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Marine Habitat Transitions and Body-Shape Evolution in Lizardfishes and Their Allies (Aulopiformes)

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In this study, we use a geometric morphometric and a character evolution approach to study the evolutionary patterns of body-shape change and habitat transition in the Aulopiformes. Aulopiform fishes (lizardfishes; 289 spp.) inhabit diverse marine habitats from coral reefs to the deep sea and exhibit a wide range of body morphologies. Herein, we examine over 400 aulopiform specimens representing 38 of 44 genera and all families and identify that there are distinct patterns of body-shape change across the aulopiform radiation that coincide with habitat. A fusiform (torpedo-shaped) body is predominant among aulopiforms distributed in inshore-benthic and deep-sea benthic environments (e.g., Aulopidae, Bathysauridae, Synodontidae). There is a trend towards body elongation in taxa distributed in deep-sea pelagic habitats at depths of 200–4,000 meters (e.g., Alepisauridae, Lestidiidae, Notosudidae, Paralepididae) and a trend of body elongation with more centrally positioned dorsal and anal fins in the deep-benthic family Ipnopidae (tripodfishes). Additionally, deep-sea pelagic aulopiforms exhibit the largest variance in body-shape disparity with significant shape disparity compared to aulopiforms found in inshore-benthic and deep-sea environments. Deep-sea benthic lineages also have significantly higher body-shape variance and disparity compared to inshore-benthic lineages. We identify that there are considerable changes in body shape as aulopiform lineages transitioned to differing marine habitats. We infer the common ancestor of aulopiforms to have lived in a deep-sea benthic environment with a single transition to an inshore-benthic environment in the common ancestor of the Aulopoidei (lizardfishes, flagfin fishes) and two independent transitions into deep-sea pelagic environments, once in the common ancestor of Giganturidae, and once in the common ancestor of Alepisauroidea + Notosudoidea. This is the first study to quantitatively investigate changes in the body shape of aulopiform fishes tied to habitat transitions in marine environments from the deep sea to coral reefs. Our findings suggest that aulopiform body plans have broadly diversified in deep-sea pelagic and benthic habitats while remaining comparatively conservative in inshore-benthic habitats.

AULOPIFORM fishes (lizardfishes and their allies) are a lineage of marine fishes that includes 44 genera and 289 species (Fricke et al., 2019). They live in habitats ranging from near-shore coral reefs to the deep sea ($>$200 m), and many aulopiforms are key predators in their ecosystems (Sweatman, 1984). Deep-sea lizardfishes and their allies have evolved a wide variety of unique morphological and physiological adaptations, including reduced (Baldwin and Johnson, 1996; Somiya et al., 1996) or tubular (Davis and Fielitz, 2010) eyes, bioluminescence (Ghedotti et al., 2015; Davis et al., 2016), and simultaneous hermaphroditism (Davis and Fielitz, 2010). There are three main lineages within the Aulopiformes, the Aulopoidei, Paraulopoidei, and Alepisauroidei (Davis, 2010). The phylogenetic relationships of this group have been well studied, and the monophyly of aulopiform fishes is well supported by both morphological (Rosen, 1973; Baldwin and Johnson, 1996; Sato and Nakabo, 2002) and molecular data (Davis, 2010; Davis and Fielitz, 2010; Near et al., 2012; Davis et al., 2016; Smith et al., 2016). They are inferred to be the sister group to the Ctenosquamata (e.g., Rosen, 1973; Davis, 2010; Near et al., 2012; Davis et al., 2016) that includes the lanternfishes and spiny-rayed fishes (Acanthomorpha).

Aulopoidei includes lineages such as the predatory lizardfishes (Synodontidae), flagfin fishes (Aulopidae), and sand-diving lizardfishes (Pseudotrichonotidae). Aulopoid fishes predominantly occupy inshore-benthic environments throughout the world's tropical and temperate oceans on the continental shelf to upper regions of the continental slope. Paraulopoidei includes the cucumberfishes (*Paraulopus*) that occupy deep-sea benthic environments on the continental slope (Sato and Nakabo, 2002). Alepisauroidei includes taxa found exclusively in deep-sea environments, such as the benthic tripodfishes (Ipnopidae), the pelagic lancetfishes (Alepisauridae), and barracudinas (Paralepididae). The Alepisauroidei is the most diverse radiation of aulopiform fishes with $\sim$173 species (Fricke et al., 2019). Species in the Alepisauroidei possess many adaptations for living in the deep sea. Several pelagic alepisauroid species, including the telescopefish (Giganturidae), lancetfish (Alepisauridae), and barracudinas (Paralepididae), have elongated bodies and orient themselves vertically in the water column to hunt (Kupchik et al., 2018). Other pelagic aulopiforms, such as the sabertooth fishes (Evermannellidae) and pearleyes (Scopelarchidae), have dorsally directed tubular and semi-tubular eyes that allow them to hunt prey located vertically above them in the water column (Davis and Fielitz, 2010). Deep-benthic tripod fishes (*Bathypterois*) have highly reduced eyes (Baldwin and Johnson, 1996; Somiya et al., 1996) and have evolved extended pelvic and caudal fin-ray elements that allow for landing and perching on sea-floor substrates (Goode and Bean, 1886; Sulak, 1977; Davis and

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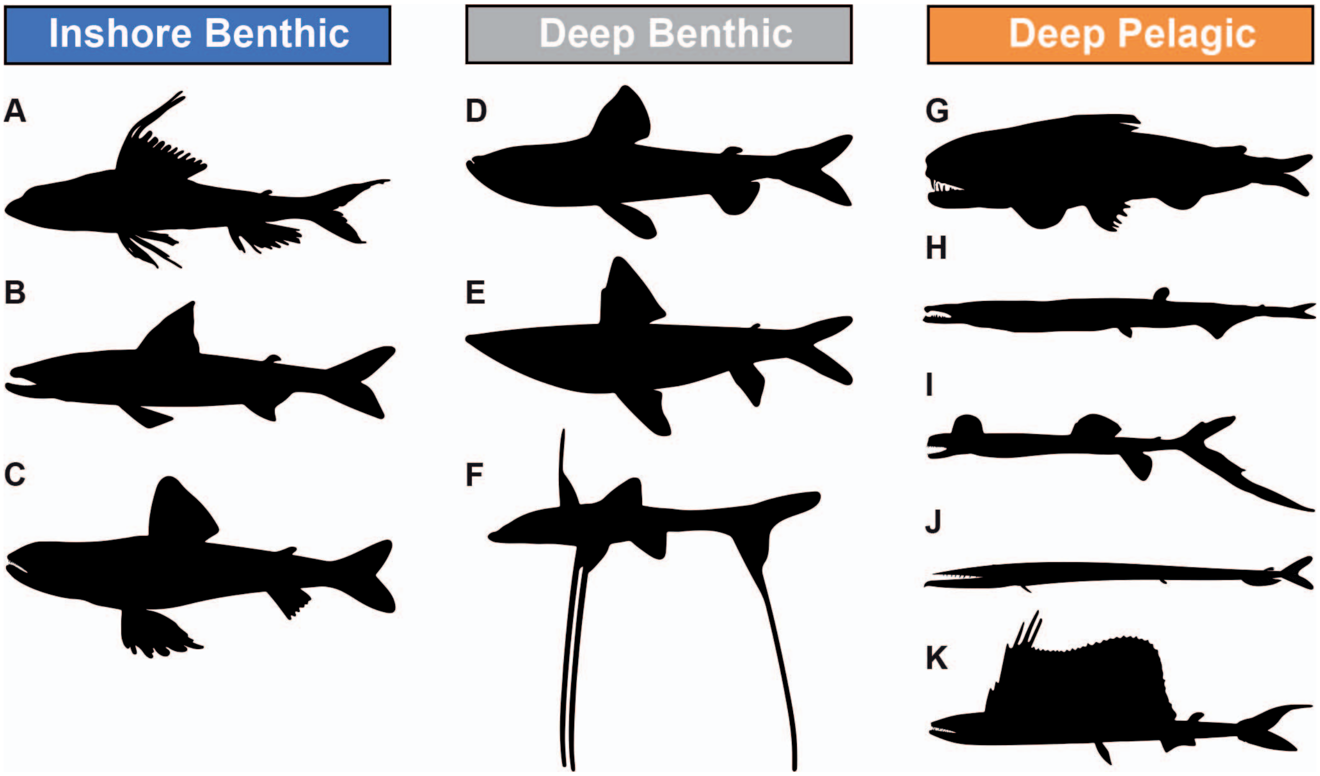

Fig. 1. Illustrations of aulopiform biodiversity with associated habitats. (A) Aulopidae; (B) Synodontidae: Harpadontinae; (C) Synodontidae: Synodontinae; (D) Paraulopidae; (E) Chlorophthalmidae; (F) Ipnopidae; (G) Evermannellidae; (H) Lestidiidae; (I) Giganturidae; (J) Alepisauridae: *Anotopterus*; (K) Alepisauridae: *Alepisaurus*.

Chakrabarty, 2011). Several species of deep-sea lizardfishes possess ventrally oriented bioluminescent organs (e.g., Merrett et al., 1971; Dunlap and Ast, 2005; Ghedotti et al., 2015), including bioluminescent liver tissue (Ghedotti et al., 2015). Among the 17 families of aulopiform fishes, there exists tremendous phenotypic diversity in body shape and appearance.

Previous works have demonstrated that variation in body shape across lineages of fishes have evolved in response to differing habitats and niches (e.g., Marcil et al., 2005; Russo et al., 2008; Muschick et al., 2012; Torres-Dowdall et al., 2012; Denton and Adams, 2015; Farré et al., 2016; Martin and Davis, 2016; Buser et al., 2017; Tuset et al., 2018; Friedman et al., 2020). This includes differences among closely related taxa found in benthic and pelagic habitats (Marcil et al., 2005). Only a handful of studies have investigated the evolution of body shape across lineages of deep-sea fishes (Orlov and Binohlan, 2009; Neat and Campbell, 2013; Denton and Adams, 2015; Farré et al., 2016; Tuset et al., 2018), and most of these have focused exclusively on pelagic taxa (Marcil et al., 2005; Hirst et al., 2014; Denton and Adams, 2015; Hooker et al., 2016).

The Aulopiformes are a fascinating lineage for studying the evolution of body shape in marine environments, as they possess a large breadth of phenotypic diversity and occupy both benthic and pelagic marine environments ranging from inshore to the depths of the deep sea (Fig. 1). Geometric morphometric techniques have been used in numerous studies to quantify body shapes in fishes and explore their evolution (e.g., Cavalcanti et al., 1999; Sibbing and Nagelkerke, 2000; Kerschbaumer and Sturmbauer, 2011). The focus of this study is to quantitatively investigate the body shape of lizardfish taxa using a geometric-morphometric approach incorporated with a previously published phylogeny of the Aulopiformes (Davis and Fielitz, 2010) and infer habitat transitions across the aulopiform radiation. In this study, we address the following questions: (1) What are the patterns of body-shape evolution among lizardfishes and their allies? (2) What are the patterns of marine habitat transitions among aulopiforms? (3) Are there trends in aulopiform body shapes that are correlated with marine habitats and/or phylogenetic signal? (4) Is there greater variation in body shape among aulopiforms that inhabit shallow or deep-sea environments?

MATERIALS AND METHODS

Taxonomic sampling.—Adult aulopiform specimens were used in this study and include material from the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), The Field Museum (FMNH), the University of Kansas Biodiversity Institute (KU), the Natural History Museum of Los Angeles County (LACM), the Museum of Comparative Zoology (MCZ), Scripps Institution of Oceanography (SIO), the National Museum of Natural History Smithsonian Institution (USNM), and the Virginia Institute of Marine Science (VIMS). Please refer to the Material Examined section for catalog information. Institutional abbreviations follow Sabaj (2020).

The left lateral side of specimens were imaged using a DSLR camera (Canon EOS Rebel t7i) after being placed on a copy stand or inside an OrTech Photo Box Plus1419. Additional images were included in this study from FishBase (Froese and Pauly, 2018), *The Fishes of the Japanese Archipelago* (Masuda et al., 1984), and from ROV footage (Kupchik et al., 2018).

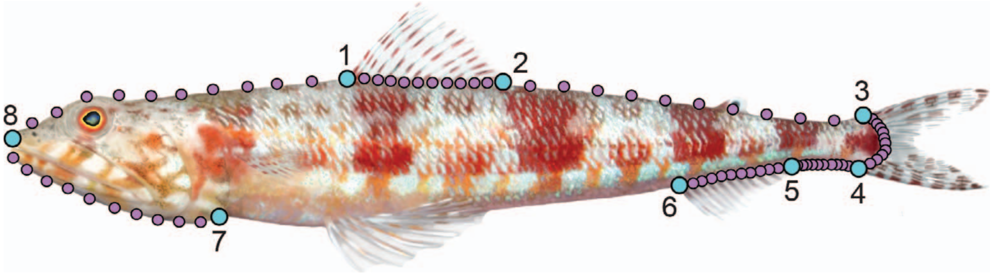

Fig. 2. Example of fixed landmark (blue circles) and sliding semi-landmark (purple circles) locations on a lizardfish (*Synodus variegatus* illustrated). Homologous fixed landmarks follow those from McMahan et al. (2011) and include: 1, anterior insertion of the dorsal fin on body; 2, posterior insertion of the dorsal fin on the body; 3, dorsal insertion of caudal fin; 4, ventral insertion of caudal fin; 5, posterior insertion of anal fin on the body; 6, anterior insertion of anal fin on body; 7, the point at which the interopercle meets the ventral body outline; 8, anterior tip of premaxilla. Digital image by R. P. Martin.

References to additional images are listed in Supplementary Table 1 (see Data Accessibility). Any specimens that exhibited significant body warping were excluded from analyses. In total, 404 specimens representing 78 species, 38 of 44 genera, and all families are included in this study. This study does include images of individuals from differing preservations in order to maximize taxonomic diversity; however, the findings of Fruciano et al. (2019) indicate that preservation may only have minor effects on analyses of shape variation.

Geometric morphometrics and statistical analyses.—A landmark-based geometric morphometric approach was used to quantify the variation in body shape among aulopiforms using the tps series of programs (Rohlf, 2015, 2018a, 2018b). The program tpsDig2 (Rohlf, 2018a) was used to assign fixed landmarks and sliding semi-landmarks onto digital images of lizardfishes. Fixed landmarks were placed on homologous structures and follow the landmark positions recommended by McMahan et al. (2011). The eight homologous landmarks (blue circles; Fig. 2) include: (1) anterior insertion of the dorsal fin on body, (2) the posterior insertion of the dorsal fin on the body, (3) the dorsal insertion of the caudal fin, (4) the ventral insertion of the caudal fin, (5) posterior insertion of the anal fin on the body, (6) the anterior insertion of the anal fin on the body, (7) the point at which the interopercle meets the ventral body outline, and (8) the anterior tip of the premaxilla. In addition to the homologous landmarks, 70 semi-landmarks were used to further describe aulopiform body shape. A total of seven semi-landmark curves were positioned between each set of fixed landmarks following the contour of bodies and were populated with ten landmarks each (purple circles; Fig. 2). In order to prevent the inclusion of shape variation due to stomach fullness (Martinez and Sparks, 2017), we excluded semi-landmarks around the stomach area in our analyses (Fig. 2). The relative warp analysis was performed with tpsRelw (Rohlf, 2015, 2018b) to quantify the changes in body shape without *a priori* group assignment with a default alpha such that the relevant warp is equivalent to a principal component analysis (Zelditch et al., 2012). This included conducting a Procrustes superimposition prior to the relative warp analysis to scale, rotate, and translate specimen data and create a consensus configuration (Rohlf, 2015, 2018a, 2018b).

Using the same dataset, we performed an additional general Procrustes analysis in R (R Core Team, 2018) using bending energy in the geomorph package v. 3.1.1 (Adams and Otárola-Castillo, 2013) that included the eight homologous fixed landmarks. Downstream analyses were performed using the output from this general Procrustes analysis followed by a principal component analysis (PCA). The phylogeny from Davis and Fielitz (2010), which included fossil calibrations to estimate divergence times among lizardfishes, was integrated with scores from the PCA and used with phytools (Revell, 2012) in R to create a genus-level phylomorphospace (Sidlauskas, 2008). We calculated morphological disparity using geomorph (Adams and Otárola-Castillo, 2013) to compare potential differences in the amount of body-shape variability among aulopiform families, suborder/superfamily, and habitats. We also performed an ANOVA of mean shapes in relation to habitat in geomorph. We assessed phylogenetic signal of body-shape variation using the K_{mult} statistic and phylosig function from phytools (Adams, 2014). *P*-values were based on 1,000-iteration permutations and used the average shapes of species from genera that were present in the divergence-time phylogeny of Davis and Fielitz (2010). Because of the lack of scale data for all specimens, we were unable to test for potential impacts of allometry, but we included only adult specimens in this study.

Habitat transitions.—The fossil-calibrated phylogeny of the Aulopiformes from Davis and Fielitz (2010) was used to infer the patterns and timing of marine habitat transitions. Habitat character states included outgroup taxa as well. These states included: (0) predominantly freshwater, (1) predominantly anadromous, (2) predominantly inshore benthic or benthopelagic on continental shelf and/or upper continental slope, (3) predominantly deep benthic or benthopelagic on lower continental slope and/or abyssal plain, and (4) predominantly deep pelagic. The break from the continental shelf is typically around 200 meters (m); however, it can vary from 200 to 500 m depending on the region (Angel, 1997), and fishes coded for state 2 are predominantly found among depth ranges from 0 to 500 m on the continental shelf or upper continental slope. Fishes coded for state 3 are predominantly found from the deep continental slope to the abyssal plain, with deep pelagic (state 4) encompassing pelagic lineages predominantly found in open ocean depths below 200 m. Outgroups from Davis and Fielitz (2010) were coded as: *Amia calva* (0), *Hiodon* *alosoides* (0), *Danio rerio* (0), *Dorosoma cepedianum* (0), *Argentina sialis* (2), *Oncorhynchus mykiss* (1), *Diplophos taenia* (4), *Thaleichthys pacificus* (1), *Ijimaia antillarum* (3), *Neoscopelus macrolepidotus* (3), *Nannobrachium lineatum* (4), *Benthosema glaciale* (4), *Polymixia japonica* (3), *Metavelifer multiradiatus* (3), and *Morone chrysops* (0). The character evolution of habitat transitions was reconstructed with ancestral state methods using Mesquite 3.51 (Maddison and Maddison, 2018) with parsimony and maximum-likelihood methods.

RESULTS

Variation and body-shape disparity across lizardfishes and their allies.—The consensus configuration of the relative warp analysis infers the average aulopiform body as fusiform (torpedo-shaped), with the dorsal fin positioned along the midpoint. The results of the principal component analysis indicate considerable variation in body shape among aulopiforms (Fig. 3, Supplementary Figs. 1–4; see Data Accessibility) with principal components (PCs) 1 and 2 describing 61% of the overall variation. The first two principal components describe body-shape variation associated with depth and elongation and the length and position of median fins in aulopiforms. The morphospace on the low score extreme along PC 1 includes taxa with an elongated and slender body, with the dorsal fin positioned posteriorly, closer to the caudal peduncle (Fig. 3). The morphospace on the high score extreme of PC 1 includes taxa with a deeper fusiform body with a more anteriorly positioned dorsal-fin insertion relative to the midpoint of the body. The morphospace on the low score extreme of PC 2 includes species with a fusiform body and a dorsal and anal fin positioned along the midpoint of the body. The morphospace along the high score extreme of PC 2 includes taxa with a slender body that is slightly elongated with the dorsal and anal fin positioned along the midpoint of the body (Fig. 3). For graphical representations of the distribution of each genus in the morphospace described by PC 1 and 2, please refer to Supplementary Figures 1–4 (see Data Accessibility).

In general, taxa within the aulopoid families Aulopidae, Pseudotrichonotidae, and Synodontidae exhibit a fusiform body and were located on or around the consensus shape of the Aulopiformes (Fig. 3). Overall, species in the Aulopoidei have significantly lower disparity in body shape compared to species within the Alepisauroidei superfamilies Ipnopoidea ($P = 0.007$) and Alepisauroidea ($P = 0.001$) as seen in Table 1. Taxa within the Paraulopoidei (Paraulopidae) exhibit a deeper, fusiform body and are restricted in morphospace on the high score side of PC 1 with a dorsal fin positioned along the midpoint of the body (Fig. 3). Species in the Paraulopoidei were not found to have significant disparity in body shape relative to the other suborders/superfamilies; however, this lineage is represented by a single genus and had a smaller number of samples in the analyses.

The Alepisauroidei exhibited a wide range of quantified body shapes. The superfamily Ipnopoidea had the second largest disparity in body shape among aulopiform suborders/superfamilies (Table 1), with the family Ipnopidae (tripodfishes) exhibiting a unique range of body morphologies located in two distinct clusters (Fig. 3). The first cluster included the genera *Bathytyphlops* and *Ipnops* and is distributed near the consensus body shape that exhibits a dorsal fin positioned along the midline of the body with a fusiform shape. The second cluster included the genera *Bathymicrops* and *Bathypterois* and is located along the low score extreme of PC 2 in morphospace and with a slightly elongated posterior region with a deeper anterior body (Fig. 3). In *Bathymicrops* and *Bathypterois,* the dorsal fin is positioned along the midline of the body and the anal fin is located just slightly posterior to the midline of the body. Giganturidae have body elongation with a dorsal fin positioned posteriorly near the caudal peduncle and are clustered along the low score side of PC 1 in morphospace (Fig. 3). While two individuals were included from ROV footage within the Giganturidae (Supplementary Table 1; see Data Accessibility) along with a formalin-fixed giganturid, these individuals occupied similar regions in morphospace within this family. On the high score side of PC 1, Bathysauroididae and Bathysauropsidae exhibited a robust, fusiform body with a dorsal fin positioned along the midpoint of the body. Bathysauridae exhibited a fusiform body located near the consensus shape of Aulopiformes, with a dorsal fin positioned along the midpoint of the body (Fig. 3). Overall, the superfamily Ipnopoidea had significantly higher body-shape disparity than Aulopoidei ($P = 0.007$) and Cholorophthalmoidea ($P = 0.02$), and significantly lower body-shape disparity than the Alepisauroidea ($P = 0.002$) as seen in Table 1.

The superfamily Chlorophthalmoidea (family Chlorophthalmidae) was distributed on the high score side of PC 1 with a robust fusiform body and a dorsal fin positioned along the midpoint of the body (Fig. 2). The Chlorophthalmoidea had significantly lower body-shape disparity than the Ipnopoidea ($P = 0.02$) and the Alepisauroidea ($P = 0.001$) as seen in Table 1. Fishes in the superfamily Notosudoidea (family Notosudidae) possessed elongated bodies with the dorsal fins positioned slightly posterior to the midpoint of the body and are located on the low score side of PC 1 (Fig. 3) with a significantly lower body-shape disparity than the Alepisauroidea ($P = 0.004$) as seen in Table 1.

The superfamily Alepisauroidea had the largest disparity in body shape among all aulopiform fishes, with significantly greater body-shape disparity than all other aulopiform lineages other than the Paraulopoidei ($P = 0.058$; Table 1). The families Evermannellidae and Scopelarchidae have deep fusiform bodies on the high score side of PC 1 with dorsal fins positioned along the midpoint of the body (Fig. 3). The families Lestidiidae, Paralepididae, and Sudidae had elongated bodies with dorsal fins positioned posteriorly near the caudal peduncle and were distributed on the low score side of PC 1 (Fig. 3). The family Alepisauridae (*Alepisaurus, Anotopterus*, and *Omosudis*) had the widest range in morphospace with each of the three genera occupying distinct clusters. *Anotopterus* was located on the low score extreme of PC 1 in morphospace with the most extreme elongation within Aulopiformes with a dorsal fin posteriorly positioned near the caudal peduncle (Fig. 3). *Omosudis* had a shorter and deeper body relative to *Alepisaurus* and *Anotopterus* and was located closer to the consensus configuration on the low score side of PC 1 (Fig. 3). *Alepisaurus* was located along the high score extreme of PC 2 and had an elongated body with a uniquely long dorsal fin that covers the majority of the dorsal surface of the body (Fig. 3).

Phylomorphospace and phylogenetic signal.—There was significant phylogenetic signal in body shape for all lizardfishes

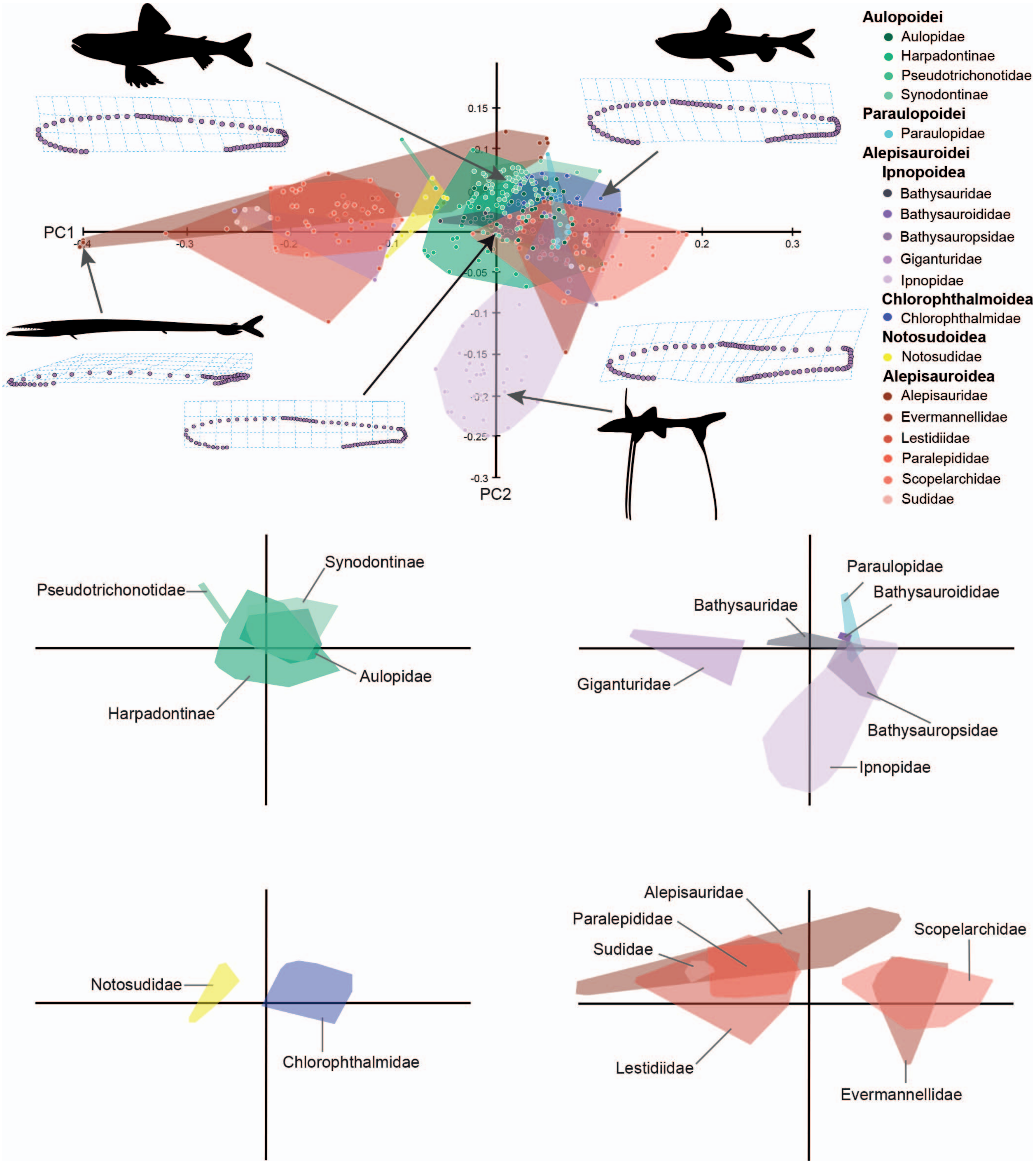

Fig. 3. Results of principal component analysis depicting principal component 1 and principal component 2 with eight homologous landmarks and 70 semi-landmarks. Colored polygons highlight distribution of specimens within families of lizardfishes.

combined ($K_{mult} = 1.0069$, $P = 0.001$) and for the Alepisauroidea ($K_{mult} = 1.0727$, $P = 0.001$). In most instances, closely related genera within suborders/superfamilies tended to cluster nearer to each other in shape space, with less closely related taxa being more morphologically divergent (Figs. 3, 4). For example, some taxa in the superfamily Alepisauroidea (Fig. 4) had similar elongated body shapes to the families Alepisauridae (*Anotopterus*), Lestidiidae, Paralepididae, and Sudidae.

However, there are some deep-sea pelagic lineages within the Alepisauoridea or the deep-sea benthic and pelagic Ipnopoidea, where closely related genera are significantly morphologically divergent, such as within the families Alepisauridae (*Alepisaurus*, *Anotopterus*, *Omosudis*), Ipnopidae

Table 1. Lizardfish disparity values from the morphological disparity test by suborder and superfamily. Asterisks denote significant values.

			Alepisauroidei			
	Aulopoidei	Paraulopoidei	Ipnopoidea	Chlorophthalmoidea	Notosudoidea	Alepisauroidea
Variance	0.008814591	0.004405217	0.021614454	0.008162117	0.00385712	0.037560784
P-values						
Aulopoidei	–	0.721	0.007*	0.884	0.569	0.001*
Paraulopoidei	0.721	–	0.148	0.777	0.964	0.058
Alepisauroidei						
Ipnopoidea	0.007*	0.148	–	0.02*	0.061	0.002*
Chlorophthalmoidea	0.884	0.777	0.02*	–	0.639	0.001*
Notosudoidea	0.569	0.964	0.061	0.639	–	0.004*
Alepisauroidea	0.001*	0.058	0.002*	0.001*	0.004*	–

(*Bathypterois*, *Ipnops*), and between the deep-sea lizardfishes *Bathysaurus* and the telescopefishes *Gigantura*.

Variation in body shape across marine habitats.—The relative warp and disparity analyses indicate a quantitative differentiation in body shape across differing habitats in the Aulopiformes (Fig. 5). Aulopiforms occupying inshore-benthic habitats in the suborder Aulopoidei (e.g., Aulopidae, Harpadontinae, Pseudotrichonotidae, and Synodontinae) possess fusiform bodies and form a tight cluster around the consensus configuration (Fig. 5). Inshore-benthic aulopiforms had the lowest overall variance in body shape among the three habitats (0.00879) and significantly lower body-shape disparity compared to deep-sea benthic aulopiforms on the deeper continental slope and abyssal plain ($P = 0.001$) or deep-sea pelagic aulopiforms ($P = 0.001$; Table 2). Deep-sea benthic aulopiforms (Bathysauridae, Bathysauroididae, Bathysauropsidae, Chlorophthalmidae, Ipnopidae, Paraulopidae) have significantly higher body-shape disparity than inshore-benthic aulopiforms ($P = 0.001$), but significantly lower disparity when compared to deep-sea pelagic aulopiforms ($P = 0.001$, Table 2). In general, benthic aulopiforms found in deep-sea habitats have predominantly deeper, fusiform bodies with the exception of Ipnopidae. Taxa in the Ipnopidae are unique in that *Bathymicrops* and *Bathypterois* possess a slight body elongation with an anal

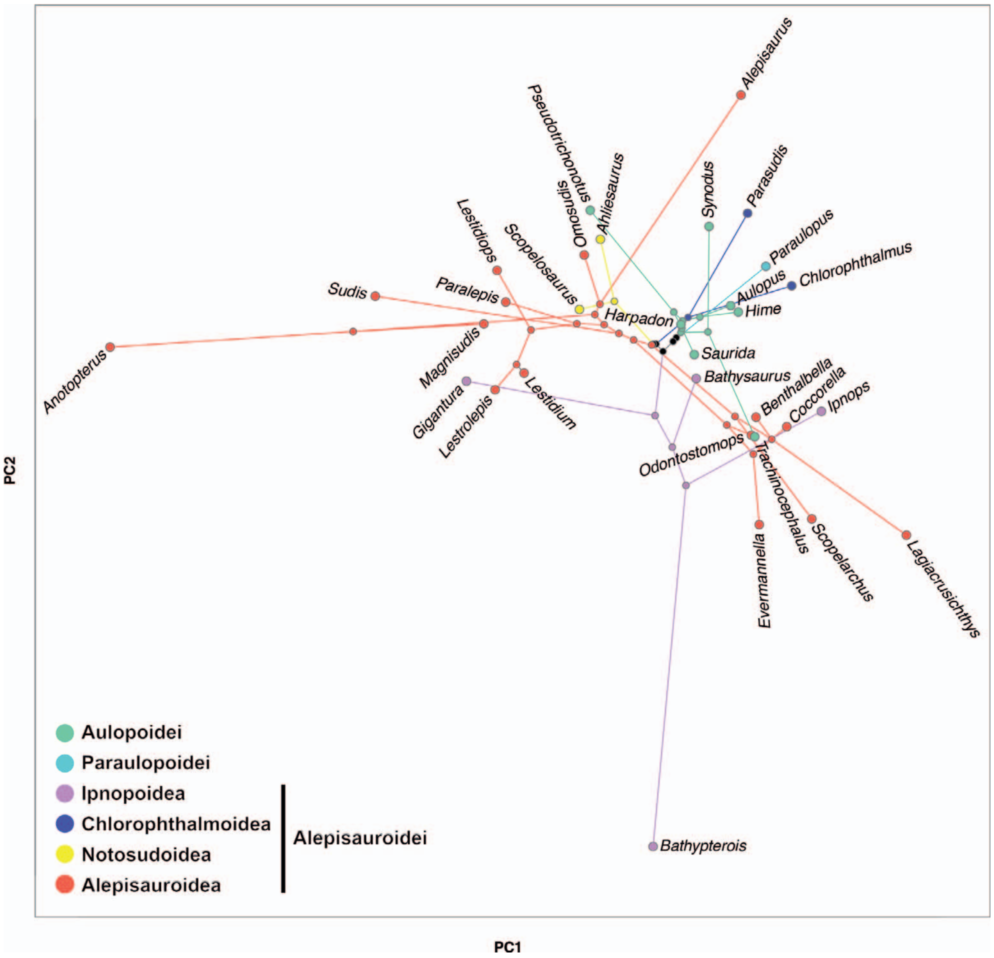

Fig. 4. Phylomorphospace visualization plot of principal component 1 and principal component 2 incorporating the phylogeny from Davis and Fielitz (2010). Circle positions represent the average location in morphospace for each genus.

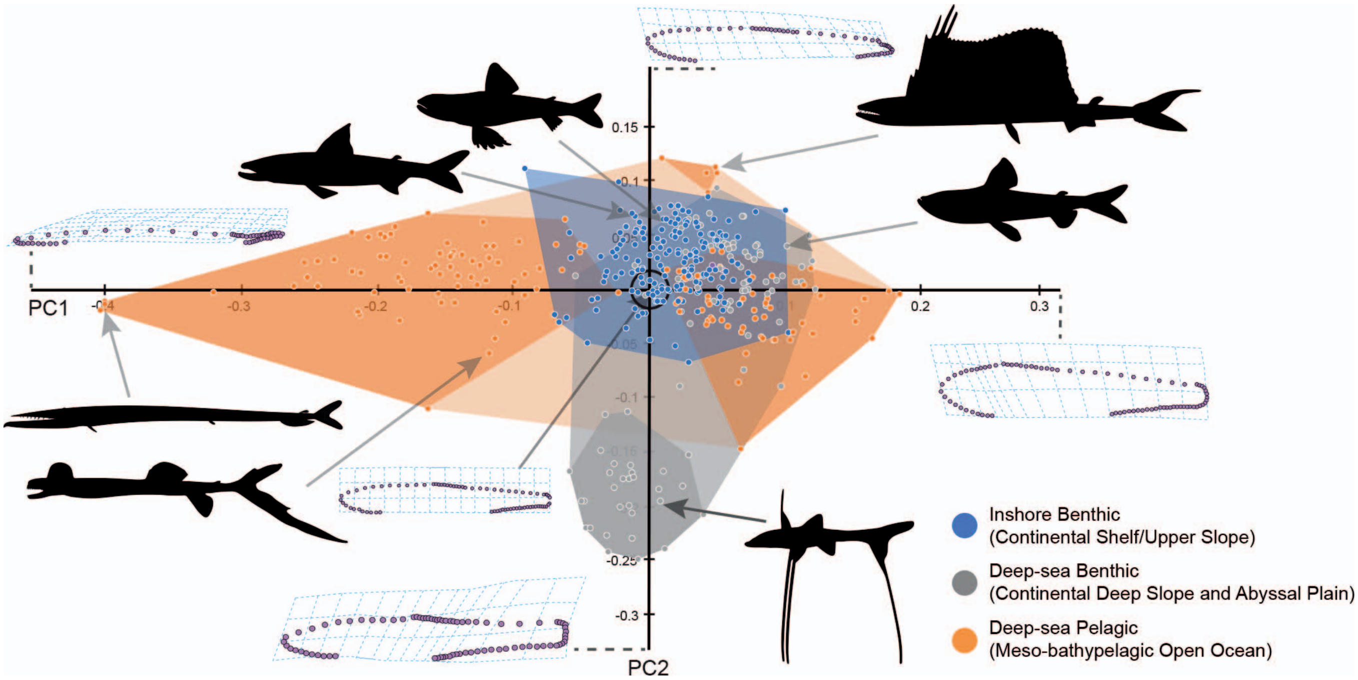

Fig. 5. Results of principal component analysis depicting principal component 1 and principal component 2 with eight homologous landmarks and 70 semi-landmarks. Colored polygons represent distribution by marine habitat.

fin positioned just slightly posterior to the midline of the body (Fig. 5), whereas the rest of aulopiform taxa possess anal fins located near the caudal fin. The deep-sea pelagic aulopiforms (Alepisauridae, Evermannellidae, Giganturidae, Lestidiidae, Notosudidae, Paralepididae, Scopelarchidae, Sudidae) reside among three areas of morphospace (Fig. 5), with body morphologies ranging from a deeper anterior body (Evermannellidae, Scopelarchidae) on the high score side of PC 1 to an elongate body on the low score side of PC 1 (Alepisauridae, Giganturidae, Lestidiidae, Paralepididae, Sudidae). The deep-pelagic lancetfishes (*Alepisaurus*) occupy a distinct area of morphospace as a result of its uniquely enlarged dorsal fin (Figs. 3, 5). As a group, deep-sea pelagic aulopiforms had the highest body-shape variability (0.0356), significantly higher than both deep-sea benthic (0.0228; $P = 0.001$) and inshore-benthic (0.00879; $P = 0.001$) taxa. Deep-sea benthic aulopiforms also had significantly higher body-shape variability than inshore-benthic ($P = 0.001$) taxa. An ANOVA of means for body shape with habitat as an independent character also inferred that the average body shapes by habitat are statistically significantly different from each other among all pairwise comparisons ($P = 0.001$).

Table 2. Lizardfish disparity values from the morphological disparity test by marine habitat. Asterisks denote significant values.

	Inshore benthic	Deep-sea benthic	Deep-sea pelagic
Variance	0.00879	0.02282	0.03559
P-values			
Inshore benthic	–	0.001*	0.001*
Deep-sea benthic	0.001*	–	0.001*
Deep-sea pelagic	0.001*	0.001*	–

Marine habitat transitions in lizardfishes and their allies.—The common ancestor of the Aulopiformes is inferred to have inhabited a deep-benthic environment when the lineage first evolved during the Upper Jurassic to Lower Cretaceous (Fig. 6). A habitat transition from a deep-benthic to an inshore-benthic environment occurred in the common ancestor of the Aulopoidei during the Upper Jurassic to Lower Cretaceous (Fig. 6). Two independent habitat transitions occurred from a deep-benthic environment to a deep-pelagic environment within the Aulopiformes (Fig. 6). The first transition occurred in the common ancestor of the Notosudoidea + Alepisauroidea during the Lower Cretaceous (Fig. 6). The second transition occurred in the common ancestor of Giganturidae within Ipnopoidea, with that family likely evolving between the Paleogene to Neogene (Fig. 6). The maximum-likelihood and the maximum-parsimony reconstruction inferred the same ancestral habitat states with the most likely state from the likelihood analysis being the most parsimonious state in the parsimony analysis.

DISCUSSION

This study aims to understand the evolution of body shape in aulopiform fishes that have evolved in different marine habitats and to investigate habitat transitions in this diverse lineage of fishes. We found significant quantitative evidence of body-shape change among the radiation of lizardfishes and their allies (Fig. 3) and that there is distinct clustering of body-shape patterns associated with marine habitats (Fig. 5). We identified that the common ancestor of the Aulopiformes was most likely benthic/benthopelagic in deep-sea environments with aulopiforms first evolving during the Upper Jurassic to Lower Cretaceous (Fig. 6). Our study shows that extant aulopiforms have experienced three habitat transitions across their evolutionary history (Fig. 6) and the body

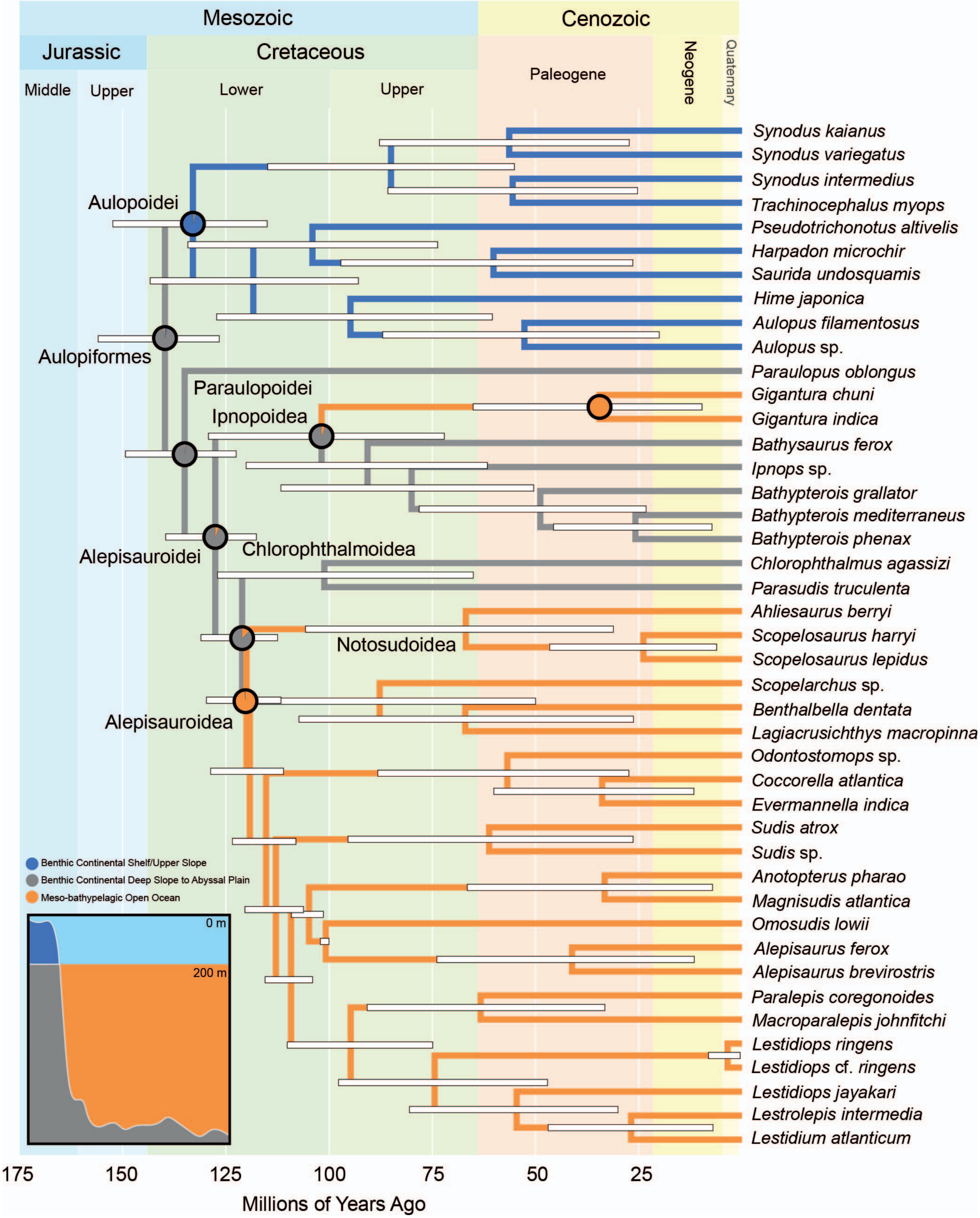

Fig. 6. Marine habitat transitions among Aulopiformes inferred on the time-calibrated phylogeny from Davis and Fielitz (2010). Outgroups trimmed from tree to highlight Aulopiformes. Benthic continental shelf to upper slope may range from approximately 0 to 500 meters depending on region, with most continental shelves breaking at 200 m. Deep-sea pelagic includes the zones below the epipelagic starting with the mesopelagic at 200 m. Maximum-likelihood character reconstruction of habitat shown with probabilities of states represented at nodes.

shapes of taxa found in these differing habitats occupy different regions of morphospace (Figs. 3, 5). We identify that aulopiforms living in deep-sea environments have greater disparity and variance in body shape than those distributed among inshore environments. We hypothesize that it is likely the transition to deep-sea habitats in aulopiforms facilitated the extraordinary diversity of aulopiform body plans as these lineages evolved adaptations for living in their deep-sea benthic and pelagic environments and began to broaden their evolutionary ecology into new niche spaces.

Inshore-benthic lizardfishes in the suborder Aulopoidei (Aulopidae, Pseudotrichonotidae, Synodontidae: Synodontinae and Harpadontinae) are commonly found in reef and sandy environments. Inshore lizardfishes are ambush predators that have evolved a fusiform body shape that allows for quick bursts to capture prey items (Pettersson and Hedenström, 2000; Fisher and Hogan, 2007). While species richness is high among shallow inshore taxa, such as within *Synodus*, the body plans of inshore taxa are generally more conserved with a fusiform/torpedo shape. Aulopoid taxa were inferred to be clustered around the consensus configuration in morphospace (Figs. 3, 5, Supplementary Figs. 1–4; see Data Accessibility) and were comparatively more restricted in body shape and median fin placement than taxa found in deep-sea habitats (Figs. 3, 5) which have significantly higher variance and disparity in body shape than inshore aulopiforms (Table 1). The evolutionary history of aulopoid lizardfishes includes a single habitat transition from a deep-sea benthic environment to an inshore-benthic environment in the common ancestor of the Aulopoidei, from which this lineage continued to diversify among inshore habitats along the continental shelf and upper continental slope, with no transitions back to predominantly deep-sea environments (Fig. 6). Aulopoidei likely diverged during the Upper Jurassic to Lower Cretaceous (115–152 MYA, Fig. 5) in predominantly inshore habitats.

The common ancestor of the Aulopiformes was inferred to live in a deep-sea benthic habitat (Fig. 6), and we identify that aulopiforms which have evolved in deep-sea benthic habitats have a significantly broader range of body-shape morphologies than inshore-benthic lizardfishes in Aulopoidei (Figs. 3, 5; Table 2). This significant variation in body-shape disparity indicates that within the Aulopiformes, evolution in the deep sea has facilitated a vast array of body forms when compared to the more conservative torpedo-shaped body plans found in more inshore lizardfishes. The broad variation in deep-sea benthic lizardfishes includes the position of their median fins. For example, the tripodfishes (Ipnopidae, *Bathypterois*) have a slightly elongated fusiform body with an anal fin near the center of the body, with this genus highlighted in a darker shade in Figure 5 within the broader deep-sea benthic morphospace. Tripodfishes are the only lineage of lizardfishes that elevate themselves with elongated caudal and pelvic fin elements on the sea floor (Sulak, 1977; Davis and Chakrabarty, 2011). Sulak (1977) hypothesized that this elevation is to acquire benthopelagic plankton floating above the substrate. Other deep-benthic aulopiforms in the Paraulopoidei (Paraulopidae), Ipnopoidea (Bathysauridae, Bathysauroididae, Ipnopidae) have a fusiform shape with an anal fin positioned closer to the caudal fin and variation regarding depth of the body anteriorly (Figs. 3, 5).

Aulopiforms living in deep-sea pelagic habitats include ~40 percent of their species richness, and we inferred two independent habitat transitions into deep-pelagic environments from a deep-benthic ancestor. The first transition from a deep-benthic ancestor to a deep-pelagic habitat occurs in the common ancestor of the Notosudoidea (waryfishes) + Alepisauroidea (lancetfishes and allies) during the Lower Cretaceous (Fig. 6). The majority of extinct fossil aulopiform lineages that have been included in phylogenetic analyses that incorporate extinct and extant aulopiforms (e.g., Fielitz, 2004) are inferred to be within the deep-pelagic Alepisauroidea, and it is likely many of these taxa (e.g., Enchodontoidei, Cimolichthyoidei) were inhabiting pelagic environments from the Early to Late Cretaceous (Davis and Fielitz, 2010) and have adaptations for pelagic environments seen in extant alepisauroid taxa including enlarged fangs. The second independent invasion into a pelagic habitat from deep-benthic ancestors occurs in the Giganturidae (telescopefishes) likely from the Late Cretaceous to the Paleogene (Fig. 6).

The deep-sea pelagic aulopiforms have the greatest variance and body-shape disparity within morphospace (Table 2), and their body morphologies trend in three directions, with these trends highlighted by darker shades in Figure 5. One trend includes a slender and more elongated body, which has convergently evolved in the telescopefishes (Ipnopoidea: Giganturidae) and the Notosudoidea (Notosudidae) + Alepisauroidea taxa (Alepisauridae, Lestidiidae, Paralepididae, Sudidae). In general, pelagic lineages of fishes have been documented to have trends towards body elongation (Friedman et al., 2020), and this is the case among aulopiform fishes that have transitioned to pelagic habitats from benthic ancestors. Among the elongated and slender taxa there is a pattern of the dorsal fin shifting to an increasingly posterior position on the body in some lineages, with the extreme being *Anotopterus* (Figs. 3, 5). The lancetfishes (*Alepisaurus*) represent the second deep-pelagic trend with a slender and elongated body but an enlarged sail-like dorsal fin that extends across the length of their body (Figs. 3, 5) in a distinct region of morphospace. Deep-sea pelagic aulopiforms with laterally compressed and elongated bodies such as the lancetfishes (Alepisauridae), telescopefishes (Giganturidae), naked barracudinas (Lestidiidae), and barracudinas (Paralepididae) have been documented to orient themselves vertically in the water column to hunt prey items above them while simultaneously limiting the silhouette of their body (Bailey et al., 2003; Kupchik et al., 2018). This behavior is found in a few other elongated pelagic marine fishes including the cutlassfishes and oarfishes (Benfield et al., 2013; Kupchik et al., 2018).

While most of the deep-pelagic aulopiforms have elongated bodies, two lineages (Evermannellidae and Scopelarchidae) have evolved a fusiform body that is deeper anteriorly and represent the third trend in morphospace for the deep-pelagic aulopiforms (Figs. 3, 5). Taxa in Evermannellidae (sabertooth fishes) and Scopelarchidae (pearleyes) have independently evolved tubular and semitubular eyes that are dorsally directed (Davis and Fielitz, 2010; Davis, 2015) that they use to hunt prey items above them in the water column. Sabertooth fishes and pearleyes are not known to vertically orient like many of the slender and elongated pelagic aulopiformes, and some species of pearleyes may obscure their silhouette through bioluminescence. Unlike many other lineages of deep-sea pelagic fishes (dragonfishes, lanternfishes), most pelagic aulopiform taxa do not use bioluminescence for camouflage in the deep sea (Hastings, 1971; Young and Roper, 1976; Davis et al., 2014, 2016), although there are a few exceptions. Species in the families Lestidiidae (naked barracudinas) and Scopelarchidae (pearleyes) have evolved bioluminescence to illuminate their ventral surface, which is hypothesized to aid in counter illumination (Davis, 2015; Ghedotti et al., 2015; Davis et al., 2016) in their pelagic environment.

Conclusison.—Overall, the evolutionary history of aulopiform fishes includes multiple transitions into differing marine habitats from a deep-sea benthic common ancestor, and there is a significant increase in the variation of body-shape disparity among lineages of aulopiforms distributed in deep-sea environments relative to inshore environments. Habitat transitions include a single invasion into inshore marine habitats in the common ancestor of the Aulopoidei (e.g., lizardfishes, flagfin fishes; Fig. 6), which we found to be restricted in morphospace with fusiform torpedo-shaped bodies (Fig. 5). There have been two independent invasions into deep-sea pelagic habitats from a deep-sea benthic common ancestor, including in the telescopefishes (Giganturidae) and the common ancestor of the waryfishes (Notosudidae) + lancetfishes and allies (Alepisauroidea; Fig. 6). We saw a trend toward slender and elongated bodies in many deep-sea pelagic aulopiform lineages (Figs. 3, 5), and overall, taxa within the exclusively pelagic superfamily Alepisauroidea had the greatest variance in body shape of all aulopiform fishes with significantly greater body disparity (Table 1) than nearly all other suborders/superfamilies. Our findings indicate that there has been considerable evolution in the body shape of aulopiforms as they evolved in various marine environments from coral reefs, to the bottom of the sea floor, to the open ocean and we find that there is greater variation in body morphologies of deep-sea aulopiform lineages relative to those found living in inshore/coral reef habitats.

DATA ACCESSIBILITY

Supplemental material is available at https://www.copeiajournal.org/cg-19-300.

MATERIAL EXAMINED

Ahliesaurus berryi: MCZ 161661 (1), 163249 (1).

Alepisaurus ferox: BMNH 1833 (1).

Anotopterus pharao: MCZ 43141 (1), 164375 (1).

Arctozenus risso: MCZ 62039 (5), 188113 (1); VIMS 01764 (5).

Aulopus bajacali: SIO 25-650 (5).

Bathymicrops regis: VIMS 06114 (1).

Bathypterois atricolor: FMNH 81860 (1).

Bathypterois bigelowi: VIMS 06362 (7).

Bathypterois guentheri: FMNH 81645 (2).

Bathypterois phenax: FMNH 64423 (1).

Bathypterois quadrifilis: FMNH 117871 (3), 81860 (1).

Bathypterois viridensis: FMNH 64423 (3), 64434 (1); VIMSC 6149 (4).

Bathysauropsis gracilis: MCZ 130274 (2).

Bathysaurus ferox: MCZ 138024 (1).

Bathysaurus mollis: BMNH 1878 (1).

Bathytyphlops sewelli: BMNH 178-8285 (2).

Benthalbella dentata: SIO 88-53 (1).

Benthalbella infans: FMNH 79258 (1); SIO 94-79 (1).

Benthalbella linguidens: MCZ 157117 (1).

Chlorophthalmus agassizi: BMNH 1840 (5).

Chlorophthalmus atlanticus: FMNH 117863 (3).

Chlorophthalmus brasiliensis: VIMS 100755 (5).

Coccorella atlantica: FMNH 79706 (1), 82275 (1); MCZ 73021 (1).

Coccorella atrata: FMNH 82775 (1), 85312 (1).

Coccorella sp.: USNM 077A (1).

Evermannella balbo: FMNH 94562 (1).

Evermannella indica: FMNH 79729 (1), 82745 (1); SIO 73-148 (2).

Evermannella melanoderma: FMNH 49867 (1).

Gigantura indica: USNM 215421 (1).

Harpadon microchir: SU 20714 (4).

Hime japonica: FMNH 89115 (1), 121176 (1); LACM 38702-1 (1).

Ipnops agassizii: USNM 54618 (1).

Ipnops meadi: USNM 149041 (1).

Ipnops murrayi: FMNH 64080 (1).

Lagiacrusichthys macropinna: MCZ 125832 (1).

Lestrolepis intermedia: MCZ 91583 (2).

Magnisudis atlantica: MCZ 164296 (4).

Odontostomops normalops: MCZ 127271 (1), 165564 (1).

Omosudis lowii: MCZ 163185 (1).

Paralepis atlantica: MCZ 136896 (1).

Paralepis brevirostris: MCZ 164300 (1).

Paralepis coregonoides: MCZ 128216 (1); USNM 49347 (1).

Paralepis elongata: MCZ 43140 (3).

Parasudis fraserbrunneri: FMNH 117870 (1).

Parasudis truculenta: BMNH 1986.4.3.10-13 (1), 1986.4.3.10-14 (1), 1986.4.3.10-15 (1), 1986.4.3.10-16 (1); FMNH 46309 (1); VIMS 03261 (4).

Rosenblattichthys volucris: SIO 68-582-25 (2).

Saurida brasiliensis: FMNH 64828 (3), 67270 (1), 117860 (6).

Saurida caribbaea: FMNH 64828 (3).

Saurida cf. undosquamis: FMNH 120832 (2).

Saurida gracilis: CAS 69571 (4); FMNH 75362 (1).

Saurida grandisquamis: FMNH 45828 (1).

Saurida macrolepis: FMNH 120828 (2).

Saurida normani: FMNH 64916 (1).

Saurida tumbil: CAS 69927 (5); FMNH 57255 (1).

Saurida wanieso: SU 60886 (1).

Scopelarchoides danae: MCZ 127125 (1).

Scopelarchoides signifer: SIO 61-32 (2).

Scopelarchus analis: FMNH 79651 (3), 79652 (1), 79653 (1), 79716 (1), 79719 (1), 79720 (2), 79722 (1), 79727 (1), 88141 (1), 88144 (1); MCZ 127130 (2); SIO 71-386 (1), 96-34 (2).

Scopelarchus guentheri: FMNH 79712 (1), 88137 (1), 88138 (1); MCZ 70909 (2).

Scopelarchus michealsarsi: FMNH 79709 (1).

Sudis hyalina: MCZ 43077 (1).

Synodus binotatus: FMNH 75388 (1).

Synodus dermatogenys: FMNH 125034 (3).

Synodus doaki: FMNH 110273 (1).

Synodus foetens: FMNH 5429 (1), 8275 (1).

Synodus intermedius: FMNH 5434 (2).

Synodus kaianus: FMNH 120833 (1).

Synodus poeyi: AMNH 76393 (4).

Synodus scituliceps: FMNH 8271 (3).

Synodus ulae: FMNH 89527 (1).

Synodus variegatus: FMNH 44413 (1), 51363 (1), 75582 (1).

Trachinocephalus myops: BMNH 300-55380 (4).

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