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# Phylogenomics of Lanternfishes and the Evolution of Feeding Structures

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# Phylogenomics of Lanternfishes and the Evolution of Feeding Structures

by

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## Abstract

Mechanisms of speciation in the deep-sea, an environment with few physical isolating barriers, are relatively understudied in deep-sea fishes. This research focuses on the lanternfishes (Myctophiformes ~250 species) as a study system to investigate speciation in deep-sea environments and to test new phylogenomic approaches at resolving contested phylogenetic relationships. Previous phylogenetic hypotheses of lanternfishes identify two monophyletic families (Myctophidae and Neoscopelidae) and two monophyletic subfamilies within Myctophidae (Myctophine and Lampanyctinae), based on morphological and molecular data. Although subfamily relationships have generally remained the same, hypotheses of higher order (tribe, genus, species) relationships lack resolution. This study is the first to infer the evolutionary relationships of lanternfishes with a genome scale target-enrichment approach with ultraconserved elements (UCEs), which are noncoding areas of the genome that are highly conserved across distantly related taxa. Our results infer a phylogeny of lanternfishes that includes a monophyletic Neoscopelidae, a monophyletic Myctophinae, and a paraphyletic Lampanyctinae. We elevate two tribes to subfamilies (Gymnoscopelinae and Diaphinae both previously within Lampanyctinae) in addition to Lampanyctinae and Myctophinae. Gymnoscopelinae was resolved as the stem myctophid group and Diaphinae as sister to Myctophinae. Little is known regarding how lanternfish achieved such high species richness in the deep sea, and many studies have focused on their bioluminescence. This study also focuses on the evolution of feeding structures in lanternfishes and the potential for niche differentiation in this group. Geometric morphometrics were performed on 955 lanternfish specimens, and an ancestral character-state reconstruction was used to examine patterns of evolution in mouth size in lanternfishes. We identify that mouth size in lanternfishes is highly variable, with general trends towards larger mouths in Lampanyctinae and Gymnoscopelinae and shorter mouths in Myctophinae. Of particular note, Diaphinae was found to occupy a large range of morphospace, with broad plasticity in mouth size among the examined species. To further investigate the evolution of feeding structures, we examined 229 lanternfish specimens within Myctophiformes, assessing variation in tooth anatomy, presence on tooth bearing bones, and presence of heterodonty. An ancestral character-state reconstruction was also used to examine the evolution of heterodonty in this group. Our results support at least four separate evolutions of heterodonty in lanternfishes. Once in the common ancestor of the tribe Lampanyctini, once in *Diogenichthys*, once in *Centrobranchus*, and possible multiple evolutions in *Diaphus.* Heterodonty tooth types are expressed by four different anatomical variations around a global ‘hook’ shape, which have allowed for specialization in feeding.

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# Table of Contents

Chapter Page

Chapter Page

## List of Tables

## List of Figures

## Nomenclatural Disclaimer

The taxonomic changes presented herein, including new taxa, combinations, and synonymy, are disclaimed as nomenclatural acts and are not available, in accordance with Article 8.3 of the International Code of Zoological Nomenclature.

# CHAPTER I: EVOLUTIONARY RELATIONSHIPS OF LANTERNFISHES (TELEOSTEI: MYCTOPHIFORMES) USING ULTRACONSERVED ELEMENTS

## Introduction

Lanternfishes are among the most species-rich groups of fishes endemic to open-ocean environments, containing approximately 257 species in 36 genera (Eschmeyer, Fricke, & Van der Laan, 2017). They include six species in the family Neoscopelidae (blackchins) and 251 species in the family Myctophidae (lanternfishes). Lanternfishes reside in the mesopelagic and bathypelagic zones between 200–3,000 m deep and are common worldwide, accounting for more than half of all midwater-fish biomass (Paxton, 1972; Sutton, Wiebe, Madin, & Bucklin, 2010). They move from the mesopelagic and bathypelagic zones during the day into the shallower epipelagic zone at night following their prey (e.g. copepods, ostracods; Paxton, 1967; Holton, 1969; Gaskett, Bulman, He, & Goldsworthy, 2001), and their vertical migration plays a major role in the oceanic ecosystem by transferring energy from shallower to deeper oceanic levels (Paxton, 1972; Springer, Piatt, & Vliet, 1996; Collins et al., 2008; Davis, 2015).

Lanternfishes possess bioluminescent photophores and light organs located in various positions on the body, that produce light endogenously (Davis, Sparks, & Smith, 2016). Photophores situated in lateral rows along the ventral surface of the body are thought to counter illuminate and provide camouflage by mimicking the limited downwelling light from above (Lawry, 1974; Case, Warner, Barnes, & Lowenstine, 1977; Haddock, Moline, & Case, 2010). In

contrast to ventral photophores, Davis, Holcroft, Wiley, Sparks, and Smith (2014) demonstrated that lateral photophores are species specific and are potentially involved in species recognition. Lanternfishes illustrate extensive variation in sexually dimorphic bioluminescent light organs, including the presence and/or size of specialized light organs at the base of the tail, known as supracaudal and infracaudal light organs, and those located on the head (Herring, 2007). Bioluminescent marine fishes that display sexually dimorphic light organ systems are thought to undergo sexual selection and increased rates of diversification (Davis et al., 2014; Davis et al., 2016), and the increased diversity of lanternfishes may have been aided by selective pressures on their bioluminescent systems (Davis et al., 2014; Davis et al., 2016) in combination with niche differentiation (Martin & Davis, 2016).

Previously, the myctophiform fishes have been hypothesized to be closely related to aulopiform fishes (lizardfishes; Gosline, Marshall, & Mead, 1966). Rosen (1973) separated the Myctophiformes from the Aulopiformes based on the presence of an uncinate process on the second epibranchial in lizardfishes to the exclusion of myctophiforms, and the presence of ctenoid scales that lanternfishes share with members of the Acanthomorpha (spiny-rayed fishes). Taxonomically robust phylogenetic studies on the evolutionary relationships of ray-finned fishes have consistently inferred the monophyly of the lanternfishes based on molecular sequence data (e.g., Near et al., 2012; Betancur-R. et al., 2013; Davis et al., 2014; Davis et al., 2016; Smith, Stern, Girard, & Davis, 2016).

The two families within Myctophiformes (Figure 1.1) include Neoscopelidae (blackchins) and Myctophidae (lanternfishes). Neoscopelidae is comprised of six species in three genera, whereas, Myctophidae includes 251 species and 33 genera (Eschmeyer et al., 2017).

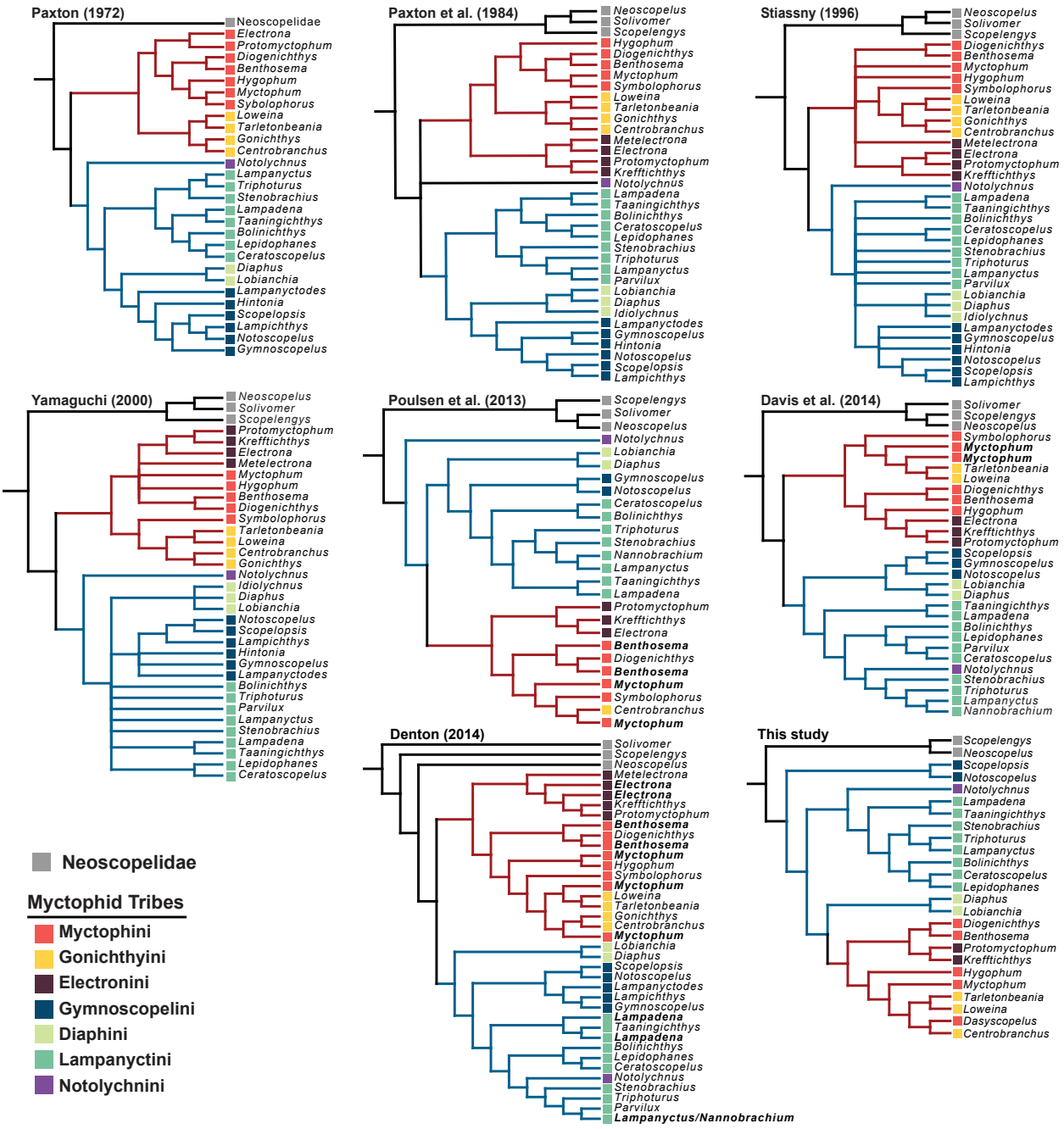


Figure 1.1. Previous and current phylogenetic hypotheses of Myctophiformes. Myctophinae is represented by red lines and Lampanyctinae is represented by blue lines. Previous hypotheses include Paxton (1972), osteology and photophores; Paxton et al. (1984), synapomorphy based reconstruction using osteology, photophore, and larval characters; Stiassny (1996), a maximum parsimony strict consensus analysis of Paxton et al. (1984) character matrix plus four new characters; Yamaguchi (2000), a maximum parsimony strict consensus reanalysis of Stiassny (1996) with polymorphic characters coded as "?"; Poulsen et al. (2013), mitogenomic gene sequences; Denton (2014), six nuclear and one mitochondrial genes; Davis et al. (2014), two nuclear and one mitochondrial genes. Taxa in bold were recovered as non-monophyletic in their respective studies.

Previous phylogenetic analyses have of lanternfishes have repeatedly hypothesized two monophyletic subfamilies within the family Myctophidae (Figure 1.1): Lampanyctinae and Myctophinae. The recognition of these subfamilies is based on adult and larval morphological features (Paxton, 1972; Paxton, Ahlstrom, & Moser, 1984; Stiassny, 1996; Yamaguchi, 2000) and molecular characters (Poulsen et al., 2013; Davis et al., 2014; Denton, 2014, Davis et al., 2016).

Within Myctophidae there are currently seven recognized tribes, including three in the subfamily Myctophinae (Myctophini, Gonichthyini, and Electronini) and four in the subfamily Lampanyctinae (Gymnoscopelini, Diaphini, Lampanyctini, and Notolychnini) as seen in Table 1.1. Paxton (1972) recognized six tribes (Figure 1.1), excluding the tribe Electronini due to it having only one distinguishing character, the location of the PLO photophore being below or near the ventral margin of the pectoral base. This is in comparison to the rest of the taxa in the tribe Myctophini, where the PLO is distinctly above the pectoral base. The tribe Electronini was later recognized by Paxton et al. (1984), and all seven tribes have been recognized and used in subsequent studies on the evolutionary relationships of lanternfishes (Table 1.1; Paxton et al. 1984; Yamaguchi, 2000; Poulsen et al., 2013; Davis et al., 2014; Denton, 2014). The monophyly of the subfamilies within Myctophidae has remained constant with the exception of the phylogenetic placement of tribe Notolychnini, which includes a single species *Notolynchnus valdiviae* (Figure 1.1). The tribe Notolychnini has been placed as the stem tribe within Lampanyctinae (Paxton, 1972; Stiassny, 1996; Yamaguchi, 2000), nested within the tribe Lampanyctini (Davis et al., 2014; Denton, 2014) or in a polytomy with the subfamilies Myctophinae and Lampanyctinae (Figure 1.1; Paxton et al., 1984). Although historically both subfamilies have remained consistent in taxonomic composition (with the exception of

Table 1.1 Historical lanternfish subfamilies, tribes, and genera.

**Order Myctophiformes**
- **Family Neoscopelidae**
  - *Neoscopelus, Scopelengys, Solivomer*
- **Family Myctophidae**
  - **Subfamily Myctophinae**
    - Tribe Myctophini: Fowler, 1925
      - *Benthosema, Diogenichthys, Hygophum, Myctophum, Symbolophorus*
    - Tribe Gonichthyini: Paxton, 1972
      - *Centrobranchus, Gonichthys, Loweina, Tarletonbeania*
    - Tribe Electronini: Wisner, 1963
      - *Electrona, Krefftichthys, Metelectrona, Protomyctophum*
  - **Subfamily Lampanyctinae**
    - Tribe Gymnoscopelini: Paxton, 1972
      - *Gymnoscopelus, Hintonia, Lampanyctodes, Lampichthys, Notoscopelus, Scopelopsis*
    - Tribe Diaphini: Paxton, 1972
      - *Diaphus, Idiolychnus, Lobianchia*
    - Tribe Lampanyctini: Paxton, 1972
      - *Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux, Stenobrachius, Taaningichthys, Triphoturus*
    - Tribe Notolychnini: Paxton, 1972
      - *Notolychnus*

Notolychnini*)*, the phylogenetic relationships among tribes and genera within each subfamily has been more fluid (Figure 1.1).

The aim of this study is to infer the relationships among lanternfishes using genome-scale approach with phylogenomic methods that involve sequence capture of nuclear regions that includes ultraconserved elements (UCEs). Ultraconserved elements are regions of the genome that are highly conserved among evolutionarily distant taxa, and sequence capture probes sets can pull out hundreds of UCE regions (~100-1500 bp each) from a sequenced specimen for use in phylogenetic analyses (Bejerano et al., 2004; Wang, Lee, Kodzius, Brenner, & Venkatesh, 2009; Faircloth et al., 2012). This approach to estimating relationships has been successfully used on various vertebrate groups (e.g. mammals, McCormack et al., 2012; birds, Faircloth et al., 2012; and fishes, Gilbert et al., 2015). In this study we use high-throughput phylogenomic methodology to create a UCE based phylogenomic tree. From this we infer the relationships of lanternfishes and test the monophyly of currently recognized families, subfamilies, and tribes. We compare this work to previous hypotheses of lanternfish relationships based on morphology, mitochondrial genomes, and nuclear and mitochondrial gene fragments (Sanger sequencing). We focus on addressing the following questions: (1) What is the hypothesis of relationships among lanternfishes using genome-scale data? (2) How does this hypothesis compare to previous hypotheses, and how does it differ from previous studies of lanternfish evolution and taxonomy?

# Materials and Methods

## Taxon Sampling

We sequenced 25 lanternfish species representing 25 of 30 genera, and our analysis included six additional species representing closely related euteleosts and acanthomorphs as outgroups (Table 1.2). All analyses were rooted with *Guentherus altivelis* (Ateleopodiformes). All DNA was extracted from muscle or fin clips using a DNeasy Tissue Extraction Kit (Qiagen) following the manufacturer's protocol. The first and second elution from a Qiagen filter were combined and dried down with a DNA SpeedVac Concentrator (Thermo Fisher) to a 102 µL volume. Using 2µL, we quantified each template using a Qubit fluorometer (Life Technologies) using the dsDNA BR Assay Kit following the manufacturer's protocol. Quantified samples (100µL volume) were sent to MYcroarray (Ann Arbor MI) who performed library preparation (e.g., DNA shearing, size selection, cleanup), target capture (using the 500 UCE actinopterygian loci probe set; Faircloth, Sorenson, Santini, & Alfaro, 2013) and enrichment, sequencing using an Illumina HiSeq 2500, and demultiplexing of samples. Institutional abbreviations for museum and collection acronyms used for anatomical and tissue vouchers follow Sabaj (2016).

## UCE Assembly and Phylogenetic Analysis

We used software programs to analyze ultraconserved data received from MYcroarray in Fastq format, and to create a phylogenetic tree of lanternfishes using UCEs. Sequences were cleaned of indices and adapters using illumiprocessor (Faircloth, 2013) and trimmomatic (Bolger, Lohse, & Usadel, 2014). Reads were assembled, by species, into contigs using ABySS (Simpson et al., 2009), with the kmer value set to 60. After assembly, we used a software package that utilized LASTZ (Large-Scale Genome Alignment Tool; Harris, 2007), and the

Table 1.2. Voucher specimens for new UCE sequences.

| Taxon | Tissue/Voucher |
|---|---|
| **Outgroup** | |
| *Alepisaurus ferox* | SIO 96-3 |
| *Chloropthalmus nigromarginatus* | FMNH 121202 |
| *Guentherus altivelis* | USNM 386478 |
| *Hoplostethus mediterraneus* | A. Dettai Pers. Coll. |
| *Polymixia berndti* | Uncat. AMNH 364 |
| *Synodus variegatus* | SIO 04-63 |
| | |
| **Ingroup** | |
| *Benthosema glaciale* | KU 3058 |
| *Bolinichthys longipes* | SIO 10-164 |
| *Centrobranchus* sp. | Uncat. AMNH A23 |
| *Ceratoscopelus townsendi* | SIO 06-91 |
| *Dasyscopelus orientale* | KU T10933 |
| *Diaphus theta* | KU 2135 |
| *Diogenichthys atlanticus* | SIO 09-99 |
| *Hygophum reinhardti* | SIO 09-320 |
| *Krefftichthys andersoni* | CSIRO GT 390 |
| *Lampadena speculigera* | KU 5916 |
| *Lampanyctus macdonaldi* | KU 7446 |
| *Lepidophanes guentheri* | KU 3796 |
| *Lobianchia gemellari* | SIO 10-171 |
| *Loweina rara* | SIO 10-171 |
| *Myctophum auroleternatum* | SIO 06-295 |
| *Neoscopelus macrolepidotus* | KU 3291 |
| *Notolychnus valdiviae* | SIO 10-166 |
| *Notoscopelus caudispinosus* | KU 5301 |
| *Protomyctophum thompsoni* | KU 2133 |
| *Scopelengys tristis* | KU 3240 |
| *Scopelopsis multipunctatus* | CSIRO GT 3776 |
| *Stenobrachius leucopsarus* | Uncat. |
| *Taaningichthys bathyphilus* | SIO 10-174 |
| *Tarletonbeania crenularis* | SIO 06-88 |
| *Triphoturus oculeum* | SIO 06-293 |

Faircloth et al. (2013) fish probe set, to find reciprocally unique UCE matches and aligned them to the species-specific contigs. LASTZ was set at 80% for the minimum coverage and 80% for the minimum identity for identifying UCEs. This software package also contained a custom Python program (match_contigs_to_probes.py) that removed reciprocal and non-reciprocal duplicate hits from the data set, and created a relational database of matches to UCE loci by taxon. FASTA files of the UCE data identified across all taxa were constructed by PHYLUCE (Faircloth et al., 2012). Contigs were aligned using MAFFT (Katoh & Standley, 2013), and Python (seqcap_align_2.py) then trimmed the contigs representing UCEs, in parallel, across the selected taxa prior to phylogenetic analysis. A 65% data matrix was created and concatenated in MAFFT for RAxML. We performed 20 independent runs in RAxML (Randomized Axelerated Maximum Likelihood; Stamatakis, 2014) of the concatenated data utilizing a GTR+G substitution model and picked the best tree of 20. The rapid bootstrapping algorithm was set at 1,000 and stopped at 250 bootstrap replicates based on MRE bootstrapping criterion. A total of 445 UCE fragments were used for a final length of 335,071 bps. Sequence fragment lengths were ~100–1,400 bps. Phylogenetic trees were created in FigTree (Rambaut, 2007). Additionally, we ran an independent likelihood analysis (RAxML) on each UCE and used Astral II (Mirarab & Warnow, 2015) to create a species tree from all the individual gene trees. The likelihood analysis on each UCE had the best tree of 5 replicates. A run of 100 bootstraps were done on each of the 445 UCEs and were summarized in ASTRAL II. Bootstrap support of species-tree nodes were denoted on the concatenated tree (Figure 1.2).

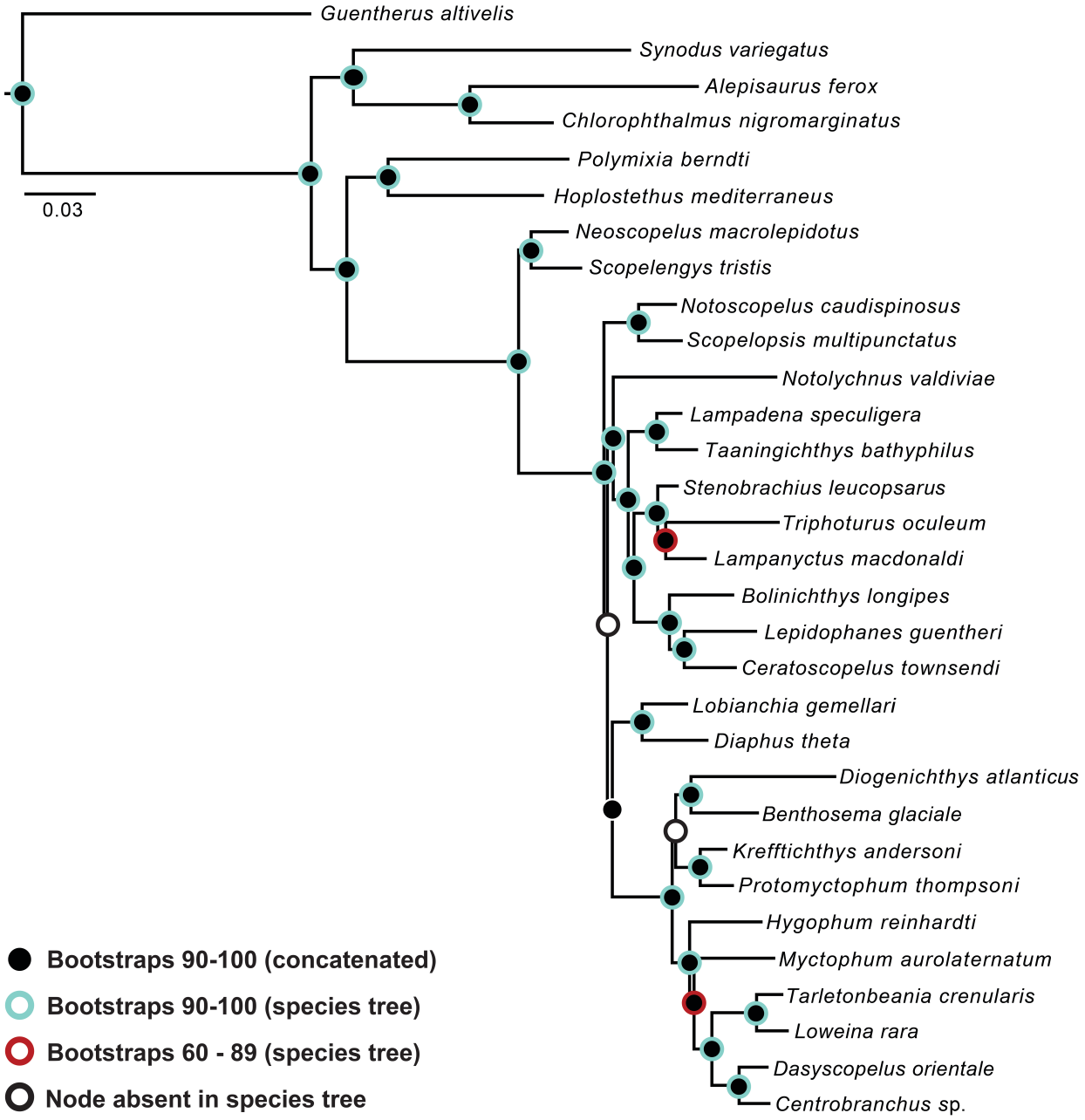


Figure 1.2. Maximum likelihood phylogeny of lanternfish relationships based upon UCE sequences. All nodes except for two are supported by bootstrap proportions ≥ 0.90 in concatenated tree.

## Results

The results from our maximum likelihood analysis inferred a monophyletic Myctophiformes as the sister group to Acanthomorpha (Figure 1.2). These findings are consistent with previous morphological (e.g., Rosen, 1973; Mirande, 2016) and molecular (e.g., Near et al., 2012; Davis et al., 2016; Smith et al., 2016) work (Figure 1.1). The two families within Myctophiformes, Neoscopelidae and Myctophidae, were recovered as monophyletic sister groups with strong bootstrap support (≥ 0.90; Figure 1.2). Within Myctophidae, taxa from the subfamily Lampanyctinae are recovered as paraphyletic with respect to Myctophinae with three distinct clades recognized herein as three subfamilies. The first clade includes fishes from the tribe Gymnoscopelini (bootstrap ≥ 0.90; *Gymnoscopelus, Hintonia*, *Lampanyctodes, Lampichthys, Notoscopelus,* and *Scopelopsis*) and requires the recognition of this clade as the subfamily Gymnoscopelinae (Figures 1.2, 1.3), a name first described by Paxton (1972). This Gymnoscopelinae is the stem myctophid lineage and was sister to a clade that includes the tribes Notolychnini, Lampanyctini, Diaphini, Myctophini, Electronini, and Gonichthyini (Figures 1.2, 1.3). A second recovered clade includes the monophyletic group comprised of genera from the Lampanyctini *(Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux, Stenobrachius, Taaningichthys,* and *Triphoturus*) and Notolychnini (*Notolychnus*), with a bootstrap support of ≥ 0.90 (Figures 1.2, 1.3) and is recognized here as Lampanyctinae. Lampanyctinae was recovered as the sister group to a clade containing the tribes Diaphini, Myctophini, Electronini, and Gonichthyini. The Diaphini + Myctophini + Electronini + Gonichthyini clade contains a monophyletic group that includes the tribe Diaphini (*Diaphus* and *Lobianchia*; bootstrap ≥ 0.90) and requires the recognition of the Diaphinae, (Figures 1.2, 1.3).

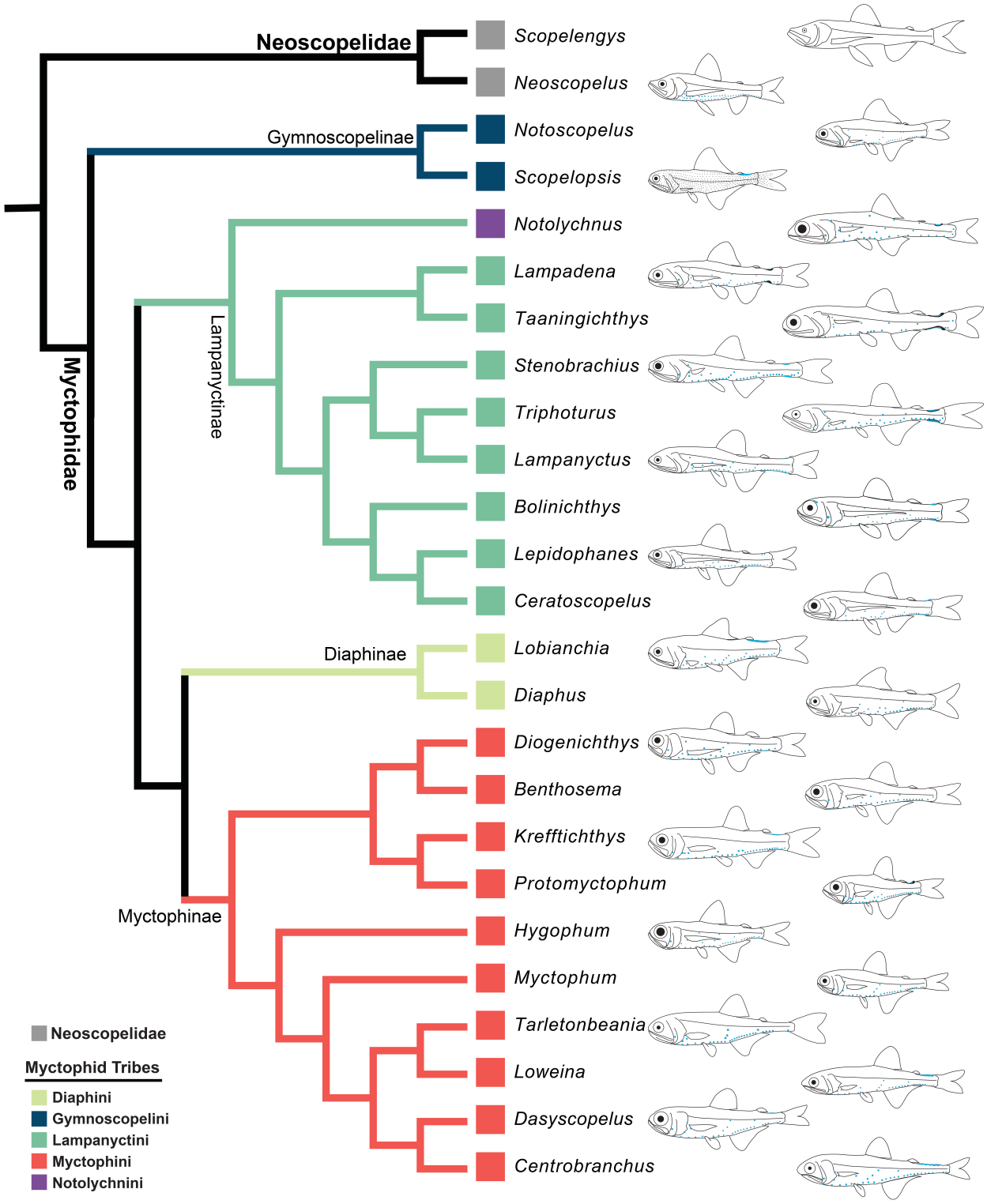


Figure 1.3. Cladogram of maximum likelihood UCE phylogeny of lanternfishes presenting new proposed subfamilies and taxanomic revision of Myctophini. Lanternfish drawings based on work done by Nafpaktitis (1977) and Nafpaktitis et al. (1977).

Diaphinae is the sister group to Myctophinae (bootstrap ≥ 0.90), which includes the tribes Myctophini, Gonichthyini, and Electronini (Figures 1.2, 1.3).

## Discussion

### Evolutionary Relationships of Myctophiformes

This work seeks to resolve the interrelationships of myctophid tribes and genera with the analysis of a genome-wide (UCE) dataset. 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; Davis et al., 2016) in recovering a monophyletic Myctophiformes, Myctophidae, and Neoscopelidae (Figures 1.2, 1.3). The monophyly of Myctophiformes is historically supported by seven anatomical synapomorphies (Wiley & Johnson, 2010), six are described from Stiassny (1996): a median dorsal keel present on mesethmoid, median maxillo-premaxillary buccal ligaments (VIII) insert on contralateral buccal elements, large tooth plate fused to proximal face of fourth ceratobranchial, first external levator reduced or absent, first centrum with enlarged, cone-like parapophyses, and adipose fin support ventrally inserted into supracarinalis posterior muscle mass. Springer and Johnson (2004) identified an additional anatomical synapomorphy for Myctophiformes: possessing tranversus pharyngobranchials 2a and 2b.

Most previous studies have inferred a monophyletic Neoscopelidae (blackchins) based on molecular and morphological data (Figure 1.1), which is also recovered with our genome-wide study (Figures 1.2, 1.3). We also recover a monophyletic Myctophidae, consistent with all previous studies (Figure 1.1). The monophyly of Myctophidae is described by numerous

synapomorphic characters, some of which are described in Stiassny (1996), which include but are not limited to: reduction of the dorsal hypohyal element (HH1), first levator muscle subdivided into two heads independently inserted onto the second pharyngobranchial element, bony connection between the descending process of the third hypobranchial element with the urohyal, bony articulation between the urohyal and the second, or second and third, basibranchial element, and cylindrical median rostral cartilage firmly bound to mesethmoid, loosely bound to buccal jaws.

Our results inferred unique relationships within the lanternfishes (Myctophidae) wherein Lampanyctinae *sensu* Paxton (1972) was recovered as a paraphyletic grade with Myctophinae nested within it, as the sister group to the tribe Diaphini (Figures 1.2, 1.3). Previous studies using morphological (Paxton, 1972; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000) and molecular data (Poulsen et al., 2013; 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 Lampanyctinae 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).

The paraphyletic grade of lampanyctine myctophids is composed of three distinct clades that we herein recognize as the subfamilies: Gymnoscopelinae, Lampanyctinae, and Diaphinae (Figure 1.3). Gymnoscopelinae (Gymnoscopelini) was recovered as the sister group to all other myctophids. Subsequently, a restricted Lampanyctinae (Lampanyctini and Notolynchnini) was recovered as the sister group to Diaphinae+Myctophinae clade. The monophyly of Lampanyctinae+Diaphinae+Myctophinae is supported by the loss of the supramaxillae

(Yamaguchi, 2000: Character 6). Finally, Myctophinae was recovered as the sister group to Diaphinae, with the monophyly of these two subfamilies supported by the transition from zero to one or more ossified distal pectoral radials (Yamaguchi, 2000: Character 25). With the exception of tribes within the Myctophinae, historically recognized tribes (Figure 1.1, Table 1.1) are recovered as monophyletic with our genome-wide study (Figures 1.2, 1.3). The phylogenetic placement of myctophiform genera within tribes have been largely consistent among molecular studies (Figure 1.1), thus we will be placing the few genera that were not included in our analysis (noted with an asterisk) into our classification following their phylogenetic placement as presented in previous molecular studies (Poulsen et al., 2013; Davis et al., 2014; Denton, 2014).

**Relationships within Gymnoscopelinae**

This study resolves Gymnoscopelinae (*Gymnoscopelus*, Hintonia*, Lampanyctodes*, Lampichthys*, Notoscopelus,* and *Scopelopsis*) as the stem clade of myctophids (Figure 1.3). Optimizing the characters from Yamaguchi (2000) on our hypothesis of evolutionary relationships (Figure 1.3) infers six unambiguous synapomorphies for the Gymnoscopeline: an increase in the number of procurrent ventral rays (Yamaguchi, 2000: Character 5); presence of slightly hooked teeth in posterior dentary (Yamaguchi, 2000: Character 11); presence of dorsal process of opercular head of hypomandibula (Yamaguchi, 2000: Character 16); presence of keel or ridge on fifth circumorbital (Yamaguchi, 2000: Character 26); accessory luminous tissue present (Yamaguchi, 2000: Character 48); larval photophores (except $Br_2$) present (Yamaguchi, 2000: Character 53; Figure 1.4).

This subfamily is atypical among myctophids in that it includes four monotypic genera (*Hintonia, Lampanyctodes, Lampichthys,* and *Scopelopsis*). *Scopelopsis multipunctatus,* unlike

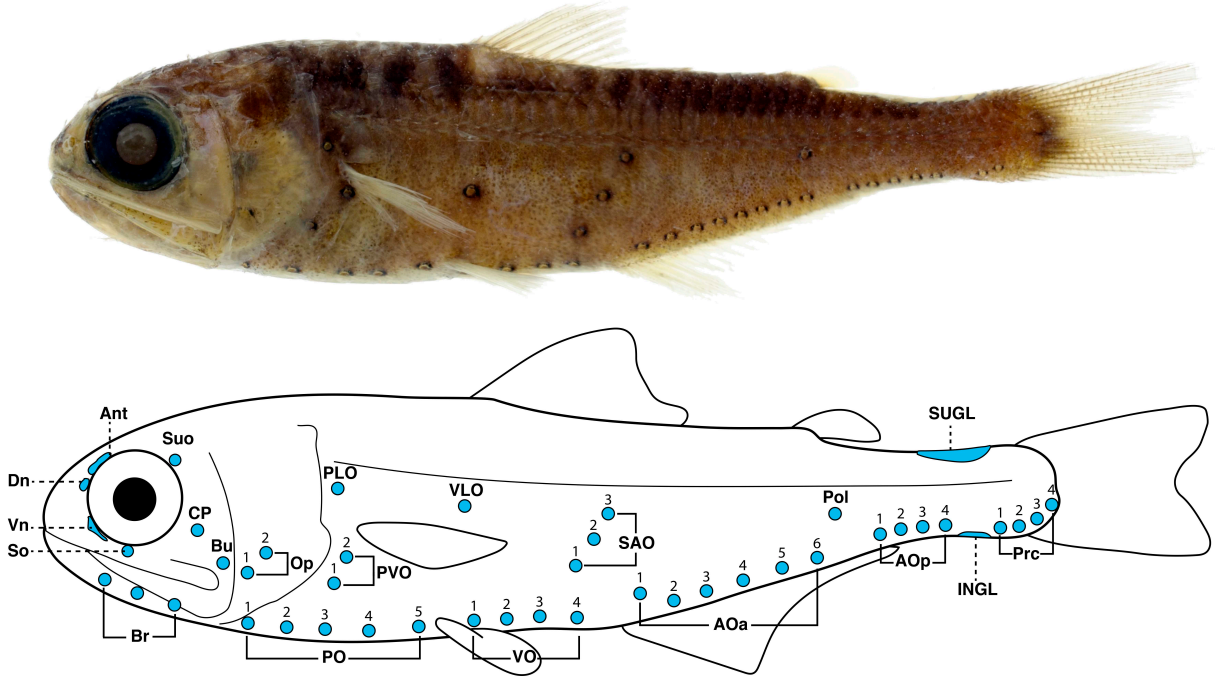


Figure 1.4. Example of photophores located on a specimen *Myctophum affine* (FMNH 59974). Diagram exhibiting general placement of bioluminescent photophores and luminous glands on species within Myctophidae. **Ant**, antorbital organ; **AOa**, anterior anal organs; **AOp**, posterior anal organs; **Br**, branchiostegal organs; **Bu**, buccal organ; **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**, sub pectoral luminous glands; **SAO**, supraanal organs; **So**, suborbital organ; **Suo**, supraorbital organ; **SUGL**, supracaudal luminous gland; **VLO**, supraventral organ; **Vn**, ventronasal organ; **VO**, ventral organs.

all other myctophids, possesses secondary photophores on every scale (Moser & Ahlstrom, 1972). Most species in this subfamily are restricted to oceans in the southern hemisphere, with the exception of species in *Notoscopelus,* which are found in oceans globally (Paxton, 1972).

**Relationships within Lampanyctinae**

Our revised Lampanyctinae includes the tribes Lampanyctini (*Bolinichthys, Ceratoscopelus, Lampadena, Lampanyctus, Lepidophanes, Parvilux*, Stenobrachius, Taaningichthys,* and *Triphoturus*) and the monotypic Notolychnini (*Notolychnus*). Our study indicates that the traditionally taxonomically difficult Notolychnini belongs within Lampanyctinae (Figures 1.2, 1.3). The problematic placement of *Notolychnus* in previous phylogenetic hypotheses based on morphological characters (Figure 1.1) is likely because *Notolychnus* exhibits "intermediate" states among species of Lampanyctinae and Myctophinae (Paxton, 1972). For example, *Notolychnus* lacks a postero-medial shelf similar to taxa in Myctophinae; whereas, this shelf is present in all other Lampanyctinae taxa (Paxton, 1972). Additionally, *Notolychnus* only has two Prc photophores on their caudal peduncle similar to the number observed in species within Myctophinae, where, in comparison, other lampanyctines (*sensu stricto*) have three to nine Prc photophores (Figure 1.4). Additionally, larval myctophine eyes are elliptical in outline; whereas, the eyes are round in lampanyctines. *Notolychnus* has intermediate semi-elliptical eyes (Moser & Ahlstrom, 1970). Most other characters exhibited by *Notolychnus* suggest a close affinity with lampanyctines (Paxton, 1972). Poulsen et al. (2013) placed *Notolychnus* as the stem myctophid lineage based on an analysis of mitochondrial genomic data. In contrast, recent studies utilizing three to seven mitochondrial or nuclear gene fragments derived from Sanger sequencing have inferred *Notolychnus* as nested within the

Lampanyctini (Davis et al., 2014; Denton, 2014). There are no unambiguous anatomical characters that unite the Lampanyctinae as recognized in this study. This is not surprising given the historically problematic placement of *Notolychnus* based on anatomy alone. However, the tribe Lampanyctini (i.e., all lampanyctines except *Notolychnus*) within Lampanyctinae is united by three unambiguous morphological characters: presence of moderately to strongly hooked teeth in posterior dentary (Yamaguchi, 2000: Character 4); presence of Dn photophore (Yamaguchi, 2000: Character 45); presence of sexual dimorphism in caudal luminous organs (Yamaguchi, 2000: Character 47).

This study finds that the relationships of genera within Lampanyctini grouped into three main lineages. *Lampadena* and *Taaningichthys* form a clade, which is sister to all remaining lampanyctine lineages distributed in two broader clades (Figure 1.3). The first clade includes the genera *Stenobrachius, Lampanyctus,* and *Triphoturus,* with these taxa identified as having a shared unique mitochondrial gene rearrangement (Poulsen et al., 2013). Davis et al. (2014) indicated that *Lampanyctus* exhibits exceptional species richness given the clade age. The other clade contains *Bolinichthys, Lepidophanes*, and *Ceratoscopelus.* The presence of these three clades within Lampanyctini (with the exception of the presence or absence of *Notolychnus*) is consistent throughout most historical myctophid phylogenies (e.g., Paxton, 1972; Paxton et al., 1984; Poulsen et al., 2013; Denton, 2014; Davis et al., 2014), but the relationships of these clades to each other has lacked corroboration among studies (Figure 1.1).

As noted above, one synapomorphy of the Lampanyctini is the presence of anterior facing ‘recurved’ teeth on the posterior portion of the dentary. These specialized teeth are hypothesized to inhibit the loss of prey items in the mouth cavity (Paxton, 1972). Many of the species in this

group display additional cheek and secondary photophores (Figure 1.4; Paxton 1972;). Denton (2014) called into question the monophyly of *Nannobrachium* and suggested that the validity of the genus be revisited. Given the results of Poulsen et al. (2013), Davis et al. (2014), and Denton (2104), we consider *Nannobrachium* to be a synonym of *Lampanyctus* (type species *Lampanyctus crocodilus*; Risso, 1810).

**Relationships within Diaphinae**

The subfamily Diaphinae (tribe Diaphini) is comprised of three genera, *Lobianchia, Idiolychnus** and the species-rich genus *Diaphus* (~30% of myctophid diversity; Froese & Pauly, 2016). Our results corroborate all previous hypotheses that recovered Diaphinae as a monophyletic group (Figure 1.1). Some previous studies using either morphological (Paxton, 1972; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000) or molecular (Poulsen et al., 2013; Davis et al., 2014) data resolved Diaphini nested within Lampanyctinae *sensu* Paxton (1972) as seen in Figure 1. Denton (2014) resolved Diaphini as the stem lineage within Lampanyctinae *sensu* Paxton (1972). Our study infers a novel placement for the clade, resolving Diaphinae (Diaphini) as the sister group to Myctophinae (Figures 1.2, 1.3), separate from Lampanyctinae (*sensu lato*). Optimizing the characters from Yamaguchi (2000) on our resulting tree (Figure 1.3) recognizes five synapomorphes for the Diaphinae: presence of a wide pubic plate (Yamaguchi, 2000: Character 7); a raised $PO_4$ photophore (Yamaguchi, 2000: Character 32); a raised $VO_3$ photophore (Yamaguchi, 2000: Character 34); presence of larval photophores, except $BR_2$ (Yamaguchi, 2000: Character 53); lack of pigment on the head (Yamaguchi, 2000: Character 60; Figure 1.4). Poulsen et al. (2013) also found a unique mitochondrial gene rearrangement in Diaphinae taxa.

*Diaphus* is the most species rich genus in the Myctophidae, containing 77 species (Froese & 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); alternatively, it has evolved a diverse system of anteriorly facing light organs on the head (Figure 1.4). These additional head light organs may be used to find or stun prey items, are often sexually dimorphic, and may play an important role in the radiation of this lineage (Paxton, 1972; Sparks, Dunlap, & Smith, 2005). Recent work looking at the evolution of mouth size in lanternfishes (Martin & Davis, 2016) identified *Diaphus* as being one of the few myctophid lineages to have species with both long and short upper jaws. 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 & Davis, 2016).

**Relationships within Myctophinae**

This study resolves a monophyletic Myctophinae including 14 genera (*Benthosema, Centrobranchus, Dasyscopelus, Diogenichthys, Electrona*, Gonichthys*, Hygophum, Krefftichthys, Loweina, Metelectrona*, Myctophum, Protomyctophum, Symbolophorus*, Tarletonbeania*). 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 Figure 1.1. The Myctophinae are united by eight unambiguous morphological synapomorphies: presence of comparatively short jaw length (Yamaguchi, 2000: Character 1); loss of an extrascapular (Yamaguchi, 2000: Character 2); lack of a fused third epibranchial toothplate (Yamaguchi, 2000: Character 27); presence of an elongate second basibranchial (Yamaguchi, 2000: Character 28); absence of a urohyal with elongated anterior process and reduced articular facet (Yamaguchi,

2000: Character 29); absence of a dorsally projecting metapterygoid strut (Yamaguchi, 2000: Character 30); one Pre photophore (Yamaguchi, 2000: Character 31); narrow larval eyes (Yamaguchi, 2000: Character 50). The Myctophinae genera within the present study can be grouped into two major clades. The first clade contains *Diogenichthys+Benthosema* as sister to *Kerfftichthys+Protomyctophum* (Figure 1.3). The sister groups within this clade have high bootstrap support (≥ 0.90), but the clade itself was poorly supported (Figure 1.2). The second major clade resolves *Hygophum* as the stem genus, followed by *Myctophum,* which is then sister to a crown group containing *Tarletonbeania+Loweina* sister to *Dasyscopelus+Centrobranchus* (Figure 1.3). Species within Myctophinae have reduced their non-photophore luminous tissue to the supracaudal and infracaudal glands (Figure 1.4). Sexual dimorphism is exhibited in many species that posses these caudal light organs, which are found in most or all members within Myctophinae (Paxton, 1972; Herring, 2007).

Since the work of Paxton et al. (1984), there have been three recognized tribes within the Myctophinae: Myctophini, Gonichthyini, and Electronini. The phylogenetic hypothesis of lanternfishes presented by Paxton et al. (1984) used a diversity of morphological characters in a synapomorphic reconstruction using a parsimony criterion, to support the monophyly of these three tribes (Figure 1.1). More recent studies have utilized maximum parsimony (Stiassny, 1996; Yamaguchi, 2000) and maximum likelihood and bayesian computational analyses (Poulsen et al., 2013; Davis et al., 2014; Denton, 2014, Davis et al., 2016). In these studies, the relationships of lanternfishes within Myctophini, Gonichthyini, and Electronini, have lacked consistent monophyletic composition (Figure 1.1). Stiassny (1996) resolved Myctophinae as a polytomy, and Gonichthyini as the only monophyletic tribe within the subfamily. Yamaguchi (2000),

building off of Paxton (1984) and Stiassny (1996), had similar results, resolving two clades within Myctophinae, a monophyletic Gonichthyini and a clade comprising a polytomy of Myctophini and Electronini (Figure 1.1). Poulsen et al. (2013) and Denton (2014) resolved a monophyletic Electronini and a paraphyletic Myctophini. Davis et al. (2014) had similar findings, with a monophyletic Electronini nested within a paraphyletic Myctophini (Figure 1.1). This study resolved a monophyletic Electronini nested within a paraphyletic Myctophini, and resolves a paraphyletic Gonichthyini (Figures 1.1, 1.2). These previous studies show a lack of consistent monophyly in the tribes Electronini, Myctophini, and Gonichthyini (Stiassny, 1996; Yamaguchi, 2000; Poulsen et al., 2013; Davis et al., 2014; Denton 2014.). Due to this inconsistency, the genera *Centrobranchus, Electrona, Gonichthys, Krefftichthys, Loweina, Metelectrona, Protomyctophum,* and *Tarletonbeania* were previously recognized as members of the tribes Gonichthyini and Electronini, are recognized here as belonging to the tribe Myctophini (Figure 1.3).

Within Myctophini, we resolved a paraphyletic *Myctophum,* with *M. orientale* nested within Gonychthyini, separate from *M. aurolaternatum*. This finding corroborates Paulson et al. (2013) who resolved *M. asperum* and *M. orientale* as separate from a clade containing *M. affine, M. nitidulum,* and *M. punctatum*. Poulsen et al. (2013) also found the *M. affine+M. nitidulum+M. punctatum* clade to have a unique mitochondrial gene rearrangement, whereas *M. asperum+ M. orientale* displayed the typical myctophid gene order. Denton (2014) resolved a clade of *Myctophum* that included *M. asperum, M. brachygnathum, M. lychnobium, M. obtusirostre, M. orientale, M. selenops,* and *M. spinosum,* as separate from *M. affine, M. aurolaternatum*, *M. nitidulum*, and *M. punctatum* (type species, Rafinesque, 1810). Based on our

work and these previous studies, the polyphyly of fishes traditionally recognized in the genus *Myctophum* requires the recognition of *M. asperum, M. brachygnathum, M. lychnobium, M. obtusirostre, M. orientale, M. selenops,* and *M. spinosum* in *Dasyscopelus* (Günther, 1864), type species *Dasyscopelus asperum* (Figure 1.3).

**Classification**

We present a new classification of myctophiform families, subfamilies, tribes, and genera (Table 1.3). Asterisks indicate genera not included in analyses. Classification follows phyletic sequence, and reflects the results of both the maximum-likelihood and species-tree analyses.

## Conclusions

We recovered a well-supported phylogeny of lanternfishes using UCE data that includes a monophyletic subfamily Myctophinae, and a paraphyletic historical subfamily Lampanyctinae. We elevated the tribes Gymnoscopelini and Diaphini to subfamily level (Gymnoscopelinae and Diaphinae) in addition to a revised Lampanyctinae and the historical Myctophinae. We synonymized the tribes Electronini and Gonichthyini into Myctophini. We revised the genus *Myctophum* and reinstated the genus *Dasyscopelus* based on support from this study and previous studies (Paulson et al., 2013; Denton, 2014). Additionally, we synonymized the genus *Nannobrachium* into the genus *Lampanytus*.

Table 1.3. Revised classification of Myctophiformes.

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

# CHAPTER II: PATTERNS OF PHENOTYPIC VARIATION IN THE MOUTH SIZE OF LANTERNFISHES (TELEOSTEI: MYCTOPHIFORMES)

## Introduction

Lanternfishes (Teleostei: Myctophiformes) are one of the most species-rich groups of fishes endemic to deep-sea open-ocean environments, containing approximately 257 species in 36 genera (Nelson, 2006; Eschmeyer et al., 2017). They include members from two families, Neoscopelidae (blackchins) and Myctophidae (lanternfishes). Lanternfishes are common worldwide and account for greater than 50% of all midwater-fish biomass (e.g., Paxton, 1972; Sutton et al., 2010; Olivar et al., 2012). They are predominantly found in the mesopelagic zone between 200–1000 m and make up a large percentage of the deep scattering layer. This layer was identified when sonar waves bounced off of the gas-filled swim bladders of millions of mesopelagic fishes and emulated a 'false seafloor' (Barham, 1966; Tont, 1976). Most lanternfishes perform diel vertical migrations, moving from the mesopelagic to the epipelagic zone at night to feed and retreating to the relative darkness of the mesopelagic during the day. Lanternfishes are prey for a variety of organisms (e.g., dragonfishes and lizardfishes), and this daily migration plays a major role in the oceanic ecosystem by transferring energy from shallower to deeper oceanic levels (Barham, 1966; Paxton, 1972; Collins et al., 2008; García-Seoane, Dalpadado, & Vázquez, 2013; Davis, 2015).

Previous phylogenetic hypotheses of lanternfishes have identified two monophyletic subfamilies within the family Myctophidae, Lampanyctinae and Myctophinae, based on both

morphological (Paxton, 1972; Stiassny, 1996) and molecular data (Poulsen et al., 2013; Davis et al., 2014; Denton, 2014). Our recent study using phylogenomics identified two additional subfamilies (Gymnoscopelinae and Diaphinae) in addition to Lampanyctinae and Myctophinae. Lanternfishes are known for the species-specific bioluminescent photophores and organs that cover their bodies. These structures produce endogenously generated light and are situated along the ventral and lateral surfaces of their bodies.

The ventral photophores produce counter illumination (Lawry, 1974; Case et al., 1977). This type of camouflage involves the excitation of the bioluminescent photophores to match the intensity of downwelling light to hide the ventral profile from predators lurking below. Bioluminescent marine fishes that live in shallow-water marine environments with sexually dimorphic bioluminescent organs have been hypothesized to undergo sexual selection (Sparks et al., 2005; Chakrabarty, Davis, Smith, Baldwin, & Sparks, 2011a; Chakrabarty et al., 2011b). The bioluminescent photophores of lanternfishes located in lateral positions on the body may be involved with species recognition and sexual selection (Mensinger & Case, 1990; De Busserolles, Fitzpatrick, Paxton, Marshall, & Collin, 2013a; De Busserolles, Hart, Hunt, Davies, & Justin, 2013b; Davis et al., 2014; Davis et al., 2016). Additionally, the eyes of lanternfishes are attuned to see wavelengths that match the light given off by bioluminescent organisms (Turner, White, Collins, Partridge, & Douglas, 2009). Despite the common occurrence of this group in deep-sea environments, little is known currently about how lanternfishes have achieved such high species richness in the open ocean, which has few reproductive isolating barriers.

Many planktivorous fishes and fish larvae display size preferences for prey based on gape size (Arthur, 1976; Munk, 1997). Studies on the larvae of lanternfishes have indicated that gape

size is important to the ecological niches the larvae occupy (Conley & Hopkins, 2004; Tanimata, Yamamura, Sakurai, & Azumaya, 2008). Paxton (1972) suggested that adult lanternfishes have a high degree of variation in mouth size across their radiation, but currently no studies have investigated the degree of this variation, the pattern of its evolution across lanternfishes, or whether mouth size may be similarly important to feeding in adults. Additionally, studies have indicated that the jaw morphology of fishes plays a crucial role in determining the type of prey it consumes and how morphological variation can lead to changes in foraging ability and subsequently differential use of food resources (Karpouzi & Stergiou, 2003; Price, Friedman, & Wainright, 2015). Correlations between mouth size and prey size have been studied in many fishes (e.g., alewife, Janssen, 1976; roach, Prejs, Lewandowski, & Stańczykowska-Piotrowska, 1990; largemouth bass, Hambright, 1991). The presence of variation in the mouth size of lanternfishes and subsequent selective feeding based on prey size, coupled with reproductive isolating mechanisms (species-specific and sexually dimorphic bioluminescent structures; Davis et al., 2014; Davis et al., 2016) could be a potential mechanism of diversification, if it allows for niche differentiation in the open ocean.

The focus of this work is to investigate the evolution of variation in mouth size across the lanternfish radiation. Paxton (1972) has suggested that there is variation in jaw morphology across lanternfishes, however this variation has never been quantitatively investigated. If significant variation exists in the size of the mouth (Figure 2.1A-F) among lanternfish species, and there is evidence this variation is having a potential impact on their diet as adults, then the possibility exists that niche partitioning is occurring in lanternfishes. In this study, the elongation of the upper jaw in lanternfishes is quantitatively investigated and the evolutionary pattern of

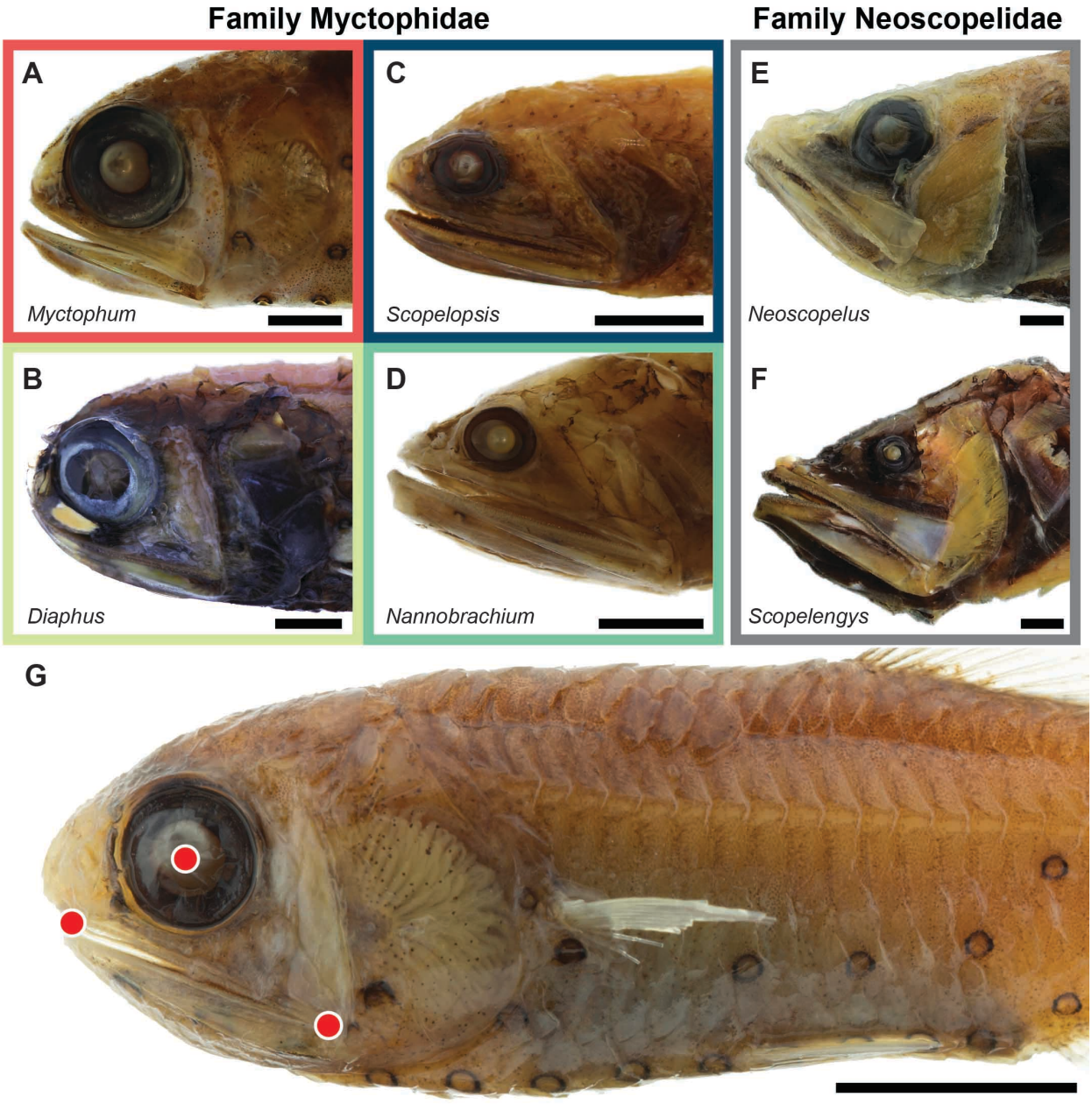


Figure 2.1. Examples of variation in upper-jaw morphology among the four lanternfish subfamilies. Scale bars represent 5 mm. Representative for Myctophinae (A) *Myctophum obtusirostre* (MCZ 51389); Representative for Diaphinae (B) *Diaphus rafinesquii* (MCZ 118953); Representative for Gymnoscopelinae (C) *Scopelopsis multipunctatus* (MCZ 102571); Representative for Lampanyctinae (D) *Nannobrachium cuprarium* (MCZ 112776); (E) *Neoscopelus macrolepidotus* (FMNH 112581); (F) *Scopelengys tristis* (USNM 201152); Geometric morphometric landmark placement sites on lanternfish specimens (G) *Gonichthys tenuiculus* (FMNH 71685).

changes in mouth size is reconstructed within a phylogenetic framework. We focused on addressing the following questions: (1) Is there quantitative evidence that mouth size changes across the lanternfish radiation, and what is the degree of that variation? (2) What is the character evolution of mouth size across the evolutionary history of lanternfishes? (3) Is there any evidence that variation in mouth size may influence the diet of lanternfishes?

## Materials and Methods

### Specimens

Lanternfish specimens from the Museum of Comparative Zoology, the Smithsonian Institution, and the Field Museum were used in this study. Photographs of 955 alcohol preserved specimens, representing 30 of 36 genera and 124 species (see Material Examined) were taken using a Canon EOS Rebel SL1 Digital SLR camera. Museum abbreviations follow Sabaj (2016).

### Geometric Morphometrics

In order to investigate the variation in mouth size across lanternfishes, digital landmarks were placed on three analogous areas using the geometric morphometric software tps (Rohlf, 2010a, 2010b). Analogous areas include: the most anterior part of the premaxilla, the most posterior medial part of the maxilla, and the middle of the eye (Figure 2.1G). These landmarks were chosen as they provide a general estimate of variation in mouth shape and length in comparison to the eye. A relative warp analysis, which is a principal component analysis, was conducted to quantify the amount of variation in mouth size of each specimen from a consensus configuration that was created from a Procrustes superimposition (Rohlf & Slice, 1990). A Procrustes superimposition scales and rotates all of the shapes created based on landmark

placements prior to running the relative warp analysis. This removes any artifacts that may have been created due to inconsistencies in image size and specimen rotation.

**Character Evolution**

Likelihood and parsimony ancestral-state reconstructions were performed in Mesquite 2.75 (Maddison & Maddison, 2015). Our UCE based phylogeny of lanternfishes was used to reconstruct the character evolution of upper-jaw length. Character states for upper-jaw lengths were inferred from the quantitative results of the relative warp analysis following MacLeod (2002). For genera not included in the morphometric analysis, a character state was assigned based on the anatomy of the fish (*Krefftichthys*). The morphological character used to infer the ancestral character states among Myctophiformes is described below.

1. Length of upper jaw relative to the position of the eye

   ($01_0$) Anterior margin of premaxilla extends well beyond eye, posterior margin of maxilla extends slightly behind eye.

   ($01_1$) Anterior margin of premaxilla extends slightly beyond eye, posterior margin of maxilla extends slightly behind eye.

   ($01_2$) Anterior margin of premaxilla extends slightly beyond eye, posterior margin of maxilla extends well behind eye.

## Results

**Variation in Mouth Size Across Lanternfishes**

The relative warp analysis shows a quantitative differentiation in morphospace as represented by the center of the eye, the anteriormost margin of the premaxilla, and the distal

most margin of the maxilla in Myctophidae and Neoscopelidae, and also between the four lanternfish subfamilies, Gymnoscopelinae, Lampanyctinae, Diaphinae, and Myctophinae (Figure 2.2), relative to other clades. Neoscopelidae (blackchins) trend towards a longer anterior portion of the upper jaw with an enlarged snout in relation to the eye. Within the family Myctophidae (lanternfishes), genera in the subfamily Gymnoscopelinae have a small overlapping distribution along the right side of the X-axis, indicating a trend towards longer upper jaws (Figure 2.2), with only small differences in upper-jaw length between genera (Figure 2.3A). In contrast, genera in the subfamily Myctophinae have a broad overlapping distribution across the left side of the X-axis, indicating a trend towards shorter upper jaws (Figure 2.2). While there is broad overlap of the genera within this subfamily (Figure 2.3C), there are also differences between various genera in morphospace (e.g., *Loweina, Metelectrona, Protomyctophum,* and *Tarletonbeania*) showing distinctive clumping and separation (Figure 2.4A, B). *Tarletonbeania* is an exception to the general trend in that is contains species with both long and short upper jaws (Figure 2.4B). Genera within Lampanyctinae indicate a trend towards a longer posterior portion of the upper jaw in relation to the eye (Figure 2.2). While there is significant overlap of genera within Lampanyctinae across the right side of the X-axis (Figure 2.3B), only a few genera in this subfamily have a broad distribution in morphospace (Figure 2.4C) showing higher variation among species within a genus (i.e., *Bolinichthys,* and *Lampanyctus*). However, the overall variation among species within a genus is generally reduced across Lampanyctinae (Figure 2.4D). *Bolinichthys,* and *Ceratoscopelus* both contain species that have both long and short upper jaws, and are exceptions to the general trend (Figure 2.4C, D). Additionally, there are multiple genera that do not overlap in morphospace (e.g., *Ceratoscopelus,* and *Taaningichthys*; Figure

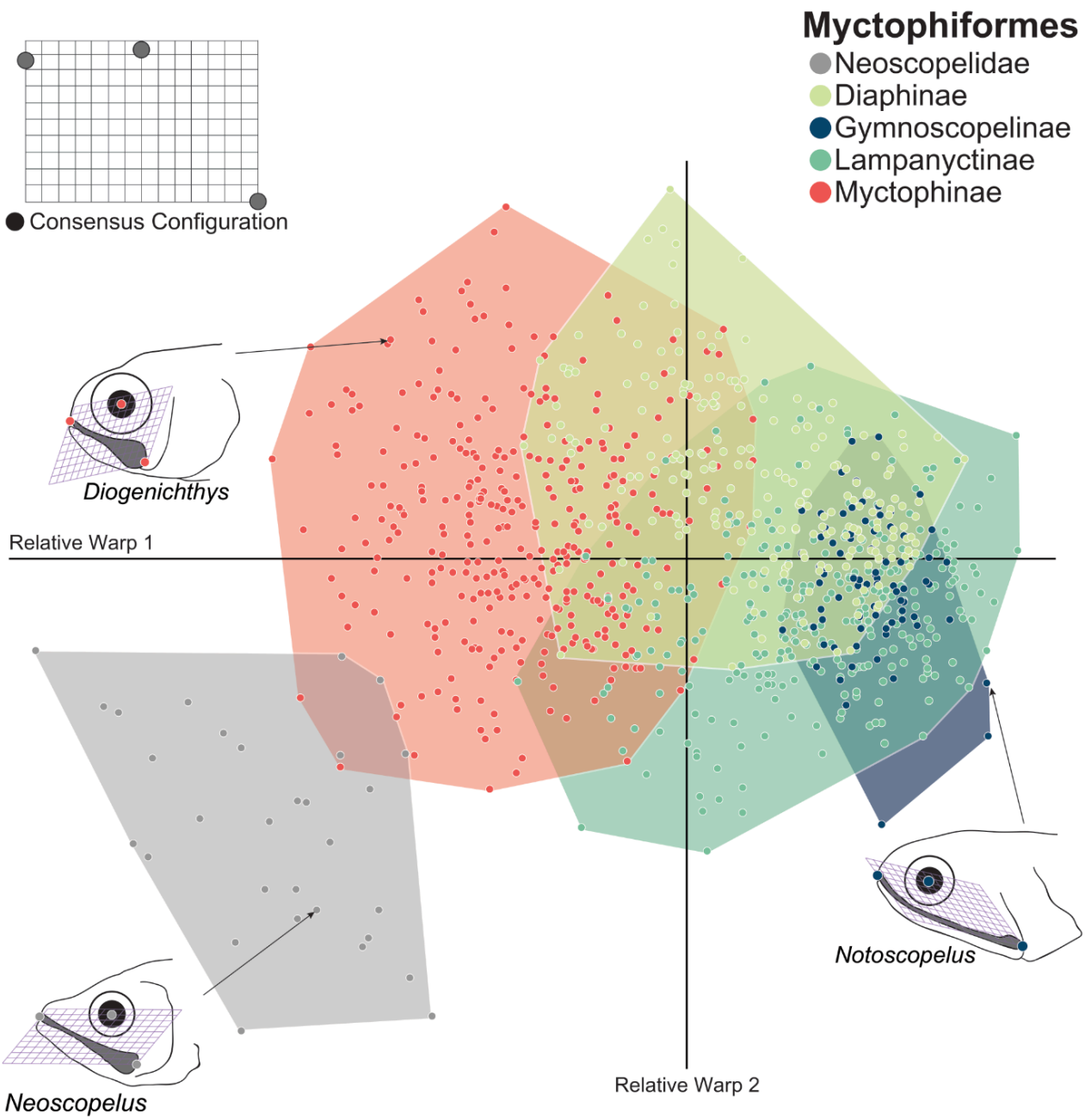


Figure 2.2. Relative warp analysis of jaw landmarks for Myctophiformes.

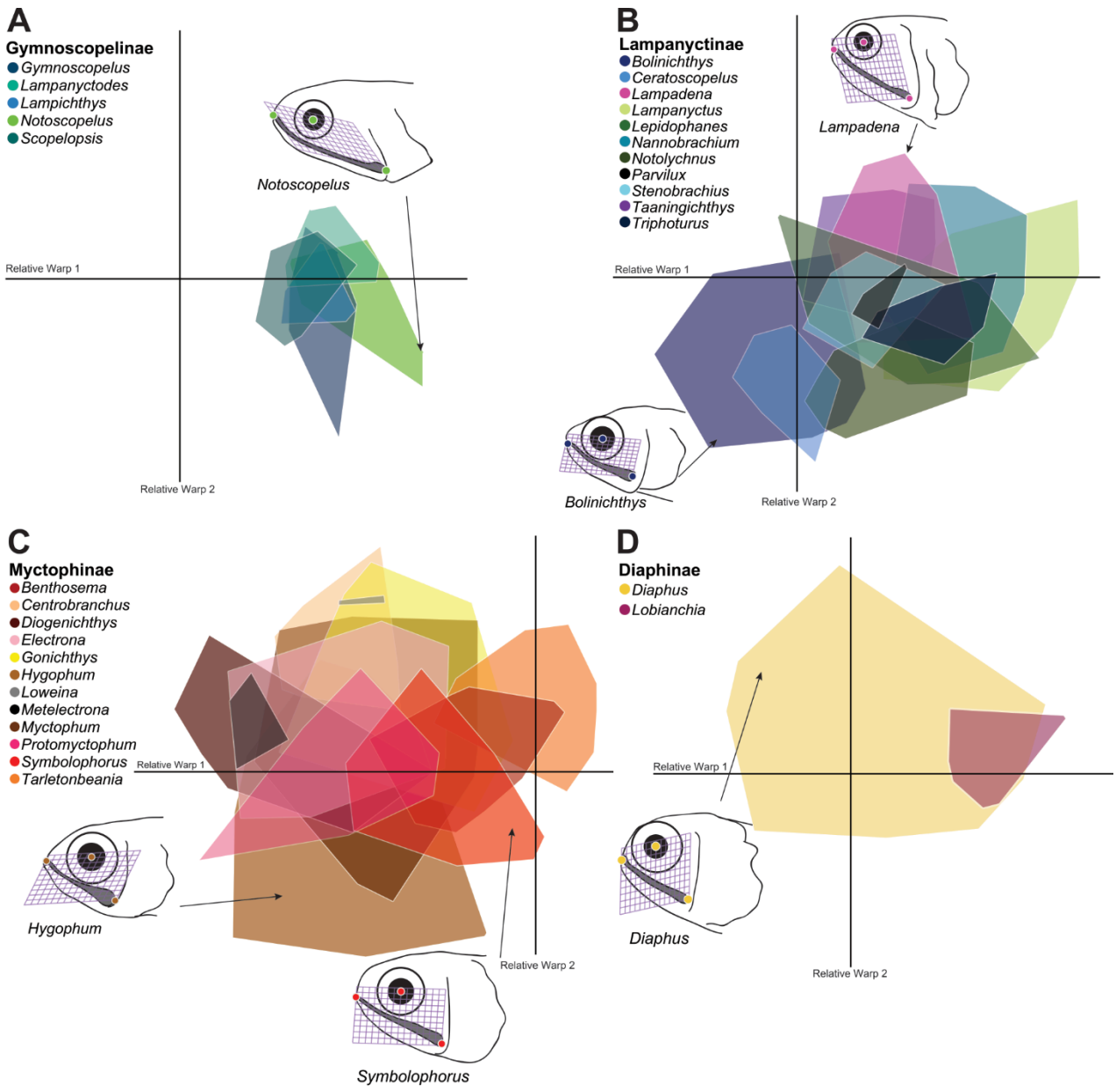


Figure 2.3. Breakdown of relative warp analysis of mouth size in: (A) Gymnoscopelinae genera; (B) Lampanyctinae genera; (C) Myctophinae genera; (D) Diaphinae genera.

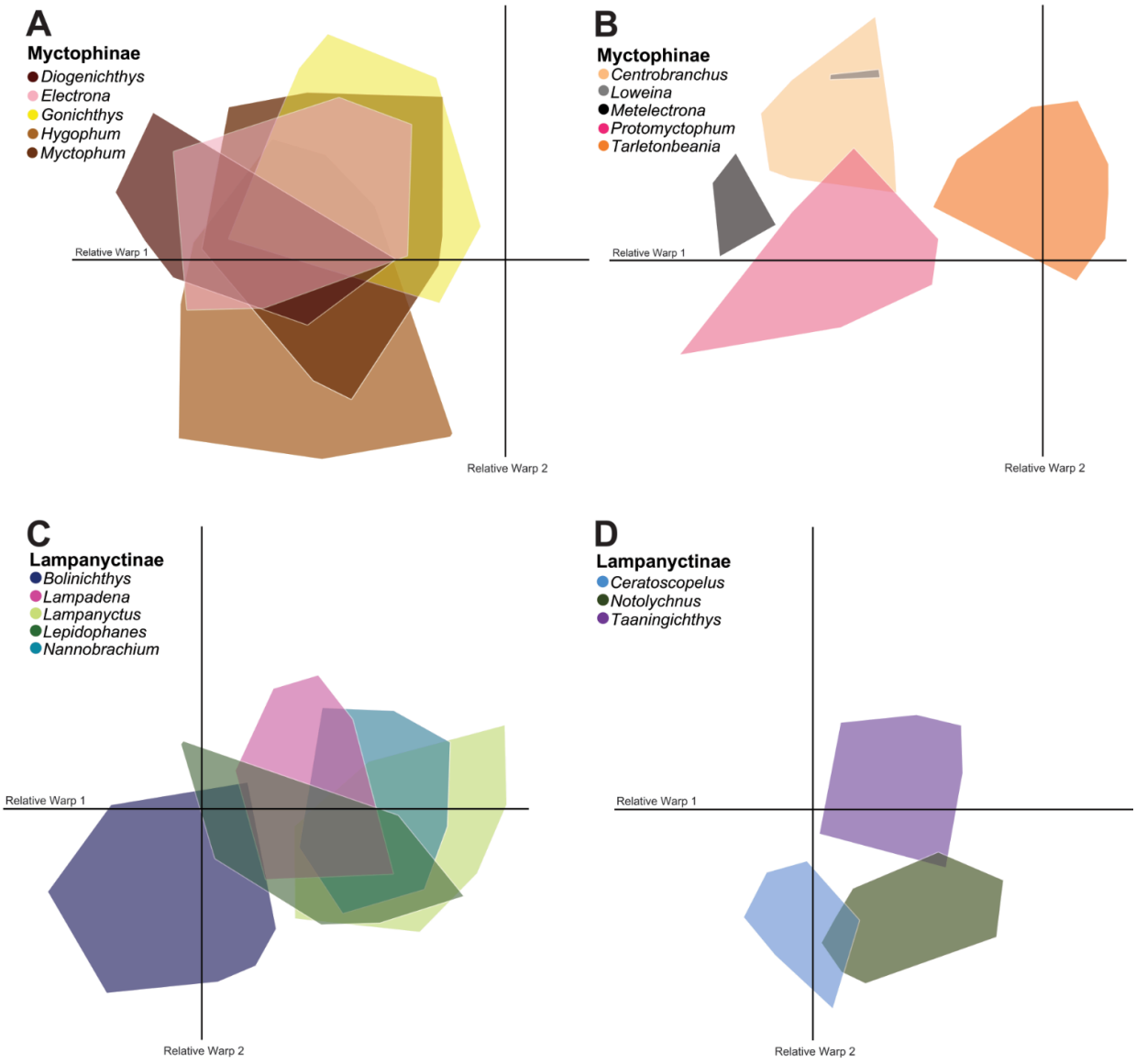


Figure 2.4. Breakdown of relative warp analysis of mouth size in Myctophinae and Lampanyctinae genera. (A) myctophine genera with high morphospace variation; (B) examples of myctophine genera with separation in morphospace; (C) lampanyctine genera with high morphospace variation; (D) examples of lampanyctine genera with separation in morphospace.

2.4D). The genus *Diaphus* within Diaphinae have upper-jaw lengths that span across the morphospace of the other three subfamilies (Figures 2.2, 2.3D).

### Character Evolution of Mouth Size

Ancestral character states are indicated at nodes (Wiley et al., 2011). The common ancestor of the Myctophiformes either had a larger upper jaw with a robust snout, similar to that of the family Neoscopelidae, or a longer upper jaw similar to Gymnoscopeline and Lampanyctinae. This node was equivocal for both states under a parsimony reconstruction (Figure 2.5). The common ancestor of the Myctophidae most likely had a longer upper jaw, similar to that of the subfamily Lampanyctinae, under parsimony (Figure 2.5). The subfamily Myctophinae most likely evolved shorter upper jaws in its common ancestor.

## Discussion

### Evolution of Mouth Size in Myctophiformes

This work seeks to understand the evolution of mouth size in lanternfishes and its potential impact on the radiation of this species-rich group in the open ocean. Overall, the results indicate that there is considerable variation in mouth size among lanternfish lineages (Figure 2.2). Within the family Neoscopelidae, the anterior portion of the mouth and snout are elongated in relation to the position of the eye. The relative warp analysis indicates that within the morphospace, this upper-jaw length is markedly different from species in the family Myctophidae (Figure 2.2). The ancestral character-state reconstruction inferred under parsimony (Figure 2.5) suggests that the upper-jaw length similar to that of Neoscopelidae may be the ancestral jaw length for all Myctophiformes. Fossil evidence of stem Myctophiformes, including

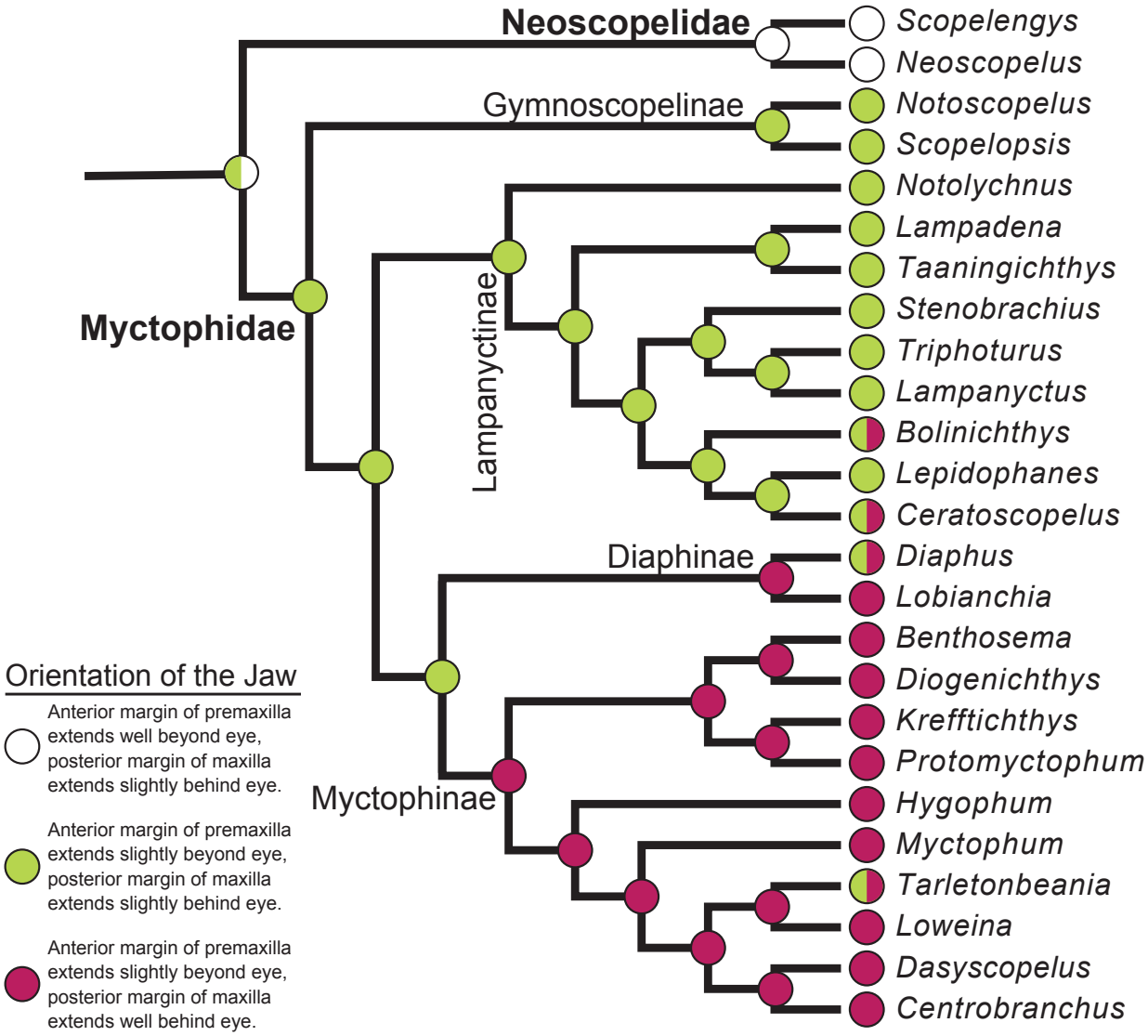


Figure 2.5. Parsimony ancestral character-state reconstruction of the evolution of upper-jaw length shown at nodes on a maximum likelihood phylogeny of lanternfish relationships based upon UCE sequences.

†*Sardinoides* (Cretaceous), †*Neocassandra* (Paleocene), and †*Beckerophotus* (Eocene; Prokofiev, 2006), indicates that stem lanternfish had a neoscopelid-like mouth, which coincides with our ancestral character-state reconstruction. In general, the family Neoscopelidae has upper jaws that are not as shortened or as elongated as species in the family Myctophidae (Figure 2.2). The family Neoscopelidae has low species diversity with three genera and approximately six species (Eschmeyer et al., 2017). In contrast, the species-rich family Myctophidae possesses higher variability in the length of the upper jaw (Figures 2.1, 2.2), which may have facilitated the broad diversification of the lanternfishes.

Paxton (1972) described two general trends in the mouth size in myctophids. He noticed a trend towards larger mouths in Lampanyctinae and smaller mouths in Myctophinae. This study identified similar trends in mouth-size evolution in lanternfishes (Figures 2.2, 2.3). There is a distinct elongation of the posterior portion of the upper jaw in relation to the eye in Gymnoscopelinae and Lampanyctinae, with only a few exceptions (e.g., some species of *Bolinichthys*, and *Ceratoscopelus*). Myctophinae shows a shortening of the upper jaw in relation to the eye (Figures 2.2, 2.3C). Paxton (1972) suggested that the ancestral character state for Myctophidae was a small mouth, with lampanyctines evolving larger mouths. The results of the parsimony character-state reconstruction indicate otherwise, inferring that the ancestral character state for myctophids was likely larger mouths with Myctophinae evolving shorter mouths (Figure 2.5). A stem fossil lineage of Myctophidae known from Oligocene deposits, †*Eomyctophum* (Prokofiev, 2006), also has an elongated upper jaw which is consistent with the results of our ancestral character-state reconstructions. Not all lineages within Myctophidae follow the observed general trends of mouth size identified in their respective subfamilies. The genera

*Tarletonbeania, Diaphus, Bolinichthys,* and *Ceratoscopelus* all contain species that have evolved both smaller and larger mouths (Figure 2.4).

**Evolution of Mouth Size in *Diaphus***

The genus *Diaphus* was found to occupy the largest amount of morphospace for any lanternfish genus (Figures 2.2, 2.3D), and it is one of the only myctophid lineages to have species with both long and short upper jaws (Figure 2.2). In contrast, many taxa within a given genus of lanternfishes are generally restricted in their overall pattern of upper-jaw length (Figure 2.4B, D). The genus *Diaphus* contains approximately 77 species (Eschmeyer et al., 2017), 30% of the total lanternfish species richness. Davis et al. (2014) found that the genus *Diaphus* has exceptional species richness given its clade age, indicating that this lineage of lanternfishes has been diversifying at a significantly elevated rate relative to all other lanternfish lineages. It is possible that the increased variation in the upper jaws of *Diaphus*, coupled with the variation of the head bioluminescent organs found in species of this genus, may have impacted its diversification. *Diaphus* is unique among all other lanternfish taxa in that species within this genus have evolved a complex system of anteriorly oriented light organs on the head. These additional light organs are often sexually dimorphic and may be used additionally to stun, confuse, illuminate, or induce fluorescence in prey (Sparks et al., 2014; Haddock et al., 2010). Many deep-sea fishes (e.g., dragonfishes, barracudinas) also use light organs associated with the eye to seek out prey items (Douglas & Partridge, 1997; Douglas et al., 1998; Douglas, Bowmaker, & Mullineaux, 2002; Ghedotti, Barton, Simons, & Davis, 2015).

The evolution of the upper jaw within the genus *Diaphus* indicates that mouth size is highly variable with species exhibiting either long or short upper jaws, and these species are

distributed throughout the evolutionary history of the lineage (Figure 2.6). This indicates that the evolutionary history of *Diaphus* is punctuated with changes in jaw length (Figure 2.6) and that the evolution of their jaws may have had an impact on shifts in ecological specializations within this lineage. To further elucidate the pattern and direction of jaw evolution in *Diaphus*, further work is needed to examine the jaws of additional species within the genus in relation to a densely sampled species phylogeny of the group. The high anatomical variation of upper-jaw length in *Diaphus* indicates that there is a possibility that niche differentiation may have played a role in their diversification if there are dietary changes that correlate with the variation in mouth size observed in this study (Figure 2.6). A study that focused on the diets of two species of *Diaphus* that are comparable in body size found that the diet of the short-jawed *D. garmani* included small copepods, euphausiids, ostracods, and amphipods, whereas the diet of the long-jawed *D. chrysorhynchus* included larger cephalopods and myctophids, in addition to zooplankton (Tanaka, Sassa, Ohshimo, & Aoki, 2013).

**Mouth Size and Feeding in Lanternfishes**

Previous work on the diets of lanternfishes have identified that their diets consist predominantly of epipelagic zooplankton: copepods, amphipods, ostracods, and euphausiids (e.g., Pakhomov, Perissinotto, & McQuaid, 1996; Gaskett et al., 2001). Many of these studies also found variation in lanternfish diets based on the size of prey items (e.g., Hopkins, Sutton, & Lancraft, 1996; Williams, Koslow, Terauds, & Haskard, 2001; Conley & Hopkins, 2004; Shreeve et al., 2009). This further indicates that both mouth and body size may play a role in niche partitioning in this group. Because the diet of lanternfishes includes predominantly different species of epipelagic zooplankton, this enables the co-occurrence of many lanternfish species

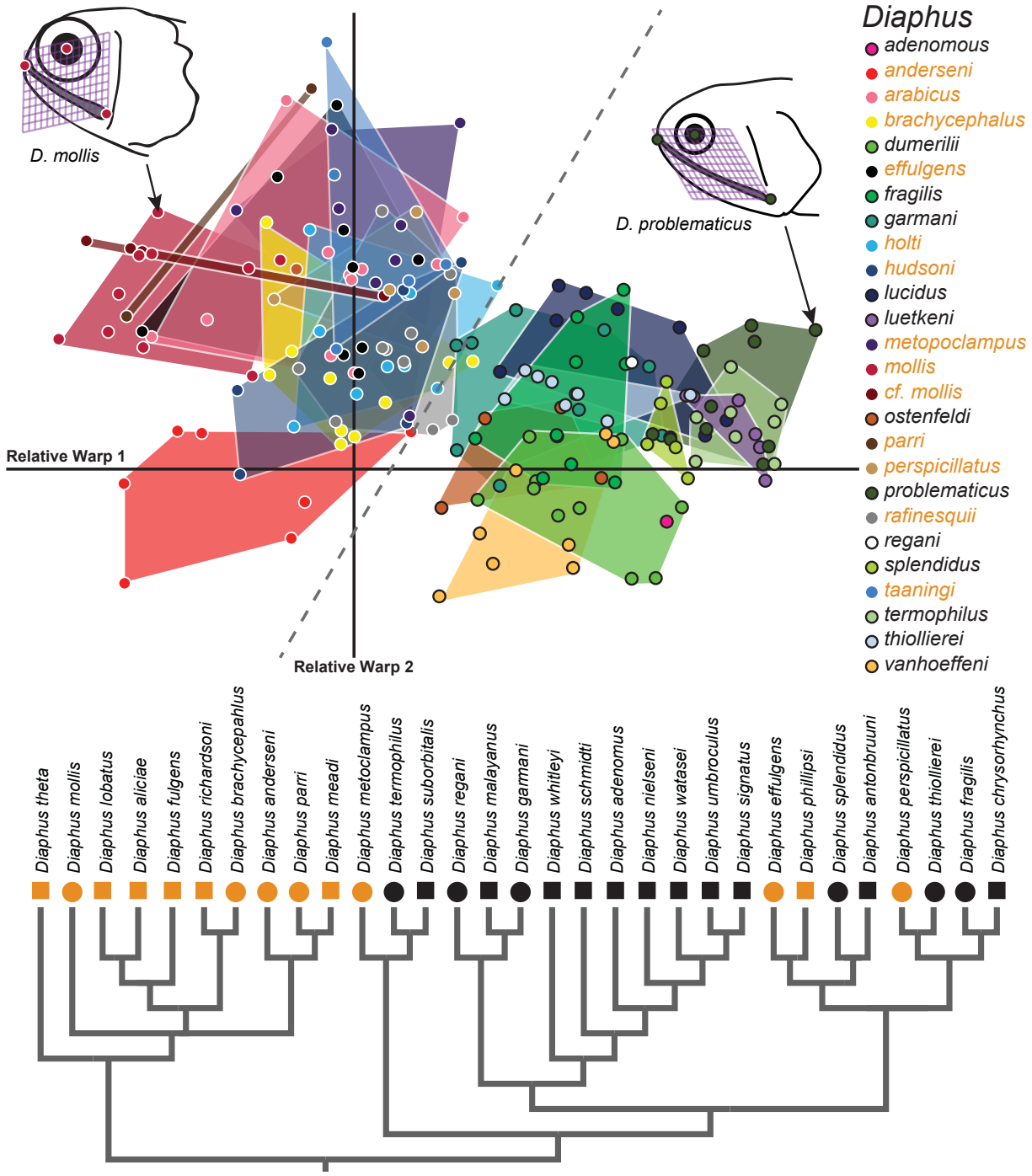


Figure 2.6. Relative warp analysis of upper-jaw length among species of *Diaphus*. The two main trends of mouth size are represented by text color and outlines on the circles representing specimens; black text and outlines indicate longer upper jaws and orange text with white outlines indicate shorter upper jaws. The presence of short and long upper jaws are indicated on a summary phylogeny of species within *Diaphus* (Denton, 2014), with species included in this study indicated by a circle and species coded from an external source indicated by a square (Froese and Pauly, 2016). Circles and squares colored black indicate longer upper jaws, whereas orange indicates shorter upper jaws.

during nightly feeding migrations into the epipelagic zone. Lanternfishes are hypothesized to exhibit ‘diffuse competition’ for food resources, which could result in competitive exclusion and niche separation (Hopkins & Gartner, 1992). Differences in the diets and prey size of lanternfishes with similar body sizes but varying mouth sizes have been identified in previous studies. For example, *Myctophum obtusirostre*, a short-jawed species, was found to eat molluscs and bivalve larvae, compared to *Diaphus watasei*, a long-jawed species, which was found to eat zooplankton, squids, and other larval and adult myctophids (Alwis & Gjøsæter, 1988). As body length and mouth size increases within lanternfishes, there is usually a shift in the size of prey consumed, and species become more opportunistic, feeding on both large and small prey items and becoming more piscivorous (Takagi, Yatsu, Itoh, Moku, & Nishida, 2009; Bernal, Olivar, & de Puelles, 2013).

The variation we have found in the mouth size of lanternfishes may be the result of divergence due in part to differences in the size of prey items consumed and the result of divergent natural selection because of resource competition. Conley and Hopkins (2004) indicated that larvae of species within the subfamilies Gymnoscopelinae, Lampanyctinae, and Diaphinae exhibit a high diversity of prey type, with size restrictions of prey set by mouth size. This pattern continued in the postmetamorphic stages, with larger mouth sizes allowing for a greater range of prey size (Conley & Hopkins, 2004). Additional ontogenetic studies on lanternfishes also found this pattern in prey selectivity (e.g., Sabatés & Saiz, 2000; Tanimata et al., 2008; Bernal et al., 2013). A larger mouthed gymnoscopeline, lampanyctine, or diaphine species may be more successful at prey capture on larger prey items than a smaller mouthed

myctophine species, due to gape size. This may result in shifts into divergent diets over time and further facilitate diversification.

There are few studies that have investigated variation in mouth size across a lineage of deep-sea fishes, but similar studies on vertebrates have indicated that variation in dentition and the size and shape of the mouth has an impact on niche differentiation (Liem, 1973; Rosenberger, 1992; Danley & Kocher, 2001; Lovette, Bermingham, & Ricklefs, 2002; Hulsey, Mims, Parnell, & Streelman, 2010; Muschick, Barluenga, Salzburger, & Meyer, 2011). The role of niche differentiation in the open ocean has been comparatively understudied compared to other aquatic habitats. There are few physical barriers to gene flow in the open ocean, and greatly separated areas may be connected genetically due to the reproductive strategies of many marine species that have high fecundity and rely on ocean currents to disperse their young (Palumbi, 1994; Gordeeva, 2011). Additionally, marine populations can be large, which may slow genetic divergence between populations (Palumbi, 1994).

Lanternfishes are among the most species-rich lineages of open-ocean fishes, a habitat with few physical barriers to gene flow, and niche partitioning can promote speciation in these kinds of habitats (Brawand et al., 2014). Many species within a given genus in Myctophidae are restricted in their upper-jaw morphospace, indicating a possible differentiation into specialized niches across the broader lanternfish radiation (Figure 2.4B, D). Taxa that overlap in morphospace (Figure 2.4A, C) likely prey on similar food sources, while species that do not overlap in morphospace potentially occupy different niches and are not directly in competition with each other for resources. In general, there is potential evidence for niche partitioning across the evolution of lanternfish lineages. Future studies will compare diets across all lanternfishes in

order to get a clearer picture of patterns of diet change and the potential for niche differentiation in this lineage. Other morphological characters that could impact diet, including the variation in dentition, body size, and geographic distribution will also be assessed.

## Conclusions

Overall, our results indicate that there is considerable variation in mouth size among lanternfish lineages (Figure 2.2), including general trends towards smaller mouths in Myctophinae, and larger mouths in Gymnoscopelinae, and Lampanyctinae (Figure 2.2, 2.3). The parsimony character-state reconstruction indicates that the ancestral state for Myctophiformes and Myctophidae was likely longer jaws (Figure 2.5). The broad variation in mouth size of lanternfishes indicates that this group may have undergone shifts in ecological specializations. Of particular note, Diaphinae and the genus *Diaphus* has high variation in upper-jaw length within morphospace and is one of the only lineages to exhibit species with both short and long jaws (Figure 2.6), which indicates that species of *Diaphus* may have an evolutionary history that is punctuated with niche partitioning. Further work is needed to compare the overall diets of all lanternfish species with variation in feeding anatomy.

## Material Examined

*Benthosema glaciale*: MCZ 53426, 5, 37–60 mm SL; MCZ 125916, 5, 36–59 mm SL.

*Benthosema pterotum*: MCZ 151480, 6, 24–40 mm SL; MCZ 151484, 7, 34–41 mm SL.

*Benthosema suborbitale*: MCZ 92374, 9, 27–30 mm SL.

*Bolinichthys indicus*: MCZ 124300, 5, 35–39 mm SL; MCZ 124302, 3, 34–40 mm SL; MCZ 124320, 3, 41–46 mm SL.

*Bolinichthys longipes*: MCZ 151750, 2, 42–43 mm SL; MCZ 151781, 3, 15–38 mm SL.

*Bolinichthys photothorax*: MCZ 123846, 4, 26–51 mm SL; MCZ 127392, 4, 18–25 mm SL.

*Bolinichthys supralateralis*: MCZ 123602, 3, 18–19 mm SL; MCZ 157865, 5, 25–29 mm SL.

*Centrobranchus nigroocellatus*: FMNH 64611, 1, 38 mm SL; FMNH 64711, 2, 24–30 mm SL; MCZ 98844, 10, 25–37 mm SL.

*Ceratoscopelus maderensis*: MCZ 100705, 5, 58–66 mm SL.

*Ceratoscopelus townsendi*: MCZ 164690, 3, 47–51 mm SL.

*Ceratoscopelus warmingii*: MCZ 92411, 7, 40–52 mm SL.

*Diaphus adenomus*: FMNH 58702, 1, 43 mm SL.

*Diaphus anderseni*: MCZ 103200, 7, 22–27 mm SL.

*Diaphus arabicus*: MCZ 151691, 12, 28–35 mm SL.

*Diaphus brachycephalus*: MCZ 121432, 7, 29–40 mm SL; MCZ 121662, 3, 32–33 mm SL.

*Diaphus dumerilii*: MCZ 120885, 5, 43–52 mm SL; MCZ 120888, 5, 24–37 mm SL.

*Diaphus effulgens*: MCZ 109969, 2, 52–62 mm SL; MCZ 110019, 5, 37–56 mm SL; MCZ 157869, 1, 57 mm SL; USNM 300852, 1, 98 mm SL.

*Diaphus fragilis*: MCZ 90437, 5, 45–70 mm SL; MCZ 120741, 5, 44–70 mm SL.

*Diaphus garmani*: MCZ 90863, 4, 48–52 mm SL; MCZ 151630, 5, 36–42 mm SL.

*Diaphus holti*: MCZ 120623, 3, 22–47 mm SL; MCZ 120625, 7, 29–36 mm SL.

*Diaphus hudsoni*: MCZ 97005, 3, 34–54 mm SL; MCZ 114101, 2, 45–56 mm SL.

*Diaphus lucidus*: MCZ 120329, 5, 33–58 mm SL; MCZ 120456, 4, 35–48 mm SL.

*Diaphus luetkeni*: MCZ 120166, 6, 39–44 mm SL.

*Diaphus metopoclampus*: MCZ 157871, 8, 26–32 mm SL.

*Diaphus mollis*: MCZ 90306, 5, 39–48 mm SL; MCZ 119262, 5, 31–54 mm SL.

*Diaphus cf. mollis*: MCZ 120148, 4, 38–44 mm SL.

*Diaphus ostenfeldi*: MCZ 119162, 2, 42–45 mm SL; MCZ 119163, 2, 47–48 mm SL.

*Diaphus parri*: MCZ 151451, 2, 32–52 mm SL.

*Diaphus perspicillatus*: MCZ 126693, 5, 34–52 mm SL.

*Diaphus problematicus*: MCZ 119046, 5, 54–66 mm SL; MCZ 128058, 5, 45–60 mm SL.

*Diaphus rafinesquii*: MCZ 118651, 4, 37–40 mm SL; MCZ 118953, 4, 62–75 mm SL; MCZ 151065, 2, 68–72 mm SL.

*Diaphus regani*: MCZ 90115, 1, 59 mm SL.

*Diaphus splendidus*: MCZ 118342, 5, 53–70 mm SL.

*Diaphus taaningi*: MCZ 159064, 5, 62–70 mm SL.

*Diaphus termophilus*: MCZ 118159, 4, 34–52 mm SL; MCZ 118161, 4, 30–49 mm SL.

*Diaphus thiollierei*: MCZ 151465, 4, 57–59 mm SL; MCZ 151467, 5, 46–64 mm SL.

*Diaphus vanhoeffeni*: MCZ 118098, 8, 27–31 mm SL.

*Diogenichthys atlanticus*: FMNH 120916, 3, 65–75 mm SL; MCZ 55530, 8, 20–22 mm SL.

*Electrona antarctica*: MCZ 149056, 10, 18–23 mm SL; USNM SOSC-38 IK-1, 4, 66–76 mm SL.

*Electrona carlsbergi*: USNM 206858, 4, 82–86 mm SL. Electrona risso: MCZ 62188, 8, 18–23 mm SL.

*Gonichthys barnesi*: MCZ 103190, 7, 31–47 mm SL.

*Gonichthys cocco*: MCZ 116669, 8, 43–52 mm SL.

*Gonichthys tenuiculus*: FMNH 71685, 6, 31–41 mm SL; MCZ 103199, 3, 45–49 mm SL; USNM 150085, 3, 38–47 mm SL.

*Gymnoscopelus braueri*: MCZ 148792, 3, 89–94 mm SL; MCZ 148797, 3, 70–96 mm SL; USNM 206612, 4, 102–122 mm SL; USNM 206645, 5, 55–95 mm SL.

*Hygophum benoiti*: MCZ 116153, 7, 40–44 mm SL.

*Hygophum brunni*: MCZ 98555, 7, 22–37 mm SL.

*Hygophum hanseni*: MCZ 115977, 4, 29–40 mm SL.

*Hygophum hygomii*: MCZ 92776, 7, 47–55 mm SL; MCZ 115383, 5, 32–48 mm SL; USNM 253214, 5, 51–58 mm SL.

*Hygophum macrochir*: MCZ 115225, 6, 39–51 mm SL; MCZ 115290, 4, 44–52 mm SL.

*Hygophum proximum*: MCZ 148705, 4, 36–43 mm SL.

*Hygophum reinhardtii*: MCZ 114759, 7, 29–34 mm SL.

*Hygophum taaningi*: MCZ 114511, 2, 46–54 mm SL; MCZ 157874, 4, 24–28 mm SL.

*Lampadena chavesi*: MCZ 98534, 1, 73 mm SL; MCZ 103117, 2, 62–71 mm SL.

*Lampadena luminosa*: MCZ 102986, 4, 28–70 mm SL; MCZ 102987, 3, 60–66 mm SL.

*Lampadena pontifex*: FMNH 117877, 2, 121–126 mm SL; MCZ 96997, 2, 60–62 mm SL.

*Lampadena speculigera*: MCZ 55526, 2, 85–87 mm SL; MCZ 114311, 2, 51–53 mm SL; MCZ 164146, 1, 127 mm SL.

*Lampadena urophaos*: MCZ 114235, 2, 55–58 mm SL.

*Lampanyctodes hectoris*: MCZ 91359, 10, 44–72 mm SL.

*Lampanyctus alatus*: MCZ 113992, 9, 39–47 mm SL.

*Lampanyctus australis*: MCZ 55034, 2, 80–87 mm SL.

*Lampanyctus crocodilus*: FMNH 63115, 1, 171 mm SL; MCZ 55470, 5, 60–105 mm SL.

*Lampanyctus festivus*: MCZ 112559, 8, 29–55 mm SL.

*Lampanyctus iselinoides*: MCZ 102845, 5, 57–84 mm SL.

*Lampanyctus macdonaldi*: MCZ 164406, 9, 79–156 mm SL.

*Lampanyctus mexicanus*: MCZ 45398, 6, 42–65 mm SL.

*Lampanyctus niger*: MCZ 49150, 2, 73–82 mm SL.

*Lampanyctus nobilis*: MCZ 110299, 8, 42–82 mm SL.

*Lampanyctus photonotus*: MCZ 111820, 5, 47–61 mm SL; MCZ 157875, 5, 41–65 mm SL.

*Lampanyctus pusillus*: MCZ 102137, 8, 29–33 mm SL.

*Lampanyctus vadulus*: MCZ 110183, 4, 56–83 mm SL; MCZ 110187, 4, 40–83 mm SL.

*Lampichthys procerus*: USNM 265347, 3, 30–34 mm SL.

*Lampichthys rectangularis*: MCZ 51782, 10, 69–88 mm SL.

*Lepidophanes gaussi*: MCZ 109655, 5, 17–33 mm SL; MCZ 109657, 5, 41–42 mm SL.

*Lepidophanes guentheri*: FMNH 113578, 2, 27–46 mm SL; MCZ 108541, 8, 40–64 mm SL; USNM 254406, 5, 53–69 mm SL.

*Lepidophanes supralateralis*: USNM 327068, 2, 59–102 mm SL.

*Lobianchia dofleini*: MCZ 108030, 10, 24–29 mm SL; USNM 284037, 5, 32–57 mm SL.

*Lobianchia gemellari*: FMNH 78441, 1, 46 mm SL; FMNH 78468, 5, 40–50 mm SL; MCZ 107215, 7, 64–70 mm SL.

*Loweina rara*: USNM 274182, 2, 20–25 mm SL.

*Metelectrona ventralis*: USNM 206602, 4, 94–108 mm SL; USNM 209344, 1, 40 mm SL.

*Myctophum affine*: MCZ 106578, 7, 30–39 mm SL.

*Myctophum asperum*: FMNH 59979, 1, 68 mm SL; MCZ 106460, 8, 31–62 mm SL.

*Myctophum fissunovi*: MCZ 81734, 8, 37–57 mm SL.

*Myctophum nitidulum*: MCZ 157588, 8, 23–50 mm SL.

*Myctophum obtusirostre*: MCZ 51389, 4, 65–80 mm SL; MCZ 105868, 3, 30–47 mm SL.

*Myctophum phengodes*: MCZ 105757, 4, 78–87 mm SL; MCZ 105766, 3, 73–87 mm SL.

*Myctophum punctatum*: MCZ 105563, 10, 65–83 mm SL.

*Myctophum selenops*: MCZ 105306, 4, 25–39 mm SL.

*Myctophum sp.*: FMNH 39659, 5, 42–53 mm SL.

*Myctophum spinosum*: MCZ 151450, 8, 41–71 mm SL.

*Nannobrachium atrum*: MCZ 113519, 6, 57–92 mm SL.

*Nannobrachium cuprarium*: MCZ 112776, 6, 55–67 mm SL; MCZ 112823, 4, 43–63 mm SL.

*Nannobrachium indicum*: MCZ 151729, 6, 32–84 mm SL.

*Nannobrachium isaacsi*: MCZ 55141, 6, 52–70 mm SL.

*Nannobrachium lineatum*: MCZ 159035, 2, 59–66 mm SL; MCZ 164479, 2, 59–71 mm SL.

*Nannobrachium wisneri*: MCZ 58390, 6, 55–65 mm SL.

*Neoscopelus macrolepidotus*: FMNH 112580, 5, 96–118 mm SL; FMNH 112581, 6, 130–173 mm SL; MCZ 28159, 2, 90–124 mm SL.

*Neoscopelus microchir*: FMNH 119741, 7, 78–161 mm SL; FMNH 120855, 5, 97–138 mm SL.

*Notolychnus valdiviae*: MCZ 104374, 8, 18–20 mm SL; MCZ 104620, 6, 14–15 mm SL; USNM 274026, 6, 15–20 mm SL.

*Notoscopelus bolini*: MCZ 103988, 8, 36–56 mm SL.

*Notoscopelus caudispinosus*: MCZ 104040, 2, 47–58 mm SL; MCZ 157882, 3, 59–66 mm SL.

*Notoscopelus elongatus kroyeri*: MCZ 104150, 6, 62–72 mm SL.

*Notoscopelus resplendens*: MCZ 166099, 8, 32–66 mm SL.

*Parvilux boschmai*: USNM 269450, 3, 63–107 mm SL.

*Parvilux ingens*: USNM 298057, 1, 57 mm SL.

*Protomyctophum anderssoni*: USNM 206597, 3, 51–62 mm SL.

*Protomyctophum arcticum*: MCZ 102601, 7, 31–41 mm SL.

*Protomyctophum beckeri*: USNM 269393, 4, 35–40 mm SL.

*Protomyctophum crockeri*: FMNH 120663, 1, 21 mm SL; FMNH 124688, 1, 33 mm SL.

*Protomyctophum subparallelum*: MCZ 102557, 7, 23–29 mm SL.

*Scopelengys clarkei*: FMNH 76368, 1, 40 mm SL.

*Scopelengys tristis*: USNM 201152, 4, 97–131 mm SL.

*Scopelopsis multipunctatus*: MCZ 102571, 8, 41–52 mm SL; USNM 274110, 3, 42–50 mm SL; USNM 274205, 3, 49–52 mm SL.

*Stenobrachius leucopsarus*: FMNH 71832, 6, 38–51 mm SL; FMNH 122276, 1, 67 mm SL; MCZ 88957, 10, 42–71 mm SL; SIO 58–20, 5, 58–68 mm SL.

*Symbolophorus barnardi*: MCZ 96811, 7, 40–59 mm SL.

*Symbolophorus boops*: MCZ 103573, 5, 65–93 mm SL; MCZ 103574, 6, 66–91 mm SL.

*Symbolophorus evermanni*: FMNH 71681, 1, 53 mm SL; MCZ 148717, 4, 64–76 mm SL; MCZ 148720, 3, 44–72 mm SL.

*Symbolophorus kreffti*: MCZ 102259, 6, 37–49 mm SL; MCZ 103553, 6, 42–52 mm SL.

*Symbolophorus rufinus*: MCZ 103536, 2, 69–90 mm SL; MCZ 148934, 3, 55–75 mm SL.

*Symbolophorus veranyi*: MCZ 45333, 5, 72–98 mm SL; MCZ 111606, 6, 64–74 mm SL.

*Taaningichthys bathyphilus*: FMNH 85121, 1, 50 mm SL; FMNH 85184, 2, 55–59 mm SL; MCZ 102467, 3, 35–52 mm SL; MCZ 102500, 2, 37–62 mm SL; USNM 252592, 3, 62–69 mm SL.

*Taaningichthys paurolychnus*: FMNH 121661, 2, 24–27 mm SL.

*Taaningichthys spp.*: USNM 407721, 1, 98 mm SL.

*Tarletonbeania crenularis*: FMNH 74222, 7, 34–62 mm SL; MCZ 45847, 10, 44–64 mm SL.

*Triphoturus mexicanus*: MCZ 125392, 5, 49–51 mm SL.

*Triphoturus nigrescens*: MCZ 89185, 8, 28–34 mm SL.

# CHAPTER III: EVOLUTION OF HETERODONTY ON THE ORAL JAWS OF LANTERNFISHES (TELEOSTEI: MYCTOPHIFORMES)

## Introduction

Lanternfishes are among the most abundant and species-rich groups of fishes endemic to the deep sea, containing 257 species in 36 genera (Eschmeyer et al., 2017) and two families, Neoscopelidae (blackchins) and Myctophidae (lanternfishes). Lanternfishes reside in the meso- and bathypelagic zones (≥ 200 meters deep), and most perform diel vertical migrations, moving to the epipelagic (open-ocean photic zone) at night to feed, and retreating to the darkness of the mesopelagic (open-ocean non-photic zone) during the day. They feed mainly on oceanic zooplankton (e.g. copepods, amphipods, euphausiids; Bernal, Olivar, Maynou, & de Puelles, 2015), and play a major role in the oceanic ecosystem by transferring energy to deeper oceanic levels (Sutton et al., 2010). Little is known regarding how lanternfishes became so species rich in the deep sea, and the majority of previous studies that investigated diversification in this group have focused predominantly on bioluminescence (Davis et al., 2014). Studies that focus on diversification in association with variation in feeding structures are common for terrestrial organisms (e.g., birds, termites), but comparatively few studies have examined these features in deep-sea organisms (Kenaley, 2012; Martin & Davis, 2016).

Tooth morphology confers information regarding diet in many extant and extinct vertebrates (Massare, 1987; Van Valkenburgh, 1989; Anthony & Kay, 1993), and it is generally hypothesized that tooth morphology and tooth function vary together in predictable ways across

niches. The morphological adaptations of an animal's feeding structures limit its ability to utilize food resources. Consequently, animals with similar tooth morphologies may have similar diets (e.g., Karr & James, 1975; Grossman, 1986). Studies on the evolution of African cichlid biodiversity have looked at variation in the morphology of the jaw and dentition and its influence in niche differentiation (Liem, 1973; Muschick et al., 2011). Most dentition of fishes follow patterns of convergent evolution based on niche similarities (e.g., Motta, 1988; Streelman, Webb, Albertson, & Kocher, 2003). Carnivorous fishes typically have canine teeth, that are long, conical, either straight or curved, and used for piercing and holding prey items (Grubich, Rice, & Westneat, 2008). Molariform teeth are flat broad teeth used for crushing and grinding food such as mollusks (Summers, 2000). Multicuspid teeth are commonly found in fishes that scrape algae off of substrates (Streelman et al., 2003), and 'incisors' in fish are used for cutting and are highly variable, coming in a variety of shapes (e.g. beak, saw edge, incisor; Bonaldo, Krajewski, Sazima, & Sazima, 2007; Grubich, Huskey, Crofts, Orti, & Porto, 2012). Villiform teeth are fine, closely set teeth used for stabbing and direction, and are more common in deep-sea fishes (Kenaley, 2012).

Myctophiformes possess villiform teeth on four oral jaw bones (i.e. premaxilla, dentary, palatine, mesopterygoid; Figure 3.1A, B) and additionally on the branchial arches (Paxton, 1972). In lanternfishes, the premaxilla extends the entire length of the upper jaw, and is closely attached to the maxilla by ligaments and connective tissue, excluding the maxilla from the entire gape. Lanternfish teeth are made of two parts: a short base (pedicle), and a longer crown (Paxton, 1972; Figure 3.1D). Paxton (1972) found that their teeth are depressible toward the oral cavity, and bend at the line separating the base and the crown, an attachment type that was later

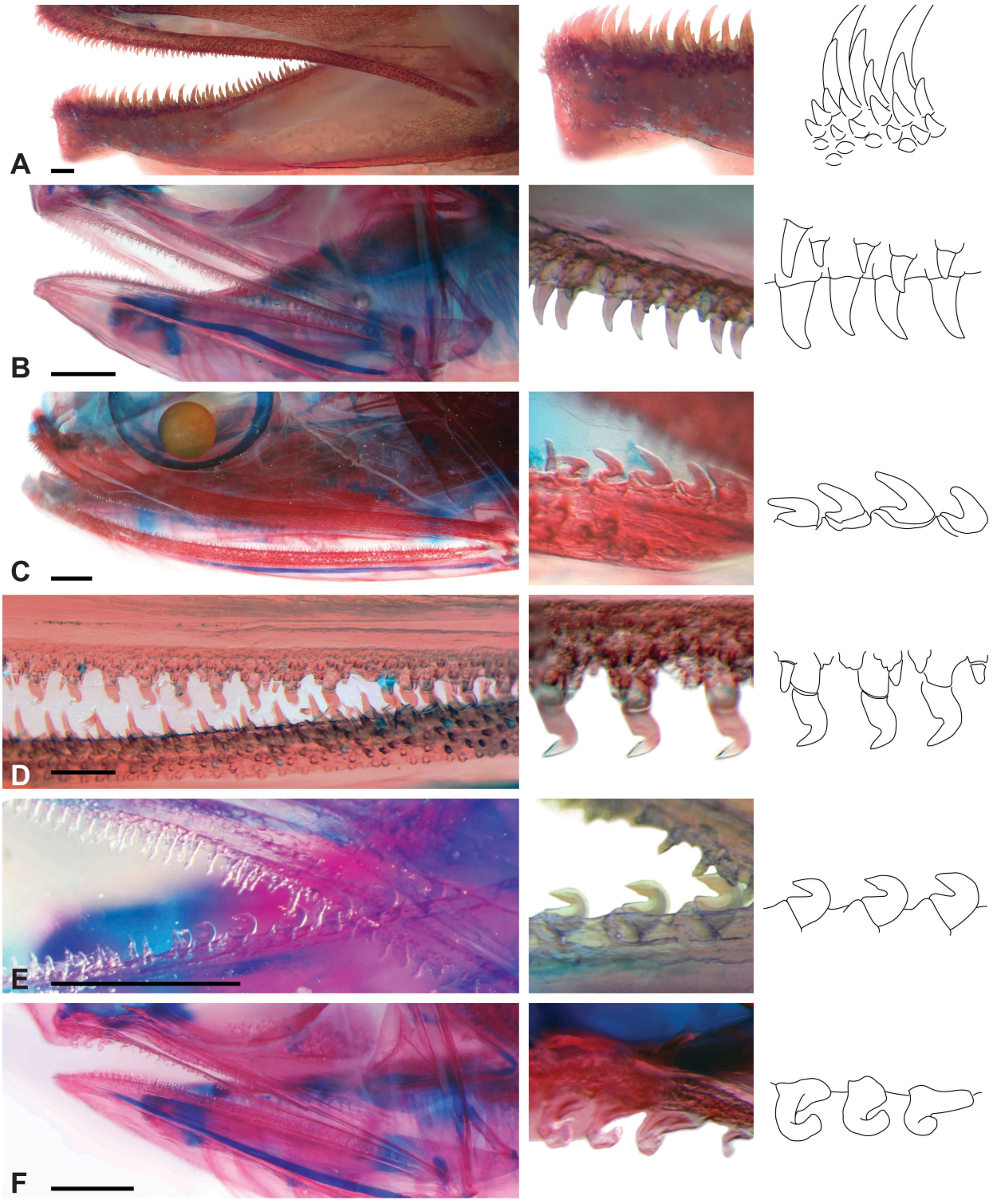


Figure 3.1. Examples of homodont (**A**, *Scopelengys tristis* FMNH 71919; **B**, *Gonichthys cocco* MCZ 98562) and heterodont (**C**, *Lampanyctus cuprarius* FMNH 49323; **D**, *Diaphus rafinesquii* MCZ 166656; **E**, *Diogenichthys laternatus* FMNH 71937; **F**, *Centrobranchus nigroocellatus* MCZ 98563) dentition in lanternfishes. Scalebars represent 1 mm.

described as ‘type 4’ by Fink (1981). Teeth located on the premaxilla and dentary, deemed villiform are generally conical, small, and aligned in numerous rows (Figure 3.1A, B). When Paxton (1972) examined multiple species of myctophids he found a variety of tooth patterns, including teeth with the tips curved slightly anteriorly or medially, and others he described as hooked (Figure 3.1C, D, E, F). The presence of these morphologically different teeth in addition to villiform on the same bone indicates that some species of lanternfishes exhibit heterodont dentition.

Heterodonty is the possession of more than one tooth morphology on the same bone. It is found extensively in mammals, and many studies focus on its presence in this group (e.g. Yamanaka, Yasui, Sonomura, Uemura, 2007; Štembírek et al., 2010) whereas very few studies investigate heterodonty in other lineages (e.g. reptiles; Dessem, 1985). The presence of heterodont dentition allows animals to utilize food sources they may not normally be able to (Kay, 1975). Very few studies have investigated heterodonty in fishes (e.g. Bemis & Bemis, 2015; Conway, Bertrand, Browning, Lancon, & Clubb, 2015), and those that do have focused on heterodonty in the pharyngeal teeth (e.g. Webb, Wallwork, & Elgood, 1981). There are currently no comprehensive anatomical studies on the presence and evolution of heterodonty across the lanternfish lineage.

This study investigates the evolution of heterodonty and anatomical variation in dentition across lanternfishes (e.g., hooked, villiform, caniniform), and reconstructs the repeated evolution of heterodonty within a phylogenetic framework. Previous studies assessing variation in dentition of lanternfishes (e.g. Paxton, 1972) did not investigate these traits within a phylogenetic framework. In this study we address the following questions related to the evolution of dentition

in lanternfishes: (1) What variation in dentition exists among the lanternfishes? (2) How many times has heterodonty on the oral jaws repeatedly evolved in lanternfishes?

## Materials and Methods

### Survey of Oral Dentition

We examined 229 lanternfish specimens covering 32 of 36 genera, and 85 species within Myctophiformes (see Material Examined). We assessed variation in tooth anatomy, presence on oral tooth-bearing bones (i.e. premaxilla, dentary, palatine, and mesopterygoid), and presence or absence of heterodonty. Specimen types include alcohol preserved, and clear and stained. Specimens used in this study are on loan from the Museum of Comparative Zoology, Scripps Institution of Oceanography, University of Kansas, Field Museum of Natural History, and the American Museum of Natural History. Museum abbreviations follow Sabaj (2016). Clear and staining followed Alcian blue (cartilage) and Alizarin red (bone) standard operating procedure (Taylor & Van Dyke, 1985).

### Character Evolution of Heterodonty

Likelihood ancestral-character state reconstructions were performed in Mesquite 3.04 (Maddison & Maddison, 2015). We used a maximum likelihood phylogeny of lanternfishes based on UCE sequences to reconstruct the character evolution of heterodonty in lanternfishes. Character states include presence and absence for heterodonty on any oral tooth-bearing bones. For genera not included in the anatomical analysis (*Loweina*), a character state was assigned based on previous publications on the anatomy of the genus (Paxton, 1972). The morphological character used to infer the ancestral character states among Myctophiformes is described below.

1. Multiple tooth types (Heterodonty) on tooth-bearing bone of the oral jaws

   ($01_0$) Absent.

   ($01_1$) Present.

**Phylogeny of *Diaphus***

To assess the evolutionary patterns of heterodonty in *Diaphus,* genetic data from 43 species were downloaded from GenBank to infer a species-level phylogeny using five nuclear (bmp4, 579 bp; glyt, 783 bp; h3, 375 bp; tbr1, 723 bp; zic1, 810 bp) and two mitochondrial (12S, 178 bp; COI, 690 bp) genes (Table 3.1). Each gene was aligned separately in MAFFT (Katoh & Standley, 2013) and concatenated in Mesquite v3.04 (Maddison & Maddison, 2015). The dataset was separated into 21 partitions, representing the three codon positions in each gene. All partitions were assigned a GTR + G substitution model in GARLI v2.01 (Zwickl, 2006) to conduct a maximum-likelihood analysis. The tree with the best likelihood score from 25 independent analyses was selected as the preferred hypothesis. The resulting phylogenetic tree was visualized with FigTree (Rambaut, 2007).

## Results

**Survey of Oral Dentition**

Villiform teeth were present on all assessed specimens within the family Neoscopelidae (blackchins) and Myctophidae (lanternfishes; Table 3.2, Figure 3.1). Heterodonty was present in 13 genera, only in Myctophidae, and only located on the premaxilla and/or dentary. Villiform teeth were present on all oral tooth-bearing bones (i.e. dentary, premaxilla, palatine, mesopterygoid) and on all specimens, with the exception of the teeth located on the palatine of

Table 3.1. Genbank accession numbers and associated gene sequences used in the phylogenetic reconstruction of *Diaphus*.

| Taxon | COI | 12S | zic1 | tbr1 | glyt | H3 | bmp4 |
|---|---|---|---|---|---|---|---|
| **Outgroup** | | | | | | | |
| *Lobianchia gemellarii* | KJ190063.1 | | KJ190148.1 | KJ556068.1 | KJ555596.1 | KJ555780.1 | KJ555292.1 |
| *Lobianchia dolfeini* | KP337918.1 | | KJ556256.1 | KJ556067.1 | KJ555595.1 | KJ555779.1 | KJ555291.1 |
| *Lampanyctus jordani* | KJ555413.1 | LC026533.1 | KJ556245.1 | KJ556055.1 | KF139781.1 | KJ555768.1 | KJ555282.1 |
| **Ingroup** | | | | | | | |
| *D. adenomas* | KJ555343.1 | | KJ556155.1 | KJ555963.1 | KJ555499.1 | KJ555686.1 | KJ555227.1 |
| *D. aliciae* | KJ555344.1 | LC146161.1 | KJ556156.1 | KJ555964.1 | KJ555500.1 | KJ555687.1 | KJ555228.1 |
| *D. anderseni* | KJ555346.1 | LC146170.1 | KJ556158.1 | KJ555966.1 | KJ555502.1 | KJ555689.1 | |
| *D. antonbruuni* | KJ555347.1 | | KJ556159.1 | KJ555967.1 | KJ555503.1 | KJ555690.1 | KJ555229.1 |
| *D. bertelseni* | EU148145.1 | | | | | | |
| *D. brachycephalus* | KJ555348.1 | LC146156.1 | KJ556160.1 | KJ555968.1 | | KJ555691.1 | KJ555230.1 |
| *D. chrysorhynchus* | AP012230 | LC146157.1 | KJ556165.1 | KJ555973.1 | KJ555506.1 | KJ555694.1 | KJ555233.1 |
| *D. danae* | KC136590.1 | LC146369.1 | | | | | |
| *D. dumerilii* | KF768169.1 | LC146176.1 | KF768161.1 | | | | |
| *D. effulgens* | KJ555350.1 | LC146168.1 | KJ190142.1 | KJ555974.1 | KJ555507.1 | KJ555695.1 | KJ555234.1 |
| *D. fragilis* | KJ555352.1 | LC146358.1 | KJ556168.1 | KJ555976.1 | KJ555509.1 | KJ555697.1 | |
| *D. fulgens* | KJ555353.1 | | KJ556169.1 | KJ555977.1 | KJ555510.1 | KJ555698.1 | KJ555235.1 |
| *D. garmani* | KJ555354.1 | LC146160.1 | KJ556170.1 | KJ555978.1 | KJ555511.1 | KJ555699.1 | |
| *D. gigas* | AP012235 | | | | | | |
| *D. holti* | KJ709514.1 | LC146356.1 | | | | | |
| *D. jenseni* | | LC146172.1 | | | | | |
| *D. knappi* | | LC146181.1 | | | | | |
| *D. kuroshio* | | LC146162.1 | | | | | |
| *D. lobatus* | KJ555355.1 | | KJ556171.1 | KJ555979.1 | KJ555512.1 | KJ555700.1 | KJ555236.1 |
| *D. lucidus* | AP012231 | LC146153.1 | | | | | |
| *D. malayanus* | KJ555356.1 | | KJ556172.1 | KJ555980.1 | KJ555513.1 | KJ555701.1 | KJ555237.1 |
| *D. meadi* | KJ555357.1 | LC145981.1 | KJ556173.1 | KJ555981.1 | KJ555514.1 | KJ555702.1 | |
| *D. metopoclampus* | KJ555358.1 | | KJ556174.1 | KJ555982.1 | KJ555515.1 | KJ555703.1 | KJ555238.1 |
| *D. mollis* | KJ555360.1 | LC146371.1 | KJ556176.1 | KJ555984.1 | KJ555517.1 | KJ555704.1 | KJ555240.1 |
| *D. nielseni* | | | KJ556177.1 | KJ555985.1 | KJ555518.1 | KJ555705.1 | KJ555241.1 |
| *D. ostenfeldi* | | LC146166.1 | | | | | |
| *D. parri* | KJ555363.1 | LC146360.1 | KJ556180.1 | KJ555988.1 | KJ555521.1 | KJ555708.1 | KJ555244.1 |
| *D. perspicillatus* | KJ555365.1 | LC146158.1 | KJ556183.1 | KJ555991.1 | KJ555524.1 | KJ555711.1 | |
| *D. phillipsi* | | | KJ556184.1 | KJ555992.1 | KJ555525.1 | KJ555712.1 | KJ555245.1 |
| *D. rafinesquii* | EU148154.1 | LC146159.1 | KF140525.1 | | KF139730.1 | | |
| *D. regani* | | LC146365.1 | KJ556185.1 | KJ555993.1 | KJ555526.1 | KJ555713.1 | |
| *D. richardsoni* | KJ555366.1 | | KJ556186.1 | KJ555994.1 | | | KJ555246.1 |
| *D. schmidti* | KJ555367.1 | LC146171.1 | KJ556187.1 | KJ555995.1 | KJ555527.1 | KJ555714.1 | KJ555247.1 |
| *D. signatus* | KJ555368.1 | | KJ556188.1 | KJ555996.1 | KJ555528.1 | KJ555715.1 | KJ555248.1 |
| *D. splendidus* | KJ555373.1 | LC146154.1 | KJ556194.1 | KJ556002.1 | KJ555534.1 | KJ555720.1 | KJ555254.1 |
| *D. suborbitalis* | | AB974487.1 | KJ556196.1 | KJ556004.1 | KJ555536.1 | KJ555721.1 | |
| *D. subtilis* | GU071745 | LC146167.1 | | | | | |
| *D. termophilus* | LC146370.1 | KJ556197.1 | KJ556005.1 | | KJ555537.1 | KJ555723.1 | KJ555255.1 |
| *D. theta* | KJ555374.1 | LC145995.1 | KJ556198.1 | KJ556006.1 | KJ555538.1 | KJ555724.1 | KJ555256.1 |
| *D. thiollierei* | KJ555376.1 | | KJ556201.1 | KJ556009.1 | KJ555541.1 | KJ555726.1 | |
| *D. umbroculus* | | | KJ556202.1 | KJ556010.1 | KJ555542.1 | KJ555727.1 | KJ555258.1 |
| *D. watasei* | KR231855.1 | LC026566.1 | KJ556204.1 | KJ556012.1 | KJ555544.1 | KJ555729.1 | KJ555260.1 |
| *D. whitleyi* | KJ555379.1 | | KJ556205.1 | KJ556013.1 | KJ555545.1 | KJ555730.1 | KJ555261.1 |

Table 3.2. Tooth types present on oral tooth bearing bones in assessed genera. Colored cells correspond to myctophid tribes. *Neoscopelus* and *Scopelengys* reside within Neoscopelidae; teal, Gymnoscopelini; purple, Notolychnini; green, Lampanyctini; light green, Diaphini; salmon, Myctophini. Letter symbols represent tooth types, V: Villiform, H: Hooked, C: Caniniform, A: Arrowhead.

| Subfamilies | Genera | Dentary | Premaxilla | Palatine | Mesopterygoid |
|---|---|---|---|---|---|
| | ***Neoscopelus*** | **V** | **V** | **V** | **V** |
| | ***Scopelengys*** | **V** | **V** | **V** | **V** |
| **Gymnoscopelinae** | ***Gymnoscopelus*** | **V** | **V** | **V** | **V** |
| | ***Lampanyctodes*** | **V** | **V** | **V** | **V** |
| | ***Lampichthys*** | **V** | **V** | **V** | **V** |
| | ***Notoscopelus*** | **V** | **V** | **V** | **V** |
| | ***Scopelopsis*** | **V** | **V** | **V** | **V** |
| **Lampanyctinae** | ***Notolychnus*** | **V** | **V** | **V** | **V** |
| | ***Bolinichthys*** | **V + H** | **V** | **V** | **V** |
| | ***Ceratoscopelus*** | **V + H** | **V** | **V** | **V** |
| | ***Lampadena*** | **V + H** | **V** | **V** | **V** |
| | ***Lampanyctus*** | **V + H** | **V** | **V** | **V** |
| | ***Lepidophanes*** | **V + H** | **V** | **V** | **V** |
| | ***Parvilux*** | **V + H** | **V** | **V** | **V** |
| | ***Stenobrachius*** | **V + H** | **V** | **V** | **V** |
| | ***Taaningichthys*** | **V + H** | **V** | **V** | **V** |
| | ***Triphoturus*** | **V + H** | **V** | **V** | **V** |
| **Diaphinae** | ***Lobianchia*** | **V** | **V** | **V** | **V** |
| | ***Diaphus*** | **V + H** | **V** | **V** | **V** |
| **Myctophinae** | ***Benthosema*** | **V** | **V** | **V** | **V** |
| | ***Centrobranchus*** | **V** | **V + H** | **V** | **V** |
| | ***Diogenichthys*** | **V** | **V + H + A** | **V** | **V** |
| | ***Electrona*** | **V** | **V** | **C** | **V** |
| | ***Gonichthys*** | **V** | **V** | **V** | **V** |
| | ***Hygophum*** | **V** | **V** | **V** | **V** |
| | ***Krefftichthys*** | **V** | **V** | **V** | **V** |
| | ***Myctophum*** | **V** | **V** | **V** | **V** |
| | ***Protomyctophum*** | **V** | **V** | **V** | **V** |
| | ***Symbolophorus*** | **V** | **V** | **V or C** | **V** |
| | ***Tarletonbeania*** | **V** | **V** | **V** | **V** |

*Electrona* and two species of *Symbolophorus.* These specimens lacked villiform teeth on the palatine, and instead had a single row of enlarged caniniform teeth (Table 3.2). Neoscopelidae (*Neoscopelus* and *Scopelengys*) displayed rows of both small and large villiform teeth that are slightly more pointed than species within Myctophidae (Figure 3.1A, B).

Within Myctophidae, the subfamily Gymnoscopelinae includes species (Table 3.2) with rows of the moderately sized, conical villiform teeth (Figure 3.1B). Numerous rows of villiform teeth were observed on the dentary and the premaxilla, with fewer rows on the palatine, and scattered depressed villiform bumps observed across the mesopterygoid (Table 3.2).

All Lampanyctinae species examined had rows of either small to moderately sized conical villiform teeth (Table 3.2). These teeth were either densely packed in numerous rows, or more widespread in a smaller number of rows on the dentary, premaxilla, and palatine. On the mesopterygoid they are more scattered, but with similarly densely packed or widespread pockets of villiform teeth. Lampanyctinae contains two lanternfish tribes, the monotypic Notolychnini (*Notolychnus*) and the speciose Lampanyctini (Table 3.2). All specimens examined within Lampanyctini exhibited morphologically similar heterodont dentition. Other than the regular villiform teeth, the additional heterodont teeth were located on the posterior portion of the dentary in a single row (3-11 teeth). They were anteriorly facing ‘C’ shaped hooked teeth that were generally larger than regular villiform teeth (Figure 3.1C). They were always found on the most posterior position of the dentary, either nested among regular villiform teeth, or as a stand-alone row (Figure 3.1C). Specimens representing all genera within Lampanyctini (9 total, *Nannobrachum* designated as synonym of *Lampanyctus*) were assessed (Table 3.2), and all exhibited this type of heterodont dentition.

Diaphinae includes two genera, *Lobianchia* and *Diaphus. Lobianchia* exhibited villiform teeth on the dentary, premaxilla, palatine, and mestopterygoid. *Diaphus* had higher variation in their tooth morphology (Table 3.2). Some species of *Diaphus* possessed homodont dentition, exhibiting only villiform teeth on all of their oral tooth bearing bones (e.g. *D. garmani, D. luetkeni, D. roei, D. splendidus*; Figure 3.2A). Others possessed heterodont dentition on either the premaxilla or the dentary. Heterodont teeth in *Diaphus* were either recurved, with a slight anteriorly directed angular bend approximately halfway up the crown of the tooth (e.g. *D. fragilis, D. sagamiensis, D. thiollierei*; Figure 3.2B), or had a hook shape, with a combination of the base and crown forming an 'S' like hook (e.g. *D. mollis, D. rafinesquii, D. vanhoeffeni*; Figures 3.1D, 3.2C). Within *Diaphus,* these types of heterodont teeth were either on the dentary or the premaxilla. These teeth usually formed one row either along the entire length of the bone, present on the most posterior portion of the bone, or in a row that stopped partway along it. A few species within *Diaphus* exhibited both recurved and hooked teeth (e.g. *D. holti, D. anderseni, D. brachycephalus*).

Most Myctophinae species had rows of either small or moderately sized, conical villiform teeth (Table 3.2). These teeth were either densely packed in numerous rows, or more widespread in a smaller number of rows on dentary, premaxilla, and palatine. They were scattered across the mesopterygoid, either similarly densely packed or widespread. Two genera within Myctophinae (*Electrona* and *Symbolophorous*) contained species that did not exhibit villiform teeth on the palatine (e.g. *E. antarctica, E. risso, S. boops, S. veranyi*), and instead had a single row of large, elongated caniniform teeth (Table 3.2). Two additional genera within Myctophinae exhibited heterodont dentition (*Diogenichthys* and *Centrobranchus*; Table 3.2). *Diogenichthys* exhibited

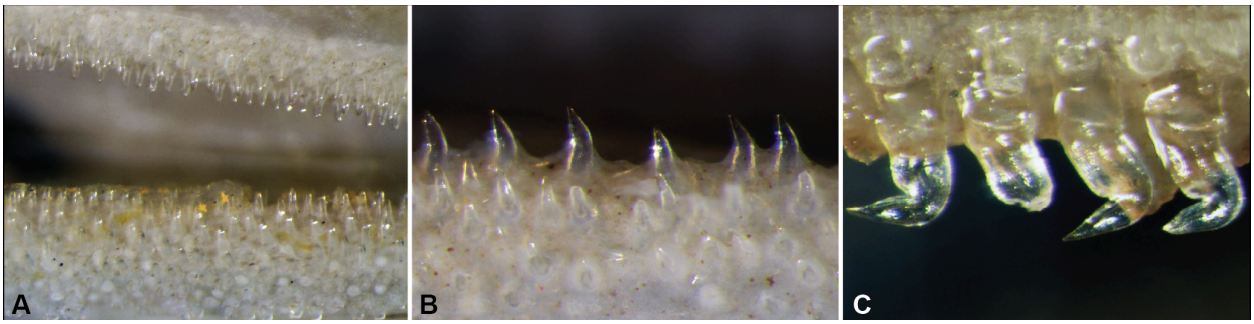


Figure 3.2. Examples of homodont (A, *D. problematics* MCZ 119046), recurved heterodont (B, *D. holti* MCZ 120623), and hooked heterodont (C, *D. rafinesquii* MCZ 166656) dentition in species of *Diaphus*.

anteriorly facing ‘C’ shaped hooked teeth, that were generally more robust and rounded than those of the Lamapnyctini (Figure 3.1E). They were found in a single row on the most posterior position of the dentary. This group also possessed arrowhead shaped teeth on both the dentary and the premaxilla (Figure 3.1E). In addition to having regular villiform teeth, *Centrobranchus* possessed heterodont dentition in the form of 4-5 posteriorly facing rounded ‘C’ shaped hooked teeth located on the most anterior portion of the premaxilla (Figure 3.1F).

**Ancestral Character Reconstruction of Heterodonty**

The common ancestor of the Myctophiformes most likely did not have heterodont dentition (Figure 3.3) as inferred under a likelihood character reconstruction. The common ancestor of the Myctophidae most likely had homodont dentition (Figure 3.3). The common ancestor of Gymnoscopelinae likely had homodont dentition (Figure 3.3). The common ancestor of Lampanyctinae likely had homodont dentition (83%), but the common ancestor of Lampanyctini likely had heterodont dentition (96%), with a single row of anterior facing hooked teeth on the posterior end of the dentary. The common ancestor of Diaphinae likely had homodont dentition (Figure 3.3). The common ancestor of Myctophinae likely had homodont dentition, and the *Dasyscopelus* + *Centrobranchus* clade likely had homodont dentition (Figure 3.3). Results of the species-level hypothesis of relationships for *Diaphus* (Figure 3.4) indicate that heterodonty is widespread throughout the clade. An explicit analysis for character evolution was not run due to missing taxa, and species that exhibit heterodonty are highlighted on Figure 3.4.

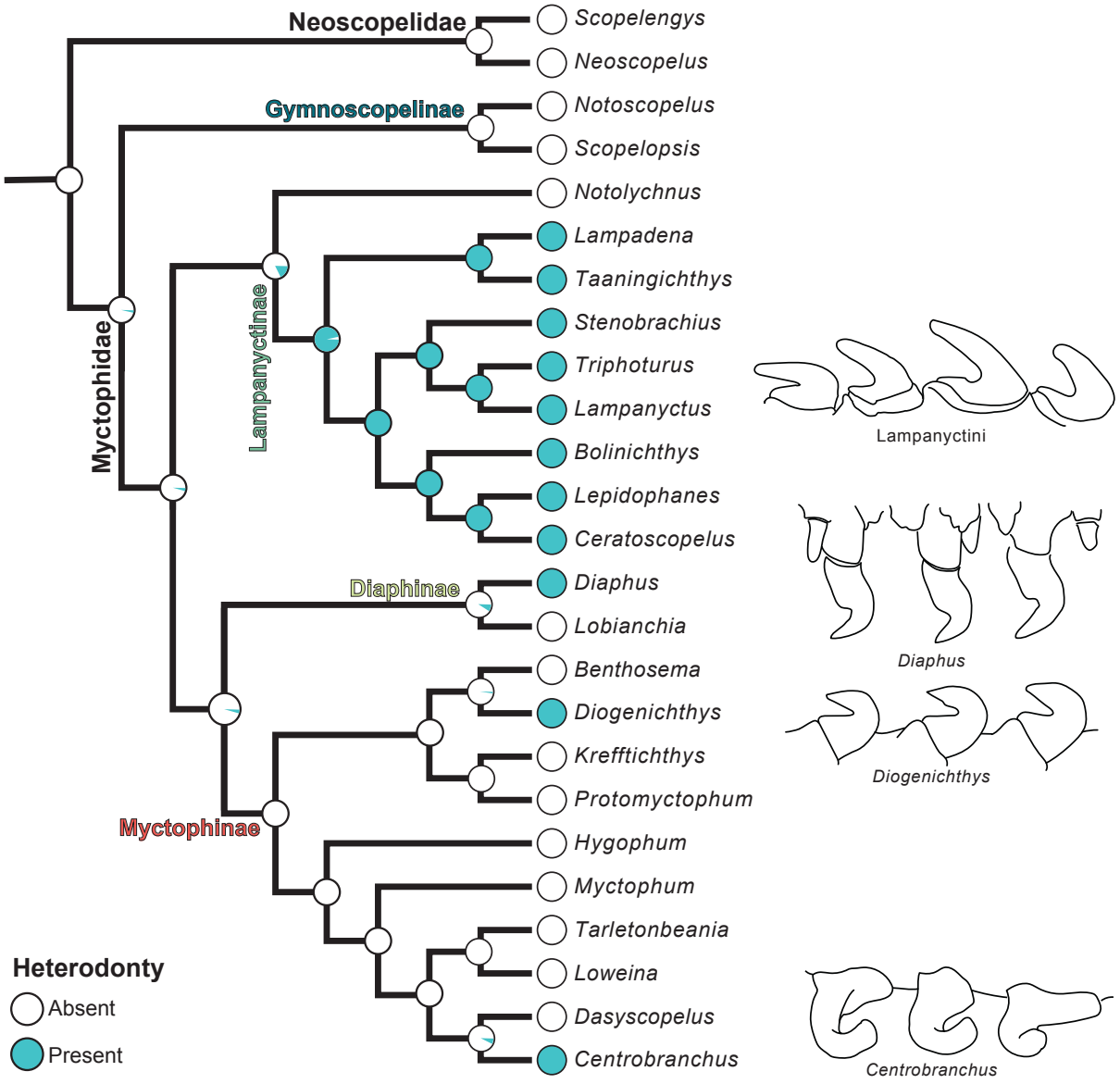


Figure 3.3. Maximum likelihood ancestral character-state reconstruction of heterodonty shown at nodes on a maximum likelihood phylogeny of lanternfish relationships based upon UCE sequences.

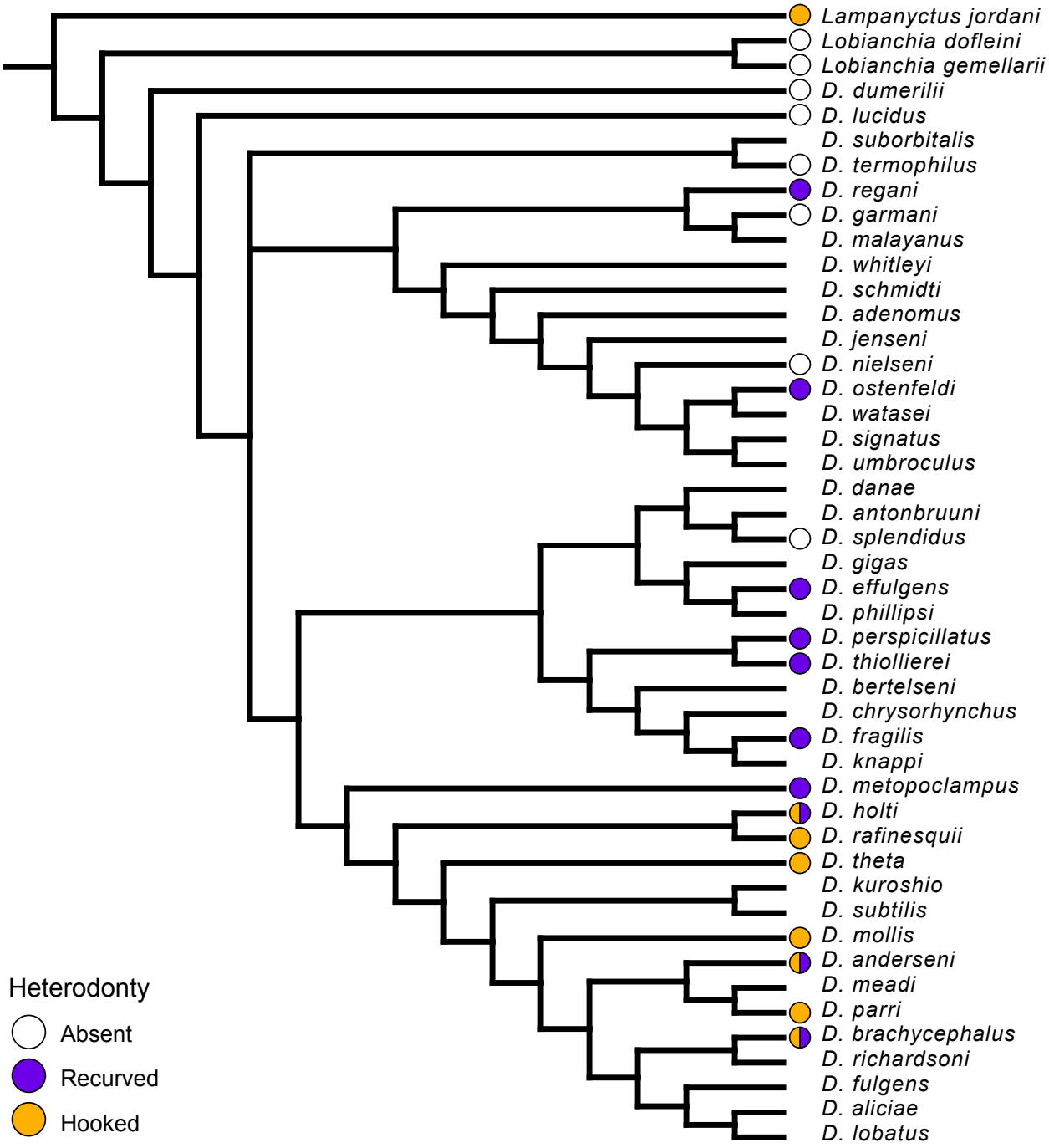


Figure 3.4. The presence of homodont dentition, recurved heterodont, or hooked heterodont dentition are indicated on a summary phylogeny of species within *Diaphus* created from a maximum-likelihood analysis of molecular data.

# Discussion

## Evolution of Heterodonty

In this study we examine the evolution of heterodonty on the oral tooth-bearing bones in lanternfishes. Heterodont dentition has evolved at least four different times within lanternfishes, and are expressed by four different anatomical variations around a global 'hook' shape (Figure 3.1). Our survey shows that species within Neoscopelidae are homodonts, with the dentary, premaxilla, palatine, and mesopterygoid possessing villiform teeth (Figure 3.1A). The maximum likelihood ancestral character-state reconstruction suggests homodont dentition is likely the ancestral state of Myctophiformes (Figure 3.3). Examination of the more speciose Myctophidae (lanternfishes) indicates that heterodonty likely evolved at least four separate times within this lineage (Figure 3.3): once in the last common ancestor of the tribe Lampanyctini, one or more times in *Diaphus*, once in *Diogenichthys*, and once in *Centrobranchus* (Figure 3.3). Paxton (1972) additionally noted 'hooked' dentition on the anterior portion of the premaxilla in specimens of *Taaningichthys*, *Lampadena*, and *Lepidophanes*. Our analysis of these genera did not corroborate these findings under our use of the term 'hooked,' describing the characteristic 'C' or 'S' shape. Instead we observed elongation and a slight increase in robustness of these teeth, a characteristic trending towards recurved. In this study, heterodonty was found to occur in 13 of the 32 assessed genera and at least 61 species. There are likely greater than 100 species that exhibit heterodonty due to the character being a synapomorphy in Lampanyctini (Figure 3.3).

## Heterodonty in Lampanyctini

All Lampanyctini specimens examined exhibited the posteriorly positioned, anteriorly facing heterodont teeth (Figure 3.1C). These findings, combined with our ancestral character-

state reconstruction (Figure 3.3) corroborate the presence of this feature as a synapomorphy of this tribe, evolving in their last common ancestor. Paxton (1972) also noted all species he examined within Lampanyctini exhibited this similar type of dentition, and had used the character 'posterior portion of dentary with row of moderately or strongly hooked teeth' in his key to identify taxa within the family Myctophidae (Figure 3.1C). Ahlstrom, Moser, and O'Toole (1976) analyzed specimens of *Lampanyctus hectoris* and found six to eight anteriorly facing hooked teeth on the posterior two-thirds of each dentary bone early in the larval stage in this species. Additionally, Paxton (1972) noted that the regular villiform teeth seemed to increase in size with an increase in size of the individual, but the posterior hooked teeth did not. This feature of the posteriorly positioned heterodont teeth (Figure 3.1C) may aid with specialized feeding in smaller individuals when the size difference between tooth types is more pronounced. Large hooked teeth, not seen in other lanternfish lineages, may make it harder for prey items to escape the oral cavity in larval and juvenile individuals before villiform teeth are fully grown. Some studies note that as body and mouth length increase with age in lanternfishes, there is often times a shift in the size and type of prey consumed. Takagi et al. (2009) notes an increase in the length of prey size consumed between juvenile and adult individuals of *Symbolophorus californiensis, Ceratoscopelus warmingii,* and *Myctophum asperum*. Bernal et al. (2013) found that as mouth width increased in *Lamapnyctus pusillus,* there was a similar increase in prey size. Some myctophid species become more opportunistic, and feed on both large and small prey items. In many carnivorous fishes (e.g. dragonfishes, anglerfishes), teeth are long, pointed, and curved slightly posteriorly towards the mouth interior, which functions primarily for holding and swallowing prey (Moore, 2002; Kenaley, 2009). The association of prey selectivity, mouth size,

and the presence of these large dentary teeth in early developmental stages of species within Lampanyctini, may support the increase in feeding potential that these hooked teeth may offer, especially to smaller individuals.

**Heterodonty in *Diogenichthys***

The genus *Diogenichthys* contains three species (Eschmeyer et al., 2017), all of which we examined in this study *(D. atlanticus, D. laternatus,* and *D. panurgus*). All three exhibited similar heterodont dentition on the dentary, showing robust anteriorly facing hooked teeth (Figure 3.1E). Paxton (1972) noted the hooked teeth of *Diogenichthys* in his key to this lineage, stating: 'posterior portion of dentary with row of strongly hooked teeth.' Taxa within *Diogenichthys* are among the smallest of lanternfish species, ranging from 20-30 mm, and they have been found to eat copepods, tunicates, and fish eggs (Oliva, Ulloa, & Bleck, 2006). Species of *Diogenichthys* are closely related to species in *Benthosema* (Poulsen et al., 2013; Denton, 2014), a genus containing individuals that do not exhibit heterodont dentition. A study assessing the diet of *Benthosema suborbitale* found large amounts of copepods in their diet (Pakhomov et al., 1996), which is the general prey item found in most lanternfish diet studies. The anteriorly facing hooked teeth present on species of *Diogenichthys* may have allowed them to specialize on food items like fish eggs, where the anatomy of the hook makes it harder for food items to escape the oral cavity in comparison to straighter teeth. Interestingly, *Diogenichthys* also exhibit arrow-shaped teeth (Figure 3.1E) on the premaxilla, but the functional role of these teeth is unknown and requires further study.

**Heterodonty in *Centrobranchus***

In *Centrobranchus,* the presence of posterior facing hooked teeth on the most anterior portion on the premaxilla (Figure 3.1F) may function in a similar way to other types of hooked teeth, by holding prey in the oral cavity. In one study, *Centrobranchus andreae* fed predominately on cavolinid pteropods (Van Noord, 2013), marine molluscs that have a tough outer shell. In addition to the villiform and hooked teeth on their oral jaw bones, *Centrobranchus* is known to have surprisingly different gill rakers than other lanternfishes. Instead of long thin rakers, the ventral area of the pharyngobranchial is covered by a plate that possesses many moderate to strong teeth (Paxton, 1972; Wisner, 1976). The adaptation of specialized anterior hooked dentition allow for species in this genus to specialize on prey items not normally sought after by other lanternfishes, and to take advantage of niches other lanternfishes do not utilize. These specialized hooked teeth may enable *Centrobranchus* to hold pteropods in the oral cavity, while their modified branchial teeth crush their hard shells.

**Heterodonty in *Diaphus***

In this study we surveyed 29 of 77 species of *Diaphus.* Heterodonty was present throughout this group and is represented by two morphological types, recurved and ’S’ shaped hooked teeth (Figures 3.1, 3.2). The evolution of heterodonty within *Diaphus* (Figure 3.4) indicates that this trait may have evolved multiple times throughout the history of this lineage, and not as a single event in a recent common ancestor. Bolin (1959) characterized *Diaphus* as possessing moderately hooked teeth in the posterior portion of the premaxilla. Similar to our study, Nafpaktitis (1966) found intermediate forms between hooked and conical teeth of *Diaphus,* and noted that these tooth morphologies aren't a definitive character for describing the

group (Figure 3.2). Paxton (1972) also mentions the presence of hooked teeth on some species of *Diaphus*, but that this morphology type has no clear pattern of evolution in this lineage. We had similar difficulties in describing the evolution of heterodonty in this group. Our phylogeny of taxa within *Diaphus* (Figure 3.4) does not show support for a single evolution of heterodonty in this lineage, and instead supports the potential for multiple evolutions or losses of heterodont dentition. Species of *Diaphus* eat a wide range of food items (e.g. molluscs, chaetognaths, polychaetes, other myctophids), many of which are uncommon prey items for other lanternfishes, who feed mainly on copepods, amphipods, ostracods, and euphausiids (Collard, 1970; Baird, Hopkins, & Wilson, 1975; Pakhomov et al., 1996; Tanaka et al., 2013). The 'S' shaped hooked dentition found on either the premaxilla or dentary in many species of *Diaphus* may have evolved multiple times in this group to aid in specialized feeding.

The genus *Diaphus* contains ~30% of all lanternfish species, and has been diversifying faster than other lanternfish lineages (Davis et al., 2014). Species in *Diaphus* are known for their diverse and sometimes sexually dimorphic headlight organs (Haddock et al., 2010 ), and were found to have high variation in their upper-jaw length (Martin & Davis, 2016). Multiple evolutions of heterodonty, combined with variation in jaw length and diverse bioluminescent head light organs, may have had an impact on diversification in this group. Additional molecular and morphological work is needed to expand on the phylogeny of *Diaphus* to further elucidate the pattern of evolution of heterodonty and diversification in this group. Streelman and Danley (2003) propose three stages of vertebrate evolutionary radiations. Stage one is divergence into a novel habitat, which for lanternfishes is the movement into bathy- and mesopelagic areas. The second and third stages are divergence in trophic morphology, focusing predominantly on

feeding structures, and in communication, which includes characteristics of coloration, behavior, and sexual dimorphism. In this study we show that lanternfishes exhibit multiple evolutions of specialized heterodont dentition, and they are known to exhibit evolutionary patterns of variation in mouth size (Martin & Davis, 2016). Alternative studies have found species specific, and sexually dimorphic bioluminescent structures (Herring, 2007; Davis et al., 2014) on lanternfishes, which are hypothesized to be used in communication. This evidence is similar to other groups (sticklebacks, Taylor & McPhail, 1999; finches, Grant & Grant, 1997; cichlids, Deutsch, 1997) that similarly follow the hypothesized stages of radiation and diversification proposed by Streelman and Danley (2003).

## Conclusions

Our study finds at least four separate evolutions of heterodonty in lanternfishes (Figure 3.3): once in the last common ancestor of Lampanyctini, *Centrobranchus, Diogenichthys,* and at least once in *Diaphus,*. Heterodont teeth are expressed by a global 'hook' shape in addition to the regular villiform teeth found on all lanternfishes. These hooks are only found on the premaxilla or the dentary. Heterodonty likely evolved multiple times within *Diaphus* (Figure 3.4), which indicates that species in this lineage may have an evolutionary history that is interspersed with specializations in feeding.

## Material Examined

*Benthosema glaciale*: MCZ 53426, 3, 37–60 mm SL.

*Benthosema pterotum*: MCZ 151484, 3, 34-41 mm SL.

*Bolinichthys indicus*: MCZ 124320, 3, 41-46 mm SL.

*Bolinichthys photothorax*: MCZ 123846, 3, 26-51 mm SL.

*Centrobranchus nigroocellatus*: MCZ 98563, 1; MCZ 98844, 3, 25-37 mm SL.

*Ceratoscopelus maderensis*: MCZ 100705, 3, 58-66 mm SL.

*Certaoscopelus warmingii*: MCZ 92411, 3, 40-52 mm SL.

*Diaphus anderseni*: MCZ 103200, 3, 22-27 mm SL.

*Diaphus arabicus*: MCZ 151691, 3, 28-35 mm SL.

*Diaphus brachycephalus*: MCZ 121662, 3, 32-33 mm SL.

*Diaphus dumerilii*: MCZ 120885, 3, 43-52 mm SL.

*Diaphus effulgens*: MCZ 110019, 3, 37-56 mm SL.

*Diaphus fragilis*: MCZ 120741, 3, 44-70 mm SL.

*Diaphus garmani*: FMNH 64636, 3, 50-65 mm SL.

*Diaphus holti*: MCZ 120623, 3, 22-47 mm SL.

*Diaphus hudsoni*: MCZ 97005, 3, 34-54 mm SL.

*Diaphus lucidus*: MCZ 120329, 3, 33-58 mm SL.

*Diaphus luetkeni*: FMNH 71834, 3, 28-45 mm SL.

*Diaphus metapoclampus*: MCZ 157871, 3, 26-32 mm SL.

*Diaphus minax*: FMNH 64627, 2, 47-52 mm SL.

*Diaphus mollis*: MCZ 90306, 3, 39-48 mm SL.

*Diaphus nielseni*: FMNH 121332, 1, 87 mm SL.

*Diaphus ostenfeldi*: MCZ 119163, 2, 47-48 mm SL.

*Diaphus parri*: MCZ 151451, 2, 32-52 mm SL.

*Diaphus perspicillatus*: MCZ 126693, 3, 34-52 mm SL.

*Diaphus problematicus*: MCZ 119046, 3, 54-66 mm SL.

*Diaphus rafinesquii*: MCZ 118953, 3, 62-75 mm SL; MCZ 166656, 1.

*Diaphus regani*: MCZ 90115, 1, 59 mm SL.

*Diaphus roei*: FMNH 113577, 1, 77 mm SL.

*Diaphus rolfbolini*: FMNH 78461, 2, 43-57 mm SL.

*Diaphus sagamiensis*: FMNH 120847, 1, 87 mm SL.

*Diaphus splendidus*: FMNH 120701, 3, 85-137 mm SL.

*Diaphus taaningi*: MCZ 159064, 3, 62-70 mm SL.

*Diaphus termophilus*: MCZ 118159, 3, 34-52 mm SL.

*Diaphus thiollierei*: MCZ 151467, 3, 46-64 mm SL.

*Diaphus vanhoeffeni*: MCZ 118089, 3, 27-31 mm SL.

*Diogenichthys atlanticus*: MCZ 55530, 3, 20-22 mm SL.

*Diogenichthys laternatus*: FMNH 71937, 3, 13-24 mm SL.

*Diogenichthys panurgus*: FMNH 71942, 1, 17 mm SL.

*Electrona antarctica*: MCZ 149056, 3, 18-23 mm SL.

*Electrona risso*: MCZ 62188, 3, 18-23 mm SL.

*Gonichthys cocco*: MCZ 98562, 1.

*Gonichthys tenuiculus*: MCZ 103199, 3, 45-49 mm SL.

*Gymnoscopelus braueri*: MCZ 148797, 3, 70-96 mm SL.

*Hygophum benoiti*: MCZ 116153, 3, 40-44 mm SL.

*Hygophum hygomii*: MCZ 92776, 3, 47-55 mm SL.

*Hygophum macrochir*: MCZ 115225, 3, 39-51 mm SL.

*Hygophum proximum*: MCZ 148705, 3, 36-43 mm SL.

*Krefftichthys anderssoni*: MCZ 148635, 1, 41 mm SL.

*Lampadena chavesi*: MCZ 98534, 1, 73 mm SL.

*Lampadena luminosa*: MCZ 102987, 3, 60-66 mm SL.

*Lampadena speculigera*: MCZ 55526, 2, 85-87 mm SL.

*Lampanyctodes hectoris*: MCZ 91359, 3, 44-74 mm SL.

*Lampanyctus australis*: MCZ 55034, 2, 80-98 mm SL.

*Lampanyctus crocodilus*: MCZ 55470, 3, 60-106 mm SL.

*Lampanyctus cuprarius*: FMNH 49323, 1.

*Lampanyctus macdonaldi*: MCZ 164406, 3, 79-156 mm SL.

*Lampanyctus vadulus*: MCZ 110183, 3, 56-83 mm SL.

*Lampichthys rectangularis*: MCZ 51782, 3, 69-88 mm SL.

*Lepidohpanes guentheri*: MCZ 108541, 3, 40-65 mm SL.

*Lobianchia gemellarii*: MCZ 107215, 3, 64-70 mm SL.

*Myctophum fissunovi*: MCZ 81734, 3, 37-57 mm SL.

*Myctophum phengodes*: MCZ 105757, 3, 78-89 mm SL.

*Myctophum punctatum*: MCZ 105563, 3, 65-85 mm SL.

*Myctophum spinosum*: MCZ 151450, 3, 41-71 mm SL.

*Nannobrachium atrum*: MCZ 113519, 3, 57-92 mm SL.

*Nannobrachium cuprarium*: MCZ 112776, 3, 55-67 mm SL.

*Nannobrachium indicum*: MCZ 151729, 3, 32-85 mm SL.

*Neoscopelus macrolepidotus*: MCZ 28159, 2, 90-121 mm SL.

*Notolychnus valdiviae*: FMNH 49465, 1, 23 mm SL.

*Notoscopelus caudispinosus*: MCZ 157882, 3, 59-67 mm SL.

*Notoscopelus elongatus kroyeri*: MCZ 104150, 3, 62-72 mm SL.

*Notoscopelus resplendens*: MCZ 166099, 3, 32-66 mm SL.

*Parvilux boschmai*: USNM 298170-5, 1.

*Protomyctophum arcticum*: MCZ 102601, 3, 31-42 mm SL.

*Scopelengys tristis*: FMNH 71919, 1; MCZ 140533, 3, 66-109 mm SL.

*Scopelopsis multipunctatus*: MCZ 102571, 3, 41-52 mm SL.

*Stenobrachius leucopsarus*: MCZ 88957, 3, 42-71 mm SL.

*Symbolophorus boops*: MCZ 103574, 3, 66-92 mm SL.

*Symbolohporus evermanni*: MCZ 148717, 3, 64-76 mm SL.

*Symbolophorus rufinus*: MCZ 103536, 2, 69-90 mm SL.

*Symbolophorus veranyi*: MCZ 111606, 3, 64-74 mm SL.

*Taaningichthys bathyphilus*: MCZ 102500, 2, 37-63 mm SL.

*Tarletonbeania crenularis*: MCZ 45847, 3, 44-64 mm SL.

*Triphoturus mexicanus*: MCZ 125392, 3, 49-51 mm SL.

## References

Ahlstrom, E. H., Moser, H. G., and O'Toole, M. J. 1976. Development and distribution of larvae and early juveniles of the commercial lanternfish, *Lampanyctodes hectoris* (Gunther), off the west coast of southern Africa with a discussion of phylogenetic relationships of the genus. *Bulletin of Southern California Academy of Sciences*, 75:138–152.

Alwis, A. D., and Gjøsæter, J. 1988. Some aspects of the feeding ecology of myctophids in the waters off central east Africa. In: Flødevigen Rapportserie No. 1, 1988. Havforsknings instituttet.

Anthony, M. R., and Kay, R. F. 1993. Tooth form and diet in ateline and alouattine primates: reflections on the comparative method. *American Journal of Science*, 293:356–382.

Arthur, D. K. 1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. *Fishery Bulletin U.S.,* 74:517–530.

Baird, R. C., Hopkins, T. L., and Wilson, D. F. 1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. *Copeia*, 356–365.

Barham, E. G. 1966. Deep scattering layer migration and composition: observations from a diving saucer. *Science,* 151:1399–1403.

Bejerano, G., Pheasant, M., Makunin, I., Stephen, S., Kent, W. J., Mattick, J. S., and Haussler, D. 2004. Ultraconserved elements in the human genome. *Science*, 304:1321–1325.

Bemis, K. E., and Bemis, W. E. 2015. Functional and developmental morphology of tooth replacement in the Atlantic Wolffish, *Anarhichas lupus* (Teleostei: Zoarcoidei: Anarhichadidae). *Copeia*, 103:886–901.

Betancur-R., R., Broughton, R. E., Wiley, E. O., Carpenter, K., Lopez, J. A., Li, C., Holcroft, N. I., Arcila, D., Sanciangco, M., Cureton, J., Zhang, F., Buser, T., Campbell, M., Rowley, T., Ballesteros, J. A., Lu, G., Grande, T., Arratia, G., Ortí, G. 2013. The tree of life and a new classification of bony fishes. PLOS Curr. Tree Life. April 18.

Bernal, A., Olivar, M. P., and de Puelles, M. L. F. 2013. Feeding patterns of *Lampanyctus pusillus* (Pisces: Myctophidae) throughout its ontogenetic development. *Marine Biology,* 160:81–95.

Bernal, A., Olivar, M. P., Maynou, F., and de Puelles, M. L. F. 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. *Progress in Oceanography*, *135:*1–17.

Bolger, A. M., Lohse, M., and Usadel, B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*, 30:2114–2120.

Bolin, R. L., 1959. Iniomi. Myctophidae from the ‘‘Michael Sars’’ North Atlantic Deep-Sea Expedition 1910. Scientific Results of the Michael Sars North Atlantic Deep- Sea Expedition 1910. University of Bergen, Bergen, Norway, 1–45.

Bonaldo, R. M., Krajewski, J. P., Sazima, C., and Sazima, I. 2007. Dentition damage in parrotfishes feeding on hard surfaces at Fernando de Noronha Archipelago, southwest Atlantic Ocean. *Marine Ecology Progress Series,* 342:249–254.

Brawand, D., Wagner, C. E., Li, Y. I., Malinsky, M., Keller, I., Fan, S., Simakov, O., Ng, A. Y., Lim, Z. W., Bezault, E., and Turner-Maier, J. 2014. The genomic substrate for adaptive radiation in African cichlid fish. *Nature,* 513:375–381.

Case, J. F., Warner, J., Barnes, A. T., and Lowenstine, M. 1977. Bioluminescence of lanternfish (Myctophidae) in response to changes in light intensity. *Nature,* 265:179–181.

Chakrabarty, P., Davis, M. P., Smith, W. L., Baldwin, Z. H., and Sparks, J. S. 2011a. Is sexual selection driving diversification of the bioluminescent ponyfishes (Teleostei: Leiognathidae)? *Molecular Ecology,* 20:2818–2834.

Chakrabarty, P., Davis, M. P., Smith, W. L., Berquist, R., Gledhill, K. M., Frank, L. R., and Sparks, J. S. 2011b. Evolution of the light organ system in ponyfishes (Teleostei: Leiognathidae). *Journal of Morphology,* 272:704–721.

Collard, S. B. 1970. Forage of some eastern Pacific midwater fishes. *Copeia*, 348–354.

Collins, M. A., Xavier, J. C., Johnston, N. M., North, A. W., Enderlein, P., Tarling, G. A., Waluda, C. M., Hawker, E. J., and Cunningham, N. J. 2008. Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biology,* 31:837–851.

Conley, W. J., and T. L. Hopkins. 2004. Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. *Bulletin of Marine Science,* 75: 361–379.

Conway, K. W., Bertrand, N. G., Browning, Z., Lancon, T. W., and Clubb Jr, F. J. 2015. Heterodonty in the New World: An SEM Investigation of Oral Jaw Dentition in the Clingfishes of the Subfamily Gobiesocinae (Teleostei: Gobiesocidae). *Copeia*, 103:973–998.

Danley, P. D., and T. D. Kocher. 2001. Speciation in rapidly diverging systems: lessons from Lake Malawi. *Molecular Ecology,* 10:1075–1086.

Davis, M. P. 2015. Evolutionary relationships of the deep-sea pearleyes (Aulopiformes: Scopelarchidae) and a new genus of pearleye from Antarctic waters. *Copeia,* 103:64–71.

Davis, M. P., Holcroft, N. I., Wiley, E. O., Sparks, J. S., and Smith, W. L. 2014. Species-specific bioluminescence facilitates speciation in the deep sea. *Marine Biology,* 161:1139–1148.

Davis, M. P., Sparks, J. S., and Smith, W. L. 2016. Repeated and widespread evolution of bioluminescence in marine fishes. PLOS ONE 11:e0155154.

De Busserolles, F., Fitzpatrick, J. L., Paxton, J. R., Marshall, N. J., and Collin, S. P. 2013a. Eye-size variability in deep-sea lanternfishes (Myctophidae): an ecological and phylogenetic study. PLOS ONE 8:e58519.

De Busserolles, F., Hart, N. S., Hunt, D. M., Davies, W. L., and Justin, N. 2013b. Spectral tuning in the eyes of lanternfishes (Myctophidae): description of a novel sexually dimorphic intra-ocular filter. In: Myctophid vision: seeing and being seen in the mesopelagic zone 169.

Denton, J. S. 2014. Seven-locus molecular phylogeny of Myctophiformes (Teleostei; Scopelomorpha) highlights the utility of the order for studies of deep-sea evolution. *Molecular Phylogenetics and Evolution,* 76:270–292.

Dessem, D. 1985. Ontogenetic changes in the dentition and diet of Tupinambis (Lacertilia: Teiidae). *Copeia*, 1985:245–247.

Deutsch, J. C. 1997. Colour diversification in Malawi cichlids: evidence for adaptation, reinforcement, or sexual selection? *Biological Journal of the Linnaean Society,* 62:1–14

Douglas, R. H., and Partridge, J. C. 1997. On the visual pigments of deep-sea fish. *Journal of Fish Biology,* 50:68–85.

Douglas, R. H., J. C. Partridge, K. Dulai, D. Hunt, C. W. Mullineaux, A. Y. Tauber, and P. H. Hynninen. 1998. Dragon fish see using chlorophyll. *Nature,* 393:423–424.

Douglas, R. H., Bowmaker, J. K., and Mullineaux, C. W. 2002. A possible retinal longwave detecting system in a myctophid fish without farred bioluminescence; evidence for a sensory arms race in the deep-sea, p. 391–394. In: Bioluminescence and Chemiluminescence, Progress and Current Applications. P. E. Stanley and L. J. Kricka (eds.). World Scientific, River Edge, New Jersey.

Eschmeyer, W. N., Fricke, R., van der Laan, R. 2017. Catalog of Fishes: Genera, Species, References. California Academy of Sciences. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 15.04.17).

Faircloth, B.C. 2013. illumiprocessor: A trimmomatic wrapper for parallel adapter and quality trimming. http://dx.doi.org/10.6079/J9ILL.

Faircloth, B.C., McCormack, J.E., Crawford, N.G., Harvey, M.G., Brumfield, R.T., and Glenn, T.C. 2012. Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology*, sys004.

Faircloth, B. C., Sorenson, L., Santini, F., and Alfaro, M. E. 2013. A Phylogenomic Perspective on the Radiation of Ray-Finned Fishes Based upon Targeted Sequencing of Ultraconserved Elements (UCEs). PLoS ONE 8: e65923.

Fink, W. L. 1981. Ontogeny and phylogeny of tooth attachment modes in actinopterygian fishes. *Journal of Morphology,* 167:167–184.

Froese, R., and D. Pauly. 2016. FishBase. World Wide Web electronic publication. www.fishbase.org. Version (10/2016).

García-Seoane, E., Dalpadado, P., and Va´zquez, A. 2013. Feeding ecology of the glacier lanternfish *Benthosema glaciale* (Actinopterygii, Myctophidae) in the Flemish Cap (north Atlantic Ocean). *Hydrobiologia,* 717:133–146.

Gaskett, A. C., Bulman, C., He, X., and Goldsworthy, S. D. 2001. Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *New Zealand Journal of Marine and Freshwater Research,* 35: 469–476.

Ghedotti, M. J., Barton, R. W., Simons, A. M., and Davis, M. P. 2015. The first report of luminescent liver tissue in fishes: evolution and structure of bioluminescent organs in the deep-sea naked barracudinas (Aulopiformes: Lestidiidae). *Journal of Morphology,* 276:310–318.

Gilbert, P. S., Chang, J., Pan, C., Sobel, E. M., Sinsheimer, J. S., Faircloth, B. C., and Alfaro, M. E. 2015. Genome-wide ultraconserved elements exhibit higher phylogenetic informativeness than traditional gene markers in percomorph fishes. *Molecular Phylogenetics and Evolution*, 92:140–146.

Gordeeva, N. V. 2011. On structure of species in pelagic fish: the results of populational-genetic analysis of four species of lanternfish (Myctophidae) from the southern Atlantic. *Journal of Ichthyology,* 51:152–165.

Gosline, W. A., Marshall, N. B., and Mead, G. W. 1966. Order Iniomi. Characters and synopsis of families. *Fishes of the western North Atlantic, Memorial Sears Foundation. Marine Research,* 1:1–18.

Grant, P. R. and Grant, B. R. 1997. Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences*, 94:7768–7775.

Grossman, G. D. 1986. Food resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology,* 1:317–355.

Grubich, J. R., Rice, A. N., and Westneat, M. W. 2008. Functional morphology of bite mechanics in the great barracuda (*Sphyraena barracuda*). *Zoology,* 111:16–29.

Grubich, J. R., Huskey, S., Crofts, S., Orti, G., and Porto, J. 2012. Mega-Bites: Extreme jaw forces of living and extinct piranhas (Serrasalmidae). *Scientific reports 2*.

Günther, A., 1864. Catalogue of the Physostomi, containing the families Siluridae, Characinidae, Haplochitonidae, Sternoptychidae, Scopelidae, Stomiatidae in the collection of the British Museum. *Catalogue of Fisheries British Museum,* 5:1–455.

Haddock, S. H., Moline, M. A., and Case, J. F. 2010. Bioluminescence in the sea. *Annual Review of Marine Science,* 2:443–493.

Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society,* 120:500–508.

Harris, R. S. 2007. Improved pairwise alignment of genomic DNA. Ph.D. Diss., Pennsylvania State Univ., Pennsylvania.

Herring, P. J. 2007. Review. Sex with the lights on? A review of bioluminescent sexual dimorphism in the sea. *Journal of the Marine Biological Association of the United Kingdom*, 87:829–842.

Holton, A. A. 1969. Feeding behavior of a vertically migrating lanternfish. *Pacific Science,* 23:325–331.

Hopkins, T. L., and J. V. Gartner, Jr. 1992. Resource- partitioning and predation impact of a low-latitude myctophid community. *Marine Biology,* 114:185–197.

Hopkins, T. L., Sutton, T. T., and Lancraft, T. M. 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. *Progress in Oceanography,* 38: 205–239.

Hulsey, C. D., Mims, M. C., Parnell, N. F., and Streelman, J. T. 2010. Comparative rates of lower jaw diversification in cichlid adaptive radiations. *Journal of Evolutionary Biology,* 23:1456–1467.

Janssen, J. 1976. Feeding modes and prey size selection in the alewife (*Alosa pseudoharengus*). *Journal of the Fisheries Board of Canada,* 33:1972–1975.

Karpouzi, V. S., and Stergiou, K. I. 2003. The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. *Journal of Fish Biology,* 62:1353–1365.

Karr, J. R., and James, F. C. 1975. Eco-morphological configurations and convergent evolution in species and communities. *Ecology and Evolution of Communities*, 258–291.

Katoh, K., and Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution,* 30:772–780.

Kay, R. F. 1975. The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology,* 43:195–215.

Kenaley, C. 2009. Revision of Indo-Pacific species of the loosejaw dragonfish genus *Photostomias* (Teleostei: Stomiidae: Malacosteinae). *Copeia*, 2009:175–189.

Kenaley, C. P. 2012. Exploring feeding behaviour in deep−sea dragonfishes (Teleostei: Stomiidae): jaw biomechanics and functional significance of a loosejaw. *Biological Journal of the Linnaean Society,* 106:224–240.

Lawry, J. V. 1974. Lantern fish compare downwelling light and bioluminescence. *Nature,* 247:155–157.

Liem, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Biology,* 22: 425–441.

Lovette, I. J., Bermingham, E., and Ricklefs, R. E. 2002. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society B: Biological Sciences,* 269:37–42.

MacLeod, N. 2002. Phylogenetic signals in morphometric data, p. 100–138. In: Morphology, Shape, and Phylogeny. N. MacLeod and P. L. Forey (eds.). Taylor and Francis, London and New York.

Maddison W. P., and Maddison D. R. 2015. Mesquite: A modular system for evolutionary analysis. Version 3.04 http://mesquiteproject.org.

Martin, R. P., and Davis, M. P. 2016. Patterns of Phenotypic Variation in the Mouth Size of Lanternfishes (Teleostei: Myctophiformes). *Copeia,* 104:795–807.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, 7:121–137.

McCormack, J. E., Faircloth, B. C., Crawford, N. G., Gowaty, P. A., Brumfield, R. T., and Glenn, T. C. 2012. Ultraconserved elements are novel phylogenomic markers that resolve

placental mammal phylogeny when combined with species-tree analysis. *Genome Research*, 22:746–754.

Mensinger, A. F., and J. F. Case. 1990. Luminescent properties of deep sea fish. *Journal of Experimental Marine Biology and Ecology,* 144:1–15.

Mirande, J. M. 2016. Combined phylogeny of ray−finned fishes (Actinopterygii) and the use of morphological characters in large−scale analyses. *Cladistics,* 10.1111/cla.12171

Mirarab, S., and Warnow, T. 2015. ASTRAL-II: Coalescent-based species tree estimation with many hundreds of taxa and thousands of genes. *Bioinformatics*, 31:i44–i52.

Moore, J. A., 2002. Upside-down swimming behavior in a whipnose anglerfish (Teleostei: Ceratioidei: Gigantactinidae). *Copeia*, 2002:1144–1146.

Moser, H. G., and Ahlstrom, E. H. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae, *Bulletin of the Natural History Museum, Los Angeles City,* 7:1–145.

Moser, H. G., and Ahlstrom, E. H. 1972. Development of the lanternfish, *Scopelopsis multipunctatus* Brauer 1906, with a discussion of its phylogenetic position in the family Myctophidae and its Role in a proposed mechanism for the evolution of photophore patterns in lanternfishes. *Fishery Bulletin*, 70:541–564.

Motta, P. J. 1988. Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environmental Biology of Fishes,* 22:39–67.

Munk, P. 1997. Prey size spectra and prey availability of larval and small juvenile cod. *Journal of Fisheries Biology,* 51:340–351.

Muschick, M., Barluenga, M., Salzburger, W., and Meyer, A. 2011. Adaptive phenotypic plasticity in the Midas cichlid fish pharyngeal jaw and its relevance in adaptive radiation. *BMC Evolutionary Biology* 11:116.

Nafpaktitis, B. G. 1966. Two new fishes of the myctophid genus *Diaphus* from the Atlantic Ocean. *Bulletin of the Museum of Comparative Zoology*, *Harvard*, 133:401–424.

Nafpaktitis, B. G. 1977. Family Neoscopelidae in Fishes of the Western North Atlantic, Part 7: Neoscopelids, Lanternfishes, Atlantic Mesopelagic Zoogeography. Memorial Sears Foundation for Marine Research, Yale University, New Haven, CT, pp. 1–12.

Nafpaktitis, B. G., Backus, R. H., Craddock, J. E., Haedrich, R. L., Robison, B. H., and Karnella, C. 1977. Family Myctophidae in Fishes of the Western North Atlantic, Part 7: Neoscopelids, Lanternfishes, Atlantic Mesopelagic Zoogeography. Memorial Sears Foundation for Marine Research, Yale University, New Haven, CT, pp. 3–265.

Near, T. J., Eytan, R. I., Dornburg, A., Kuhn, K. L., Moore, J. A., Davis, M. P., Wainwright, P. C., Friedman, M. and Smith, W. L. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences*, 109:13698–13703.

Nelson, J. S. 2006. Fishes of the World. Fourth edition. John Wiley & Sons, Hoboken, New Jersey.

Oliva, A., Ulloa, H., and Bleck, Z. 2006. Feeding habits of four species of mesopelagic fishes from the Northern Chilean. *Revista de biología tropical*, 54:613–622.

Olivar, M. P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., Miquel, J., and Massutí, E. 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the

western Mediterranean. *Deep Sea Research Part I: Oceanographic Research Papers* 62:53–69.

Pakhomov, E. A., Perissinotto, R., and McQuaid, C. D. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology Progress Series,* 134:1–14.

Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics,* 25:547–572.

Paxton, J. R. 1967. A distributional analysis for the lanternfishes (family Myctophidae) of the San Pedro Basin, California. *Copeia*, 1967:422–440.

Paxton, J. R. 1972. Osteology and relationships of the lanternfishes (family Myctophidae). *Bulletin of the Natural History Museum of Los Angeles County,* 13:1–78.

Paxton, J.R., Ahlstrom, E.H., and Moser, H.G., 1984. Myctophidae: relationships. In: Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W., Jr., Richardson, S.L. (Eds.), Ontogeny and Systematics of Fishes. *American Society of Ichthyologists and Herpetologists, Lawrence, Kansas,* 239–244.

Poulsen, J. Y., I. Byrkjedal, E. Willassen, D. Rees, H. Takeshima, T. P. Satoh, G. Shinohara, M. Nishida, and M. Miya. 2013. Mitogenomic sequences and evidence from unique gene rearrangements corroborate evolutionary relationships of Myctophiformes (Neoteleostei). *BMC Evolutionary Biology,* 13:111.

Prejs, A., Lewandowski, K., and Stańczykowska-Piotrowska, A. 1990. Size-selective predation by roach (*Rutilus rutilus*) on zebra mussel (*Dreissena polymorpha*): field studies. *Oecologia*, 83:378–384.

Price, S. A., Friedman, S. T., and Wainwright, P. C. 2015. How predation shaped fish: the impact of fin spines on body form evolution across teleosts. *Proceedings of the Royal Society B: Biological Sciences,* 282:20151428.

Prokofiev, A. M. 2006. Fossil myctophoid fishes (Myctophiformes: Myctophoidei) from Russia and adjacent regions. *Journal of Ichthyology,* 46:S38–S83.

Rafinesque, C. S., 1810. Indice d'ittiologia Siciliana, ossia, Catalogo Metodico dei Nomi Latini, Italiani, e Siciliani dei Pesci, Che si Rinvengono in Sicilia. Presso Giovanni del Nobolo, con approvazzione, Messina, Italy.

Rambaut, A. 2007. FigTree. Version 1.4.3. Program and documentation. http://tree.bio.ed.ac.uk/software/figtree/ (accessed 15.01.17).

Risso, A. 1810. Ichthyologie de Nice, ou histoire naturelle des poissons du département des Alpes Maritimes. F. Schoell, Paris, France.

Rohlf, F. J. 2010a. tpsrelw. Department of Ecology and Evolution, State University of New York at Stony Brook. Version 2.16. http://life.bio.sunysb.edu/morph

Rohlf, F. J. 2010b. tpsDIG. Department of Ecology and Evolution, State University of New York at Stony Brook. Version 1.49. http://life.bio.sunysb.edu/morph

Rohlf, F. J., and Slice, D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology,* 39:40–59.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes. *Zoological Journal of the Linnaean Society,* 53:397–513.

Rosenberger, A. L. 1992. Evolution of feeding niches in New World monkeys. *American Journal of Physical Anthropology,* 88:525–562.

Sabaj, M. H. 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). Electronically accessible at http://www.asih.org/, American Society of Ichthyologists and Herpetologists, Washington, DC.

Sabatés, A., and Saiz, E. 2000. Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. *Marine Ecology Progress Series,* 201:261–271.

Shreeve, R. S., Collins, M. A., Tarling, G. A., Main, C. E., Ward, P., and Johnston, N. M. 2009. Feeding ecology of myctophid fishes in the northern Scotia Sea. *Marine Ecology Progress Series,* 386:221–236.

Simpson, J. T., Wong, K., Jackman, S. D., Schein, J. E., Jones, S. J., and Birol, I. 2009. ABySS: a parallel assembler for short read sequence data. *Genome Research*, 19:1117–1123.

Smith, W. L., Stern, J. H., Girard, M. G., and Davis, M. P. 2016. Evolution of venomous cartilaginous and ray-finned fishes. *Integrative and Comparative Biology* 56:doi: 10.1093/icb/icw070

Sparks, J. S., Dunlap, P. V., and Smith, W. L. 2005. Evolution and diversification of a sexually dimorphic luminescent system in ponyfishes (Teleostei: Leiognathidae), including diagnoses for two new genera. *Cladistics,* 21:305–327.

Sparks, J. S., Schelly, R. C., Smith, W. L., Davis, M. P., Tchernov, D., Pieribone, V. A., and Gruber, D. F. 2014. The covert world of fish biofluorescence: a phylogenetically widespread and phenotypically variable phenomenon. PLoS ONE, 9:e83259.

Springer, A. M., Piatt, J. F., and Vliet, G. V. 1996. Sea birds as proxies of marine habitats and food webs in the western Aleutian Arc. *Fisheries Oceanography*, 5:45–55.

Springer, V. G., and Johnson, G. D. 2004. Study of the dorsal gill-arch musculature of teleostome fishes, with special reference to the Actinopterygii. *Bulletin of the Biological Society of Washington,* 11:1–260.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30:1312–1313.

Štembírek, J., Buchtová, M., Král, T., Matalová, E., Lozanoff, S., and Míšek, I. 2010. Early morphogenesis of heterodont dentition in minipigs. *European Journal of Oral Sciences*, 118:547–558.

Stiassny, M. L. 1996. Basal ctenosquamate relationships and the interrelationships of the myctophiform (scopelomorph) fishes, p. 405–426. In: Interrelationships of Fishes. M. L. J. Stiassny, L. R. Parenti, and G. D. Johnson (eds.). Academic Press, San Diego.

Streelman, J. T., and Danley, P. D. 2003. The stages of vertebrate evolutionary radiation. *Trends in Ecology & Evolution*, 18:126–131.

Streelman, J. T., Webb, J. F., Albertson, R. C., and Kocher, T. D. 2003. The cusp of evolution and development: a model of cichlid tooth shape diversity. *Evolution & development,* 5:600–608.

Summers, A. P. 2000. Stiffening the stingray skeleton-an investigation of durophagy in myliobatid stingrays (Chondrichthyes, Batoidea, Myliobatidae). *Journal of Morphology,* 243:113–126.

Sutton, T. T., Wiebe, P. H., Madin, L., and Bucklin, A. 2010. Diversity and community structure of pelagic fishes to 5000m depth in the Sargasso Sea. *Deep Sea Research Part II: Topical Studies in Oceanography,* 57:2220–2233.

Takagi, K., Yatsu, A., Itoh, H., Moku, M., and Nishida, H. 2009. Comparison of feeding habits of myctophid fishes and juvenile small epipelagic fishes in the western North Pacific. *Marine Biology,* 156:641–659.

Taylor, E. B. and McPhail, J. D. 1999. Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (Gasterosteus): insights from mitochondrial DNA. *Biological Journal of the Linnaean Society,* 66:271–291.

Taylor, W. R., and Van Dyke, G. C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium,* 9:107–119.

Tanaka, H., Sassa, C., Ohshimo, S., and Aoki, I. 2013. Feeding ecology of two lanternfishes *Diaphus garmani* and *Diaphus chrysorhynchus*. *Journal of Fish Biology,* 82:1011–1031.

Tanimata, N., Yamamura, O., Sakurai, Y., and Azumaya, T. 2008. Dietary shift and feeding intensity of *Stenobrachius leucopsarus* in the Bering Sea. *Journal of Oceanograph*y, 64: 185–194.

Tont, S. A. 1976. Deep scattering layers: patterns in the Pacific. *California Cooperative Oceanic Fisheries Investigations Report,* 18:112–117.

Turner, J. R., White, E. M., Collins, M. A., Partridge, J. C., and Douglas, R. H. 2009. Vision in lanternfish (Myctophidae): adaptations for viewing bioluminescence in the deep-sea. *Deep Sea Research Part I: Oceanographic Research Papers,* 56:1003–1017.

Van Noord, J. E. 2013. Diet of five species of the family Myctophidae caught off the Mariana Islands. *Ichthyological Research*, 60:89–92.

Van Valkenburgh, B. 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds, pp. 410–436. In: Carnivore behavior, ecology, and evolution. Springer US.

Wang, J., Lee, A. P., Kodzius, R., Brenner, S., and Venkatesh, B. 2009. Large number of ultraconserved elements were already present in the jawed vertebrate ancestor. *Molecular Biology and Evolution*, 26:487–490.

Webb, J. E., Wallwork, J. A., and Elgood, J. H. 1981. Carps, Catfish & allies. In *Guide to Living Fishes,* 91–102. Macmillan Education UK.

Wiley, E. O., and Johnson, G. D. 2010. A teleost classification based on monophyletic groups in Origin and Phylogenetic Interrelationships of Teleosts. München, Germany, pp. 123–182.

Wiley, E. O., P. Chakrabarty, M. T. Craig, M. P. Davis, N. I. Holcroft, R. L. Mayden, and W. L. Smith. 2011. Will the real phylogeneticists please stand up? *Zootaxa,* 2946:7–16.

Williams, A., Koslow, J., Terauds, A., and Haskard, K. 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. *Marine Biology,* 139:1177–1192.

Wisner, R. L. 1963. A new genus and species of myctophid fish from the South-Central Pacific Ocean, with notes on related genera and the designation of a new tribe, Electronini. *Copeia*, 24-28.

Wisner, R. L. 1976. The taxonomy and distribution of lanternfishes (family Myctophidae) of the eastern Pacific Ocean. *Scripps Institution of Oceanography La Jolla California*.

Yamaguchi, M., 2000. Phylogenetic analyses of myctophid fishes using morphological characters: progress, problems, and future perspectives. *Japan Journal of Ichthyology,* 47:87–108.

Yamanaka, A., Yasui, K., Sonomura, T., and Uemura, M. 2007. Development of heterodont dentition in house shrew (*Suncus murinus*). *European journal of oral sciences*, 115: 433–440.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phy- logenetic analysis of large biological sequence datasets under the maximum likelihood criterion [Unpublished PhD Dissertation]. [Austin]: The University of Texas.