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Light in the darkness: New perspective on lanternfish relationships and classification using genomic and morphological data

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ABSTRACT

Massive parallel sequencing allows scientists to gather DNA sequences composed of millions of base pairs that can be combined into large datasets and analyzed to infer organismal relationships at a genome-wide scale in non-model organisms. Although the use of these large datasets is becoming more widespread, little to no work has been done in estimating phylogenetic relationships using UCEs in deep-sea fishes. Among deep-sea animals, the 257 species of lanternfishes (Myctophiformes) are among the most important open-ocean lineages, representing half of all mesopelagic vertebrate biomass. With this relative abundance, they are key members of the midwater food web where they feed on smaller invertebrates and fishes in addition to being a primary prey item for other open-ocean animals. Understanding the evolution and relationships of midwater organisms generally, and this dominant group of fishes in particular, is necessary for understanding and preserving the underexplored deep-sea ecosystem. Despite substantial congruence in the evolutionary relationships among deep-sea lanternfishes at higher classification levels in previous studies, the relationships among tribes, genera, and species within Myctophidae often conflict across phylogenetic studies or lack resolution and support. Herein we provide the first genome-scale phylogenetic analysis of lanternfishes, and we integrate these data from across the nuclear genome with additional protein-coding gene sequences and morphological data to further test evolutionary relationships among lanternfishes. Our phylogenetic hypotheses of relationships among lanternfishes are entirely congruent across a diversity of analyses that vary in methods, taxonomic sampling, and data analyzed. Within the Myctophiformes, the Neoscopelidae is inferred to be monophyletic and sister to a monophyletic Myctophidae. The current classification of lanternfishes is incongruent with our phylogenetic tree, so we recommend revisions that retain much of the traditional tribal structure and recognize five subfamilies instead of the traditional two subfamilies. The revised monophyletic taxonomy of myctophids includes the elevation of three former lampanyctine tribes to subfamilies. A restricted Lampanyctinae was recovered sister to Notolychninae. These two clades together were recovered as the sister group to the Gymnoscopelinae. Combined, these three subfamilies were recovered as the sister group to a clade composed of a monophyletic Diaphinae sister to the traditional Myctophinae. Our results corroborate recent multilocus molecular studies that infer a polyphyletic *Myctophum* in Myctophinae, and a para- or polyphyletic *Lampanyctus* and *Nannobrachium* within Lampanyctinae. We resurrect *Dasyscopelus* and *Ctenoscopelus* for the independent clades traditionally classified as species of *Myctophum*, and we place *Nannobrachium* into the synonymy of *Lampanyctus*.

1. Introduction

1.1. Lanternfish background

The lanternfishes (Myctophidae) and blackchins (Neoscopelidae) are the two families that reside within the Myctophiformes. They are found in all oceans and are best known for their bioluminescent photophores and light organs that are distributed in various positions along the sides of their bodies (Beebe, 1934; Haygood et al., 1994). Davis et al. (2014) demonstrated that these lateral photophores in myctophid lanternfishes are species specific and potentially involved in species recognition, supporting previous assertions (reviewed in Paxton, 1972). Among myctophid light organs, we see extensive sexually dimorphic variation in the presence and/or size of specialized light organs at the base of the tail and anterior end of the head (Herring, 2007). Bioluminescent animals such as myctophids that possess sexually dimorphic

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light-organ systems are thought to undergo sexual selection and experience increased rates of diversification (Davis et al., 2014, 2016; Ellis and Oakley, 2016). The increased diversity of lanternfishes may have been similarly aided by selective pressures on their bioluminescent systems (Davis et al., 2014; Alfaro, 2016).

Lanternfishes have been studied extensively by evolutionary biologists. They have typically been allied with the lizardfishes (Aulopiformes) and a few other fish groups in the Myctophoidei, Myctophiformes (*sensu lato*), Scopeliformes, or Iniomi (Gosline et al., 1966; Greenwood et al., 1966). Subsequent work by Rosen (1973) separated the Aulopiformes from the Myctophiformes and placed the myctophiforms sister to the Acanthomorpha (spiny-rayed fishes) in the Ctenosquamata. Rosen recognized ten features ranging from reductions in pharyngeal elements to the presence of ctenoid scales that lanternfishes share with members of the Acanthomorpha to the exclusion of the Aulopiformes and other lower euteleostean groups. Comprehensive phylogenetic studies on the evolutionary relationships of ray-finned fishes using molecular-sequence data have consistently supported Rosen's (1973) hypotheses regarding the sister-group relationship between myctophiforms and acanthomorphs and the monophyly of the lanternfishes (e.g., Davis, 2010; Near et al., 2012; Betancur-R. et al., 2013; Davis et al., 2016; Smith et al., 2016).

The two families within the Myctophiformes (Fig. 1) are the Neoscopelidae (blackchins) and Myctophidae (lanternfishes). The Neoscopelidae include six species in three genera, and the Myctophidae include 251 species in 33 genera (Eschmeyer et al., 2017). Previous phylogenetic studies of lanternfishes have typically hypothesized two monophyletic subfamilies within the Myctophidae: Lampanyctinae and Myctophinae (Fig. 1). The recognition of these subfamilies was originally based on and later supported by adult and larval morphological features (Paxton, 1972; Stiassny, 1996; Yamaguchi, 2000, but see Paxton et al., 1984), supported by molecular characters (Davis et al., 2014; Denton, 2014, but see Poulsen et al., 2013), and rejected in the one study that combined molecular and morphological characters (Mirande, 2016; Fig. 1).

Within the Myctophidae, there are currently seven recognized tribes (Paxton et al., 1984; Table 1), including three in the Myctophinae (Electronini, Gonichthyini, and Myctophini) and four in the Lampanyctinae (Diaphini, Gymnoscopelini, Lampanyctini, and Notolychnini). Five of these myctophid tribes were described by Paxton (1972) in his foundational study that outlined the modern myctophiform classification (Fig. 1). He treated the previously described Electronini (Wisner, 1963) as a synonym of the Myctophini because species in the Electronini only had one character that distinguished them from species in the Myctophini: the PLO photophore (Fig. 2) being below or near the ventral margin of the pectoral-fin base rather than distinctly above the pectoral-fin base. He and co-authors later recognized the Electronini (Paxton et al., 1984), and all seven tribes have been recognized and used in subsequent lanternfish phylogenetic studies (Table 1; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000; Poulsen et al., 2013; Davis et al., 2014; Denton, 2014). Excluding the enigmatic and monotypic Notolychnini, the monophyly of Lampanyctinae and Myctophinae has been consistently recovered across myctophiform studies (Fig. 1). Notolychnini has been placed as the stem myctophid tribe (Poulsen et al., 2013), sister to the Lampanyctinae (Paxton, 1972; Stiassny, 1996; Yamaguchi, 2000), nested within the Lampanyctini (Davis et al., 2014; Denton, 2014), sister to *Lobianchia* (Mirande, 2016), or in a polytomy with the subfamilies Myctophinae and Lampanyctinae (Fig. 1; Paxton et al., 1984). While the taxonomy of the two subfamilies have remained overwhelmingly consistent in taxonomic composition (with the exception of Notolychnini), the phylogenetic relationships among the tribes and genera within each subfamily have been more fluid (Fig. 1).

Both Paxton (1972) and Paxton et al. (1984) represented the included lanternfish tribes and genera as monophyletic. Stiassny (1996) and Yamaguchi (2000) assumed generic monophyly and analyzed adult and larval morphological characters using parsimony and recovered many polytomies among genera in both the historical Myctophinae and Lampanyctinae. In molecular studies (Poulsen et al., 2013; Davis et al., 2014; Denton, 2014), the Myctophini and *Myctophum* were consistently recovered as para- or polyphyletic. In addition, Poulsen et al. (2013) and Denton (2014) found a paraphyletic *Benthosema*, and Denton (2014) recovered *Lampadena*, *Lampanyctus*, and *Nannobrachium* as para- or polyphyletic. Combining morphological and molecular data, Mirande's (2016) analysis resulted in a dramatically different hypothesis (Fig. 1) that included *Ceratoscopelus* + *Lepidophanes* as the stem myctophid clade and *Notolychnus* sister to *Lobianchia* (typically sister to *Diaphus*). Mirande's (2016) hypothesis is the only explicit analysis to recover a paraphyletic *Protomyctophum* as well as several other unique relationships. The results of his study are inconsistent and at odds with essentially all other studies with broad myctophiform sampling. Excluding Mirande (2016) most morphological and molecular analyses have supported similar clades (Fig. 1), but there is also a lack of consistency in monophyletic taxonomic groups.

1.2. Phylogenomics

Because of the conflict across previous studies, we wanted to greatly increase the character data to help resolve relationships among the myctophiforms and allies. Ultraconserved elements (UCEs) are regions of the genome that are highly conserved among evolutionarily distant taxa (Faircloth et al., 2012), and their DNA sequences have become increasingly used to resolve the phylogenetic relationships among various organismal lineages (e.g., Crawford et al., 2012; McCormack et al., 2012; Faircloth et al., 2012; Smith et al., 2013; Sun et al., 2014) including fishes (e.g., Faircloth et al., 2013; Harrington et al., 2016; Longo et al., 2017). In order to sequence UCEs, organismal DNA libraries are enriched for up to thousands of UCEs and their flanking regions. These libraries are sequenced using massive parallel sequencing, and sequence capture probe sets can recover hundreds of UCE regions (100–1500 bp each) from a specimen for use in phylogenetic analyses (Bejerano et al., 2004; Siepel et al., 2005; Wang et al., 2009; Faircloth et al., 2012). Gilbert et al. (2015) compared the phylogenetic informativeness of core and flanking regions of UCEs to multiple protein coding genes and found UCEs to have considerably higher net phylogenetic informativeness. Ultraconserved elements and their flanking regions are excellent sources of variable and cost-effective phylogenetic characters for large, genome-wide datasets.

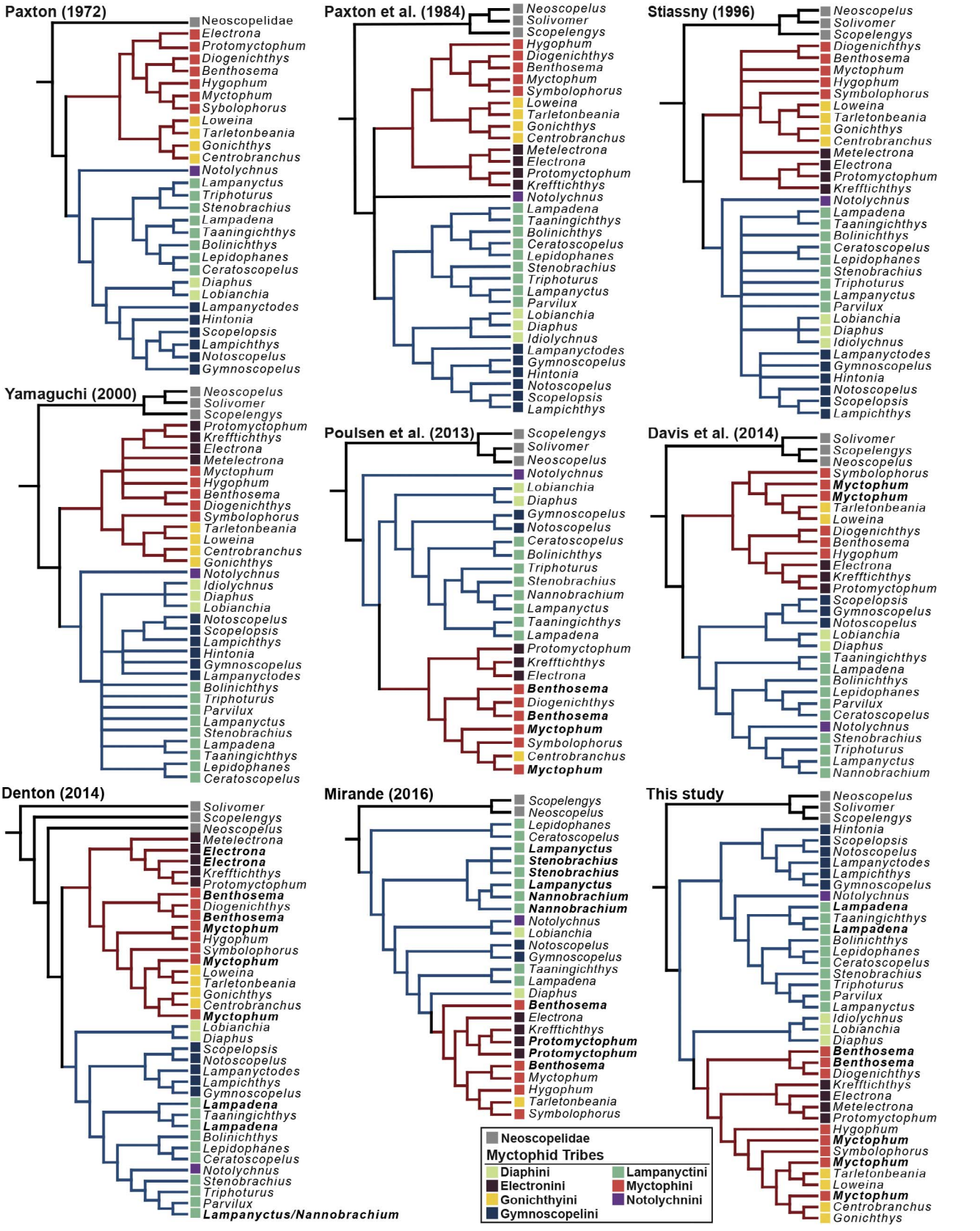
The aim of this study is to hypothesize the relationships among lanternfishes and test the monophyly of the currently recognized myctophiform families, subfamilies, tribes, and genera. We combine morphological data with sequence data from UCEs, UCE flanking regions, nuclear protein-coding genes, and mitochondrial protein-coding genes to present the most data-rich hypothesis of lanternfish evolutionary relationships to date. Our work is compared to previous hypotheses of lanternfish relationships based on morphology, mitochondrial genomes, and nuclear and mitochondrial gene fragments. We focus on addressing the following three questions: (1) What is the hypothesis of relationships among lanternfishes using genome-scale data (UCEs)? (2) What is the hypothesis of relationships among lanternfishes using an integrative approach combining morphological and molecular data (UCEs, nuclear gene fragments, the mitochondrial cytochrome oxidase I fragment)? (3) How do our genomic and integrative hypotheses compare to each other and previous hypotheses of lanternfish evolution and taxonomy?

2. Materials and methods

2.1. Taxon sampling

Taxonomic sampling for our UCE-dataset includes 32 myctophiform species representing 26 of 36 traditionally recognized genera (Eschmeyer et al., 2017) and six additional species representing closely

related euteleosts (Ateleopodiformes, Aulopiformes, and Acanthomorphs) as outgroups in order to maintain a broad taxonomic sampling of groups hypothesized to be closely related to Myctophiformes (Table 2). To assess the relationships of the Myctophiformes, we used a combination of different taxonomic and analytical strategies with either 32, 77, or 79 myctophiform species. All analyses were rooted with the



(caption on next page)

Fig. 1. Previous and current phylogenetic hypotheses of Myctophiformes. Myctophinae is represented by red lines and Lampanyctinae is represented by blue lines. Previous hypotheses include: Paxton (1972), osteology and photophores; Paxton et al. (1984), synapomorphy-based reconstruction using osteology, photophore, and larval characters; Stiassny (1996), a maximum parsimony analysis of the Paxton et al. (1984) character matrix plus four new characters; Yamaguchi (2000), a maximum parsimony reanalysis of Stiassny (1996) with polymorphic characters coded as "?"; Poulsen et al. (2013), a maximum likelihood analysis using mitogenomic gene sequences; Davis et al. (2014), a bayesian analysis using two nuclear and one mitochondrial genes; Denton (2014), a bayesian analysis using six nuclear and one mitochondrial genes; Mirande (2016), a maximum parsimony analysis using a combination of 44 nuclear, mitochondrial, and ribosomal genes and 274 morphological characters in a broad study that included 42 lanternfish taxa. Genera in bold were recovered as non-monophyletic in their respective studies. The phylogeny from this study uses maximum likelihood analyses inferred from ultraconserved elements, Sanger sequence and Illumina gene fragment data, and adult and larval morphological characters from Yamaguchi (2000). Taxa from this study are shown with the classification from Paxton et al. (1984). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Lanternfish families, subfamilies, and genera presented in Paxton et al. (1984).

Order Myctophiformes
Family Neoscopelidae
Neoscopelus, Scopelengys, Solivomer
Family Myctophidae
Subfamily Myctophinae
Tribe Myctophini
Benthosema, Diogenichthys, Hygophum, Myctophum, Symbolophorus
Tribe Gonichthyini
Centrobranchus, Gonichthys, Loweina, Tarletonbeania
Tribe Electronini
Electrona, Krefftichthys, Metelectrona, Protomyctophum
Subfamily Lampanyctinae
Tribe Gymnoscopelini
Gymnoscopelus, Hintonia, Lampanyctodes, Lampichthys, Notoscopelus, Scopelopsis
Tribe Diaphini
Diaphus, Idiolychnus, Lobianchia
Tribe Lampanyctini
Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux
Stenobrachius, Taaningichthys, Triphoturus
Tribe Notolychnini
Notolychnus

ateleopodiform, *Guentherus altivela*, and included three aulopiform and two acanthomorph outgroups.

The 32-species analysis included every myctophiform that had UCE data (Table 2). These species include 26 of 36 traditionally recognized genera (Eschmeyer et al., 2017). The results of analyses using these data will be referred to as the "UCE-concatenated tree," "UCE-species tree," or "UCE-based trees." To expand the generic- and species-level diversity in our study and allow for more comparability to previously published hypotheses of lanternfish relationships, we added 45 additional lanternfish species that had DNA sequence data for a ten-protein-coding-gene dataset (Table S1). These 77 species include 34 of 36 traditionally recognized myctophiform genera (Eschmeyer et al., 2017). The results of analyses combining the UCE data and the ten-protein-coding-gene data will be referred to as the "UCE-10 tree." Finally, to include the myctophid genera that lack sequence data and to incorporate the morphological variation that served as the basis of the traditional myctophid classification, we analyzed a dataset of 79 myctophiform species that includes all 36 traditionally recognized myctophiform genera. The results of analyses using the UCE data, the ten-protein-coding-gene data, and the morphological data will be referred to as the "total-data tree." Institutional abbreviations and acronyms for museums and collections associated with all molecular and morphological samples follow Sabaj (2016).

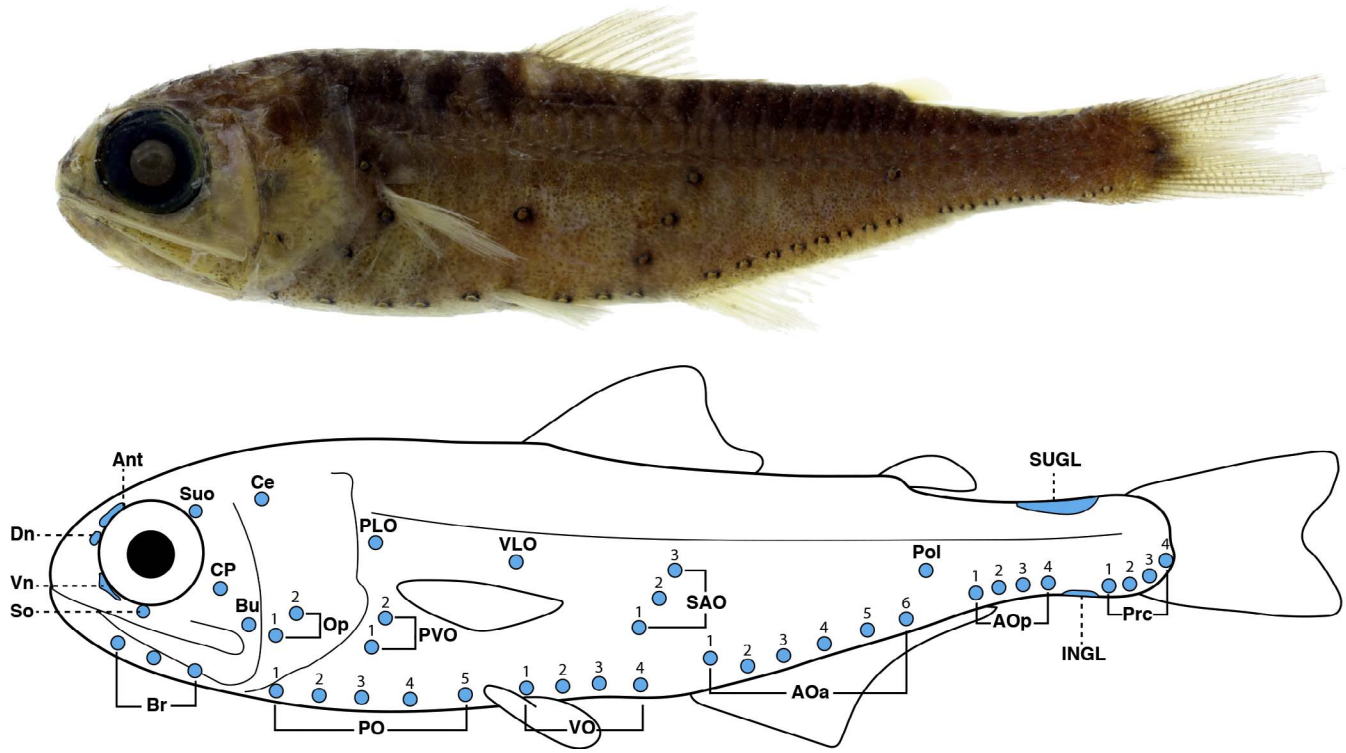


Fig. 2. Example of photophores located on a specimen *Myctophum affine* (FMNH 59974). Diagram exhibiting general placement of bioluminescent photophores and luminous glands on species within Myctophidae. **Ant**, antorbital organ; **AOa**, anterior anal organs; **AOp**, posterior anal organs; **Br**, branchiostegal organs; **Bu**, buccal organ; **Ce**, Cervical; **CP**, cheek photophore; **Dn**, dorsonasal organ; **INGL**, infracaudal luminous gland; **Op**, opercular organs; **PLO**, suprapectoral organ; **PO**, pectoral organs; **Pol**, postero-lateral organ; **Prc**, precaudal organs; **PVO**, subpectoral luminous glands; **SAO**, supraanal organs; **So**, suborbital organ; **Suo**, supraorbital organ; **SUGL**, supracaudal luminous gland; **VLO**, supraventral organ; **Vn**, ventronasal organ; **VO**, ventral organs.

Table 2
Taxa used in Illumina sequencing for UCE data and descriptive statistics for UCE loci. Asterisks denote taxa with tissue extracted using the Maxwell® RSC Whole Blood DNA Kit.

Taxon	Tissue/Voucher	SRA Accession Number	Contigs	Total bp	Mean Length
Outgroup					
Alepisaurus ferox	SIO 96-3	SRR6183952	428	395,555	924.19
Chlorophthalmus nigromarginatus	FMNH 121202	SRR6183955	430	202,991	472.07
Guentherus altivela	USNM 386478	SRR6183951	428	444,823	1039.31
Hoplostethus mediterraneus	A. Dettai personal coll.	SRR6183950	441	497,363	1127.81
Polymixia berndti	AMNH 240647	SRR6183957	454	499,151	1099.45
Synodus variegatus	SIO 04-63	SRR6183956	88	59,806	679.61
Ingroup					
Benthosema glaciale	KU 3058/MCZ 158723	SRR6183954	400	399,463	998.66
Bolinichthys longipes	SIO 10-164	SRR6183953	414	315,307	761.61
Ceratoscopelus townsendi	SIO 06-91	SRR6183949	383	310,402	810.45
Dasyscopelus orientale	KU T10933	SRR6183948	435	423,554	973.69
*Dasyscopelus spinosum**	AMNH Sol A23	SRR6183933	365	241,139	660.65
*Diaphus dumerilii**	KU 1478/KU 27150	SRR6183932	438	384,871	878.70
*Diaphus phillipsi**	SIO 10-175	SRR6183935	440	318,107	722.97
Diaphus theta	KU 2135/KU 27971	SRR6183934	415	422,458	1017.97
Diogenichthys atlanticus	SIO 09-99	SRR6183937	398	323,415	812.60
*Electrona risso**	SIO 10-173	SRR6183936	445	407,532	915.80
Hygophum reinhardtii	SIO 09-320	SRR6183939	415	412,566	994.13
Krefftichthys anderssoni	CSIRO GT 390	SRR6183938	431	249,569	579.05
Lampadena speculigera	KU 5916/MCZ 163213	SRR6183931	265	210,960	796.08
*Lampadena urophaos**	SIO 10-166	SRR6183930	426	402,721	945.35
*Lampanyctus lineatum**	KU 5971/MCZ 163698	SRR6183964	387	344,822	891.01
Lampanyctus macdonaldi	KU 7446/MCZ 164404	SRR6183965	377	329,054	872.82
*Lampichthys procerus**	CSIRO GT 3825	SRR6183966	388	317,325	817.85
Lepidophanes guentheri	KU 3796/KU 28493	SRR6183967	424	389,921	919.63
Lobianchia gemellarii	SIO 10-171	SRR6183963	440	426,533	969.39
Loweina rara	SIO 10-171	SRR6183960	421	395,725	939.96
Myctophum aurolaternatum	SIO 06-295	SRR6183961	413	412,764	999.43
*Myctophum nitidulum**	SIO 11-12	SRR6183962	438	418,361	955.16
Neoscopelus macrolepidotus	KU 3291/MCZ 155364	SRR6183958	452	457,149	1011.39
Notolychnus valdiviae	SIO 09-336	SRR6183959	392	361,469	922.11
Notoscopelus caudispinosus	KU 5301/MCZ 161883	SRR6183943	406	388,652	957.27
Protomyctophum thompsoni	KU 2133/KU 27969	SRR6183942	381	353,355	927.44
Scopelengys tristis	KU 3240/KU 28210	SRR6183941	455	420,544	924.27
Scopelopsis multipunctatus	CSIRO GT 3776	SRR6183940	413	319,466	773.53
Stenobrachius leucopsarus	FMNH 122277	SRR6183947	393	287,251	730.92
Taaningichthys bathyphilus	SIO 10-174	SRR6183946	412	380,453	923.43
Tarletonbeania crenularis	SIO 06-88	SRR6183945	437	457,500	1046.91
Triphoturus nigrescens	SIO 06-293	SRR6183944	358	263,896	737.14

2.2. Extraction, amplification, and sequencing for protein-coding genes

Nuclear and mitochondrial DNA was extracted from muscle or fin clips preserved in 95% ethanol from seven specimens prior to extraction using a DNeasy Tissue Extraction Kit (Qiagen) following the manufacturer's protocol. The polymerase chain reaction (PCR) was used to amplify all gene fragments. Double-stranded amplifications were performed in a 25 μL volume containing one Ready-To-Go PCR bead (GE Healthcare), 1.25 μL of each primer (10 pmol), and 2–5 μL of undiluted DNA extract. To amplify and sequence these gene fragments, the following primers were used: COI (L5956: 5′–CACAAAGACATTGGCAC CCT–3′, H6855: 5′–AGTCAGCTGAAKACTTTTAC–3′; Miya and Nishida, 2000); Glyt (Glyt_F559: 5′–GGACTGTCMAAGATGACCACMT–3′, Glyt_R1562: 5′–CCCAAGAGGTTCTTGTTRAAGAT–3′; Li et al., 2007); myh6 (myh6_F459: 5′–CATMTTYTCCATCTCAGATAATGC–3′, myh6_R1325: 5′–ATTCTCACCACCATCCAGTTGAA–3′; Li et al., 2007); plagl2 (plagl2_F9: 5′–CCACACACTCYCCACAGAA–3′, plagl2_R930: 5′–TTCTCAAGCAGGTATGAGGTAGA–3′; Li et al., 2007); Ptr (Ptr_F458: 5′–AGAATGGATWACCAACACYTACG–3′, Ptr_R1248: 5′–TAAGGCACA GGATTGAGATGCT–3′; Li et al., 2007); SH3PX3 (SH3PX3_F461: 5′–GTATGGTSGGCAGGAACYTGAA–3′, SH3PX3_R1303: 5′–CAAA-CAKCTCYCCGATGTTCTC–3′; Li et al., 2007); and tbr1 (tbr1_F1: 5′–TGTCTACACAGGCTGCGACAT–3′, tbr1_R820: 5′–GATGTCCT TRGWGCAGTTTTT–3′; Li et al., 2007). Amplifications for mitochondrial COI were carried out in 35 cycles using the following temperature profile: initial denaturation for 3 min at 94 °C; 35 cycles of denaturation for 15 s at 94 °C, annealing for 15 s at 53 °C, and extension for 55 s at 72 °C; and a final terminal extension at 72 °C for 7 min. For Glyt, myh6, and SH3PX3, the following temperature profile was used: initial denaturation for 3 min at 94 °C; 10 cycles of denaturation for 45 s at 94 °C, annealing for 45 s at 57 °C, and extension for 75 s at 72 °C; 30 cycles of denaturation for 45 s at 94 °C, annealing for 30 s at 55 °C, and extension for 75 s at 72 °C; and a final terminal extension at 72 °C for 7 min. For plagl2, Ptr, and tbr1, the following temperature profile was used: initial denaturation for 3 min at 94 °C; 10 cycles of denaturation for 45 s at 94 °C, annealing for 45 s at 59 °C, and extension for 75 s at 72 °C; 30 cycles of denaturation for 45 s at 94 °C, annealing for 30 s at 57 °C, and extension for 75 s at 72 °C; and a final terminal extension at 72 °C for 7 min. The double-stranded amplification products for all fragments were desalted and concentrated using AMPure (Beckman Coulter). Both strands of the purified PCR fragments were used as templates and amplified for sequencing using the amplification primers and a Prism Dye Terminator Reaction Kit v1.1 (Applied Biosystems) with minor modifications to the manufacturer's protocols. The sequencing reactions were cleaned and desalted using cleanSEQ (Beckman Coulter). The nucleotides were sequenced and the base pairs were called on a 3730 automated DNA sequencer (Applied Biosystems) or by Beckman Coulter Genomics (Danvers, MA).

2.3. Extraction, and genome-scale sequencing on an Illumina HiSeq 2500

Total genomic DNA was extracted from muscle or fin clips using a DNeasy Tissue Extraction Kit (Qiagen) following the manufacturer's protocol for 30 of the 38 specimens (Table 2). The first and second

elution from a Qiagen filter were combined and dried with a DNA SpeedVac Concentrator (Thermo Fisher) to a 102 µL volume. Total genomic DNA was extracted from muscle or fin clips for the remaining eight of the included taxa (marked with asterisks in Table 2) using the Maxwell® RSC Whole Blood DNA Kit (Promega) following the manufacturer's extraction protocol (except the replacement of the blood DNA kit's lysis buffer with Promega's tissue lysis buffer) into a 102 µL volume. We quantified each template using a Qubit fluorometer (Life Technologies) using the dsDNA BR Assay Kit following the manufacturer's protocol. If insufficient DNA was collected, multiple samples from the same specimen were combined. Final quantified samples (100 µL volume) were sent to MYcroarray (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 on an Illumina HiSeq 2500, and demultiplexing of samples.

2.4. Protein-coding gene sequences

Contigs resulting from Sanger sequencing were assembled in Geneious v8.1.8 (Kearse et al., 2012) using DNA sequences from the complementary heavy and light strands. Additional protein-coding gene fragments were extracted from sequence data received from MYcroarray in Fastq format. The Fastq sequences from multiple runs for the same species were combined into two read pair files and these combined files were cleaned of indices and adapters using illumiprocessor v2.0.7 (Faircloth, 2013) and trimmomatic v0.36 (Bolger et al., 2014). The cleaned reads were compared to existing myctophiform sequences of the ten protein-coding genes using the "map to reference" functionality in Geneious with low-sensitivity and two to five (typically three) iterations to collect homologous regions from taxa that were not successfully amplified using PCR. All newly available sequences were submitted to Genbank (Table S1) and assigned accession numbers MF966947–MF966951, MF991152–MF991209, and MG019405–MG019407. Protein-coding sequences were edited in Geneious and collated into fasta text files with sequences aligned with MAFFT v7 (Katoh and Standley, 2013). Protein-coding sequences were analyzed with genomic data or with genomic and morphological data. Previously published protein-coding sequences were drawn from the following studies: Lopez et al. (2004), Sparks and Smith (2004), Smith and Wheeler (2006), Chen et al. (2007, 2013), Miya et al. (2007), Rock et al. (2008), Davis (2010), Near et al. (2012, 2013), Betancur-R et al. (2013), Poulsen et al. (2013), Davis et al. (2014, 2016), Denton (2014), Sparks et al. (2014), Ghedotti et al. (2015), Chang et al. (2017) and Li et al. (2008), and a diversity of unpublished barcoding studies that are noted in the GenBank and Barcode Table (Table S1).

2.5. Ultraconserved element sequence data assembly and alignment

Genome-scale sequence data in Fastq format from sequences with multiple runs were combined into two read pair files and these combined files were cleaned of indices and adapters using illumiprocessor and trimmomatic. The reads were then assembled, by species, into contigs using ABySS v1.3.7 (Simpson et al., 2009), with a kmer value set to 60. After assembly, we used a software package that used LASTZ v1.02.00 (Large-Scale Genome Alignment Tool; Harris, 2007) and the Faircloth et al. (2013) actionopterygian probe set to find reciprocally unique UCE matches and align them to the species-specific contigs. We set LASTZ at 80% for the minimum coverage and 80% for the minimum identity for identifying UCEs. A custom Python program (match_contigs_to_probes.py) within PHYLUCE v1.5.0 (Faircloth et al., 2012) removed reciprocal and non-reciprocal duplicate hits from the data set and created a relational database of matches to UCE loci by taxon. We then constructed FASTA files of the UCE data identified across all taxa with PHYLUCE. Contigs were aligned using MAFFT, and a Python script within PHYLUCE (seqcap_align_2.py) was then used to trim the contigs representing UCEs, in parallel, across the selected taxa prior to phylogenetic analysis. The data matrix of aligned UCEs (Table 2) was generated and concatenated in MAFFT for RAxML v8.0.19 (Stamatakis, 2014) using only contigs found in at least 65% of the included taxa. A total of 451 aligned UCE fragments were concatenated for a final length of 357,878 bps. Sequence fragment lengths were 100–1400 bps. Nucleotide alignments are available at Mendeley Data (https://doi.org/10.17632/3shzdn6gmm.1) and raw sequencing reads at the NCBI SRA under BioProject PRJNA414237 (SRA Accession Numbers SRR6183930–SRR6183967).

2.6. Morphological data

The morphological dataset (Table S2) includes 63 characters from Yamaguchi (2000) that included characters derived primarily from Paxton et al. (1984) and Stiassny (1996). Myctophiform morphological characters were listed based on specimen observations identified in Paxton (1972) and Paxton et al. (1984). If species in our analysis were not analyzed in Paxton (1972) or Paxton et al. (1984), character states were coded with "?" for those species. Refer to the Supplementary Material for an abbreviated list of the characters from Yamaguchi (2000). Previous phylogenetic studies using morphological data (Paxton, 1972; Paxton et al., 1984, Stiassny, 1996; Yamaguchi, 2000) did not explicitly include outgroup taxa in their analyses. In this study we include character states for *Alepisaurus* (*Alepisaurus* sp., FMNH 113997), *Chlorophthalmus* (*Chlorophthalmus agassizi,* USNM 159385), *Hoplostethus* (*Hoplostethus mediterraneus,* AMNH 49718), *Polymixia* (*Polymixia lowei,* FMNH 64705), and *Synodus* (*Synodus variegatus,* USNM 140825). New character data were coded based the examination of cleared and stained specimens using multiple stereomicroscopes with varying magnification and lighting regimes. Larval characters for outgroup taxa were taken from Ambrose (1996), Stevens and Moser (1996), Konishi (1999), Ditty (2005), Ditty et al. (2005), and Richards et al. (2006).

2.7. Phylogenetic analyses

Our UCE-based trees include a total of 38 taxa. For our UCE-concatenated tree we performed 20 independent runs in RAxML using a GTR + G substitution model selected based on Darriba and Posada (2015), who found that GTR + G models maximized phylogenomic performance. We then selected the optimal tree from 20 replicates. The rapid bootstrapping algorithm was set at 1000 bootstrap replicates and stopped at 250 bootstrap replicates based on the MRE bootstrapping criterion. For our UCE-species tree, we ran an independent likelihood analyses (RAxML) on each of the 451 UCEs. Each UCE likelihood analysis used a GTR + G substitution model and selected the optimal UCE-species tree from five replicates. The results of these independent analyses were analyzed in ASTRAL II v. 4.10.12 (Mirarab and Warnow, 2015) to create a UCE-species tree. We performed 100 bootstrap runs on each of the 451 UCEs and analyzed them in ASTRAL II. Bootstrap support of UCE-species tree nodes were denoted on the UCE-concatenated tree (Fig. 3).

Our UCE-10 tree includes a total of 83 taxa. For all of the representative species, each protein-coding gene was aligned separately in MAFFT and concatenated with the UCE dataset in Geneious. Gene fragments from newly sequenced data (Sanger and Illumina) and those pulled from GenBank included nine nuclear (Glyt, 891 aligned bps; histone H3, 375 aligned bps; myh6, 702 aligned bps; plagl2, 702 aligned bps; Ptr, 708 aligned bps; RAG1, 1500 aligned bps; SH3PX3, aligned 705 bps; tbr1, aligned 844 bps; zic1, aligned 921 bps) and one mitochondrial (COI, 878 aligned bps) genes (Table S1). The combined and aligned molecular dataset (UCE + ten protein-coding genes) had a total length of 366,104 bps. To analyze this dataset, we performed 20 independent runs in RAxML with a GTR + G substitution model, and the tree with the best likelihood score was selected as the optimal tree (UCE-10; Fig. S1). The rapid bootstrapping algorithm was set at 1000

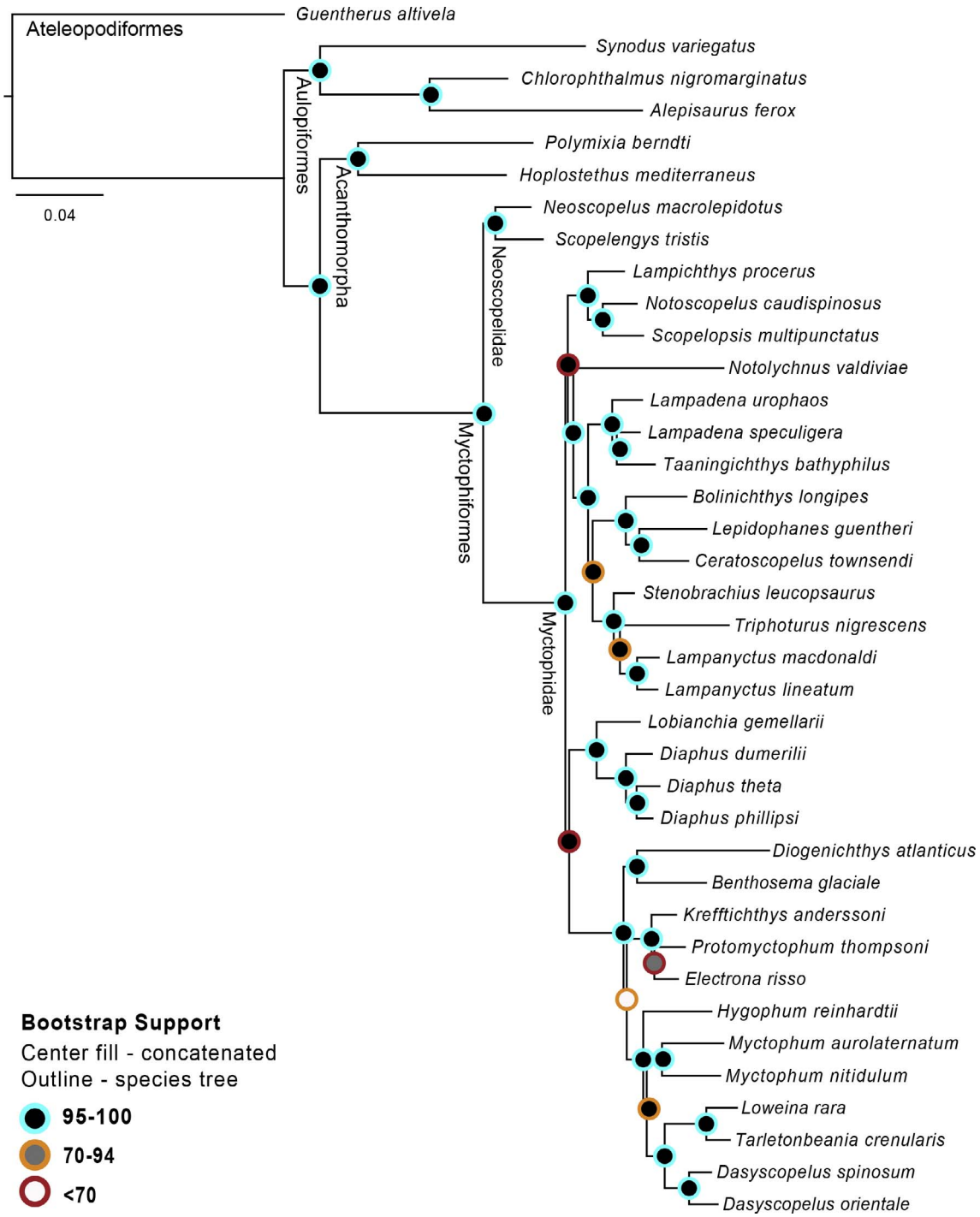


Fig. 3. A maximum-likelihood phylogeny of lanternfish relationships based upon UCE-concatenated sequences. Scale bar represents the number of substitutions per site. Circles at nodes represent bootstrap support values from the UCE-concatenated and UCE-species trees.

bootstrap replicates and stopped at 200 bootstrap replicates based on the MRE bootstrapping criterion.

The total-data tree contains 85 taxa, and combined 451 UCE sequences (Table 2), ten nuclear and mitochondrial gene fragments (Table S1), and 63 morphological characters (Table S2). Likelihood analyses for the total-data tree were performed in GARLI v2.0 (Zwickl, 2006). A single partition was used for the genetic data using a GTR + G substitution model. For the anatomical data, a single partition was used under the MK (Markov) model for morphological data (Lewis and Puterman, 2001). Twenty-five independent likelihood analyses were conducted, and the tree having the maximal likelihood score is presented here (total-data tree; Fig. 4) to evaluate evolutionary relationships. A non-parametric bootstrap analysis (Felsenstein, 1985) was performed for the total-data tree with 200 random pseudoreplicates. Morphological characters (Table S2) were optimized with parsimony on our total-data tree using Winclada v0.9.9 (Nixon, 1999) to optimize the synapomorphies across the myctophiform phylogeny. Optimizations for the myctophiform tree are presented in Fig. S2. For bootstrap-support analyses for the total-data tree, terminals represented solely by morphological data (*Hintonia* and *Idiolychnus*) were excluded because they

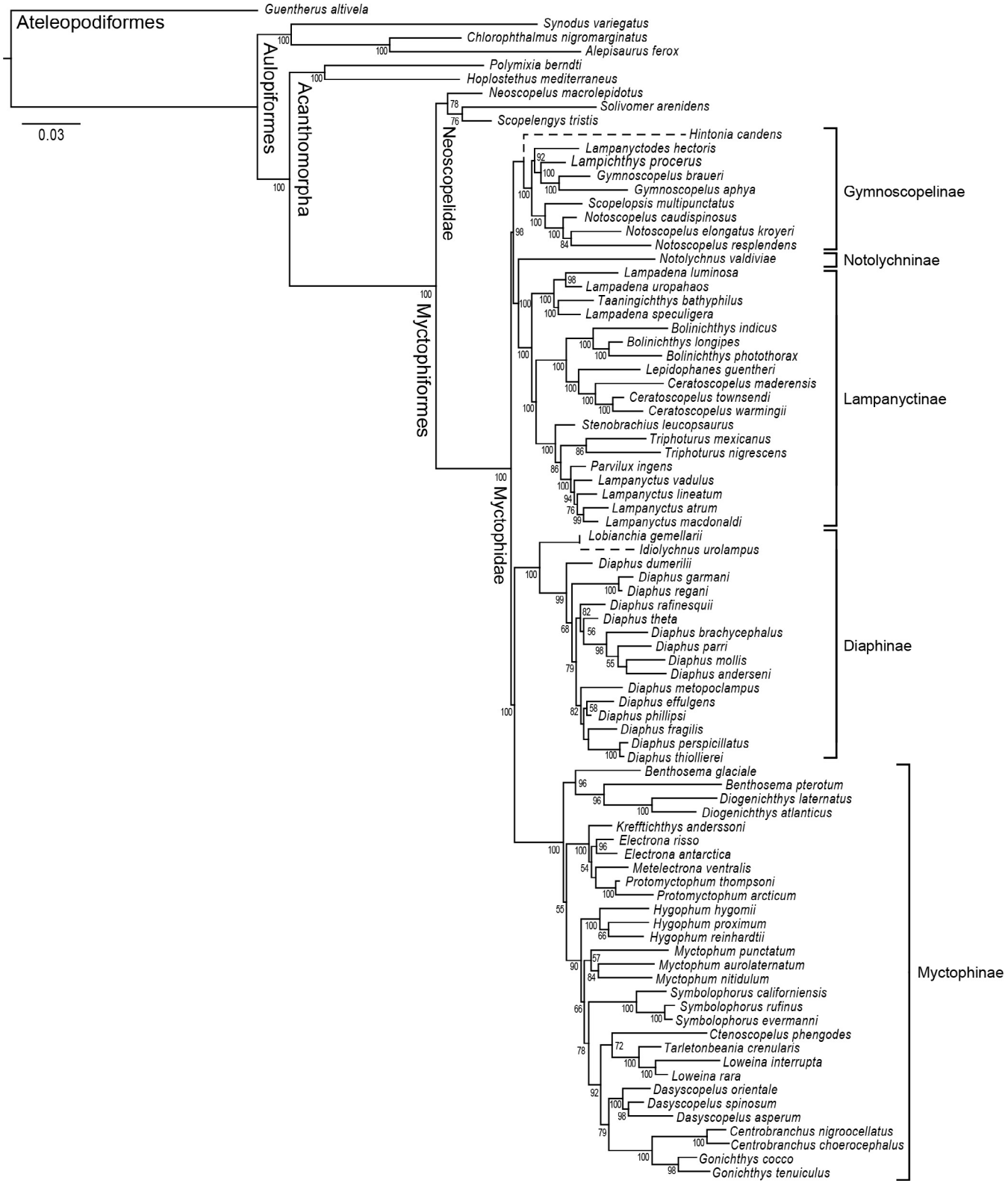


Fig. 4. A maximum-likelihood total-data tree of lanternfish relationships based upon UCE sequences, Sanger sequence and Illumina gene fragment data, and larval and adult morphological characters described in Yamaguchi (2000). Scale bar represents the number of substitutions per site. Bootstrap support values are shown at nodes. Terminals represented solely by morphological data (*Hintonia* and *Idiolychnus*) are denoted with dashed lines and were excluded from the bootstrap-support analyses.

have excessive missing data that would impact bootstrap support values disproportionally; overall, the optimal tree with these terminals excluded was otherwise identical to the total-data tree (Fig. 4). All resulting phylogenetic trees were visualized with FigTree v1.4.3 (Rambaut, 2007).

3. Results

We conducted four different analyses to resolve myctophiform relationships. All resulting trees were in perfect agreement barring the omission of taxa in the less-species rich analyses. Due to this

consistency, we will focus on the total-data tree while describing myctophiform relationships (Figs. 4 and 5). The UCE-concatenated tree recovered 34 (97%) moderately to strongly supported nodes (Fig. 3), with 1 node (3%) being moderately supported, with a bootstrap value between 70 and 94, and 33 nodes (94%) recovered with strong support, with bootstrap values ≥95. The UCE-species tree recovered 32 nodes (91%) that were moderately to strongly supported (Fig. 3), with 4 nodes (11%) moderately supported with a bootstrap value between 70 and 94, and 28 nodes (80%) being strongly supported by bootstrap values ≥ 95. All nodes recovered in the UCE-concatenated tree were recovered in the UCE-species tree. The UCE-10 tree (Fig. S1) recovered 66 nodes (83%) that were moderately to strongly supported. Twelve nodes (15%) were recovered with moderate support and bootstrap values between 70 and 94, and 54 nodes (68%) with were recovered with strong support values ≥ 95. The total-data tree (Fig. 4) recovered 67 nodes (88%) that were moderately to strongly supported, with 17 nodes (22%) being moderately supported with bootstrap values between 70 and 94. We additionally recovered 50 nodes (66%) with strong support and bootstrap values ≥95. The total-data tree inferred a monophyletic Myctophiformes as the sister group to Acanthomorpha with strong support (Fig. 4). The two myctophiform families, Neoscopelidae and Myctophidae, were recovered as reciprocally monophyletic sister groups with moderate support (Fig. 4).

Within the Neoscopelidae, the total-data tree inferred *Solivomer* sister to *Scopelengys; Neoscopelus* was recovered as the stem neoscopelid lineage (Fig. 4). Our UCE-based trees (i.e., UCE-concatenated and UCE-species trees) did not include *Solivomer* (Fig. 3). Our total-data tree recovered a monophyletic Myctophidae with strong support (Fig. 4). Taxa from the traditional Lampanyctinae were recovered as paraphyletic with respect to the traditional Myctophinae. This result is also consistent between the UCE-based trees (Fig. 3) and the UCE-10 tree (Fig. S1).

Within the Myctophidae, our total-data tree infers Gymnoscopelini + (Notolychnini + Lampanyctini) sister to (Diaphini + Myctophinae) with strong boostrap support (Fig. 4). The strongly supported clade of traditional lampanyctines (Fig. 4) includes a clade composed of the Gymnoscopelini + (Lampanyctini + Notolychnini). A strongly supported monophyletic Gymnoscopelini composed of *Gymnoscopelus*, *Hintonia*, *Lampanyctodes*, *Lampichthys*, *Notoscopelus*, and *Scopelopsis* is sister to a lineage that includes Lampanyctini + Notolychnini (Fig. 4). Within the Gymnoscopelini, *Hintonia* is recovered as the sister group to all other gymnoscopelins. The remaining gymnoscopelins are distributed in two sister clades (Fig. 4), (*Notoscopelus* + *Scopelopsis*) and *Lampanyctodes* + (*Gymnoscopelus* + *Lampichthys*). The UCE-based trees did not include *Gymnoscopelus*, *Hintonia*, *Lampanyctodes,* but they exhibited completely congruent relationships with the total-data tree for the included species (Fig. 3).

The total-data tree infers a strongly supported monotypic Notolychnini (*Notolychnus*) sister to the Lampanyctini, which is composed of *Bolinichthys*, *Ceratoscopelus*, *Lampadena*, *Lampanyctus*, *Lepidophanes*, *Nannobrachium*, *Parvilux*, *Stenobrachius*, *Taaningichthys*, and *Triphoturus* (Fig. 4). The Lampanyctini is recovered as monophyletic with strong support. Within the Lampanyctini, a clade composed of *Lampadena* + *Taaningichthys* is inferred as the sister group to all remaining lampanyctine lineages, and our total-data tree resolves *Lampadena* as paraphyletic with *Taaningichthys* nested within *Lampadena* (Fig. 4). A clade including *Bolinichthys* + (*Ceratoscopelus* + *Lepidophanes*) is the sister group to a clade including *Parvilux, Stenobrachius, Triphoturus*, and a paraphyletic grade of *Lampanyctus macdonaldi, L. vadulus, Nannobrachium atrum,* and *N. lineatum* (*Nannobrachium* species designated as *Lampanyctus* in Figs. 3 and 4). *Parvilux* was not included in our UCE-based trees, but they had congruent relationships with the total-data tree for the included species (Fig. 3).

The Diaphini + Myctophinae was found to be highly supported in our total-data tree (Fig. 4). The Diaphini is composed of three genera, with *Diaphus* inferred as the sister group to *Idiolychnus* + *Lobianchia* with strong support. The UCE-based trees had congruent relationships (Fig. 3), but they did not include *Idiolychnus*.

The Myctophinae (Fig. 4) includes the traditional myctophine genera (*Benthosema, Centrobranchus, Diogenichthys, Electrona, Gonichthys, Hygophum, Krefftichthys, Loweina, Metelectrona, Myctophum, Protomyctophum, Symbolophorus,* and *Tarletonbeania*). The total-data tree inferred *Benthosema* + *Diogenichthys* as the sister group to all other myctophine taxa and found *Diogenichthys* nested within a paraphyletic *Benthosema* (Fig. 4). The total-data tree recovered the traditional electronins in a clade with *Krefftichthys* sister to a clade composed of *Electrona* + (*Metelectrona* + *Protomyctophum*). *Hygophum* is found sister to a clade containing a non-monophyletic traditional Gonichthyini + a non-monophyletic traditional *Myctophum* + *Symbolophorus*. The clade composed of *Myctophum aurolaternatum*, *M. nitidulum,* and *M. punctatum* is sister to *Symbolophorus* + the rest of the myctophine taxa. We resolve a clade composed of *Myctophum phengodes* (designated as *Ctenoscopelus* in Fig. 4) + (*Loweina* + *Tarletonbeania*) sister to a clade composed of the remaining *Myctophum* species (*M. asperum, M. orientale,* and *M. spinosum*; labeled as *Dasyscopelus* in Figs. 3 and 4) + (*Centrobranchus* + *Gonichthys*). The UCE-based trees did not include *Metelectrona, Centrobranchus*, *Gonichthys*, *Myctophum phengodes,* and *Symbolophorus,* but they had congruent relationships with the total-data tree for the included species (Fig. 3).

3.1. Myctophiform classification

The results from our total-data tree (and UCE-based trees) are often in conflict with the traditional taxonomy of lanternfishes (Figs. 1 and 4). We present a revised classification of lanternfishes in Table 3. Our classification makes a minimal number of changes that result in a monophyletic taxonomy, retaining much of the original subfamilial and tribal structure while also having morphological synapomorphies that can aid in future placement of taxa without necessitating DNA sequencing. The myctophiform families, Myctophidae and Neoscopelidae, are recognized as monophyletic. Within the Myctophidae, the traditional Myctophinae was nested within a paraphyletic Lampanyctinae. Among myctophid tribes composed of more than one species, all tribes except the Gonichthyini and Myctophini (i.e., Diaphini, Electronini, Gymnoscopelini, and Lampanyctini) were recovered as monophyletic. (Figs. 3, 4 and S1). A monophyletic Electronini and non-monophyletic Gonichthyini were nested within a Myctophini. *Benthosema, Lampadena,* and *Myctophum* were recovered as para- or polyphyletic, and *Lampanyctus* and *Nannobrachium* were intermixed.

In light of our recovered phylogenies (Figs. 3, 4 and S1), we recognize five myctophid subfamilies, all of which possess high bootstrap-

Table 3
Revised classification of the Myctophiformes.

Order Myctophiformes
Family Neoscopelidae
Neoscopelus, Scopelengys, Solivomer
Family Myctophidae
Subfamily Gymnoscopelinae
Gymnoscopelus, Hintonia, Lampanyctodes, Lampichthys, Notoscopelus, Scopelopsis
Subfamily Notolychninae
Notolychnus
Subfamily Lampanyctinae
Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux, Stenobrachius, Taaningichthys, Triphoturus
Subfamily Diaphinae
Diaphus, Idiolychnus, Lobianchia
Subfamily Myctophinae
Benthosema, Centrobranchus, Ctenoscopelus, Dasyscopelus, Diogenichthys, Electrona, Gonichthys, Hygophum, Krefftichthys, Loweina, Metelectrona, Myctophum, Protomyctophum, Symbolophorus, Tarletonbeania

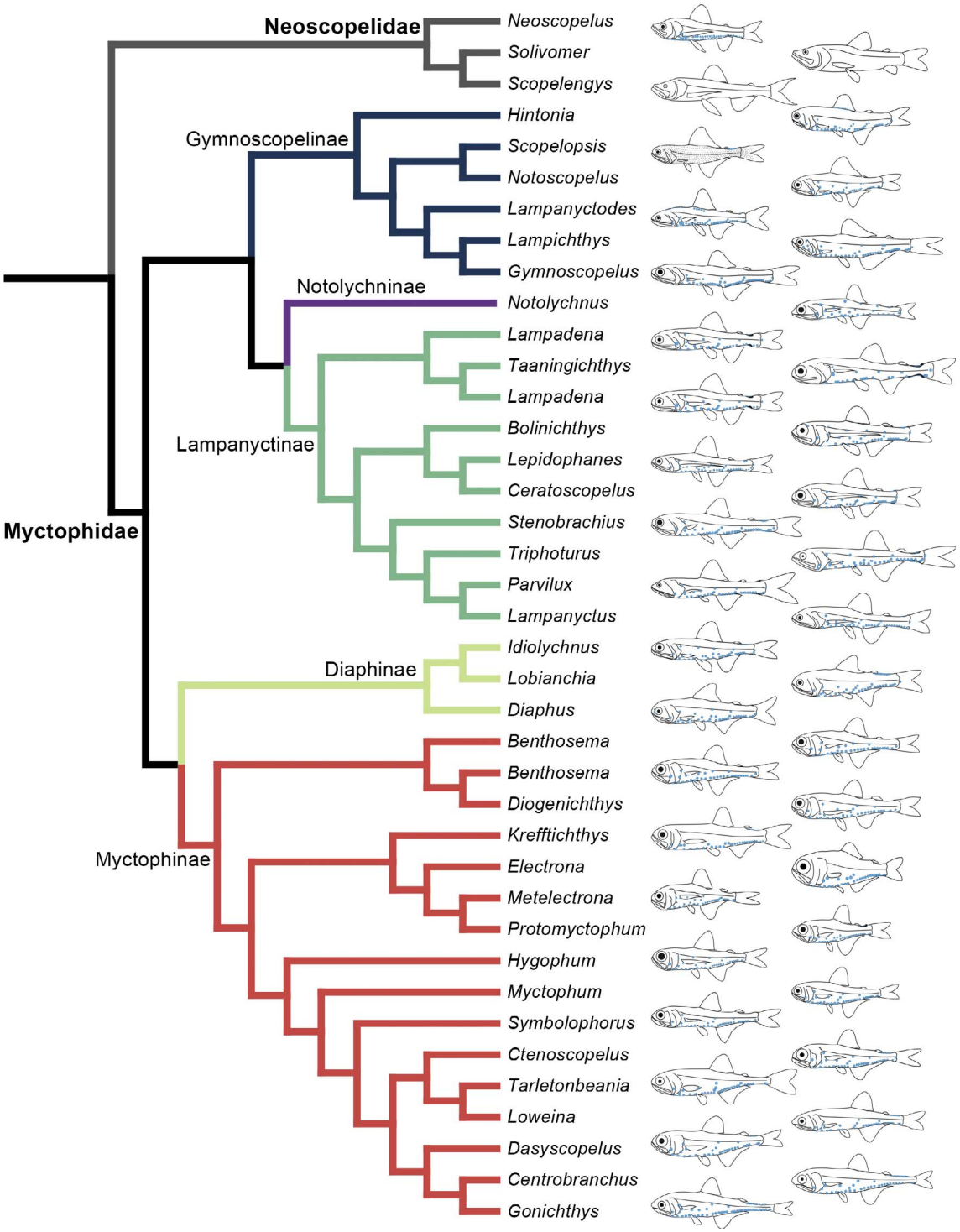


Fig. 5. A genus-level cladogram representing the preferred hypothesis of lanternfishes (total-data tree) presenting the revised phylogeny and taxonomy within Myctophidae. Lanternfish drawings based on images in Hubbs and Wisner (1964), Nafpaktitis (1977), Nafpaktitis et al. (1977), or Hulley (1986).

support values (Fig. 4). We recognize Gymnoscopelinae, which includes the clade comprised of the traditional Gymnoscopelini (*Gymnoscopelus, Hintonia*, *Lampanyctodes, Lampichthys, Notoscopelus,* and *Scopelopsis;* Fig. 5, Table 3). The monotypic Notolychnini (*Notolychnus*) is herein recognized as Notolychninae (Fig. 5, Table 3). Our restricted Lampanyctinae is comprised of the genera from the traditional Lampanyctini (*Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux, Stenobrachius, Taaningichthys,* and *Triphoturus*; Fig. 5, Table 3). The traditional Diaphini (*Diaphus, Lobianchia,* and *Idiolychnus*) is herein recognized as the Diaphinae (Fig. 5, Table 3). Lastly, this study continues to recognize the traditional Myctophinae (*Benthosema, Centrobranchus, Diogenichthys, Electrona, Gonichthys, Hygophum, Krefftichthys, Loweina, Metelectrona, Myctophum, Protomyctophum, Symbolophorus,* and *Tarletonbeania*; Fig. 5, Table 3).

The total-data tree found *Lampanyctus* and *Nannobrachium* as an intermixed paraphyletic grade (*Nannobrachium* designated as *Lampanyctus* in Fig. 4); we herein recognize *Nannobrachium* to be a synonym of *Lampanyctus* (Fig. 5, Table 3). The total-data tree found a non-monophyletic *Myctophum* (designated as *Ctenoscopelus, Dasyscopelus*, and *Myctophum* in Fig. 4), resolving three separate clades. We

herein recognize *Myctophum phengodes* in *Ctenoscopelus* (Fig. 5, Table 3). In addition to the recognition of *Ctenoscopelus*, we recognize the species *Myctophum asperum, M. orientale,* and *M. spinosum* in *Dasyscopelus* (Fig. 5, Table 3).

All of the proposed taxonomic changes in this study are congruent across all our hypotheses of relationships (Figs. 3–5, Fig. S1). The revised classification (Fig. 5, Table 3) will be used throughout the remainder of the study unless noted otherwise.

4. Discussion

4.1. Evolutionary relationships of the Myctophiformes

This study was designed specifically to resolve the relationships of lanternfishes by adding a genome-scale dataset (ultraconserved elements) to the protein-coding gene fragments and morphological characters that have been the basis of the traditional classification. Our results corroborate previous morphological and molecular studies (Paxton, 1972; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000; Poulsen et al., 2013; Davis et al., 2014) in recovering a monophyletic Myctophiformes, Myctophidae, and Neoscopelidae (Figs. 1, 3–5). A monophyletic Myctophiformes is supported by two unambiguous morphological synapomorphies including one extrascapular due to the fusion of two extrascapulars and a comparatively narrow pubic plate (Fig. S2). Wiley and Johnson (2010) summarized seven morphological synapomorphies that support this clade. Most previous studies have inferred a monophyletic Neoscopelidae (Fig. 1), which is also recovered in all of the analyses in this study (Figs. 3 and 4). Based on the 63 morphological characters from Yamaguchi (2000) used in this analysis we recovered the presence of large pectoral fins in larvae as a synapomorphy of the Neoscopelidae (Fig. S2). A monophyletic Neoscopelidae is additionally supported by two synapomorphies described by Stiassny (1996). These include the presence of an extensive cervical gap spanned by connective tissue sheets, greatly enlarged exoccipital facets, and prominent facets on the neural arch of the first vertebra; the presence of a trilobate median cartilage ligamentously attached to the maxillae and premaxillae. Contrary to previous studies, we resolved *Scopelengys* sister to *Solivomer,* with *Neoscopelus* as the stem neoscopelid lineage. *Neoscopelus* possesses ventral photophores (Fig. 2) which are similarly found in all lanternfish species within Myctophidae. Unlike other myctophiform fishes, *Scopelengys* and *Solivomer* both lack photophores. Previous morphological studies (Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000) inferred *Neoscopelus* sister to *Solivomer,* with *Scopelengys* as the stem neoscopelid (Fig. 1). Previous molecular studies have inferred *Neoscopelus* sister to *Scopelengys,* with *Solivomer* as the stem neoscopelid (Poulsen et al., 2013; Davis et al., 2014) or a paraphyletic neoscopelid grade with *Neoscopelus* sister to the Myctophidae (Denton, 2014; Fig. 1). The distinct lack of photophores in *Scopelengys* and *Solivomer* provides interesting support for this inferred clade and suggests a need for further investigation.

We recovered a monophyletic Myctophidae, consistent with all previous studies (Fig. 1). Our analysis results in three unambiguous morphological synapomorphies that support the monophyly of the Myctophidae including the presence of Dn photophore, the presence of caudal light organs, and the presence of larval photophores (except Br_2; Fig. 2). Stiassny (1996) additionally described five morphological synapomorphies that support the monophyly of the Myctophidae. Within the Myctophidae, our results recovered a paraphyletic Lampanyctinae (*sensu* Paxton, 1972) with the Myctophinae nested within it as the sister group of the revised Diaphinae (Figs. 3 and 4). Previous studies using morphological (Paxton, 1972; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000) and molecular data (Davis et al., 2014; Denton, 2014) inferred a monophyletic Lampanyctinae (*sensu* Paxton, 1972). There are two synapomorphies related to the brachial basket that supported the historical lampanyctine clade. They include the elongation of the second basibranchial element (3–4 times the length of the 1st basibranchial) and a urohyal with an elongate anterior process and reduced articulation facet (Stiassny, 1996; Yamaguchi, 2000). Our study does not support this historical clade; instead, it finds two synapomorphies that support the Gymnoscopelinae, two that support the restricted Lampanyctinae, and six characters supporting the Notolychninae.

4.2. Gymnoscopelinae

This study resolves the Gymnoscopelinae (*Gymnoscopelus, Hintonia, Lampanyctodes, Lampichthys, Notoscopelus,* and *Scopelopsis*; Table 3) as the sister group of Lampanyctinae + Notolychninae (Figs. 3–5). Our hypothesis of relationships recognizes two unambiguous synapomorphies for the Gymnoscopelinae (Fig. S2): an increase in the number of procurrent ventral rays and the presence of accessory luminous tissue. This subfamily is atypical among myctophids in that it includes four monotypic genera (*Hintonia, Lampanyctodes, Lampichthys,* and *Scopelopsis*). *Scopelopsis multipunctatus,* unlike all other myctophids, possesses secondary photophores on every scale (Moser and Ahlstrom, 1972). Most species in this subfamily are restricted to oceans in the southern hemisphere, with the exception of species within *Notoscopelus* that are found in oceans globally (Paxton, 1972).

4.3. Notolychninae

Based on the results of this study we placed *Notolychnus* within its own subfamily Notolychninae (Figs. 3–5), sister to the Lampanyctinae. There are no unambiguous anatomical characters that unite the Lampanyctinae + Notolychninae. This is not surprising given the historically problematic placement of *Notolychnus* based on anatomy alone. The phylogenetic placement of the Notolychninae in this study is sister to the Lampanyctinae in both our UCE-based trees and total-data tree. We infer six characters that separate the Notolychninae from the Lampanyctinae (Fig. S2), these include: a transition to one dorsal hypural from two or three, the presence of two Prc photophores, the PLO photophore being level with the PVO_1 photophore, the absence of sexual dimorphism in the caudal luminous organs, initially short relative gut length in larvae, and larval photophores (except Br_2) absent.

The traditional problematic placement of *Notolychnus* in previous morphological studies (Fig. 1) is likely due to *Notolychnus* exhibiting "intermediate" states between species of the Lampanyctinae (*sensu* Paxton et al., 1984) and Myctophinae. For example, *Notolychnus* lacks a posteromedial shelf on the cleithrum similar to taxa in the Myctophinae, while this shelf is present in all other myctophids (Paxton, 1972). Additionally, *Notolychnus* only has two Prc photophores (Fig. 2) on their caudal peduncle similar to the number observed in species within the Myctophinae, where, in comparison, taxa within the subfamilies Gymnoscopelinae and Lampanyctinae have three to nine Prc photophores (with the exception of *Scopelopsis*; Fig. 2). Additionally, the eyes of larval species in the Myctophinae are elliptical in outline while the eyes of larvae in the Diaphinae, Gymnoscopelinae, and Lampanyctinae are round. In comparison, *Notolychnus* exhibit intermediate semi-elliptical eyes (Moser and Ahlstrom, 1970). Poulsen et al. (2013) placed *Notolychnus* as the stem myctophid lineage based on an analysis of mitogenomic data. In contrast, recent studies using three to seven mitochondrial and/or nuclear gene fragments (Davis et al., 2014; Denton, 2014) have inferred *Notolychnus* as nested within the Lampanyctinae. Based on our total-data tree, the morphological differences that separate it from other clades, and its historical problematic placement, we have placed *Notolychnus* in its own subfamily Notolychninae (Fig. 5).

4.4. Lampanyctinae

Our revised Lampanyctinae is restricted to *Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux, Stenobrachius, Taaningichthys,* and *Triphoturus* (Table 3). This study

recognizes two unambiguous synapomorphies that support this restricted Lampanyctinae (Fig. S2). One character is the presence of a Dn (cheek) photophore (Paxton, 1972; Fig. 2), and the other character is the presence of anterior facing 'recurved' teeth on the posterior portion of the dentary. These specialized teeth are hypothesized to inhibit the escape of prey items in the mouth cavity (Paxton, 1972). This study suggests that the relationships of genera within the Lampanyctinae can be grouped into three lineages. The first lineage includes *Lampadena* + *Taaningichthys*; this clade was sister to all remaining lampanyctine lineages (Figs. 3–5). *Lampadena* was resolved as paraphyletic relative to *Taaningichthys,* a result similar to those presented in Denton's (2014) study. Although our study strives to recognize exclusively monophyletic taxonomic groups, we postpone making any taxonomic changes to *Lampadena* without gathering additional data for this small clade. The second lineage includes *Lampanyctus* + *Parvilux* + *Stenobrachius* + *Triphoturus* (Figs. 3–5), of which *Lampanyctus, Stenobrachius,* and *Triphoturus* are identified as having a shared unique mitochondrial gene rearrangement (Poulsen et al., 2013), although the condition in *Parvilux* is unknown. The remaining lampanyctine lineage contains *Bolinichthys* + *Ceratoscopelus* + *Lepidophanes*.

In this study we are addressing the intermixed clade composed of *Lampanyctus* and *Nannobrachium.* Our total-data tree infers the genera *Lampanyctus* and *Nannobrachium* as non-monophyletic (Fig. 4). *Nannobrachium* was not recognized by either Fraser-Brunner (1949) or Bolin (1959), but both suggested three evolutionary groups in *Lampanyctus* based on the length of their pectoral fins and the presence or absence of cheek and secondary body photophores. Paxton (1972) examined *Nannobrachium* and found few osteological characters that were consistent within the three previously recognized subgroups. The most reliable character he noted was poor ossification in species with short pectoral fins. Zahuranec (2000) provided an in-depth study on the species he believed should be recognized in *Nannobrachium*. After examining over 9000 specimens, he identified a set of characters shared by all species in *Nannobrachium* that included an atrophied gas bladder in adults, a "pinched" body profile with concave dorsal and ventral profiles behind the head, reduced musculature, short pectoral fins with a narrow base (or a complete lack of pectorals), and a vertically elongate squarish otolith with smooth margins. Using this character combination, Zahuranec (2000) included 17 species in five species groups in *Nannobrachium*. He further stated that many of these characters are shared with species in closely related genera including those in the *Lampanyctus macdonaldi* species group, *Parvilux*, and *Triphoturus* (i.e., the presence of short pectoral fins and weak musculature resulting in a soft flaccid body). Denton's (2014) molecular phylogenetic study included 12 species in *Lampanyctus* and nine species in *Nannobrachium.* His included species from these genera formed a clade with neither genus being recovered as monophyletic. Denton suggested that the recognition of the genus be revisited. None of the characters that Zahuranec (2000) describes fully separates species of *Nannobrachium* and *Lampanyctus*, as even he pointed out. There are characters that species in *Nannobrachium* share with the *Lampanyctus macdonaldi* species group, *Parvilux*, and *Triphoturus.* Despite the comprehensive work done by Zahuranec (2000), we consider *Nannobrachium* to be a synonym of *Lampanyctus* (Fig. 5, Table 3) based on the results of our total-data tree and the results in the more species-rich analysis of Denton (2014). Although we agree that further phylogenetic work needs to be done to assess the relationships in this species-rich group.

4.5. Diaphinae

Diaphinae is comprised of three genera, *Diaphus, Idiolychnus,* and *Lobianchia*. Our results corroborate all previous hypotheses that recovered these genera as a monophyletic group (Fig. 1). Some previous studies using either morphological (Paxton, 1972; Paxton et al., 1984) or molecular (Davis et al., 2014) data resolved this clade sister to the Gymnoscopelinae, or in a polytomy with the Gymnoscopelinae and Lampanyctinae (Stiassny, 1996; Yamaguchi, 2000) as seen in Fig. 1. Poulsen et al. (2013) resolved the Diaphinae sister to a clade composed of Lampanyctinae + Gymnoscopelinae, and Denton (2014) resolved the Diaphinae sister to a clade composed of Notolychninae + Lampanyctinae + Gymnoscopelinae. Mirande (2016) is the only study to infer a non-monophyletic Diaphinae (Fig. 1), resolving *Lobianchia* sister to *Notolychnus* and not *Diaphus*. Our study infers a highly supported Diaphinae as the sister group to the Myctophinae (Figs. 3–5), separate from the Gymnoscopelinae, Lampanyctinae, and Notolychninae. Optimizing the morphological features in our analysis on our total-data tree (Fig. S2) recognizes three synapomorphies for the Diaphinae: a raised PO_4 photophore (Fig. 2), a raised VO_3 photophore (Fig. 2), and lack of pigment on the head. Poulsen et al. (2013) also found a unique mitochondrial gene rearrangement in the diaphine genera *Diaphus* and *Lobianchia*. They did not examine *Idiolychnus.*

The genus *Diaphus* is the most species-rich myctophid genus, containing 77 species (~30% of myctophid diversity; Froese and Pauly, 2016), and recent work has identified this clade as diversifying at an accelerated rate (Davis et al., 2014). *Diaphus* is one of the few genera that does not exhibit caudal light glands (Herring, 2007); instead, species in the genus have evolved a diverse system of anteriorly facing light organs on their heads (Fig. 2). These forward-facing head light organs in *Diaphus* are often sexually dimorphic and may be used to find or induce fluorescence in their prey (Haddock et al., 2010). Previous researchers have suggested that these or similar features in other groups have played an important role in the evolution of bioluminescent fish radiations (Paxton, 1972; Sparks et al., 2005; Davis et al., 2014, 2014). Recent work looking at the evolution of mouth size in lanternfishes identified *Diaphus* as being one of the few myctophid genera to have species with either long or short upper jaws (Martin and Davis, 2016). The plasticity of upper-jaw length in this group may be an indication that jaw-length variation has enabled shifts in ecological specializations within this lineage (Martin and Davis, 2016). Although this study includes many species of *Diaphus* (Fig. 3), a more in-depth review is needed to further resolve the relationships within this species-rich lineage.

4.6. Myctophinae

This study resolves the Myctophinae as monophyletic (Figs. 3–5), including 15 genera (*Benthosema, Centrobranchus, Ctenoscopelus, Dasyscopelus, Diogenichthys, Electrona, Gonichthys, Hygophum, Krefftichthys, Loweina, Metelectrona, Myctophum, Protomyctophum, Symbolophorus,* and *Tarletonbeania*; Table 3). Our inference of a monophyletic Myctophinae corroborates all previous studies (e.g., Paxton, 1972; Stiassny, 1996; Poulsen et al., 2013; Davis et al., 2014) as seen in Fig. 1. Our study unites the Myctophinae by five unambiguous morphological synapomorphies that include: comparatively short jaw length, presence of two extrascapulars, lack of a fused third epibranchial toothplate, presence of only one Prc photophore (Fig. 2), and larvae possessing narrow eyes. In general, species within the Myctophinae have reduced their non-photophore luminous tissue to the supracaudal and infracaudal glands. Sexual dimorphism is exhibited in many myctophine species that posses these universally present caudal light organs (Paxton, 1972; Herring, 2007). Our study resolved a myctophine subclade comprised of *Benthosema* + *Diogenichthys,* with a paraphyletic *Benthosema,* (as seen in Poulsen et al., 2013; Denton, 2014). Similar to our decision to delay making taxonomic changes with *Lampadena,* we believe additional work is needed to address the paraphyly of *Benthosema*.

In this study we addressed the polyphyly of fishes traditionally classified in *Myctophum* (*sensu* Paxton, 1972) and recognized the traditional *M. phengodes* in *Ctenoscopelus.* Additionally, we placed the traditional *M. asperum, M. orientale,* and *M. spinosum* in *Dasyscopelus* (Figs. 3–5). These results are congruent with our analyses (Fig. 4) and the results of Poulsen et al. (2013), Davis et al. (2014), and Denton (2014).

4.6.1. Ctenoscopelus

Our total-data tree finds *Ctenoscopelus phengodes* in a clade with *Loweina* + *Tarletonbeania*. The taxonomic placement of *C. phengodes* based on morphological characters has been historically problematic. Fraser-Brunner (1949) recognized *Ctenoscopelus* as separate from *Myctophum* based on a set of four characters which include the presence of a toothless vomer, the last PO photophore not elevated similar to that of *Myctophum* (Fig. 2), a more forward position of the anal fin, and the strong armature of the operculum. Paxton (1972) described the toothless vomer and the position of the anal fin of *C. phengodes* as an extreme end on a broad spectrum of variation within *Myctophum*. He made similar arguments about the elevation in the PO photophore, describing this character as not being variant enough from *Dasyscopelus* (*Myctophum*) *brachygnathum*. Paxton (1972) further describes two additional differences between *Ctenoscopelus phengodes* and the rest of the *Myctophum*, including the elevation of the second Prc photophore to near the lateral line (Fig. 2) and a slight development of the orbital process of the hyomandibula in *Ctenoscopelus*. He proceeds to discuss these characters, describing the elongation of the orbital process being due to the evolutionary shift of jaw elongation seen in other myctophids, and that the Prc and PO photophore placement are not distinctive enough to recognize *Ctenoscopelus*. *C. phengodes* has ever since been placed in *Myctophum.* Similar to its placement in our study, Denton (2014) found *Ctenoscopelus phengodes* sister to *Loweina* + *Tarletonbeania*, and in light of our total-data tree, the study by Denton (2014), and the divergent morphological characters exhibited by *Ctenoscopelus,* we recognize this genus.

4.6.2. Dasyscopelus

The total-data tree found the clade containing *Dasyscopelus asperum, D. orientale,* and *D. spinosum* as separate from the clade containing the traditional *Myctophum aurolaternatum, M. nitidulum,* and *M. punctatum.* Denton (2014) similarly resolved a clade containing *Dasyscopelus asperum, D. brachygnathum, D. lychnobium, D. obtusirostre, D. orientale, D. selenops,* and *D. spinosum,* as separate from *Myctophum affine, M. aurolaternatum*, *M. nitidulum*, and *M. punctatum* (*Myctophum sensu stricto*). Poulsen et al. (2013) found that the species of *Myctophum* (*sensu stricto*) included in their study have a unique mitochondrial gene rearrangement, whereas the included species of *Dasyscopelus* displayed the typical myctophid gene order. Given the placement of *Myctophum aurolaternatum* with other species of *Myctophum* in our analyses, we explored the Illumina sequence data of *M. aurolaternatum* to assess whether it shares this clade's unusual mitogenomic gene arrangement (Poulsen et al., 2013; Satoh et al., 2016). For this assessment, the ND6 gene (positions 15,886–16,701) from the mitogenomic sequence of *Myctophum affine* (AP002922) was compared to our Illumina data using the "Map to Reference" function in Geneious. The resulting contig (GenBank MF983796) was composed of the following mitochondrial elements from 5′ to 3′: ND6, tRNA-Glu, a small intergenic spacer, and tRNA-Pro. This gene order that lacks cytochrome *b* and tRNA-Thr between ND6 and tRNA-Pro was recognized as a synapomorphy for the restricted *Myctophum* by Poulsen et al. (2013). This result provides additional evidence for the close relationship of these taxa and our treatment of this clade as a separate genus from the remainder of lanternfishes traditionally classified in *Myctophum* (i.e., *Ctenoscopelus* and *Dasyscopelus*).

Based on the evidence from our total-data tree we placed *Dasyscopelus asperum, D. orientale,* and *D. spinosum* in *Dasyscopelus.* Based on the work of Poulsen et al. (2013) and Denton (2014), we additionally place *D. brachygnathum, D. lychnobium, D. obtusirostre, and D. selenops* in *Dasyscopelus.* We restrict *Myctophum* to *Myctophum affine, M. aurolaternatum*, *M. nitidulum*, and *M. punctatum*. Finally, several species of *Myctophum* (*M. fissunovi, M. indicum, M. lunatum, M. novaeseelandiae,* and *M. ovcharovi*) are retained in *Myctophum* (*incertae sedis*) until further morphological or molecular work is completed to resolve their placement.

Fraser-Brunner (1949) found it difficult to discriminate between species in *Dasyscopelus* and those in *Myctophum,* but he identified that the two genera possessed variation in cycloid and/or ctenoid scales. Fraser-Brunner (1949) described *Myctophum aurolaternatum*, *M. punctatum, and Dasyscopelus lychnobium* as having cycloid scales, with *M. affine* possessing mostly cycloid with a few feebly ctenoid scales. He further noted that *D. asperum*, *D. brachygnathum,* and *Dasyscopelus spinosum* possess ctenoid scales. Additionally, Gibbs (1957) describes *M. nitidulum* with cycloid scales. We find most species present in *Dasyscopelus* as possessing ctenoid scales and those in *Myctophum* possessing cycloid scales, but further work is needed to study the scale morphology of *Dasyscopelus* and *Myctophum*.

Moser and Ahlstrom (1970) described two major groups of *Myctophum* based on larval photophore characters. The first group includes species that only form the Br_2 photophore (Fig. 2) during the larval period. This group includes *Myctophum affine, M. nitiduum*, and *M. punctatum,* all of which are classified in *Myctophum* (*sensu stricto*). They removed *M. aurolaternatum* due to its uniquely long larval eye stalks and trailing gut, but would have included it in this group. The second group is characterized by the additional appearance of the Dn photophore (Fig. 2) in the larval stage and includes *Dasyscopelus asperum*, *D. lychnobium*, *D. obtusirostre*, *D. selenops*, and *D. spinosum*, with a hesitant placement of *D. brachygnathum*, and *Myctophum/Dasyscopelus fissunovi*. The placement of the species in separate larval groups is congruent with our total-data tree (Fig. 4) and suggests a possible placement of *M. fissunovi* in *Dasyscopelus*.

5. Conclusion

This study is the first to examine the evolutionary relationships of lanternfishes (Myctophiformes) through an integration of ultraconserved elements, nuclear and mitochondrial gene fragments, and morphological characters. We inferred a monophyletic Neoscopelidae (blackchins) and a monophyletic Myctophidae (lanternfishes) within the Myctophiformes. Within Neoscopelidae we recover *Scopelengys* sister to *Solivomer*, with *Neoscopelus* as the stem neoscopelid. Within Myctophidae we found the historical classification incongruent with our phylogenetic tree which necessitated the taxonomic revisions presented in this manuscript. Our taxonomic revisions recognize five subfamilies instead of the traditional two, although the taxonomic composition of these subfamilies are broadly consistent with historical tribes. We promote three former lampanyctine tribes to subfamily level, including Gymnoscopelini to Gymnoscopelinae, Notolychnini to Notolychninae, and Diaphini to Diaphinae (Fig. 5). We additionally restrict Lampanyctinae to the genera that resided within Lampanyctini (*sensu* Paxton et al., 1984). We recover the Notolychninae sister to a restricted Lampanyctinae, and the Diaphinae sister to the Myctophinae. Within the Lampanyctinae we recover a paraphyletic *Lampanyctus* and *Nannobrachium* clade and place *Nannobrachium* into the synonymy of *Lampanyctus*. We resolve a polyphyletic *Myctophum* within the Myctophinae. For the resulting clades historically classified within *Myctophum* we resurrect *Ctenoscopelus* and *Dasyscopelus* (Fig. 4). Further work is needed to address the paraphyletic *Lampadena* and *Benthosema*.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ympev.2017.12.029.

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