



The impact of evolutionary trade-offs among bioluminescent organs and body shape in the deep sea: A case study on lanternfishes

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ABSTRACT

Functional innovations play major roles in constraining or contributing to the evolutionary diversification of organismal morphology. Among fish key innovations, bioluminescence is critical to the success of many deep-sea fishes. Understanding evolutionary dynamics of deep-sea fish lineages and the role bioluminescent light organs have on their evolution is a continuing effort of many deep-sea biologists. This study focused on assessing how bioluminescent structures involved with sexual communication may be impacting the evolution of body shape in the lanternfishes (Myctophiformes), a lineage of fishes possessing some of the most extensive sexual dimorphism in bioluminescent structures seen in deep-sea organisms. Results from this study using geometric morphometrics integrated with a phylogenetic hypothesis of lanternfish relationships suggest there is significant evolutionary modularity between the caudal peduncle and the rest of the body within lanternfishes. Our results also show that most lanternfish species lacking caudal light organs cluster together in morphospace (*Diaphus*, *Hintonia*, *Neoscopelidae*), possess enlarged headlight organs (*Diaphus*), and exhibit lower phylogenetic signal than species possessing caudal light organs. These results support the hypothesis that lanternfish body-shape evolution is influenced by selective pressures on their light-producing tail organs and that the importance of caudal light organs in lanternfish communication may result in differential selection on the caudal area in species that possess them. One possible interpretation for why lanternfishes without caudal light organs coalesce in morphospace may be that by removing the caudal light organ, natural selection would select for a lanternfish caudal morphology optimized for the physical landscape of the midwater that they live in, favoring more energy efficient and slow sustained swimming styles.

1. Introduction

Natural selection acts upon morphological variation tied to functions such as predation, locomotion, and communication. These functions are influenced by the constraints of an organism's natural history and physical structure, including its body shape. Analyses of body shape can be used to effectively investigate questions related to evolution, speciation, and diversification within populations, among species, and across higher taxonomic levels (Cherry et al., 1982; Streebman and Danley, 2003; Bonduriansky, 2006; Harmon et al., 2010; Friedman et al., 2019; Maile et al., 2020). The evolution of body shape in deep-sea (>200 m) or midwater fishes is poorly understood relative to many other groups, but recent work by Martinez et al. (2021) suggests that fishes living in these areas have evolved a broader array of body shapes than their shallow-water relatives and that many midwater fishes have evolved

forms ideal for slow and periodic swimming. Several deep-sea fish clades exhibit highly variable feeding and sensory system traits (Marranzino and Webb, 2018; Martinez et al., 2021), and many of these traits are tied to the evolution and use of bioluminescence (Davis et al., 2014, 2016; Martini and Haddock, 2017). Midwater fishes predominantly use bioluminescence for counterillumination, a form of camouflage in which structures on their ventrum match the color and intensity of downwelling light (Haddock et al., 2010). Bioluminescence has evolved for use in a myriad of other functions, including specializations that form lures, illuminate or surprise prey, or for use as bioluminescent distractions (Young, 1983; Haddock et al., 2010; Widder, 2010). Bioluminescence is believed to be a one of eight key functional innovations leading toward the diversification of ray-finned fishes (Wainwright and Longo, 2017). Many of the light-producing organs of bioluminescence are seemingly tied to the body shapes of fishes that use them. The ventral

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silhouette of a fish that successfully uses bioluminescence for counterillumination works in tandem with light organs to effectively obscure the silhouette. In many cases, fishes have evolved additional light organs hypothesized to be used for communication and predation (Paxton, 1972; Sparks et al., 2005; Herring, 2007; Davis et al., 2014). Often, these light organs appear similarly tied to body shape or the morphology of the structures that house them (Herring, 2007) and there are multiple groups of deep-sea fishes that use bioluminescence for these varied purposes (e.g., Herring, 2007; Chakrabarty et al., 2011; Davis et al., 2014).

One abundant and widespread lineage of deep-sea fishes notable for their bioluminescent structures (Davis et al., 2014; Denton and Adams, 2015) are the widespread lanternfishes (Myctophiformes; Paxton, 1972; Wisner, 1976; Collins et al., 2008). The Myctophiformes comprise two families (Fig. 1): Myctophidae (lanternfishes, 254 species in 34 genera) and Neoscopelidae (blackchins, 6 species in 3 genera; Fricke et al.,

2020). Nearly all lanternfishes and blackchins possess primary photophores (light organs; Figs. 1 and 2) on the ventral margins of their bodies used for counterillumination (O'Day, 1972; Paxton, 1972; Wisner, 1976). Camouflage via counterillumination is thought to be critical for lanternfish survival in the pelagic deep-sea environment. Additionally, most lanternfishes have primary photophores on the lateral sides of their bodies (Figs. 1 and 2), the positions of which have been tied to lanternfish body-shape evolution (Davis et al., 2014; Denton and Adams, 2015). Most lanternfish species possess secondary light organs on their heads, caudal peduncle, and other discrete regions of their bodies (Fig. 2). Among these bioluminescent structures, the head- and tail-light (supracaudal and infracaudal) organs are frequently sexually dimorphic and thought to be used for communication and species recognition (Paxton, 1972; Herring, 2007; Davis et al., 2014). The prevalence of primary photophores and secondary light organs on lanternfishes (Supplemental Table 1; Fig. 2), suggests that these traits have played a

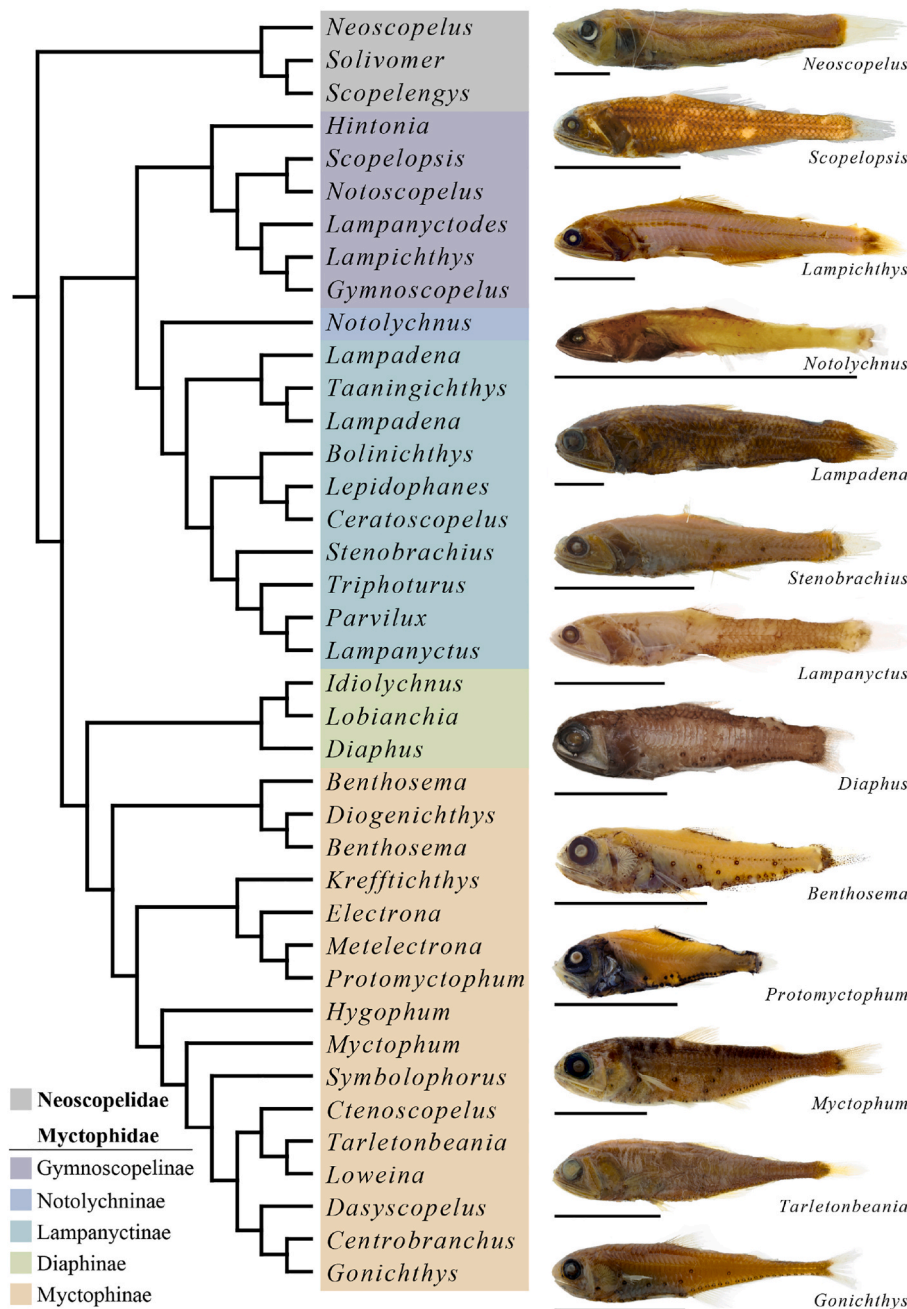


Fig. 1. A genus-level phylogeny of myctophiforms from Martin et al. (2018) with exemplars of lanternfish body shapes. Scale bars represent 2 cm. Specimen images in order from top to bottom: *Neoscopelus microchir* FMNH 120855; *Scopelopsis multipunctatus* USNM 274205; *Lampichthys procerus* MCZ 51782; *Notolychnus valdiviae* MCZ 104374; *Lampadena pontifex* FMNH 117877; *Stenobranchius leucopsarus* FMNH 71832; *Lampanyctus crypticus* USNM 274103; *Diaphus holti* MCZ 120623; *Benthoosema pterotum* MCZ 151484; *Protomyctophum crockeri* FMNH 124688; *Myctophum affine* FMNH 59974; *Tarletonbeania crenularis* FMNH 74222; *Gonichthys tenuiculus* FMNH 71685.

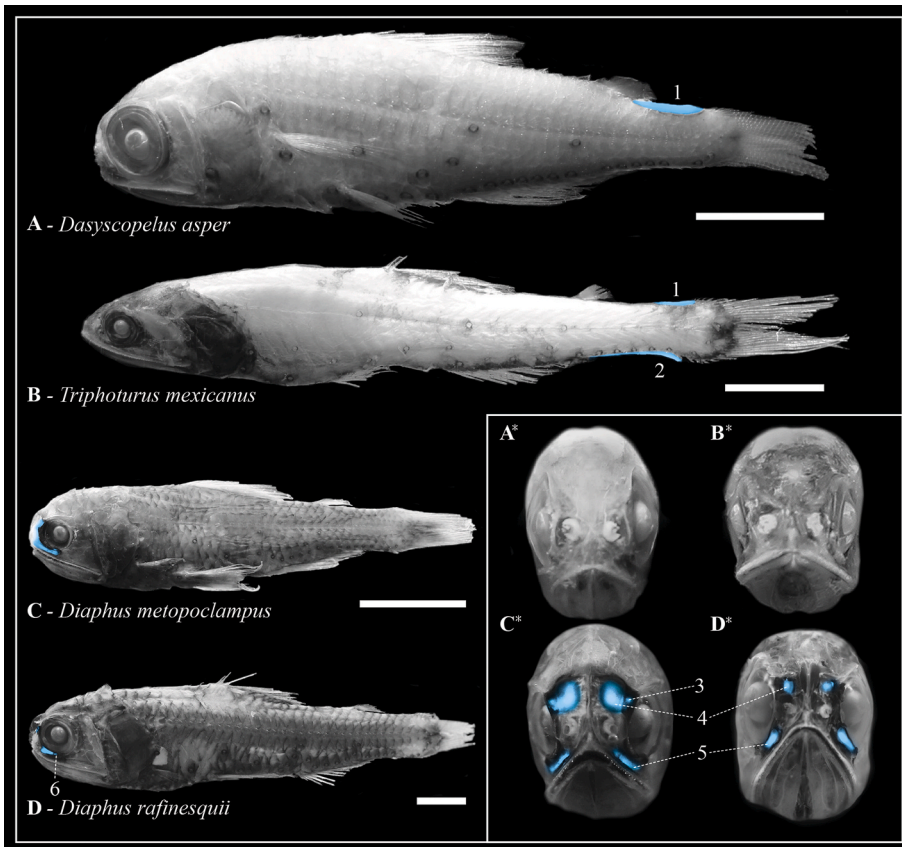


Fig. 2. Examples of the location and size of some additional light organs in lanternfishes. *Dasy Scopelus asper* (A; SIO 77–219) and *Triphoturus mexicanus* (B; KU 42113) exhibiting supracaudal (1) and infracaudal (2) glands. *Diaphus metopoclampus* (C; MCZ 157871) and *D. rafinesquii* (D; MCZ 118953) exhibiting the antorbital (3), dorsonasal (4), ventronasal (5), and suborbital (6) organs. Light organs associated with the head and tail are highlighted in blue. Scale bars represent 1 cm. Asterisks denote anterior views of specimens. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

fundamental role in the evolution of the group. Although ubiquitous throughout lanternfishes, all neoscopelids and three myctophid genera (*Diaphus*, *Gymnoscopelus*, and *Hintonia*) have species that lack caudal (tail) light organs (Herring, 2007), and many species in *Diaphus* and *Gymnoscopelus* show sexual dimorphism in the extensive secondary light organs on their heads (Fig. 2). The perpetuation of sexual dimorphism in both the caudal- or head-light organs and the use of these discrete organs for communication suggest that these structures play a substantive role in the evolution of lanternfishes and make these organs ideal candidates for testing how discrete structural innovations may affect body-shape evolution.

The synchronous analyses of functional traits like bioluminescence and body-shape disparity within a phylogenetic context is important for addressing questions regarding lanternfish evolution (de Busserolles et al., 2014; Martin and Davis, 2016, 2020; Denton, 2018). Myctophiforms share a relatively similar body plan, but there is evidence for biologically relevant body-shape disparity within the lineage (Denton and Adams, 2015). For example, the subfamily Myctophinae contains slender-tail lanternfishes (e.g., *Centrobranchus*, *Gonichthys*) and truncated lanternfishes (e.g., *Electrona*, *Protomyctophum*) and possesses a wide range of body-shape disparity compared to other lanternfish subfamilies (Paxton, 1972, Fig. 1). Additionally, the slender-tail lanternfishes within the Myctophinae were found to possess body shapes following a maneuverability/acceleration model, consistent with hydrodynamic constraints imposed on fishes (Denton and Adams, 2015). Previous qualitative (Paxton, 1972) and quantitative (Denton and Adams, 2015) accounts of lanternfish body-shape disparity, in addition to the variable use of primary photophores and secondary light organs, suggest the need for an in-depth analysis across all myctophiforms, specifically addressing body-shape disparity and the influence of caudal light organs on body-shape evolution.

The objectives of this study are to describe the evolution of myctophiform body-shape disparity and assess the possibility that there are

differential effects on body-shape evolution when caudal light organs are present. To test this, we use geometric morphometrics integrated with a phylogenetic hypothesis of myctophiforms, methods that allow us to address questions of phylogenetic signal, convergence, divergence, and constraint in body shape among all myctophiform lineages. Due to the potential differences in selective pressures on the caudal peduncle based on the presence or absence of caudal light organs and their varied functions in the ecology of these pelagic fishes and its effect on body shape that is intimately tied to locomotion, we expect modularity between the caudal peduncle region and the rest of the body in lanternfishes. We also believe that the Myctophinae will exhibit higher shape disparity and phylogenetically divergent body shapes relative to other myctophiform subfamilies. For this study, we focused on answering the following questions: (1) What are the patterns of myctophiform body-shape disparity? (2) Is there a difference in body-shape modularity between the caudal area and the rest of the body between myctophiforms with and without caudal light organs? (3) To what extent does phylogenetic history influence myctophiform body shape and are there differences in phylogenetic signal between lanternfishes with or without caudal light organs? (4) Are there any lineages that diverge from an evolutionarily constrained body shape?

2. Materials and methods

2.1. Specimens

The majority of myctophiforms used in this study were formalin-fixed and ethanol-preserved museum specimens from multiple US institutions (see Supplemental Text). Specimens from the Scripps Institution of Oceanography are stored in 50% isopropanol and our analyses included a few additional specimens that were fixed and preserved directly in 95% ethanol. The left lateral sides of 514 of the most visibly straight myctophiforms were photographed along with a scale using a

Nikon D800 or a Canon EOS Rebel SL1 Digital SLR camera representing species included in the [Martin et al. \(2018\)](#) phylogeny. These include 79 of the 260 recognized species and all 37 of the recognized genera within the Myctophiformes ([Supplemental Table 1](#)). Museum acronyms follow [Sabaj \(2020\)](#).

2.2. Geometric morphometrics

Geometric morphometrics were used to describe and compare myctophiform body-shape disparity using 11 homologous landmarks ([Fig. 3](#), white circles) and 32 sliding semilandmarks ([Fig. 3](#), black circles) situated along four curves that define lanternfish body margins. Homologous landmarks and curves were digitally placed in R ([R Core Team, 2018](#)) based on locations commonly used in geometric morphometric studies of fishes ([Loy et al., 1996](#)) using the package *Stereomorph* ([Olsen and Westneat, 2015](#)). Descriptions of homologous landmarks and curves can be found in the Supplemental Text. Stomach areas were excluded from analyses to prevent confounding shape variation due to stomach fullness ([Fig. 3](#)). A generalized Procrustes analysis (GPA) was performed using the *geomorph* package v. 3.1.1 ([Adams et al., 2019](#)) in R using bending energy for semilandmark alignment.

2.3. Allometric adjustment and shape visualization

Specimen shape values and centroid sizes were first averaged by species. A phylogenetic regression was performed on the averaged Procrustes variables using the 'procD.pgls' function for 10,000 iterations (*geomorph*) testing for an allometric effect between body shape and specimen size and incorporating the [Martin et al. \(2018\)](#) phylogeny. Regression resampling was calculated under residual randomization, where residual shape values were derived from a reduced model and then randomized in reference to the original linear model. Residuals from this analysis were subsequently used in plotting a principal component analysis (PCA), removing the observed variation on shape described by differences in specimen size and phylogenetic influence, allowing for the visualization of shape data across the Myctophiformes without the effect of phylogenetic relatedness and allometry. A phylogenetic MANOVA was performed using the function 'procD.pgls' (*geomorph*) for 10,000 iterations additionally comparing the following effects on lanternfish body shape: presence/absence of the caudal light organ, presence/absence of the caudal light organ excluding the two species of *Gymnoscopelus* used in this study (of the total eight described

species) that lack caudal light organs, and by subfamily.

2.4. Phylogenetic patterns, influence, and evolutionary rates

To evaluate evolutionary patterns of body-shape change, we created a species-level phylomorphospace ([Sidlauskas, 2008](#)) in R using the package *phytools* ([Revell, 2012](#)). We used the average location of each species in the adjusted PCA combined with the myctophiform phylogeny from [Martin et al. \(2018\)](#), which was also used to assess phylogenetic signal using the 'physignal' function from *geomorph* ([Adams, 2014](#)). The resulting K_{mult} statistic was compared to a null distribution generated from permutation tests using the average shapes of species. A significant K_{mult} value < 1 indicates that under a Brownian motion model of trait evolution closely related taxa resemble each other less than expected. A significant $K_{\text{mult}} > 1$ suggests that closely related taxa resemble each other more than anticipated. We expect the caudal light organ to be tightly associated with phylogenetic relationships, and, thus, lineages possessing them will show high phylogenetic signal and a significant K_{mult} close to 1. In order to compare relative rates of body shape evolution among lineages with and without caudal light organs, we transformed the [Martin et al. \(2018\)](#) tree into an ultrametric tree using the *phytools* and *phangorn* ([Schliep, 2011](#)) packages in R and the 'nnls.tree' and 'force.ultrametric' functions. We then used the 'compare.evol.rates' function from *geomorph*.

2.5. Modularity, disparity, and convergence

To further assess the effect of caudal light organ presence or absence on lanternfish body shape disparity, we partitioned the caudal area from the rest of the body ([Fig. 3](#), solid vs half-colored circles) and tested modularity between species with tail-light organs and species without tail-light organs using the 'phylo.modularity' function from the *geomorph* package using the size-adjusted shape array ([Adams, 2016](#)). A significant CR statistic < 1 implies that there is independence among modules ([Adams and Collyer, 2019](#)). In species with caudal light organs, we expect the caudal area housing these organs to be significantly tied to phylogeny and shape evolution and reflect low modularity, whereas species lacking a caudal light organ will have a relaxed constraint and show a significantly lower CR value. To compare differences in the amount of body-shape disparity between lanternfishes with tail-light organs and those without, we calculated Procrustes variances using the function 'morphol.disparity' from the *geomorph* package using the adjusted shape array. We were also interested in the disparity among subfamilies. To test whether non-light organ bearing lanternfish are converging in morphospace we used the function 'convratsig' from the package *convevol* ([Stayton, 2014, 2015](#)). We used species representatives (i.e., *Diaphus phillipsi*, *Gymnoscopelus braueri*, *Hintonia candens*, *Scopelengys tristis*) from each monophyletic group containing non-light organ bearing taxa. The resulting C values represent different measures of convergence, specifically a value of 0 for C1 indicates no convergence and a value of 1 means lineages are indistinguishable from each other. See [Stayton \(2014, 2015\)](#) for additional information regarding the other C values. Unless otherwise noted, P values were based on 10,000-iteration permutations for all analyses.

3. Results

3.1. Morphospace and the myctophiform body shape

The average myctophiform body shape described by the Procrustes-analysis consensus configuration is relatively slender with a tapering caudal peduncle, medially located dorsal- and anal-fin insertions, a moderately long jaw in relation to the eye, and a laterally positioned pectoral-fin insertion ([Fig. 3B](#)). Myctophiform body shapes are well differentiated at the family, subfamily, and genus level with respect to principal components (PCs) one and two, which account for 58.2% of

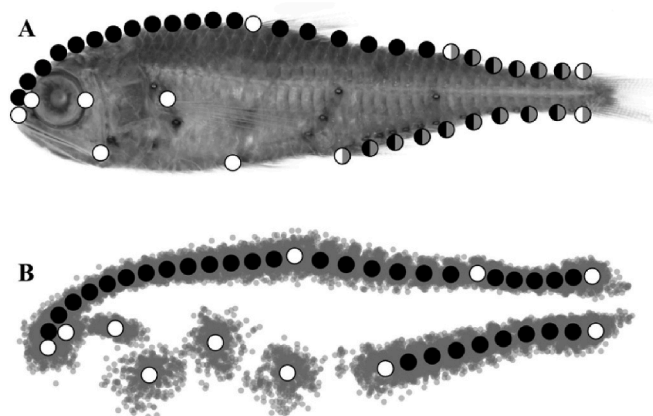


Fig. 3. A) Positions of homologous (white) and semi- (black) landmark placements used in this study. All solid-colored landmarks are associated with one partition, and all half-colored landmarks are associated with the second partition in the modularity test. B) Consensus configuration from the general Procrustes analysis of 514 specimens. White dots depict average homologous landmark locations, and black dots depict the average semilandmark locations. Gray dots depict the variation in landmark location around the average.

overall shape variation (Fig. 4). Principal component one (PC1) describes 33.4% of myctophiform body-shape variation and depicts a major axis of change in body depth in relation to body length and a shortening of the caudal peduncle area in relation to the rest of the body. Principal component two (PC2) describes 24.8% of myctophiform body-shape variation and depicts a major axis of change in the position of the anal-fin insertion and slenderness of the caudal peduncle (Fig. 4). Of note, most species lacking caudal light organs (Fig. 4 circles with black outlines) are clustered in one corner of morphospace, with the remaining lanternfishes occupying the rest of PC1 and PC2 morphospace.

Neoscopelids (blackchins) exhibit body shapes trending toward an extreme end of the first major axis of variation (Fig. 4). Blackchins possess thicker caudal peduncles with a more posteriorly displaced anal-fin insertion in relation to their dorsal-fin insertion and more ventrally positioned pectoral fins. Within the Myctophidae, the direction and breadth of variation in body shape differed substantially by subfamily except for the overlap between the Gymnoscopelinae and the Lampanyctinae. Average trends in body-shape variation by subfamily can be seen in Fig. 4. See supplemental text for a more in-depth description of shape variation by clade. An additional 17.4% of body-shape variation is described by PC3 which characterizes variation associated with the location of the dorsal- and anal-fin insertions in relation to the head. Lastly, PC4 describes 7.59% of body-shape variation and characterizes slenderness of the caudal peduncle and curvature of the myctophiform body, variation that is likely due to artifacts of preservation (Supplemental Fig. 1). Results from the three phylogenetic MANOVAs can be found in Table 1. The presence/absence of caudal light organs had a non-significant effect ($P = 0.66$) on body-shape disparity, but the same test, after removing the two individuals from *Gymnoscopelus* that do not cluster with the other lanternfish species lacking caudal light organs, resulted in a moderately significant effect ($P = 0.085$). Additionally, there was a significant effect of subfamily ($P = 0.054$) on body-shape disparity.

Table 1

Results from the phylogenetic MANOVA testing the following effects on body-shape disparity: The presence/absence of caudal light organs, presence/absence of caudal light organs *sans* the three non-caudal light organ bearing species in Gymnoscopelinae, and subfamily.

MANOVA	Df	F Value	P Value
log Centroid Size	1	2.03	0.059
Presence/Absence Caudal Light Organ	1	0.64	0.66
Presence/Absence Caudal Light Organ (<i>sans</i> <i>Gymnoscopelus</i>)	1	1.88	0.085
Subfamily	5	1.52	0.054

3.2. Phylomorphospace, phylogenetic signal, and evolutionary rates

The phylomorphospace plot (Fig. 5) positioned the body shape of the last common ancestor of the Myctophiformes near the consensus configuration (Fig. 3). In shape space, the Neoscopelidae and most of the myctophid subfamilies diverge in different directions in shape space from the average myctophiform body shape (Fig. 5) and stay relatively constrained within their respective morphospaces with limited back-crossing of subfamilial lineages. Phylogenetic signal in body shape for myctophiforms lacking caudal light organs was $K_{\text{mult}} = 0.818$ ($P < 0.001$) with closely related taxa resembling each other slightly less than expected under a Brownian motion model of trait evolution. Myctophiforms exhibiting a caudal light organ had a $K_{\text{mult}} = 0.897$ ($P < 0.001$) a slightly higher value than those lacking caudal light organs. Testing the relative rate of body-shape evolution between lineages with and without caudal light organs resulted in similar rates between groups with a non-significant ($P = 0.569$) rate ratio of 1.14. The relative evolutionary rate of body shapes for lanternfish species with and without caudal light organs was 0.0011 and 0.00097, respectively.

3.3. Body-shape modularity, disparity, and convergence

There is a significant amount of independence between the caudal area and the remainder of the body for lanternfishes lacking caudal light

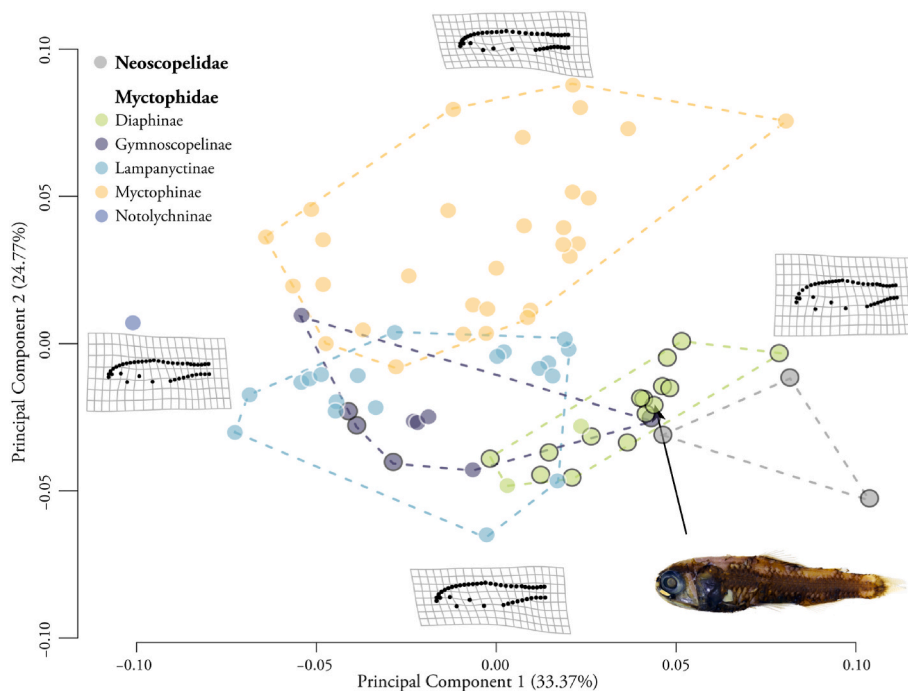


Fig. 4. Lanternfish species shown in the tangent space of PC1 and PC2 of body-shape disparity with circles representing location of species averages. Deformation grids show lanternfish body shapes at the extremes. Circle outlines highlight the location of species possessing (white outlines) or lacking (black outlines) caudal light organs. Image of *Diaphus rafinesquii* MCZ 118953.

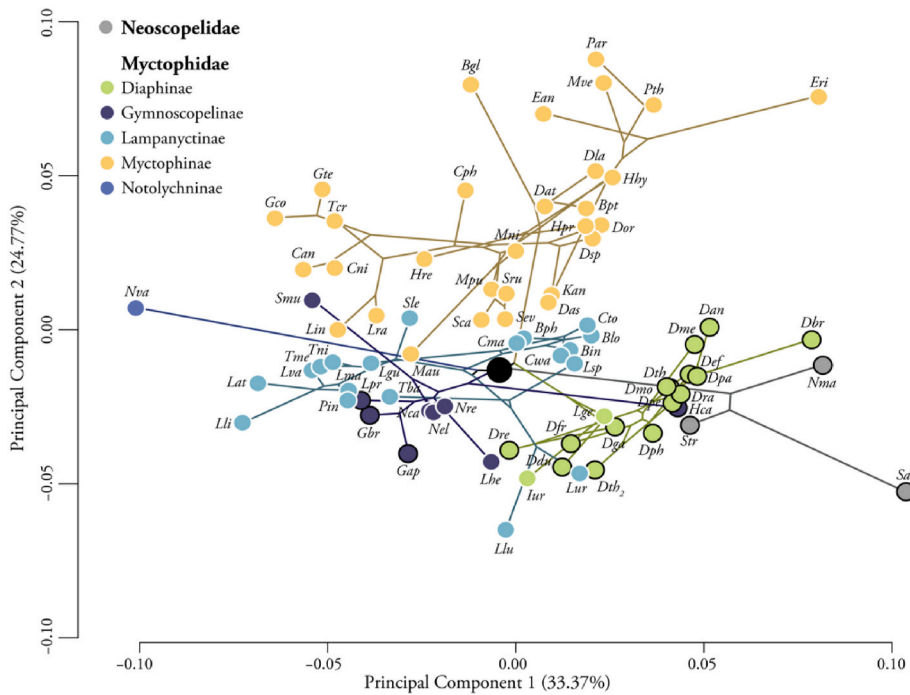


Fig. 5. Phylomorphospace plot of PC1 and PC2. Larger black circle represents ancestral myctophiform body shape. Circle positions represent the average location in morphospace at the species level. Colors correspond to Neoscopelidae and myctophid subfamilies with species names abbreviated. See [Supplemental Fig. 2](#) and material examined for unabbreviated names. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

organs (CR 0.7149, $P < 0.001$) but also for those exhibiting caudal light organs (CR 0.8255, $P < 0.001$). This finding suggests modularity and that anatomical changes in lanternfish bodies are not always accompanied by corresponding changes in the caudal peduncle, but that these differences may be occurring to a lesser extent in the lineages exhibiting caudal light organs. Body-shape disparity is variable across lanternfish subfamilies, with the Myctophinae exhibiting significantly higher disparity in their body shapes than the other myctophid subfamilies (Fig. 4; Table 2). The Diaphinae, Gymnoscopelinae, and Lampanyctinae all show relatively similar Procrustes variances and are not significantly different from each other in body-shape disparity. Additionally, body-shape disparity and Procrustes variances of lanternfishes with and without caudal light organs were 0.00439 and 0.00362 respectively. Although lanternfishes with caudal light organs had higher disparity values, Procrustes variances were not significantly different between these two groups ($P = 0.291$). The test for convergence of non-light bearing lanternfishes in morphospace yielded significant ($P < 0.001$) C values of C1: 0.5094, C2: 0.05942, C3: 0.2521, C4: 0.01137. The C1 value of 0.5094 indicates that evolution has closed 51% of the morphological distance among non-caudal light organ bearing taxa. The C3 value of 0.2521 indicates that from the most recent common ancestor all the way to the extant taxa, convergence is responsible for 25% of the total evolution in these lineages.

4. Discussion

The objectives of this study focused on understanding the evolution of lanternfish body shapes and the role that caudal light organs may be playing in their body-shape disparity. Overall, we find that using geometric morphometrics and phylogenetically informed statistical analyses, 58.2% of lanternfish body-shape disparity can be explained by principal components one and two (Fig. 4). Most lanternfishes lacking caudal light organs cluster in morphospace (i.e., *Diaphus*, *Hintonia*, Neoscopelidae) and show significant convergence (Fig. 4, C1 = 0.5094, C2 = 0.2521). The Myctophinae possess significantly more disparity in their body shapes than do the other lanternfish subfamilies (Table 2), but body-shape disparity is not significantly different between lanternfishes possessing or lacking caudal light organs. Additionally, lanternfishes with caudal light organs possess high phylogenetic signal in their body shapes ($K_{mult} = 0.897$), with a slightly lower signal in species lacking caudal light organs ($K_{mult} = 0.818$). Lastly, lanternfishes show high modularity between the caudal peduncle and the rest of the body, but that modularity is lessened in the species possessing caudal light organs (CR 0.7149 and CR 0.8255, respectively).

The evolution and trajectory of biological shape are often tied to behaviors and tasks related to environmental needs and survival (e.g., camouflage, predation). Morphological transformations in one or more regions of a body can also direct the evolution of particular groups

Table 2

Myctophiform disparity values from the morphological disparity test by Neoscopelidae and myctophid subfamily. The monotypic Notolychninae not included. Asterisks denote significant values.

	Neoscopelidae	Diaphinae	Gymnoscopelinae	Lampanyctinae	Myctophinae
Procrustes Variance	0.002354077	0.001975806	0.001958452	0.002423144	0.003826687
P values					
Neoscopelidae	-	0.763	0.762	0.957	0.21
Myctophidae	-	-	-	-	-
Diaphinae	-	-	0.981	0.536	0.00240*
Gymnoscopelinae	-	-	-	0.579	0.0214*
Lampanyctinae	-	-	-	-	0.0234*
Myctophinae	-	-	-	-	-

despite environmental and ecological pressures (Gilbert et al., 2021), especially if those features are important in communication and reproduction (Bonnet et al., 2001; Ghalambor et al., 2004). Studies on sexual selection across different groups of organisms have shown tradeoffs between expected morphology based on environmental influences and those observed in reference to reproductive success. Steppe tortoises have evolved shell and body morphologies influenced by egg laying or male-on-male combat successes rather than other environmental conditions (Bonnet et al., 2001). Many poeciliids, including mosquitofishes, show tradeoffs between evolving orange coloration, a color preferred by females, and being preyed upon (Heinen-Kay et al., 2015). The repeatedly observed pattern across vertebrate lineages that reproductive success can outweigh other environmental selective pressures in the evolution of body shape across terrestrial and aquatic habitats highlights the strength reproductive selective pressures can have on the evolution of body shape in animals. While strong selective pressures associated with living in the midwater of the open ocean would suggest a potential environmental optimal shape space for lanternfishes, in this study we demonstrate that lanternfishes may be deviating from a typical mid-water bauplan when the communication signals emitted from the caudal light organs have a stronger selective pressure than underlying environmental pressures. In particular, we identify that the presence of bioluminescent light organs on the tail may affect lanternfish body-shape evolution such that they deviate from a more environmentally functional bauplan to accommodate and take advantage of the differential signaling provided by their caudal light organ.

4.1. Impact of caudal light organs on body-shape evolution in the deep sea

As has been shown for Davis et al. (2014), selection has influenced the distribution of lateral primary photophores in lanternfishes. Our results suggest the presence of secondary light organs on the caudal peduncle may shift the selective pressures on body-shape evolution in lanternfishes. The majority of lanternfish species possess caudal light organs, such as most or all members of the Gymnoscopelinae, Lampanyctinae, Myctophinae, and Notolychninae (Supplemental Table 1). These caudal light organs are thought to be used for intraspecific communication and stunning predators and prey (Beebe and Vander-Pyl, 1944; Herring, 2007; Haddock et al., 2010). The caudal light organs of many of these species are also sexually dimorphic, and the adaptive value of these light organs in communication, anti-predation, and feeding likely make them highly selected traits for living in the pelagic deep sea. This may result in differential selection and evolution on the caudal area in lanternfishes that rely on these organs. Lanternfishes that possess caudal light organs (Supplemental Table 1) were also found to possess slightly higher phylogenetic signal ($K_{\text{mult}} = 0.897$) than those without caudal light organs ($K_{\text{mult}} = 0.818$), and caudal light organ bearing groups exhibited lower modularity ($CR = 0.82553$) between the caudal area and the rest of the body than those not bearing caudal light organs ($CR = 0.7149$). Although the phylogenetic MANOVA resulted in a non-significant effect of presence/absence of caudal light organs on body shape disparity ($P = 0.66$), if we remove the two species from *Gymnoscopelus* from the MANOVA that lack caudal light organs but have nearly identical body-shapes to the other members of the subfamily Gymnoscopelinae (that possess caudal light organs) the significance increases to $P = 0.084$. In this respect, we feel the species of *Gymnoscopelus* represent a holdover, as their overall body-shape was largely shaped by the evolution of the genus prior to the loss of these caudal-light organs and the body shape is indicative of this phylogenetic signal.

Most species in the Gymnoscopelinae (except *Gymnoscopelus* and *Hintonia*) and all species in the Lampanyctinae bear caudal light organs. Generally, these caudal light organs lack the morphological diversity seen in species in the Myctophinae (Fig. 6), a subfamily with species exhibiting extreme disparity in their caudal-light-organ morphology. Similar to the reduced variability in their caudal light organs, this study

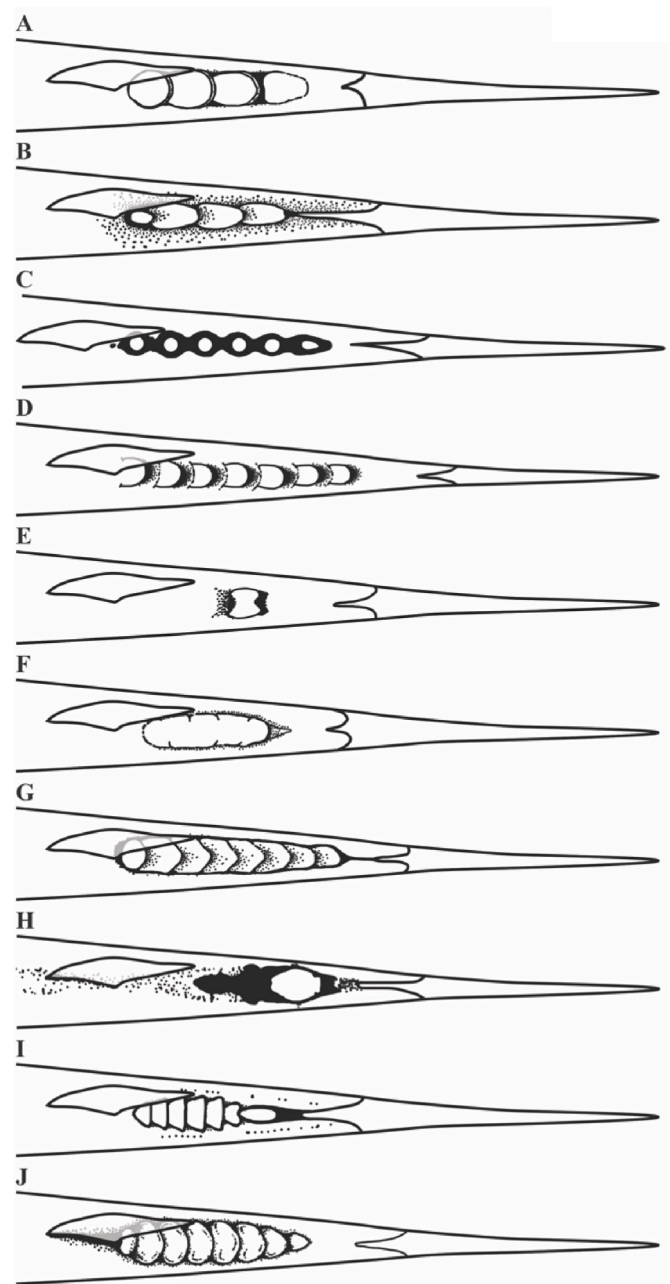


Fig. 6. Examples of the supracaudal (dorsal) light organ morphologies of myctophine lanternfishes. A) *Benthosema fibulatum*, B) *Dasyscopelus obtusirostris*, C) *Electrona antarctica*, D) *Gonichthys barnesi*, E) *Hygophum hygomi*, F) *H. reinhardtii*, G) *Myctophum affine*, H) *Protomyctophum subparalellum*, I) *P. tenisoni*, J) *Symbolophorus evermanni*.

finds that gymnoscopelines and lampanyctines are more constrained than myctophines in their body-shape variability and also overlap in morphospace (Fig. 4). Although not morphologically diverse, some lanternfish species are known to exhibit diverse and distinct flashing patterns or intensities from their caudal light organs. This has specifically been seen in species within the Lampanyctinae, the closely related *Lampanyctus niger*, *L. ritteri*, and *L. tenuiformis* (e.g., Mensinger and Case, 1990, 1997). Variability in flashing signal may negate the need for differential morphology of the caudal light organs in intraspecific communication and recognition. This may be evidence for individual lanternfish lineages following different evolutionary paths to solve the same problem, intraspecific recognition and communication in the deep sea.

The Myctophinae, which shows prominent differences in caudal-light-organ morphology among species (Wisner, 1976), is by far the most diverse in body-shape morphology across lanternfishes (Fig. 5, yellow branches). The Myctophinae is comprised of 79 species, similar in numbers to that of the Diaphinae with 81 species and the Lampanyctinae with 74 species (Fricke et al., 2020), but the myctophines possesses significantly higher body-shape disparity than other lanternfish subfamilies ($P < 0.01$; Table 2, Fig. 4). In addition to the presence or absence of caudal light organs in lanternfishes, we believe that body-shape disparity in myctophine species that possess these secondary organs is being influenced by their wide range in caudal light organ morphology, which is much more variable than are witnessed in the other lanternfish subfamilies (Fig. 6). The differences displayed in these organs can include a singular patch of luminous tissue, individual luminous scales, or coalesced luminous scales. There is also variation in the patterns and amounts of black pigmentation surrounding their caudal light organs and variation in light-organ size (Fig. 6). Myctophines are also thought to have the most extensive evidence of bioluminescent sexual dimorphism among oceanic animals (Herring, 2007). If sexual dimorphism is exhibited, males generally possess a supracaudal light organ (Fig. 2.1) while females possess an infracaudal light organ (Fig. 2.2). The high phylogenetic signal and significant disparity in body shapes we see within the Myctophinae could be due to the influence of these important and highly diverse caudal light organs. Ellis and Oakley (2016) found that among ten distantly related animal lineages (including lanternfishes), there were significantly more species in lineages with bioluminescent courtship compared to their sister groups that lacked these luminescent displays. These authors also reported that lineages with bioluminescent courtship displays had significantly higher rates of species accumulation compared to more inclusive clades that also included non-luminous relatives. Research suggests that bioluminescence may have played an early and critical role in the diversification of deep-sea fish lineages, especially when tied to courtship and sexual selection (e.g., Sparks et al., 2005; Chakrabarty et al., 2011; Davis et al., 2014, 2016). The disparity in body shapes represented by species in the Myctophinae may reflect a relationship to their highly diverse caudal light organs. As mentioned previously, studies on sexual selection across different groups of organisms have shown tradeoffs between expected morphology based on environmental influences and those observed in reference to reproductive success. The Myctophinae in particular may be demonstrating that lanternfishes could be deviating from a typical bauplan when the communication signals emitted from the caudal light organs (Fig. 6) have a stronger selective pressure than underlying environmental pressures.

A large portion of the morphospace disparity we see in the Myctophinae is due to the body morphologies of three specific genera, *Electrona*, *Metelectrona*, and *Protomyctophum* (Fig. 5 upper right). If these three genera were removed from morphospace, the disparity in the Myctophinae might be more akin to that of the Lampanyctinae. *Electrona*, *Metelectrona*, and *Protomyctophum* (Figs. 1 and 5) possess truncated body morphotypes that reflect morphological similarities to deep-sea hatchetfishes (Sternoptychidae). Deep-sea hatchetfishes are silver-sided (i.e., “mirror-like”) midwater fishes with deep and strongly compressed bodies that reflect incident light in the midwater, acting like a mirror and effectively reducing predation pressure (Denton et al., 1972). Studies on various hatchetfish species (e.g., *Argyropelecus gigas*, *A. hemigymnus*, *A. sladeni*, *Polyipnus polli*, *Sternoptyx diaphana*, *S. pseudobscura*, *S. pseudodiaphana* and, *Valenciennellus tripunctulatus*), suggest they may not take part in traveling large distances during the diurnal migration that many pelagic deep-sea species participate in and that their unique morphology has been hypothesized to have resulted in a decreased locomotory ability with less effective thrust (Hopkins and Baird, 1985; Williams and Koslow, 1997; Olivar et al., 2017; Eduardo et al., 2020). A recent study by Martinez et al. (2021) suggested that reduction of the caudal-peduncle length and width in intermediate-depth and deep-sea fishes is likely tied to reduced selection

on robust tails for use in anti-predation and maneuverability in highly structured areas. Many species of lanternfishes in *Electrona* and *Protomyctophum* have large silvery scales and have been found to be either weak or non-migrators (Watanabe et al., 1999; Collins et al., 2008; Battaglia et al., 2016). These truncated and non-migrating lanternfishes could have converged on a similar body plan and migratory behavior to those of deep-sea hatchetfishes (Hopkins and Baird, 1985; Howell and Krueger, 1987). Selective pressure toward a mirrored and truncated body would be beneficial at reducing the predation pressure on these fishes while they remain stationary in the water column at depth (Denton et al., 1972).

4.2. Convergence of body shape when caudal light organs are absent

Most species lacking caudal light organs (i.e., Neoscopelidae, *Diaphus*, *Hintonia*) were located a specific area of morphospace (Fig. 4 black outlines). Studies showing multiple transitions into particular body forms, or convergent evolution, are often linked to adaptations to specific habitats and resources (Stayton, 2008). This has been studied in multiple groups including the cichlids in Lake Tanganyika (Muschick et al., 2012) and lizards in the genus *Anolis* (Losos, 1992). As mentioned previously, Martinez et al. (2021) found a general reduction in width and depth of caudal peduncles in deep-sea teleost species (>200 m), a study that included 92 lanternfish and blackchin species. They suggested that there is a reduced need for strong maneuverability in the deep sea, which has relaxed the selection for a robust caudal peduncle for use in more dynamic types of locomotion (e.g., more turbulent waters in shallow areas and predation in well-lit and obstacle-filled environments). Although all lanternfishes possess significant phylogenetic signal and modularity in body shape, phylogenetic signal is reduced and the modularity value is lower (more modular) in lanternfishes that lack caudal light organs. This result further highlights the role light organs may be playing in influencing the caudal area in lanternfish body-shape evolution. The phylogenetic MANOVA assessing the influence of the presence/absence of caudal light organs on body shape disparity was not significant, but by removing just two species within *Gymnoscopelus* we find significance ($P = 0.084$). These species of *Gymnoscopelus* that do not cluster in morphospace with other lanternfishes lacking caudal light organs are significantly affecting the results of the phylogenetic MANOVA and suggests that increased sampling of additional species lacking caudal light organs, mainly increasing the sampling in *Diaphus* from only 15 of the 81 species, could significantly alter this finding. Clustering in morphospace of multiple species from independent myctophiform clades that lack a caudal light organ (Fig. 4) indicates that by removing the caudal light organ, natural selection could be selecting for a lanternfish body morphology that is optimized for the physical landscape of the midwater that they live in, favoring more energy efficient and slow sustained swimming styles (Martinez et al., 2021).

As previously mentioned, most lanternfishes and blackchins that lack caudal light organs cluster together in morphospace (i.e., Neoscopelidae, *Diaphus*, and *Hintonia*) with our test of convergence in morphospace resulting in significant C values. These lanternfishes are also disparately located from other lanternfish lineages and have posteriorly displaced anal-fin insertions and a general reduction in caudal-peduncle length (Fig. 4 black outlines). Their divergent caudal morphology and disparate placement in morphospace is likely related to their absence of caudal light organs (Fig. 4, Supplemental Table 1). Some species in *Diaphus* and *Gymnoscopelus* have evolved enlarged and sometimes sexually dimorphic headlight organs (Fig. 2C and D). Headlight organs are common among lanternfishes, but they are usually smaller and not as sexually dimorphic as those seen in *Diaphus* and *Gymnoscopelus* (Paxton, 1972). Enlarged headlight organs that show a wide variety of shapes and sizes may play a similar role to those of caudal light organs in species of *Diaphus* and *Gymnoscopelus* (*Diaphus* in Fig. 2C and D), since headlight organs are thought to be used in similar behaviors, such as predation and communication (Herring, 1985;

Haddock et al., 2010; de Busserolles et al., 2014). If the extensive and frequently sexually dimorphic caudal light organs are useful in the survival and reproductive success of lanternfishes, the lack of these light organs may result in reduced selective pressure on the caudal or “visual signal” area, particularly if the headlight organs in *Diaphus* and *Gymnoscopelus* are being used for similar roles in predation or intraspecific communication. Additionally, multiple species of lanternfishes, including species in *Diaphus*, are known to spawn in the epipelagic at dusk and into the night, or in the deeper and darker waters of the mesopelagic (e.g., Sassa et al., 2014, 2016). Sexually dimorphic light organs would enable intraspecific communication at night and could be tied to increased fitness.

The two species in *Gymnoscopelus* (of the total eight described species) used in this study did not cluster in morphospace with other lanternfishes lacking caudal light organs (Fig. 4). The time-calibrated phylogeny of lanternfishes by Denton (2018) suggested that *Gymnoscopelus* is a relatively young clade compared to most lanternfish genera. The lack of clustering of species in *Gymnoscopelus* with other non-caudal light organ bearing lanternfishes could be due to the high phylogenetic signal of the Gymnoscopelinae and an insufficient amount of evolutionary time for convergence to have occurred in the taxa that lack the caudal organs. Within the Gymnoscopelinae, *Hintonia candens* also lacks caudal light organs (Supplemental Table 1) and clustered with all other non-caudal-light-organ-bearing lanternfishes (Fig. 4). Unfortunately, this species is not included in the Denton (2018) time-calibrated phylogeny. *Hintonia candens* has been previously resolved as sister to the remainder of the Gymnoscopelinae (Martin et al., 2018) and is likely an older lineage than the rest of the Gymnoscopelinae, allowing for a larger amount of time for environmental pressures to act on the evolution of its body shape.

Not only are the lanternfishes lacking caudal light organs clustering in morphospace (Fig. 4), but they were also found to have lower phylogenetic signal in their body-shape disparity. This suggests that their body-shapes, at a minimum, are likely being affected by different evolutionary processes. Although it is difficult to draw major conclusions from a lower phylogenetic signal since it can be a result of a variety of evolutionary processes (Revell et al., 2008), we highlight a few possibilities for inferring it in the non-caudal-light-organ-bearing lineages. Lower phylogenetic signal could be the result of stabilizing selection. As previously mentioned, species lacking caudal light organs may have greater selection toward body shapes better suited to survival in the midwater. Another possibility is that representative species in the non-caudal-light-bearing group in our study exhibit body shapes that are more divergent from each other than is expected under a Brownian motion model of evolution. We would expect sister species within lineages with high phylogenetic signal to generally cluster nearer to each other in shape space than to less closely related taxa (Adams, 2014). Instead, we find that sister taxa within the Diaphinae occur in disparate locations within their specific portion in morphospace, exhibiting an abundance of overlapping branches in phylomorphospace (Fig. 5 green lineages) and with less closely related taxa sharing shape space. If the enlargement of head light organs and their increased use in predation and communication occurred in the common ancestor of *Diaphus*, this could result in reduced selective pressure on the caudal area that houses the caudal light organ present in almost all other myctophids. A reduction in selective pressure on the maintenance of caudal light organs could be correlated with reduced phylogenetic signal in body-shape disparity in the Diaphinae, the subfamily that makes up most of the species lacking caudal light organs. The evolution of body shapes correlated with environmental pressures may result in increased similarity in body shapes (and alternatively lower body shape disparity) since multiple species are being affected by the same environmental pressures. Natural selection for these environmentally-tailored body shapes may obscure the phylogenetic signal in lanternfishes that do not possess light organs where selective pressure tied to other functions (e.g., communication and predation) may be differentially affecting

body-shape morphology and be more tightly tied to speciation and diversification. The recurrence of a particular body shape among most lanternfishes that lack caudal light organs suggest that the average lanternfish body shape might be more akin to that seen in the non-caudal-light-bearing lineages if it were not for the presence of caudal light organs present on most other lanternfishes.

5. Conclusions

In conclusion, we find that bioluminescent organs may be impacting the evolution of body shape in deep-sea lanternfishes, particularly when they are associated with sexually dimorphic light-producing structures in the tail region. These findings provide insight on how bioluminescence used for reproductive communication can impact the evolution of body shape in other marine animals that use light for signaling and success in the deep sea and other oceanic environments. Within lanternfishes, we present trends in body-shape disparity and show lanternfishes have body-shape modularity, suggesting that the caudal area that houses the caudal light organs is not evolving in tandem with the rest of the body. The importance of these light organs in intraspecific communication or predator avoidance likely resulted in increased selective pressures on the caudal peduncle, the area that houses these light organs. Caudal light organs are sexually dimorphic in many lanternfish species, a trait that is most widespread within the Myctophinae, the subfamily that also possesses the highest body-shape disparity. The Gymnoscopelinae, Lampanyctinae, Myctophinae, and Notolychninae, include most species that possess caudal light organs, and the lineages exhibiting these caudal light organs exhibit higher phylogenetic signal. Conversely, we show lanternfishes that lack light organs on their tail have body shapes exhibiting lower phylogenetic signal, higher body-shape modularity, and cluster together in morphospace (i.e., *Diaphus*, *Hintonia*, Neoscopelidae; Fig. 4). These findings suggest there may be differential selection on shape evolution between the caudal area and the rest of the body in lanternfishes, depending on the presence or absence of a caudal light organ. Species lacking caudal light organs were found to have convergent body shapes in morphospace (Fig. 4), a shape that could be correlated with the diminishment of phylogenetic signal and would be useful to success in the midwater when not constrained by the presence of a caudal light organ. Differential selective pressures on the caudal peduncle are likely occurring within the Diaphinae, a subfamily dominated by the species-rich *Diaphus*, that lacks these light organs. Further research is needed to examine the functional morphology of the various body shapes of lanternfishes and blackchins; however, the divergent evolution of body shapes in lanternfishes highlights its potential importance to their incredible success as a diverse and abundant lineage in deep-sea ecosystems.

Author contributions

RPM imaged specimens, performed morphometric work, statistical analyses, and took the lead in manuscript writing and figure creation. MPD imaged specimens and provided instruction on geometric morphometrics. WLS provided critical feedback and helped shape the research, analysis, and manuscript. All authors helped conceive the idea, discussed the results, and contributed to the final version of the manuscript.

Data accessibility statement

R code and resulting shape files from the geometric morphometric analysis for these data are available at Mendeley data DOI: 10.17632/x6d6kcgbwg.1.

Declaration of competing interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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