-group relationship between the Echiostomini and the Melanostomiini based on morphological data. Mirande (2017) hypothesized that *Melanostomias* was polyphyletic in his total-evidence analysis.

The Bathophilini (*Bathophilus* and *Grammatostomias*) was inferred to be monophyletic in our study across all analyses with strong bootstrap support (Figures 6–8) and is consistently inferred as the sister group to the Eustomiini + Malacosteini. *Bathophilus* has a unique body form among dragonfishes, with a generally shorter body relative to the elongated bodies of most taxa in the Stomiinae (Barnett and Gibbs 1968). Species in *Grammatostomias* possess a chin barbel that can reach up to six times as long as the standard length of the fish (Morrow and Gibbs 1964). The recognition of a Bathophilini is congruent with many prior hypotheses that have identified a sister-group relationship between *Bathophilus* and *Grammatostomias* (Figures 4–5).

The most species-rich tribe of stomiine fishes is the Eustomiini (*Eustomias*) with over 100 diagnosed species (Fricke *et al.* 2025). *Eustomias* has incredible variation in its bioluminescent barbels with complex branching structures that often include bulblets (DeArmon 2019). In addition to strikingly variable bioluminescent structures, species in the Eustomiini have evolved modifications that allow a more protrusible upper jaw that is hypothesized to impact their ability to feed on larger prey (Morrow and Gibbs 1964; Gibbs *et al.* 1983). Across all of our analyses, we inferred that the Eustomiini is sister to the Malacosteini (loosejaw dragonfishes) with strong bootstrap support (Figures 6–8), and we infer the monophyly of *Eustomias* across analyses (molecular-only, total-evidence). Prior studies based on morphological data (Fink 1985) have resolved *Eustomias* as the sister group to the Bathophilini. The molecular study of Kenaley *et al.* (2014) hypothesized that *Eustomias* was nested within the loosejaw dragonfishes (*Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*) as seen in Figure 4C. Similarly, Betancur-R. *et al.* (2013) also hypothesized that *Eustomias* was nested within a clade that included a non-monophyletic Malacosteini (Figure 4D).

The loosejaw dragonfishes, Malacosteini (*Aristostomias*, *Malacosteus*, *Pachystomias*, and *Photostomias*), are distinct in having no skin between the mandibles of their lower jaws, with the exception of *Pachystomias* (Kenaley 2012). In all analyses, we find strong support for the monophyly of the Malacosteini (Figures 6–8), which has been questioned in earlier molecular studies (Betancur-R. *et al.* 2013, Figure 4D; Kenaley *et al.* 2014, Figure 4C). We support the findings of Fink (1985) and Davis *et al.* (2014) in recognizing a monophyletic loosejaw dragonfishes assemblage. While a close relationship among the taxa with no skin of the floor of the lower jaw (*Aristostomias*, *Malacosteus*, and *Photostomias*) was hypothesized historically by many studies (e.g., Morrow 1964c), *Pachystomias* was more recently aligned with the group through the phylogenetic work of Fink (1985) and studies investigating the mechanisms of the suborbital photophores that emit red fluorescence as observed in other loosejaw dragonfishes (Herring and Cope 2005). Few deep-sea fishes possess light organs that produce red-light through a combination of bioluminescence (blue emission and excitation) and biofluorescence (red re-emission), and the light-organ structures that ultimately emit red light in the loosejaw dragonfishes are hypothesized to enhance hunting for prey items in the deep sea, as most biodiversity in these environments across the tree-of-life cannot visualize red wavelengths (Denton *et al.* 1970, 1985; Widder *et al.* 1984; Partridge and Douglas 1995; Douglas *et al.* 2000).

As mentioned in the materials and methods section, there is a tenuously named species that may be allied with that Stomiinae that was not included in this study and has never been verified to exist—*Bathysphaera intacta*

(Beebe 1932). This species was described based on an observation by Beebe (1932) from a dive in the bathysphere off Nonsuch Island in Bermuda. Beebe's visual accounts of this species described it as being over six feet long with a bioluminescent chin barbel and an additional bioluminescent elongated structure near the tail (Beebe 1934). An illustration of *Bathysphaera intacta* based on Beebe's visual account appears in Beebe (1934: figure 101). While intriguing, there have been no direct observations or collections of this taxon since, and the status of this genus is considered unverified (Fricke *et al.* 2025). Currently, we do not include this genus in our classification of the Stomiinae or Stomiidae.

In this study, we provide the first genome-scale phylogeny of the barbeled dragonfishes with robust taxonomic sampling to uncover relationships among taxa previously classified in the Stomiidae *sensu* Fink (1985). Using this new framework of evolutionary relationships, we provide a revised classification of the barbeled dragonfishes, recognizing two monophyletic subfamilies Chauliodontinae and Stomiinae (14 tribes) that are all monophyletic or monotypic tribes with distinct diagnoses presented in the taxonomic accounts. This work is a step toward a stable Linnaean classification of dragonfishes, which has eluded ichthyologists for decades. Weitzman (1974), Fink (1985), Harold and Weitzman (1996), and Smith *et al.* (2024) have all been instrumental in our efforts toward a stable and evidence-based classification of the stomiiforms. With this work, only the Sternoptychidae, which is clearly monophyletic at the family level, needs additional phylogenetic work for its higher-level classification (May 2019). This work also provides an evolutionary framework for future studies on barbeled dragonfishes, which constitute one of the largest lineages of pelagic fishes distributed across the world's oceans.

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

Supplemental_Table_1_Dragonfish_Genbank

Supplemental_Table_2_Morphological_Data