

Patterns of Phenotypic Variation in the Mouth Size of Lanternfishes (Teleostei: Myctophiformes)

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Lanternfishes (Myctophiformes, ~260 species) are among the most abundant and species-rich groups of fishes endemic to the deep sea, and they play a major role in the oceanic ecosystem by transferring energy from shallower to deeper oceanic levels. Little is currently known regarding how lanternfishes have achieved such high species richness in the deep sea, and the majority of previous studies that have investigated diversification in this group have focused on bioluminescence. In this study, we investigate the variation in mouth size of lanternfishes in an effort to better understand potential mechanisms of speciation in this group, as previous studies have indicated that there is considerable variation in the size and biodiversity of prey items of lanternfishes. Geometric morphometrics were performed on 955 lanternfish specimens, and an ancestral character-state reconstruction was used to examine variation and evolution of mouth size in this group. We identify that mouth size in lanternfishes is highly variable, with general trends towards larger mouths in the subfamily Lampanyctinae (Myctophidae) and shorter mouths in the subfamily Myctophinae (Myctophidae). Within each subfamily there are discrete patterns of jaw-size differentiation among genera. Of particular note, the genus *Diaphus*, the most species-rich genus of lanternfishes (~30% of lanternfish diversity), was found to occupy a large range of morphospace, with broad plasticity in mouth size among the examined species. Ancestral character-state reconstructions indicate that a neoscopelid-like jaw was the likely ancestral state for Myctophiformes; whereas, a longer jaw, similar to that of the majority of species in the subfamily Lampanyctinae, was most likely the ancestral state for the family Myctophidae.

LANTERNFISHES (Teleostei: Myctophiformes) are one of the most species-rich groups of fishes endemic to deep-sea open-ocean environments, containing approximately 260 species in 36 genera (Nelson, 2006; Eschmeyer, 2015). 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, 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). 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 surface 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 et al., 2011a, 2011b). The bioluminescent photophores of lanternfishes located in lateral positions on the body may be involved with species recognition and sexual selection (Mensing and Case, 1990; De Busserolles et al., 2013; Davis et al., 2014, 2016). Additionally, the eyes of lanternfishes are attuned to see wavelengths that match the light given off by bioluminescent organisms (Turner et al., 2009). Despite the common occurrence of this group in deep-sea environments, little is currently known 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 and Hopkins, 2004; Tanimata et al., 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

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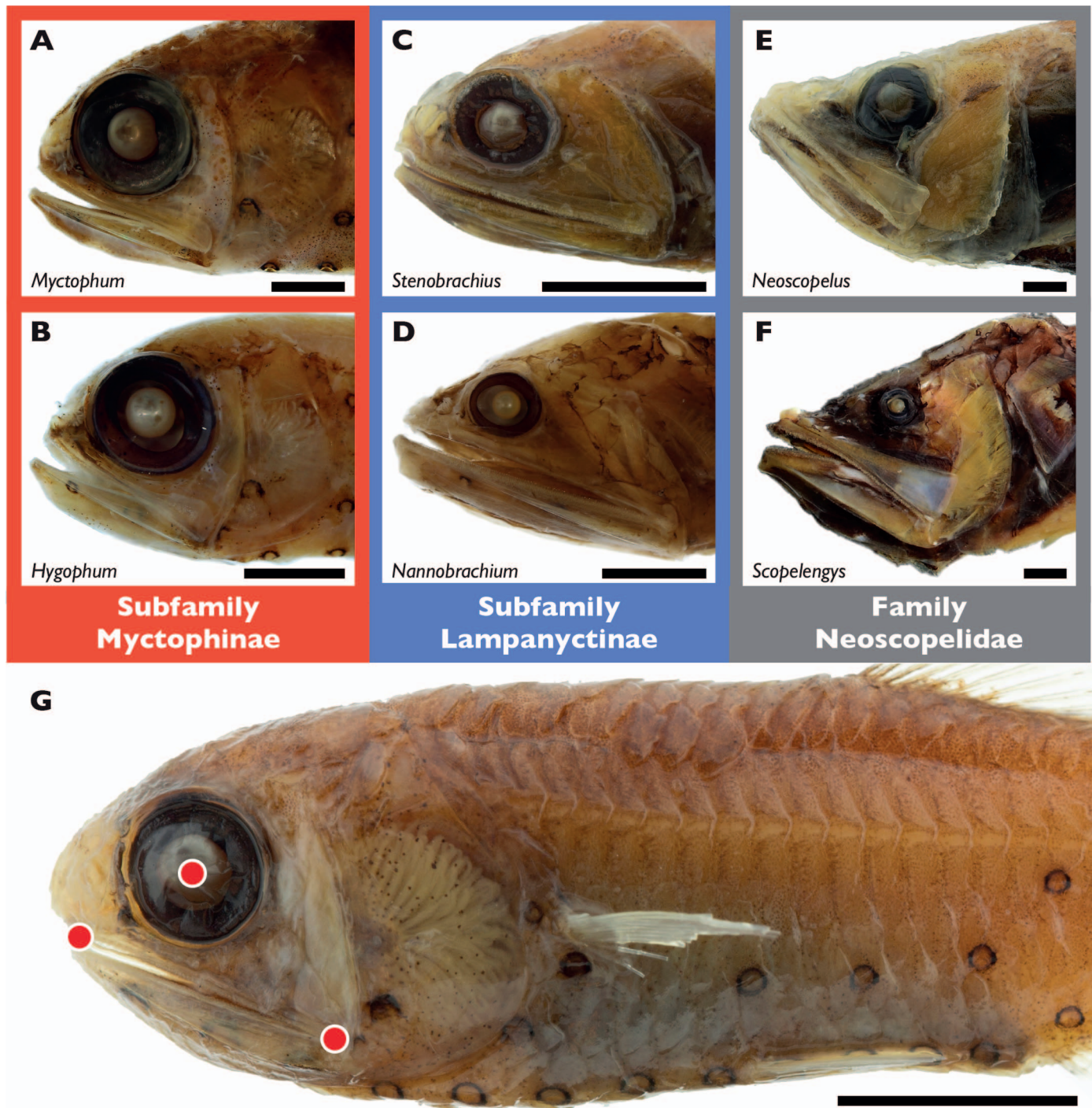


Fig. 1. Examples of variation in upper-jaw morphology among lanternfishes. Scale bars represent 5 mm. (A) *Myctophum obtusirostre* (MCZ 51389); (B) *Hygophum macrochir* (MCZ 115225); (C) *Stenobranchius leucopsarus* (FMNH 71832); (D) *Nannobranchium cuprarium* (MCZ 112776); (E) *Neoscopelus macrolepidotus* (FMNH 112581); (F) *Scopelengys tristis* (USNM 201152); (G) Landmark placement sites on lanternfish specimens. *Gonichthys tenuiculus* (FMNH 71685).

type of prey it consumes and how morphological variation can lead to changes in foraging ability and subsequently differential use of food resources (Karpouzi and Stergiou, 2003; Price et al., 2015). Correlations between mouth size and prey size have been studied in many fishes (e.g., Janssen, 1976; Prejs et al., 1990; Hambricht, 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,

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. Previous studies have suggested that there is variation in jaw morphology across lanternfishes (Paxton, 1972); however, this variation has never been quantitatively investigated. If significant variation exists in the size of the mouth (Fig. 1) 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 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 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 Pérez (2014).

Geometric morphometrics.—In order to investigate the variation in mouth size across lanternfishes, digital landmarks were placed on three homologous areas in the geometric morphometric software tps (Rohlf, 2010a, 2010b). Homologous areas include: the most anterior part of the premaxilla, the most posterior medial part of the maxilla, and the middle of the eye (Fig. 1G). These landmarks were chosen as they provide a general estimate of variation in the size of the upper jaw. 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 and 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 and Maddison, 2010). A previously published time-calibrated phylogeny of lanternfishes (Davis et al., 2014) 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 (*Solivomer* and *Krefflichthys*). 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
 - (01₀) Anterior margin of premaxilla extends well beyond eye, posterior margin of maxilla extends slightly behind eye.
 - (01₁) Anterior margin of premaxilla extends slightly beyond eye, posterior margin of maxilla extends slightly behind eye.
 - (01₂) 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 mouth size between Myctophidae and Neoscolopelidae and also between the two lanternfish subfamilies, Lampanyctinae and Myctophinae (Fig. 2), relative to other clades. Neoscolopelidae (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 Myctophinae have a broad overlapping distribution across the left side of the X-axis, indicating a trend towards shorter upper jaws (Fig. 2). While there is broad overlap of the genera within this subfamily (Fig. 3A, B), there are also differences between various genera in morphospace (e.g., *Loweina*, *Metelectrona*, *Protomyctophum*, and *Tarletonbeania*) showing distinctive clumping and separation (Fig. 3C, D, E). In contrast, genera in the subfamily Lampanyctinae indicate a trend towards a longer posterior portion of the upper jaw in relation to the eye (Fig. 2). While there is significant overlap of genera within Lampanyctinae across the right side of the X-axis (Fig. 4A), only a few genera in this subfamily have a broad distribution in morphospace (Fig. 4B) showing higher variation among species within a genus (i.e., *Bolinichthys*, *Diaphus*, and *Lampanyctus*). However, the overall variation among species within a genus is generally reduced across Lampanyctinae (Fig. 4). Additionally, there are multiple genera that do not overlap in morphospace (e.g., *Ceratoscopelus*, *Notoscolopelus*, and *Parvilux*; Fig. 4C, D, E). Some genera within the subfamilies contain species that have both long and short upper jaws and are an exception to the general trends (i.e., *Tarletonbeania*, *Diaphus*, *Bolinichthys*, and *Ceratoscopelus*; Figs. 3, 4).

Character evolution of mouth size across the evolutionary history of lanternfishes.—Ancestral character states are indicated at nodes (Wiley et al., 2011). The common ancestor of the Myctophiformes most likely had a larger upper jaw with a robust snout, similar to that of the family Neoscolopelidae. This was inferred under a likelihood character reconstruction (50%), although it is equivocal for all states under a parsimony reconstruction (Fig. 5). The common ancestor of the Myctophidae most likely had a longer upper jaw, similar to that of the subfamily Lampanyctinae (72%) under likelihood, and it is equivocal for all states under parsimony (Fig. 5). The subfamily Myctophinae most likely evolved shorter upper jaws in its common ancestor.

DISCUSSION

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 (Fig. 2). Within the family Neoscolopelidae, 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 (Fig. 2). The ancestral character-state reconstruction inferred under likelihood (Fig. 5) suggests that the upper-jaw length of Neoscolopelidae is likely to be the ancestral jaw length for all Myctophiformes. Fossil evidence of stem Myctophiformes, including †*Sardinoides* (Cretaceous), †*Neocassandra* (Paleocene), and †*Beckerophotus* (Eocene; Prokofiev, 2006), indicates that stem lanternfish had a

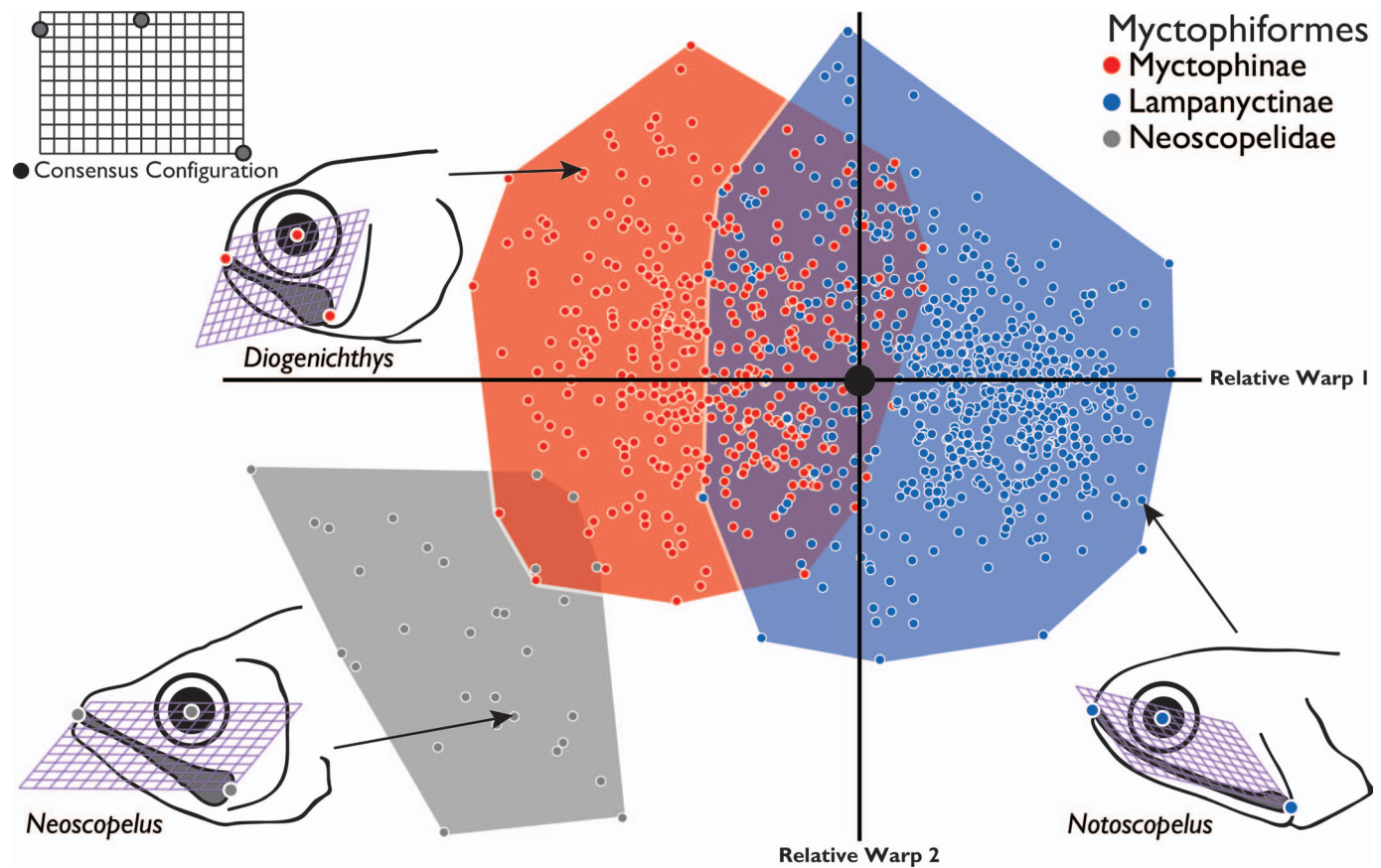


Fig. 2. Relative warp analysis of jaw landmarks for Myctophiformes.

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 (Fig. 2). The family Neoscopelidae has low species diversity with three genera and approximately six species (Eschmeyer, 2015). In contrast, the species-rich family Myctophidae possesses higher variability in the length of the upper jaw (Fig. 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 (Figs. 2, 5). There is a distinct elongation of the posterior portion of the upper jaw in relation to the eye in Lampanyctinae, with only a few exceptions (e.g., some species of *Diaphus*, *Bolinichthys*, and *Ceratoscopelus*). Myctophinae shows a shortening of the upper jaw in relation to the eye (Figs. 2, 5). Paxton (1972) also suggested that the ancestral character state for Myctophidae was a small mouth, with lampanyctines evolving larger mouths. The results of the likelihood character-state reconstruction indicate otherwise, inferring that the ancestral character state for myctophids was likely larger mouths with Myctophinae evolving shorter mouths (Fig. 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 subfam-

ilies. The genera *Tarletonbeania*, *Diaphus*, *Bolinichthys*, and *Ceratoscopelus* all contain species that have evolved both smaller and larger mouths (Figs. 3, 4).

The genus *Diaphus* was found to occupy the largest amount of morphospace for any lanternfish genus (Fig. 4A, B), and it is one of the only lampanyctine lineages to have species with both long and short upper jaws (Fig. 4). In contrast, many taxa within a given genus of lanternfishes are generally restricted in their overall pattern of upper-jaw length (Figs. 3C, D, E, 4C, D, E). The genus *Diaphus* contains approximately 77 species (Eschmeyer, 2015), 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., 2005; 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 and Partridge, 1997; Douglas et al., 1998, 2002; Ghedotti et al., 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

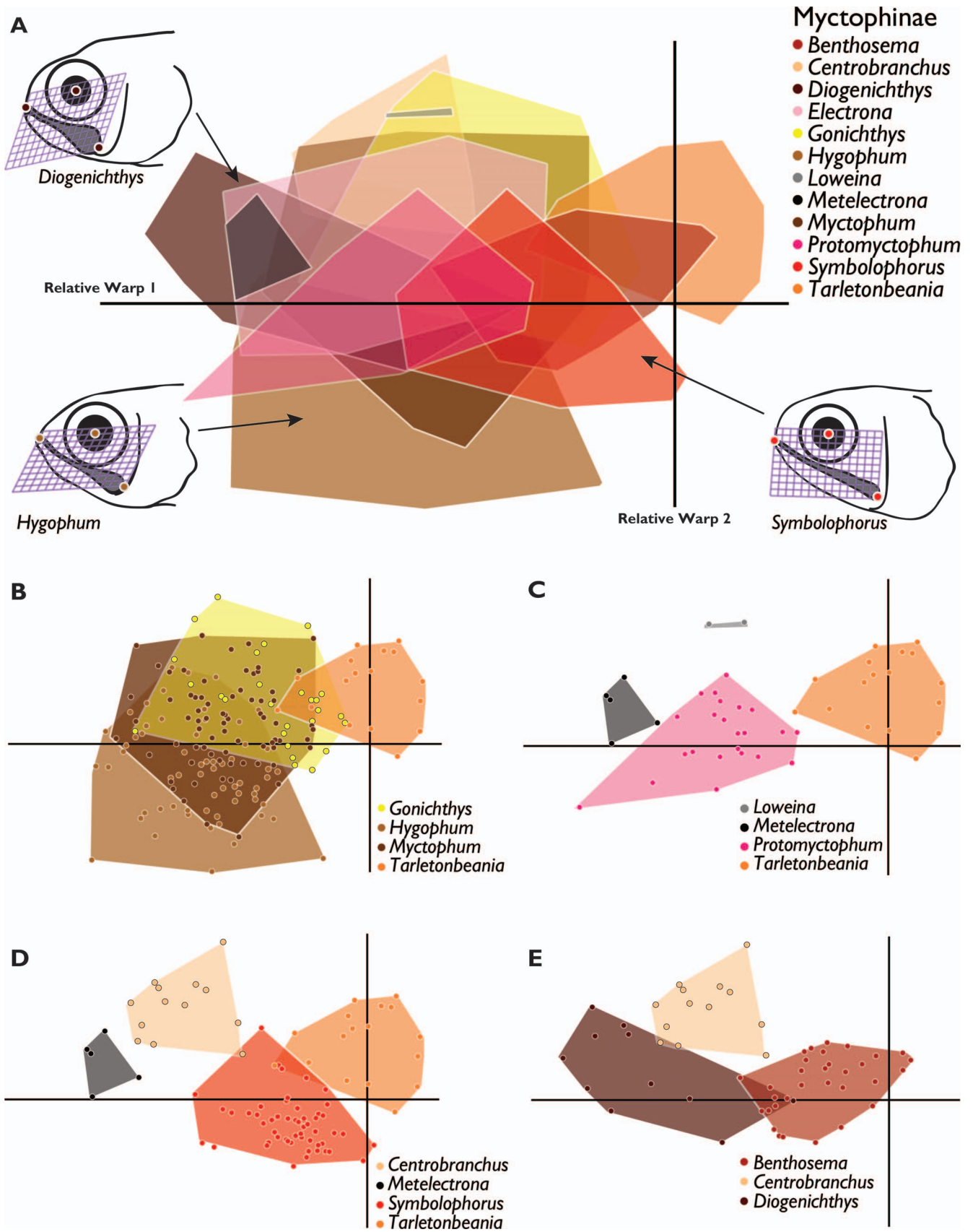


Fig. 3. Relative warp analysis of mouth size in: (A) Myctophinae; (B) myctophine genera with high morphospace variation; (C–E) examples of myctophine genera with separation in morphospace.

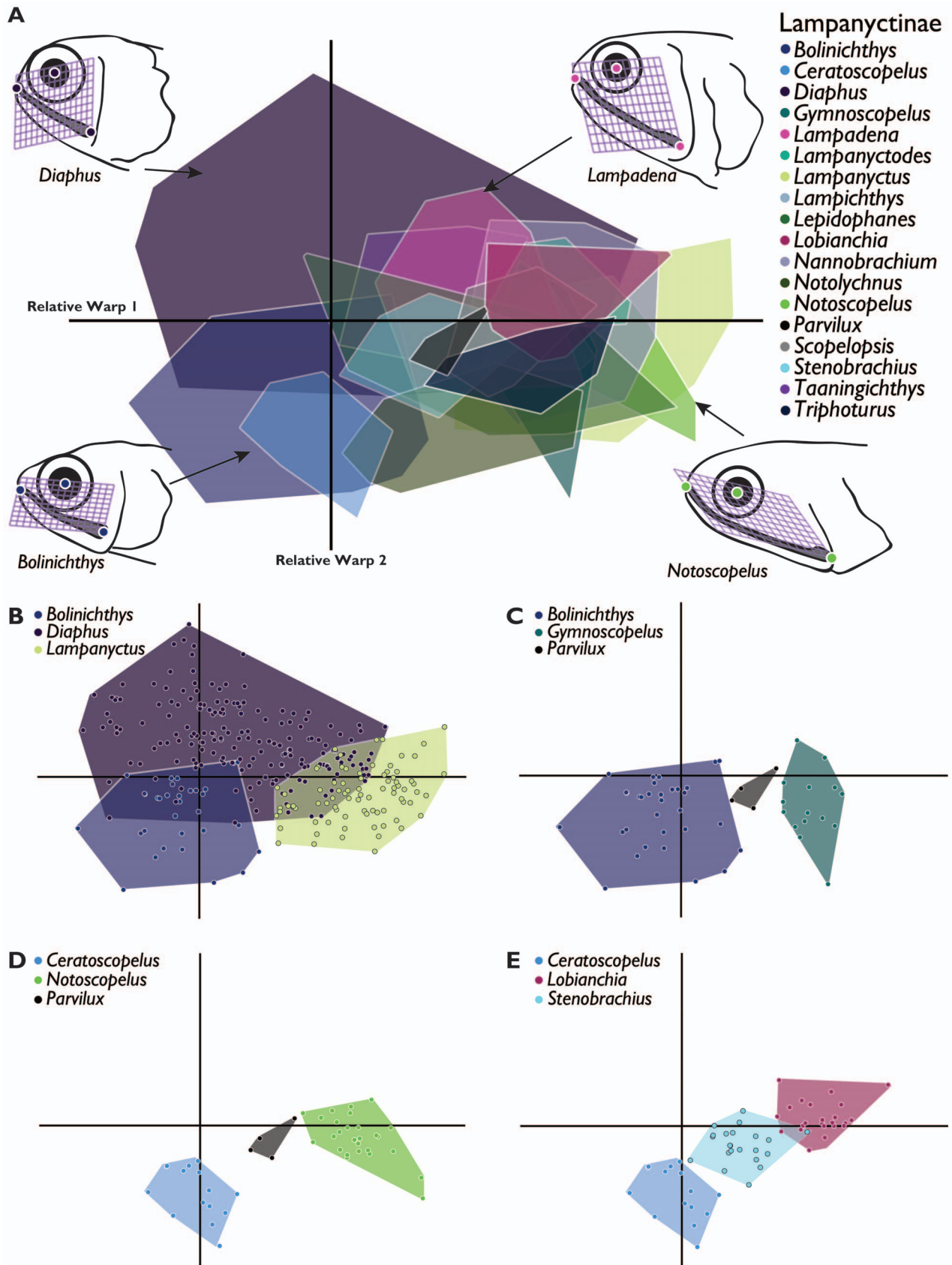


Fig. 4. Relative warp analysis of mouth size in: (A) Lampanyctinae; (B) lampanyctine genera with high morphospace variation; (C–E) examples of lampanyctine genera with separation in morphospace.

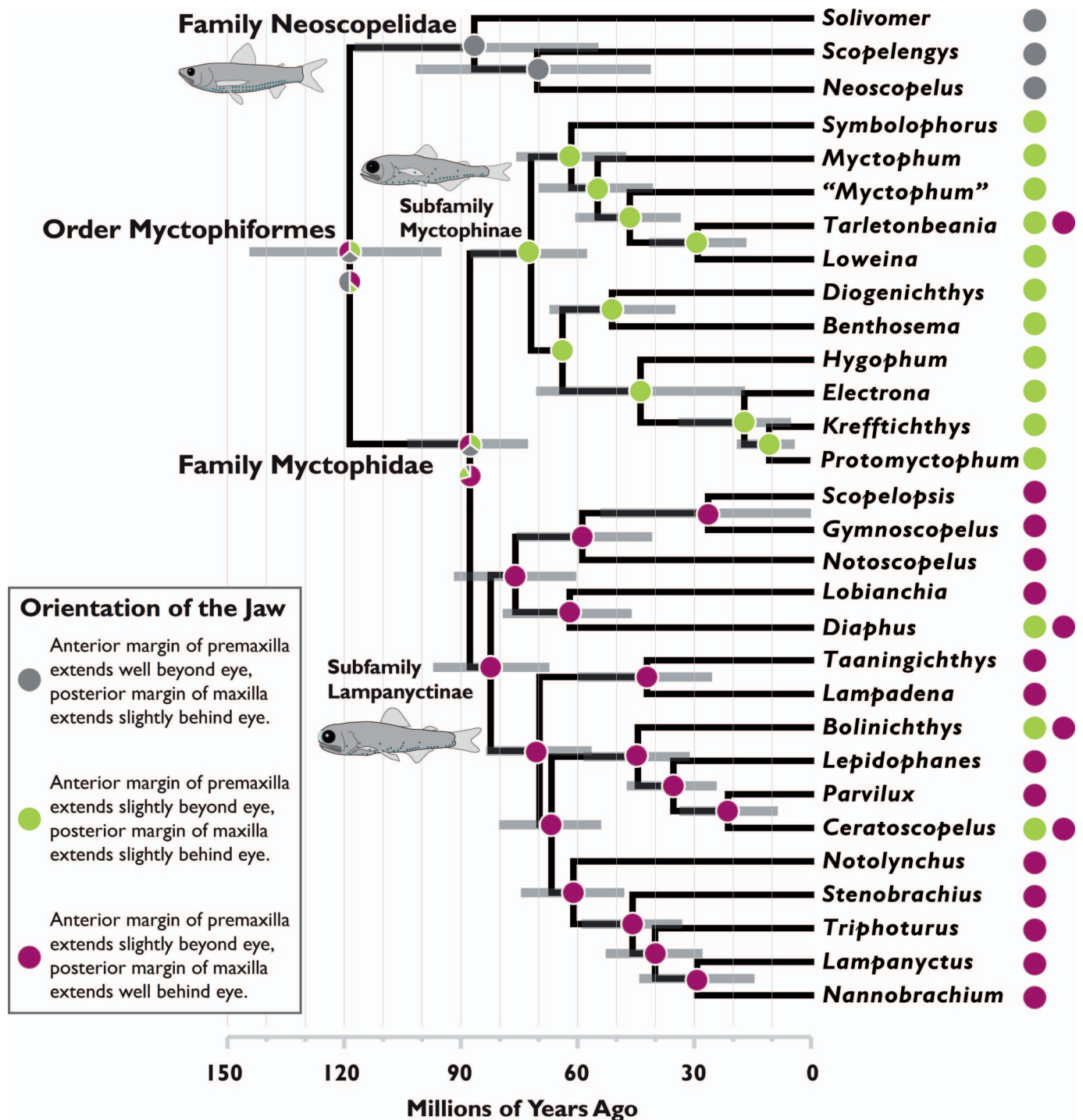


Fig. 5. Time-calibrated phylogeny of lanternfishes from Davis et al. (2014) based on nuclear and mitochondrial data. Maximum likelihood and parsimony ancestral character-state reconstructions shown at nodes. Where reconstructions differ, parsimony is above the node and likelihood is below the node.

are distributed throughout the evolutionary history of the lineage (Fig. 6). This indicates that the evolutionary history of *Diaphus* is punctuated with changes in jaw length (Fig. 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 this lineage, further work is needed to examine the jaws of additional species within the genus *Diaphus* in relation to a densely sampled species phylogeny of the lineage. 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 (Fig. 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. chryso-rhynchus* included larger cephalopods and myctophids, in addition to zooplankton (Tanaka et al., 2013).

Previous work on the diets of lanternfishes have identified that their diets consist predominantly of epipelagic zoo-

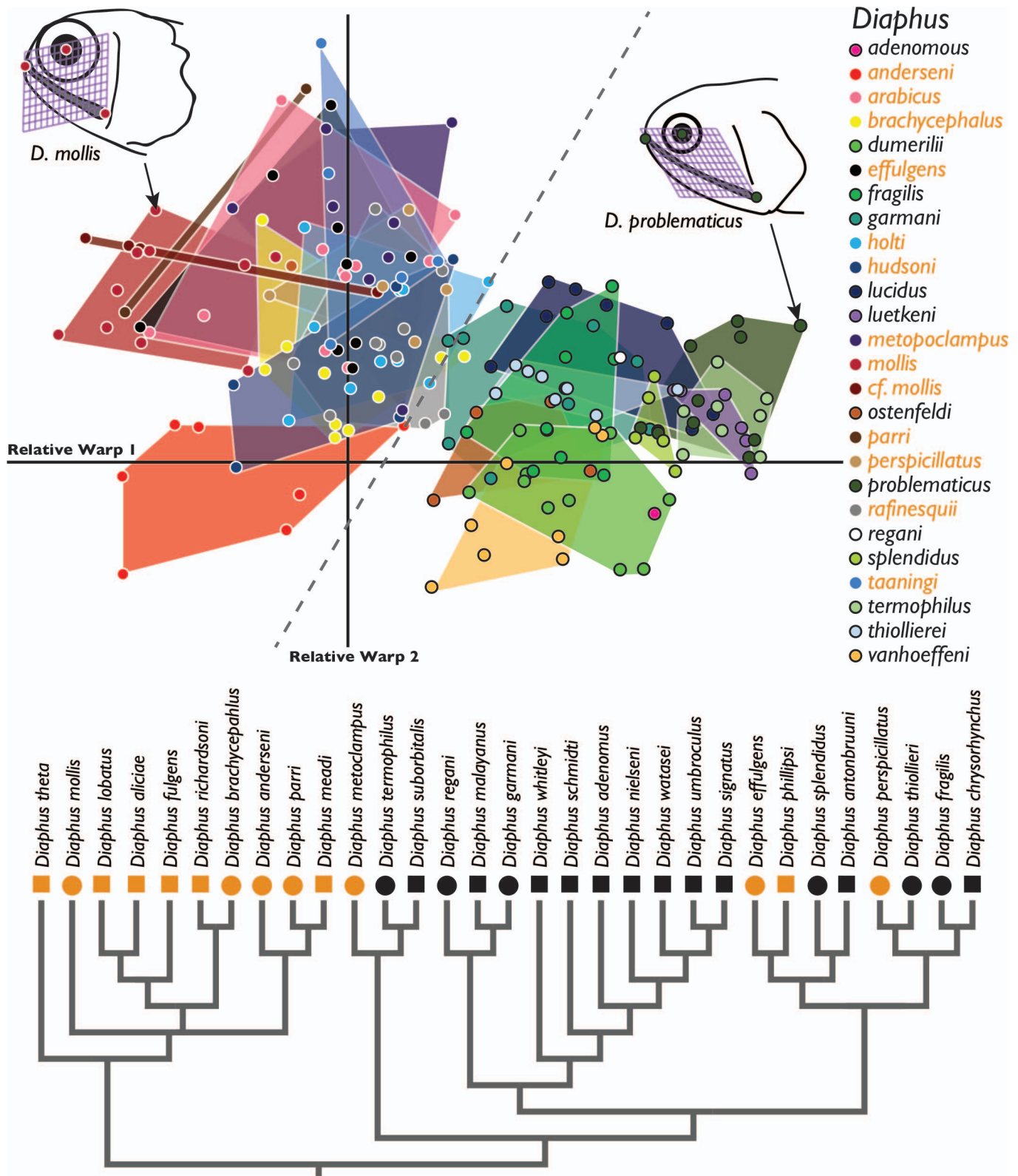


Fig. 6. Relative warp analysis of upper-jaw length among species of *Diaphus*. The two main trends of mouth size are represented by text color and outlines on the circles representing specimens; black text and outlines indicate longer upper jaws and orange text with white outlines indicate shorter upper 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, 2015). Circles and squares colored black indicate longer upper jaws, whereas orange indicates shorter upper jaws.

plankton: copepods, amphipods, ostracods, and euphausiids (e.g., Pakhomov et al., 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 et al., 1996; Williams

et al., 2001; Conley and 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 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 and 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, has been found to eat molluscs and bivalve larvae, compared to *Diaphus watasei*, a long-jawed species, which has been found to eat zooplankton, squids, and other myctophids and their larvae (Alwis and Gjøsaeter, 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 et al., 2009; Bernal et al., 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 subfamily Lampanyctinae 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 and Hopkins, 2004). Additional ontogenetic studies on lanternfishes also found this pattern in prey selectivity (e.g., Sabatés and Saiz, 2000; Tanimata et al., 2008; Bernal et al., 2013). A larger mouthed lampanyctine 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 and Kocher, 2001; Lovette et al., 2002; Hulsey et al., 2010; Muschick et al., 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 (Figs. 3C, D, E, 4C, D, E). Taxa that overlap in morphospace (Figs. 3A, 4A) 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 (Fig. 2), including general trends towards smaller mouths in Myctophinae, and larger mouths in Lampanyctinae. The likelihood character-state reconstruction indicates that the ancestral state for Myctophiformes and Myctophidae was likely longer jaws (Fig. 5). Few studies have investigated variation in mouth size across a lineage of deep-sea fishes. The broad variation in mouth size of lanternfishes indicates that this group may have undergone shifts in ecological specializations. Of particular note, the genus *Diaphus* has high variation in upper-jaw length within morphospace and is one of the only genera to exhibit species with both short and long jaws (Fig. 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

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

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

Benthoosema 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 beta*: FMNH 39659, 5, 42–53 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 spinosum*: MCZ 151450, 8, 41–71 mm SL.
- Nannobranchium atrum*: MCZ 113519, 6, 57–92 mm SL.
- Nannobranchium cuprarium*: MCZ 112776, 6, 55–67 mm SL; MCZ 112823, 4, 43–63 mm SL.
- Nannobranchium indicum*: MCZ 151729, 6, 32–84 mm SL.
- Nannobranchium isaacsi*: MCZ 55141, 6, 52–70 mm SL.
- Nannobranchium lineatum*: MCZ 159035, 2, 59–66 mm SL; MCZ 164479, 2, 59–71 mm SL.
- Nannobranchium 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.
- Stenobranchius 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 krefftii*: 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.

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