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Evolutionary Relationships of the Anglerfishes (Lophioidei) with a Total Evidence Approach: Illuminating Habitat Transition Impacts on Anglerfish Lures and Body Shapes

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Evolutionary Relationships of the Anglerfishes (Lophioidei) with a Total Evidence Approach: Illuminating Habitat Transition Impacts on Anglerfish Lures and Body Shapes

By

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Matthew Davis, Chairperson
Sarah Gibson
Jennifer Lamb

Abstract

The anglerfishes (Lophioidei) consist of carnivorous fishes renowned for their first dorsal-fin spine luring specialization used in prey capture behavior. Anglerfishes encompass a unique fish lineage (>400 species) distributed at varying oceanic depths that have resulted in fascinating evolutionary adaptations, including pseudo-walking, chemical prey attractant lures, bioluminescent lures and barbels, sexual dimorphism, and male parasitism. Chapter one of this thesis investigates the evolutionary relationships of the suborder Lophioidei using a total evidence approach. A total evidence approach is a strategy used to infer evolutionary relationships that combine different lines of evidence, such as morphological and genetic data, to provide a robust hypothesis of evolutionary relationships and is used to investigate the evolution of anglerfishes (Acanthuriformes: Lophioidei). In this thesis I explore the evolutionary relationships of Lophioidei with ultraconserved elements (UCEs), UCEs and mitochondrial genomes, and a total evidence approach that combines UCEs, mitochondrial genomes, and morphological characters. The results of these analyses recover a monophyletic Lophioidei as the sister group to Tetraodontoidei within Acanthuriformes, with Lophioidei+Tetraodontoidei sister to the boarfish *Antigonia* (Caproidae). Within Lophioidei, the goosefishes (Lophioideo) were inferred as the stem anglerfish lineage. The Lophiidae are the sister group to a clade comprised of the frogfishes (Antennarioideo) + batfishes (Ogcocephaloideo) and the coffinfishes (Chaunancoideo) + deep-sea anglerfishes (Ceratoideo). Chapter 2 explores the luring apparatus of anglerfishes, the primary tool used in prey capture and communication in certain groups. The anglerfishes have three distinctive luring strategies: mechanical luring, chemical attractant luring, and bioluminescent luring. Anglerfish specimens and photos procured from ichthyological museum collections and online public databases are used to collect morphometric data from the lures of these fishes. Depth records collected from FishNet 2 are then used to examine lure morphometrics based on various oceanic depths. Using the total evidence tree in Chapter 1, the study recovers two independent evolutionary events of a mechanical luring strategy in Lophioidei and Caulophrynidae, one independent evolutionary event of bioluminescent luring in Ceratoideo, two independent evolutionary events of chemical attractant luring in *Antennarius striatus* and Ogcocephaloideo, and a single event of the luring apparatus found in Neoceratidae. Lure total length to standard length ratios from smallest to largest include Chaunacoideo 0.047, Antennarioideo 0.186, Lophioideo 0.208, and Ceratoideo 0.443, indicating deep-sea pelagic anglerfishes have the highest lure to standard length ratios. Chapter 3 continues the investigation of habitat impacts on Lophioidei to investigate body shape changes and lure ranges. A geometric morphometric analysis is performed on the same taxa used in Chapter 2, while also measuring luring ranges in degrees based on videos and photos as a reference to set parameters for the radial range of which these fishes can move their lures. We found the luring ranges to be highly variable across Lophioidei with lateral body shapes exhibiting significant disparities between chemical lures compared to bioluminescent lures (P value: 0.064) and mechanical lures (P value: 0.069). Body shape disparities were also found between Bathypelagic and Abyssopelagic anglers and between the Ceratoideo compared to Lophioideo (P value: 0.034), Antennarioideo (P value: 0.001), and Ogcocephaloideo (P value: 0.020).

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Chapter I

Evolution of Lophioidei Using a Total Evidence Phylogenetic Approach

Introduction

Lophioidei (anglerfishes and their allies) are predatory fishes with morphologically unique taxa found in multiple habitats from benthic in-shore, deep-shelf drop-offs, and meso- and bathypelagic waters. Anglerfishes have captivated the imagination of the public and scientists as nightmares of the deep since their initial discovery in 1833 (Waterman, 1939). The suborder is distinguished by modifications to their first dorsal fin spine used as a lure (pterygiophore, illcium, and escae) that have fleshy mechanical, chemical, or bioluminescent escae to lure prey to their gaping mouths. In this thesis, we are following the classification of fishes established by Davis et al. (2016) and Smith et al. (2016), with the anglerfish clade being recognized as the suborder Lophioidei within the order Acanthuriformes. Lophioidei clades that have often been recognized as suborders in other studies (Hart et al., 2022) are recognized as infraorders herein. Currently, the suborder Lophioidei consists of 408 living species (Fricke et al., 2023) distributed throughout 74 genera and 18 families within 5 infraorders: Lophioideo (goosefishes and monkfishes, 30 species), Antennarioideo (frogfishes, 69 species), Ogcocephaloideo (batfishes, 98 species), Chaunacoideo (coffinfishes, 33 species), and Ceratioideo (deep-sea anglerfishes, 178 species) (Miya et al., 2010; Arnold and Pietsch, 2012; Chanet et al., 2013).

Interrelationships of Lophioidei

In the initial attempt to place the anglerfishes (Lophioidei) (see Figure 1.1) within the fish tree-of-life, then-known lophioid, antennarioid, and ogcocephaloid fishes were placed together with then-known batrachoidid fishes based on their “pseudo-feet” pectoral fins in a classification named “acanthoptérygiens à pectorales pédiculée”. This classification originated in Cuviers second edition of *Le Règne Animal* (Cuvier and Valenciennes, 1837) and translated to "acanthopterygii with pedunculated pectorals". Günther (1861) would simplify the name of this classification into Pediculati while still inferring these relationships.

Pediculati and its relationships of Batrachoidiformes and Lophioidei would be supported by numerous studies based on morphological data (Valenciennes, 1837; Cope, 1872; Jordan and Evermann, 1898; Jordan and Sindo, 1902; Boulenger, 1904; Jordan, 1905; Regan, 1912; Eaton et al., 1954). Regan (1926) would note that similarities found in the pectoral arch of the Batrachoidiformes and Lophioidei could not outweigh differences in other osteological characters found between the two lineages resulting in the separate of these two groups, while still emphasizing a sister group relationship between the two. This relationship would be supported by future studies (Regan and Trewavas, 1932; Gregory, 1933; Gregory and Conrad, 1936; Berg, 1940; Eaton et al., 1954; Monod, 1960; Greenwood et al., 1966; Rosen and Patterson, 1969). Greenwood et al. (1966) classified Lophioidei and the Batrachoidiformes together under the superorder Paracanthopterygii, which also included the orders Gobiesociformes (clingfishes), Percopsiformes (cavefishes), and Gadiformes (cods). Patterson and Rosen (1989) would continue to support the hypothesized sister group relationship between Lophioidei and Batrachoidiformes while citing new evidence from the dorsal gill-arch skeleton.

Pietsch and others continued the work studying the interrelationships of Lophioidei as well as the intrarelationships of the order itself using morphological (Pietsch, 1981, 1984; Pietsch and Grobecker, 1987; Pietsch and Orr, 2007) and mitochondrial genetic data (Miya et al., 2010). Miya et al. (2003) and Miya et al. (2010) would use mitochondrial genomic data to investigate multiple fish lineages including the Lophioidei. Their work included six Lophioidei taxa that were monophyletic within Percomorpha, nested as sister group to the Tetraodontiformes, Zeiformes, and Perciformes (Miya et al., 2003) rather than a direct sister group with Batracoidiformes. Miya et al. (2005) would use mitochondrial genomic data to investigate the placement of the Batrachoidiformes and found the toadfishes to be nested in a percomorph clade with the Synbranchiformes, then sister group to a clade consisting of Lophioidei, Tetraodontoidei, and other Acanthuriformes.

The current hypothesis concerning the interrelationships of the anglerfishes indicates a sister group relationship between Lophioidei to the Tetraodontoidei (pufferfishes and allies), nested in the Acanthuriformes supported by predominantly genetic data-based phylogenetic studies (Miya et al., 2003; Miya et al., 2010; Davis et al., 2016; Hart et al., 2022). Nearly all molecular phylogenetic reconstructions support a deeply nested suborder of Lophioidei in Acanthuriformes with a close relationship to the Tetraodontoidei (Yamanoue et al., 2007; Yagishita et al., 2009; Near et al., 2012; Davis et al., 2016; Mirande; 2016; Rabosky et al., 2018) using both mitochondrial and nuclear data. While genetic datasets used for phylogenetic analyses would provide resolution in the relationships between Lophioidei and other spiny-rayed fishes, there remain inconsistencies in the intraspecific relationships within the suborder among morphological, mitochondrial, and nuclear gene datasets (Shedlock et al., 2004; Pietsch and Orr, 2007; Miya et al., 2010; Mirande, 2016; Rabosky et al., 2018; Hart et al., 2022) (see Figure 1.2).

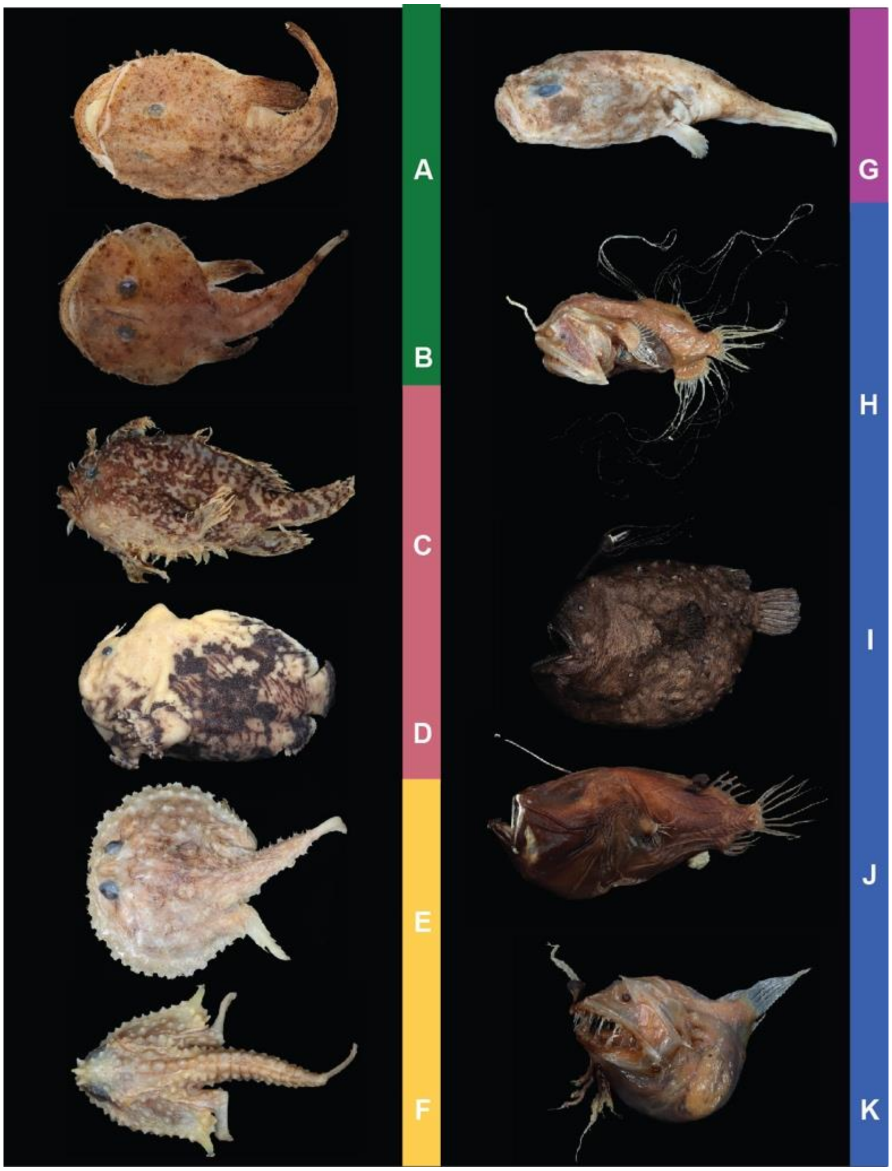
Hart et al. (2022) (see Figure 1.2) investigated the relationships of Lophioidei using ultraconserved elements, regions of the genome that are highly conserved among distant taxa. Their results inferred Tetraodontoidei as the sister group to the Lophioidei. Within Lophioidei, Lophioideo was inferred as the stem lineage and the sister group to a large clade that includes a clade of Ogcocephaloideo and Antennarioideo and a clade composed of Chaunacoidei and Ceratoideo (see Figure 1.2). Their phylogenetic hypothesis disagreed with most if not all prior hypotheses of the infraorders infraorders of Lophioidei. Their taxonomic sampling was predominantly focused on frogfishes (>75% Antennarioideo) and they proposed three new families of frogfishes including Histiophrynidae, Rhycheridae, and Tathicarpidae.

Intrarelationships of Lophioidei

Lophioideo (monkfishes and goosefishes) (see Figure 1.1) are bathydemersal and can range from inshore to up to 1000 meters deep. These fishes are dorsally compressed with broad heads and equally wide mouths. These fishes are ambush predators with cryptic color patterns and tassels on their mouths to break up their shape to avoid being detected by prey. The monkfishes are among the only anglerfishes that are commercially eaten, and their taste is compared to lobster meat. A single-family, Lophiidae, comprises the infraorder, encompassing 4 genera (Pietsch and Grobecker, 1987). This grouping has traditionally been monophyletic and is typically presented as the stem infraorder for the suborder (Regan, 1912; Pietsch, 1981; Pietsch and Grobecker, 1987; Miya et al., 2010; Mirande, 2016; Hart et al., 2022) with few exceptions (Shedlock et al., 2004) (Figure 1.2).

Figure 1.1.

Images of representative anglerfish (Lophioidei) taxa from the Natural History Museum of Los Angeles County.

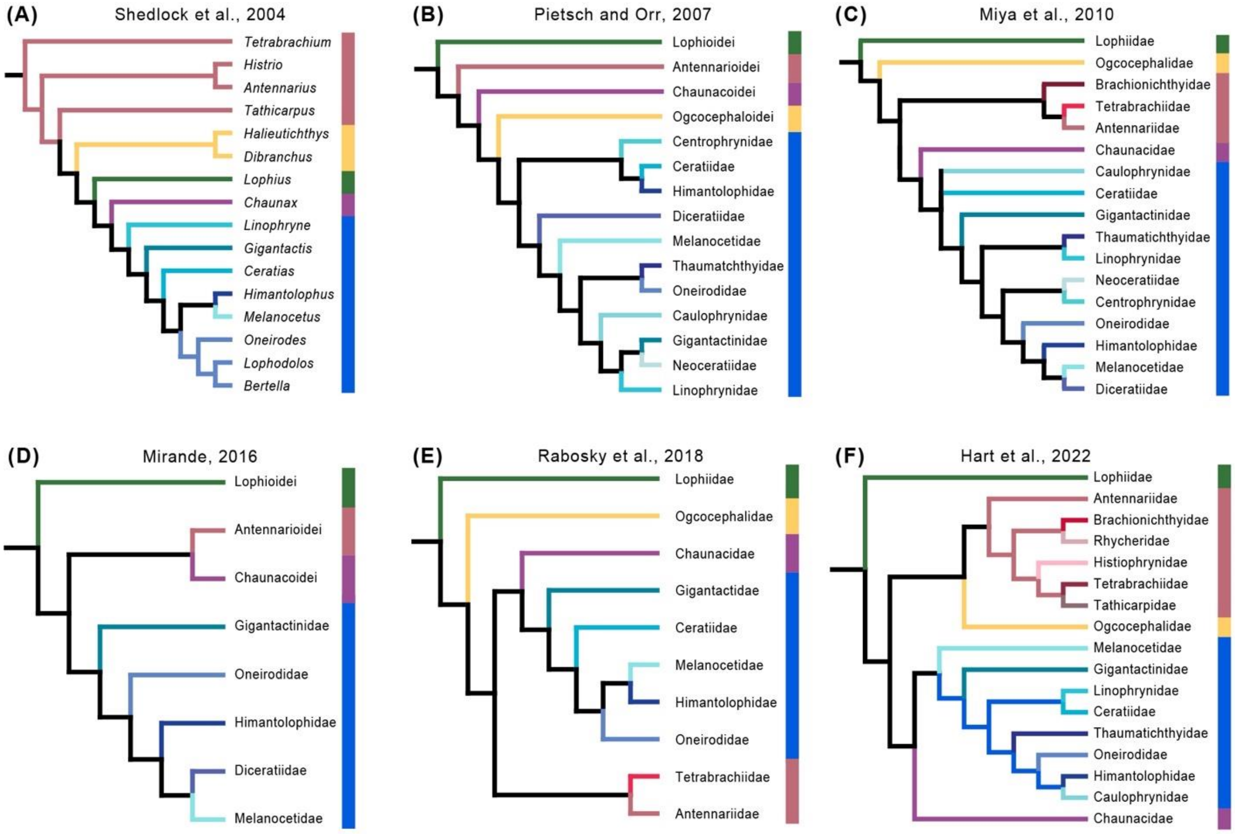


Note. Colors associated with phylogenetic tree (see Figure 1.3, 1.4, and 1.5). Lophoideo: (A) *Lophius americanus*, 251 mm SL, LACM 34328-1. (B) *Lophiomus setigerus*, 67 mm SL, LACM 44743-7. Antennarioideo: (C) *Histrio histrio*, 138 mm SL, LACM 8975-1. (D) *Antennatus strigatus*, 81 mm SL, LACM 20677. Ogcocephaloideo: (E) *Halieutaea fitzsimonsi*, 168 mm SL, LACM 44745-6. (F) *Malthopsis mitrigera*, 72 mm SL, LACM_56294-1. Chaunacoideo: (G) *Chaunax* sp., 158 mm, LACM_44750-3. Ceratoideo: (H) *Caulophryne polynema*, 131 mm SL, LACM 33923-1. (I) *Himantolophus sagamius*, 348 mm SL, LACM 60082-1. (J) *Cryptosaras couesi*, 175 mm SL, LACM 11231-1. (K) *Linophryne densiramus*, 60 mm SL, LACM_38440-1.

Antennarioideo (frogfishes) (see Figure 1.1) occupy benthic ranges from inshore and moderately deep waters. Laterally compressed with a corpulent build, most taxa have unique coloration patterns and/or modifications to their appearance allow for them to be cryptically hidden in a variety of concealed positions to ambush their prey, even going so far as allowing algae and sponges to grow on them to better blend in with their surroundings. There are seven recognized families in the infraorder Antennarioideo; Antennariidae, Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae comprised of 23 genera (Hart et al., 2022). Regan's (1912) cladistic analysis produced a paraphyletic relationship of Antennarioideo comprised of six families: Antennariidae, Tetrabrachiidae, Lophichthyidae, Brachionichthyidae, Chaunacidae, and Ogcocephalide. Pietsch (1984) contested this arrangement and produced a revised cladogram that restricted the infraorder to four families: Antennariidae, Tetrabrachiidae, Lophichthyidae, and Brachionichthyidae. This placement had Antennariidae as the sister group to Tetrabrachiidae, together being a sister group to Lophichthyidae, and the three together being a sister group to Brachionichthyidae. Miya et al. (2010) mitochondrial genomic analysis resulted in a relationship of Brachionichthyidae as the sister group to Tetrabrachiidae and Antennariidae (see Figure 1.2). Shedlock et al. (2004) recovered *Tetrabrachium* as the sister group to *Antennarius* and *Histrio*, this clade then sister group to *Tathicarpus* noting a failed 5% threshold chi-square test for nucleotide composition for *Tetrabrachium* for base composition between the three species (see Figure 1.2).

Figure 1.2.

Prior phylogenetic hypotheses of family and infraorder relationships of anglerfishes (Lophioidei).



Note. Phylogenetic hypotheses based on mitochondrial rRNA genes (A), morphology (B), mitochondrial genomes (C), mitochondria and nuclear DNA with morphology (D), and mitochondrial and nuclear DNA.

Ogcocephaloideo (batfishes) (see Figure 1.1) are found in benthic shallow to deep-water habitats and are dorsoventrally flattened with some species possessing an elongated upturned snout. Some batfishes have been hypothesized to produce a chemical attractant through their esca to increase prey attraction (Nagareda and Shenker, 2009). A single family, Ogcocephalidae, comprises the infaorder with 10 genera (Pietsch and Grobecker, 1987). The infraorder has typically been monophyletic, but relationship between Lophioidei infraorders has varied. Shedlock et al. (2004) placed ogcocephaloids as the closest sister group to lophoids, which then are sister groups to Ceratioideo (see Figure 1.2). Pietsch and Orr (2007) hypothesized Ogcocephaloideo as the sister group to Ceratioideo based strictly on morphometric characters (see Figure 1.2). Miya et al. (2010) inferred ogcocephaloids as the sister group to Antennarioideo, with that clade the sister group to Chaunacoideo based on mitochondrial genomic data (see Figure 1.2).

Chaunacoideo (coffinfishes) (see Figure 1.1) are globular benthic fishes found in on the continental shelf and deep-water ranges. Chaunacoid fishes have been documented to have specializations to their gills to increase the water intake to increase body volume by 30% as a hypothesized means of reducing energetic demands when swimming and predator evasion (Long and Farina, 2019) and are typically red or orange in coloration. A single family, Chaunacidae, comprises the infraorder, with two genera (Pietsch and Grobecker, 1987). The infraorder has typically been monophyletic, but its placement in Lophioidei has varied. In Miya et al. (2010), ogcocephaloids and antennarids had a sister group relationship to chaunacids based on mitochondrial genomic data (see Figure 1.2). Mirande (2016) had a direct sister group relationship between Chaunacids and Antennarids and together being sister group to Ceratioideo based on nuclear and mitochondrial DNA combined with morphological characters (see Figure 1.2). Other studies (Shedlock et al., 2004; Miya et al., 2010) inferred Chaunacoideo as the sister group to Ceratioideo based on mitochondrial DNA and mitochondrial genomes (see Figure 1.2).

Ceratioideo (deep-sea anglerfishes) (see Figure 1.1) are deep-sea (below 300m) pelagic and bathydemersal that are known for extreme sexual dimorphism in size between females and males in some lineages. Typically, the anglerfish females possess bacterial bioluminescent escae (Pietsch and Orr, 2007; Davis et al., 2016) with the family Linophrynidae possessing both intrinsic bioluminescent chin barbels in combination with a bacterial bioluminescent esca. Anglerfish males exhibit either a temporary, obligate, or facultative parasitic relationship with the females where they become fused with integrated blood systems with the female. The males gain motility, blood-transferred nutrients, and genetic exchange opportunities in return for the female to gain fertilization. The infraorder is comprised of eleven families; Caulophrynidae, Neoceratidae, Melanocetidae, Himantolophidae, Diceratiidae, Oneirodidae, Thaumatichthyidae, Centrophrynidae, Ceratiidae, Gigantactinidae, and Linophrynidae encompassing over 35 genera and are the most species rich taxonomic suborder with 311 currently recognized taxa (Fricke et al., 2023). The intra-ordinal relationships of this infraorder have lacked consistency, but it's clear that Ceratoideo is the crown infraorder of Lophioidei in most phylogenetic hypotheses (Shedlock et al., 2004; Pietsch and Orr, 2007; Miya et al., 2010; Mirande, 2016) (see Figure 1.2). There is little to no consistency in the intrarelationships among families within the infraorder (Shedlock et al., 2004; Pietsch and Orr, 2007; Miya et al., 2010; Mirande, 2016; Rabosky et al., 2018; Hart et al., 2022) (see Figure 1.2).

To date, no total evidence hypothesizes relationships for Lophioidei have been estimated, and in this study, we combine genome-scale nuclear (ultraconserved elements) and mitochondrial data with previously published morphological characters to infer the evolutionary relationships of anglerfishes (Lophiodei). Ultraconserved elements (UCEs) are regions of the genome that are highly conserved among distant taxa including most vertebrate genomes (Faircloth et al., 2012, Bejerano et al., 2004; Siepel et al., 2005). UCEs have been used to infer phylogenetic relationships across several lineages of organisms (e.g., Crawford et al., 2012; McCormack et al., 2012; Faircloth et al., 2012; Smith et al., 2013; Sun et al., 2014) and in fishes (Faircloth et al., 2013; Gilbert et al., 2015: Harrington et al., 2016; Longo et al., 2017; Martin et al., 2018). UCE cores and flank regions have been demonstrated to produce more resolution in inferring clades compared to traditional multi-locus gene fragment datasets for resolving phylogenetic relationships in percomorph fishes, with a nearly 10-fold increase for UCE cores and 100-fold for UCE flanks (Gilbert et al., 2015).

Modern phylogenetic studies have sought to clarify the evolutionary relationships of Lophioidei, but there remains discrepancies and inconsistencies between these studies that rely on morphological, genetic, and combined datasets. The relationships of Lophioidei requires further work and data. In this study, we use a total evidence approach (Davis, 2010; Martin et al., 2018; Girard et al., 2020) using genetic and morphological data to infer the evolutionary relationships of this captivating taxonomic group. Our study aims to test the monophyly of the currently recognized lophioid infraorders, families, and genera. We combine morphological data from Pietsch and Orr (2007), UCE sequence data, and mitochondrial DNA to produce a phylogenetic hypothesis of Lophioidei to investigate these specific questions: (1) What is the sister group to the anglerfishes (Lophioideo)? (2) What are the evolutionary relationships of the infraorders (Lophioideo, Antennarioideo, Ogcocephaloideo, Chaunacoideo, and Ceratoideo)?

(3) What are the family relationships of the frogfishes (Antennarioideo) and the deep-sea anglerfishes (Ceratoideo)?

Materials and Methods

Taxonomic Sampling

Taxonomic sampling included all families and most genera within the suborder Lophiodei covering the five suborders: Antennarioideo, Ogcocephaloideo, Lophioideo, Chaunacoideo, and Ceratoideo. For the ultraconserved element (UCE) only dataset, A total of 35 species were included with 13 outgroups and 22 anglerfishes representing 14 genera and all infraorders. Outgroups for the UCE data consisted of thirteen Acanthuriformes genera. The genus *Morone* was included as a stem representative of the order Acanthuriformes as inferred in other studies focused on the evolutionary relationships of ray-finned fishes (Near et al., 2012; Smith et al., 2016; Davis et al., 2016) and this genus was included as the outgroup root. To increase the number of anglerfish genera and species, a UCE+Mitochondrial genome dataset was assembled that included previously published mitochondrial genomes were acquired from GenBank (Table 1.1) and supplemented with newly collected mitochondrial genomes using the program MitoFinder (Allio et al., 2020) on newly sequenced taxa. This data brings the total number of included anglerfish genera to 59 for this dataset. Finally, A total evidence phylogenetic hypothesis of relationships consisted of ultraconserved elements (UCEs), mitochondrial genomes, and the 88 morphological characters from Pietsch and Orr (2007).

DNA Extraction

DNA extractions were taken from muscular tissue samples or fin clips of 35 species (22 anglerfish species, 13 outgroup species) using the Maxwell RSC Instrument with Promega Blood Kit (AS1400) following the manufacturer’s protocol. When necessary, multiple samples were combined using a Thermo Fisher SpeedVac Concentrator to a 102 µl volume. A Qubit fluorometer was used to quantify each template using the dsDNA BR Assay kit following the manufacturer's protocol. Following quantification, the samples were sent to Arbor Biosciences (Ann Arbor, MI) at a 100 µl volume for sequencing.

Ultraconserved Element Amplification, Sequencing, and Assembly

UCE quantified extraction samples were sent to Arbor Biosciences for library preparations, target capture (actinopterygian UCE probe set; Faircloth et al., 2013), and sequencing (Illumina HiSeq 2500). The UCE data was received in a Fastq file format. The Fastq data that included sequences from multiple runs was cleaned of indices and adapters using illumiprocessor and trimmomatic. Once cleaned, the reads were assembled into contigs using SPADES. UCE loci were identified for each species using the actinopterygian probe set (Faircloth et al., 2013) in combination with the software LASTZ v1.02.00 (Harris, 2007) set at 80% minimum coverage and 80% minimum identity for finding UCEs. PHYLUCE v1.7.2 (Faircloth et al., 2012) was used to create a database of UCE loci by taxon and then to construct FASTA files of the UCE data. The extracted UCE data was aligned with MAFFT with a data matrix that included only contigs found in at least 65% of the included taxa. For the 35 taxa that were sampled for UCEs, a total of 462 aligned UCE fragments were concatenated for a total length of 302,543 bps. Sequence fragment lengths ranged from 100-1400 bps. The combined dataset for UCE fragments and mitochondrial genomes included 90 taxa and 334197 base pairs.

Mitochondrial Genome Extraction from Genome-scale Data

Following the extraction of our UCEs, we also used MitoFinder (Allio et al., 2020) to extract mitogenomes from the rawfasq DNA sequence files for anglerfishes that did not have previously published mitochondrial genome data available on genbank. Mitochondrial genome data procured from Genbank to be used in conjunction with the extracted mitochondrial genomic data is shown in Table 1.1.

Phylogenetic Analyses

The UCE data alone included 35 taxa and was partitioned to find the best model of molecular evolution using an entropy-based method (Sliding-Window Site Characteristics – Entropy Method, SWSC-EN; Tagliacollo and Lanfear, 2018). Each species-specific UCE loci is split into regions of left flanking, right flanking, and ultra-conserved core by rate of evolution. These UCE segments become the output for PartitionFinder v2.1.1 (Lanfear et al., 2014; Stamatakis, 2014; Lanfear et al., 2017) where the best-fitting nucleotide substitution model for each data partition is found. PartitionFinder2 uses selected models from AICc and the recluster search method (Lanfear et al., 2014) to assign models of molecular evolution. We additionally used PartitionFinder 2 to identify the best-fitting models of molecular evolution for the combined UCE and mitochondrial genome dataset that included a total of 90 taxa. In the combined dataset the UCE data was partitioned based on the entropy-based method into segments and the protein-coding gene fragments were partitioned by gene and codon position. PartitionFinder2 identified 389 subsets for the UCE only dataset and 390 for the combined dataset with the mitochondrial genome.

The UCE data alone included 35 taxa and the evolutionary relationships were inferred using Maximum likelihood in IQ-TREE v1.5 (Nguyen et al., 2015) applying the substitution models (identified from PartitionFinder2) assigned to each UCE segment (identified from SWSC-EN) . The phylogenetic analyses were analyzed independently for 20 replicates with the topology representing the maximum likelihood of those 20 replicates presented herein as the optimal hypothesis (Figure 1.3). The same procedure was applied to the concatenated UCE + mitochondrial genome dataset that included 90 taxa, 462 UCEs, and mitochondrial genome fragments (Figure 1.4). Finally, a combined total evidence dataset that was analyzed with the same procedure that included the UCE + mitochondrial genome + morphological dataset (Figure 1.5). Bootstrap replicates were also conducted 100 times for various datasets and are denoted on the nodes of the respective analyses.

Table 1.1.

Previously published mitochondrial genomes used in phylogenetic analysis (see Figures 1.4 and 1.5) and GenBank accession numbers.

Classification	Genus	Species	Genbank Accession Numbers
Suborder Lophioideo			
Family Lophiidae	*Lophius*	*americanus*	AP004414
	Lophiomus	*setigerus*	AP004413
	Lophoides	*caulinaris*	AB282826
	Sladenia	*gardineri*	AB282827
Suborder Antennarioideo			
Family Antennariidae	*Antennarius*	*striatus*	AB282828
	Antennarius	*coccineus*	AB282830
	Histrio	*histrio*	AB282829
	Histiophryne	*cryptacanthus*	
Family Brachionichthyidae	*Brachionichthys*	*hirsutus*	AB282832
Family Tetrabrachiidae	*Tetrabrachium*	*ocellatum*	AB282831
Suborder Ogcocephaloideo			
Family Ogcocephalidae	*Ogcocephalus*	*parvus*	
	Malthopsis	*jordani*	AP005978
	Halieutaea	*stellata*	AP005977
	Coelophrys	*brevicaudata*	AB282834
	Zalieutes	*elater*	AB282835
Suborder Chaunacoidei			
Family Chaunacidae	*Chaunax*	*abei*	AP004415
	Chaunax	*tosaensis*	AP004416
	Chaunax	*pictus*	AB282833
Suborder Ceratoidei			
Family Caulophrynidae	*Caulophryne*	*jordani*	AP004417
	Caulophryne	*pelagica*	AB282836
Family Centrophrynidae	*Centrophryne*	*spinulosus*	AB282850
Family Ceratiidae	*Ceratias*	*uranoscopus*	AB282851
	Cryptopsaras	*couseii*	AB282850
Family Diceratiidae	*Bufoceratias*	*thele*	AB282841
	Diceratias	*pileatus*	AB282842
Family Himantolophidae	*Himantolophus*	*albinares*	AB282839
	Himantolophus	*groenlandicus*	AB282840
Family Melanocetidae	*Melanocetus*	*johnsonii*	AB282838
	Melanocetus	*murrayi*	AP004418
Family Neoceratidae	*Neoceratias*	*spinifer*	AB282837
Family Oneirodidae	*Bertella*	*idomorpha*	AB282846
	Chaenophryne	*melanorhabdus*	AB282845
	Lasiognathus	*sp.*	AB282848
	Oneirodes	*thompsoni*	AB282843
	Puck	*pinnata*	AB282844
Family Thaumatichthyidae	*Thaumatichthys*	*pagidostomus*	AB282847

Note. Mitochondrial genomes extracted following UCE extraction are not listed.

Results

Interrelationships of Lophioidei within Acanthuriformes

To explore the phylogenetic placement of Lophioidei within Acanthuriformes, we conducted three different phylogenetic analyses including a UCE-only dataset, a UCE and mitochondrial genome dataset, and a total evidence dataset incorporating UCE, mitochondrial genomes, and morphological characters. Bootstrap values will be described in the following order throughout the results and discussion: **(A)** UCE only tree (see Figure 1.3), **(B)** UCE and mitochondrial genome tree (see Figure 1.4), and **(C)** total evidence tree consisting of UCE, mitochondrial genomes, and morphological characters (see Figure 1.5). Results from the maximum likelihood analysis of UCE-only data (see Figure 1.3), UCE and mitochondrial genome data (see Figure 1.4), and the total evidence dataset (see Figure 1.5), recovered a monophyletic Lophioidei clade in each analysis. All three analyses recovered Lophioidei as the sister group to Tetraodontoidei supported by a bootstrap value of **(A)** 99% **(B)** 97.94 **(C)** 100%. All three analyses recover a monophyletic Lophioidei as the sister group to Tetraodontoidei within Acanthuriformes, with Lophioidei+Tetraodontoidei sister to the boarfish *Antigonia* (Caproidae) supported by a bootstrap value of **(A)** 68% **(B)** 73.2% **(C)** 63.16%.

Intrarelationships of Lophioidei

All three analyses recovered evolutionary relationships among infraorders (see Figures 1.3, 1.4, and 1.5) including: Lophioideo as the stem infraorder sister group to a clade of Antennarioideo, Ogcocephaloideo, Chaunacoideo, and Ceratoideo supported by a bootstrap value of **(A)** 100%, **(B)** 98.25%, and **(C)** 98.95%. Antennarioideo and Ogcocephaloideo are a sister group supported by a bootstrap value of **(A)** 100%, **(B)** 97.94%, and **(C)** 98.95%. Antennarioideo and Ogcocephaloideo are sister group to a sister group clade of Chaunacoideo and Ceratoideo supported by a bootstrap value of **(A)** 100%, **(B)** 97.97%, and **(C)** 98.95%. Chaunacoideo and

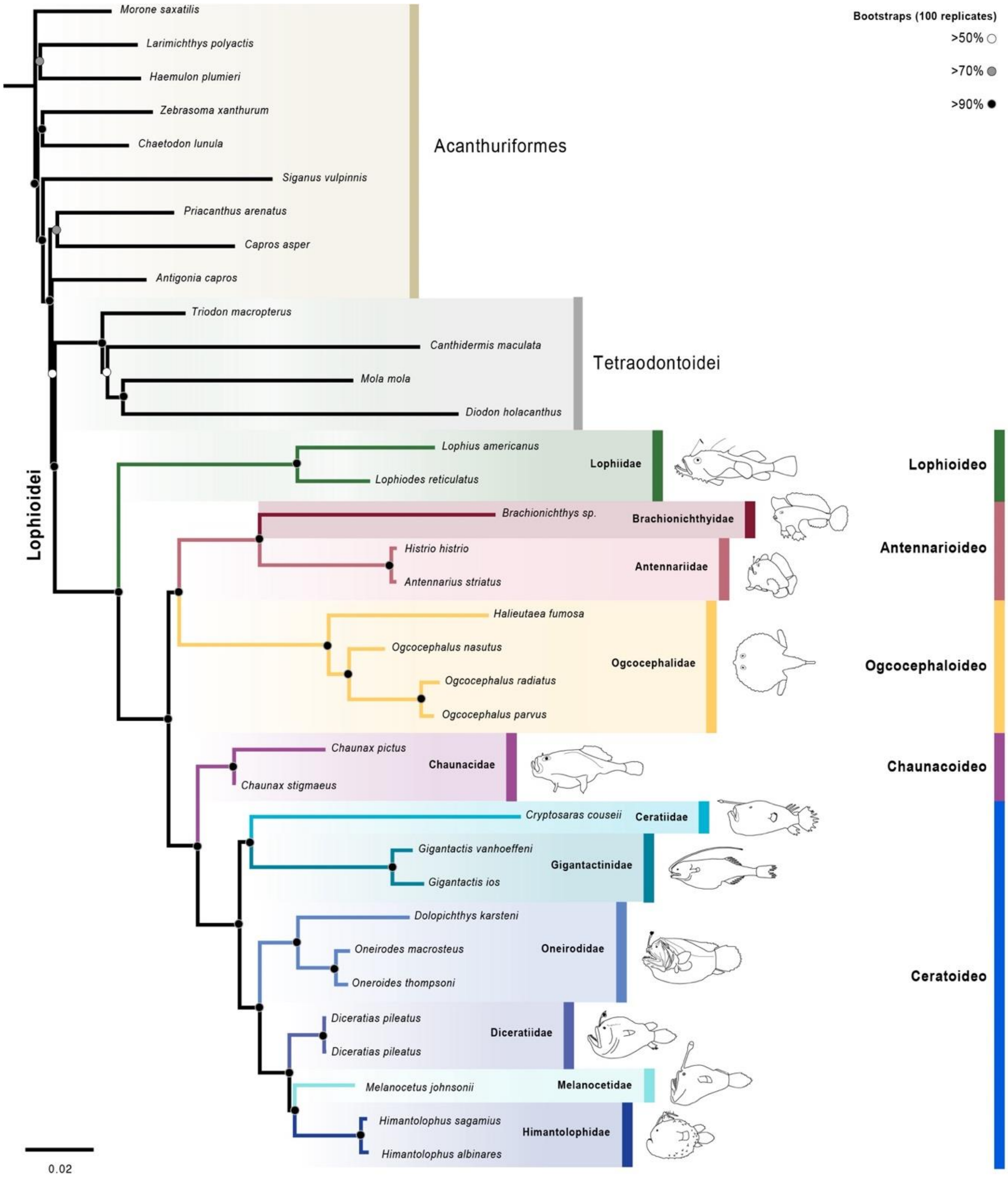
Ceratoideo are a sister group supported by a bootstrap value of **(A)** 100%, **(B)** 98.97%, and **(C)** 98.95%.

Lophioideo

The UCE analysis recovered a monophyletic Lophiidae with *Lophius* and *Lophiodes* as sister group (see Figure 1.3) supported by a bootstrap value of **(A)** 100% (see Figure 1.3). Within Lophioideo, the family Lophiidae is comprised of 4 genera inferring a monophyletic Lophiidae in the total evidence analysis and the combined UCE and mitochondrial genome data analysis(see Figure 1.4 and 1.5) that recovered a grouping of Lophiidae genera (*Sladenia* + (*Lophiomus* + (*Lophiodes* + (*Lophiodes* + *Lophius*)))) (see Figure 1.4 and 1.5). We recovered *Lophiodes* as paraphyletic. The monophyly of Lophoideo was supported by a bootstrap value of **(B)** 100% and **(C)** 100%.The infraorder Lophioideo was recovered as the sister group to a clade including Antennarioideo, Ogcocephaloideo, Chaunacoideo, and Ceratoideo supported by a bootstrap value of **(A)** 100%, **(B)** 98.25%, and **(C)** 98.95%.

Figure 1.3.

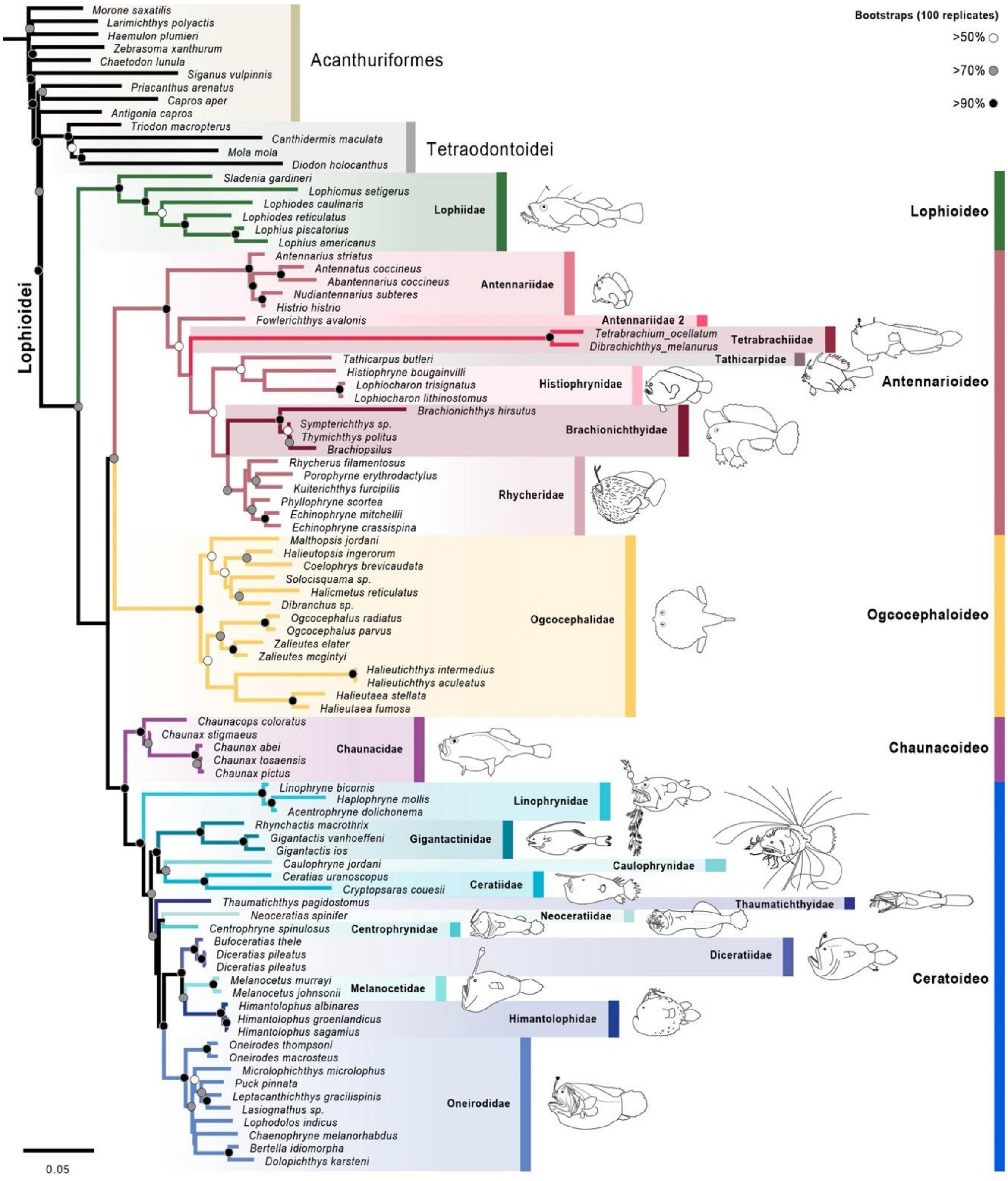
UCE maximum likelihood tree.



Note. Colored circles on nodes indicate bootstrap values as follows: White >50%, Grey >70%, Black >90% based on 100 replicates.

Figure 1.4.

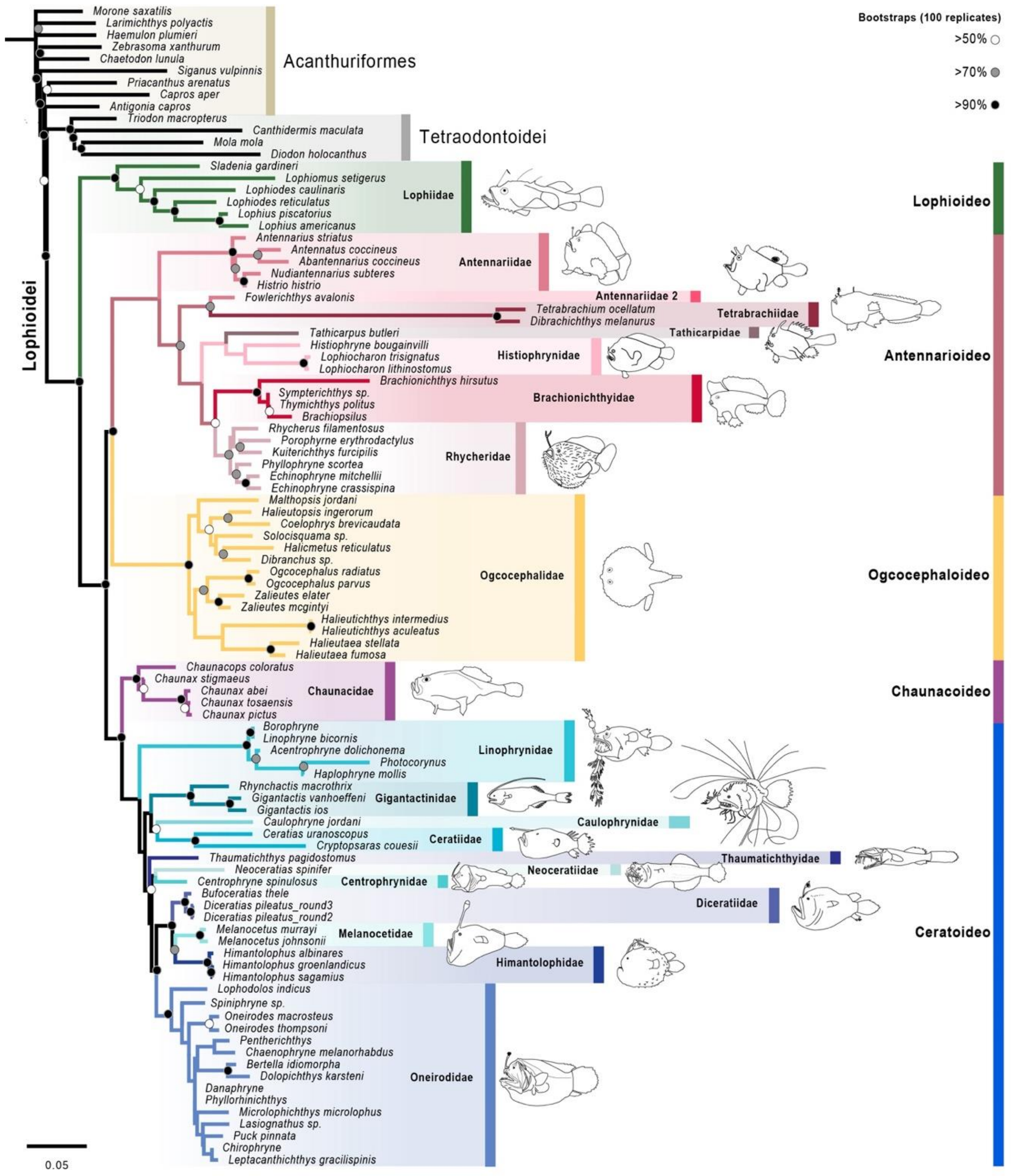
UCE and mitochondrial genome maximum likelihood tree.



Note. Colored circles on nodes indicate bootstrap values as follows: White >50%, Grey >70%, Black >90% based on 100 replicates.

Figure 1.5.

Total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data.



Note. Colored circles on nodes indicate bootstrap values as follows: White >50%, Grey >70%, Black >90% based on 100 replicates.

Antennarioideo

In the UCE-only tree (see Figure 1.3), we recovered a monophyletic Antennarioideo with Batrachionichthyidae and Antennariidae (*Antennarius* and *Histrio*) being sister groups supported by a bootstrap value of **(A)** 100% (see Figure 1.3). The total evidence analysis and the combined UCE and mitochondrial genome data analysis recovered a Antennarioideo grouping of (Antennariidae + ((Antennariidae 2 + Tetrabrachiidae) + ((Tathicarpidae + Histiophrynidae) + (Brachionichthyidae + Rhycheridae)))). The monophyly of Antennarioideo was supported by a bootstrap value of **(B)** 98.25% and **(C)** 100%.

Within Antennaroideo, the family Antennariidae is comprised of 6 genera and infers a paraphyletic Antennariidae. In the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figures 1.4 and 1.5) we recovered a grouping of Antennariidae genera (*Antennarius* + *((Anennatus* + *Abantennarius)* + *(Nudiantennarius* + *Histro)))*. This family is supported by a bootstrap value of **(A)** 100% **(B)** 100% and **(C)** 100%. Group 2 of Antennariidae consisting of *Fowlerichthys* as the stem genera sister group to Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae.

The monophyletic family Tetrabrachiidae is comprised of 2 genera. This monophyly is recovered in the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figures 1.4 and 1.5) and is supported by a bootstrap value of **(B)** 100% and **(C)** 100%. Tetrabrachiidae is sister group to Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae and is supported by a bootstrap value of **(B)** 34.02%, and **(C)** 31.58%.

The monotypic family Tathicarpidae consisting of *Tathicarpus* is sister group to Histiophrynidae recovered in the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figures 1.4 and 1.5) and is supported by a bootstrap value of **(B)** 53.61% and **(C)** 45.26%. The total evidence analysis and the combined UCE and mitochondrial genome data analysis recovered a monophyletic Histiophrynidae that is comprised of 2 genera of *Histiophryne* and *Lophiocharon* (see Figure 1.4 and 1.5). Tathicarpidae and Histiophrynidae are sister group to Brachionichthyidae and Rhycheridae and is supported by a bootstrap value of **(B)** 52.58%, and **(C)** 40%.

Brachionichthyidae and Rhycheridae were recovered as sister group in the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) and is supported by a bootstrap value of **(B)** 37.11% and **(C)** 53.68%. Brachionichthyidae was recovered as monophyletic and comprised of 4 genera. The monophyly of Brachionichthyidae is supported by a bootstrap value of **(B)** 100% and **(C)** 97.89%. In the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) we recovered a grouping of Brachionichthyidae genera (*Brachionichthys* + (*Sympterichthys* + (*Thymichthys* + *Brachiopsilus*))).

Rhycheridae, the sister family to Brachionichthyidae, is recovered as monophyletic in the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) and is supported by a bootstrap value of **(B)** 86.60% and **(C)** 83.16%. These analyses recovered a grouping of Rhycheridae genera (Rhycherus + ((Porophryne + Kuiterichthys) + (Phyllophryne + Echinophryne))).

Ogcocephaloideo:

Within Ogcocephaloideo, the monophyly of the family Ogcocephalidae was supported by all three analyses with by a bootstrap value of **(A)** 100%, **(B)** 100%, and **(C)** 98.95%. In all three analyses, the infraorder Ogcocephaloideo was recovered as the sister group to Antennarioideo supported by a bootstrap value of **(A)** 100%, **(B)** 98.25%, and **(C)** 98.95%(see

Figures 1.3, 1.4, and 1.5). In the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) recovered 10 genera in Ogcocephalidae. These analyses recovered a grouping of Ogcocephalidae genera (Malthopsis + ((Halieutopsis + Coelophrys) + (Solocisquama + (Halicmetus + Dibranchus))) + (Ogcocephalus + Zalieutes) + (Halieutichthys + Halieutaea).

Chaunacoideo:

Within Chaunacoideo, the monophyly of the family Chaunacidae is supported by all three analyses and is supported by a bootstrap value of **(A)(B)(C)** 100%. The monophyletic family Chaunacidae is comprised of two genera *Chaunacops* and *Chaunax*. The infraorder is the sister group to Ceratoideo supported by a bootstrap value of **(A)(B)(C)** 100%.

Ceratoideo

The UCE analysis recovered a Ceratoideo comprised of 6 families (Ceratiidae, Gigantactinidae, Oneirodidae, Diceratiidae, Melanocetidae, and Himantolophidae) (see Figure 1.3). The monophyly of the infraorder Ceratoideo is supported by the UCE analysis and is supported by a bootstrap value of **(A)** 100%. The UCE analysis recovered a grouping of Ceratoideo families (Ceratiidae + Gigantactinidae) + (Oneirodidae + (Diceratiidae + (Melanocetidae + Himantolophidae)). The total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) recovered a monophyletic Ceratoideo comprised of 11 families (Linophrynidae, Gigantactinidae, Caulophrynidae, Ceratiidae, Thaumatichthyidae, Neoceratidae, Centrophrynidae, Diceratiidae, Melanocetidae, Himantolophidae, and Oneirodidae). The monophyly of the infraorder Ceratoideo is supported by the total evidence analysis and the combined UCE and mitochondrial genome data analysis and is supported by a bootstrap value of **(B)** 98.97% and **(C)** 100%. The total evidence analysis and the combined UCE and mitochondrial genome data analysis recovered a grouping of Ceratoideo families (Linophrynidae + ((Gigantactinidae + (Caulophrynidae + Ceratiidae)) + (Thaumatichthyidae + ((Neoceratidae + Centrophrynidae) + ((Diceratiidae + (Melanocetidae + Himantolophidae)) + Oneirodidae))).

The relationships of Ceratoideo families and their genera recovered in the total evidence analysis and the combined UCE and mitochondrial genome data analysis (see Figure 1.4 and 1.5) are listed below.

Linophrynidae: A clade of *Borophryne* and *Linophryne* is the sister group to a clade including *Acentrophryne*, and *Photocorynus* + *Haplophryne*.

Gigantactinidae: *Rhynachactis* and *Gigantactis* were found to be sister groups.

Caulophrynidae: The family is only represented by a single genus, *Caulophryne* which was recovered as monophyletic.

Ceratiidae: *Ceratias* and *Cryptopsaras* were found to be sister groups.

Thaumatichthyidae: The family is only represented by a single genus, *Thaumatichthys* which was recovered as monophyletic. *Lasiognathus* was recovered not in Thaumatichthyidae but rather Oneirodidae.

Neoceratidae: The family is only represented by a single genus, *Neoceratias* which was recovered as monophyletic.

Centrophrynidae: The family is only represented by a single genus, *Centrophryne* which was recovered as monophyletic.

Diceratiidae: *Bufoceratias* and *Diceratias* were found to be sister groups.

Melanocetidae: The family is only represented by a single genus, *Melanocetus* which was recovered as monophyletic.

Himantolophidae: The family is only represented by a single genus, *Himantolophus* which was recovered as monophyletic.

Oneirodidae: *Lophodolos* is the stem genus of the family which is then sister group to *Spiniphryne*. *Spiniphryne* is the sister group to *Oneirodes,* which is the sister group to a clade consisting of (*Pentherichthys* + *Chaenophryne) + (Bertella* + *Dolopichthys)* + *(Danaphryne* + *Phyllorhinichtys)* + (*Microlophichthys* + (*Lasiognathus* + (*Puck* + (*Chirophryne* + *Leptacanthichthys*). *Pentherichthys* and *Chaenophryne* are sister groups and form a clade that is sister group with the clade containing *Bertella* and *Dolophichthys*. These four genera form a clade that is sister group to a clade with (*Danaphryne* + *Phyllorhinichthys*) and (*Microlophichthys* + (*Lasiognathus* + (*Puck* + (*Chirophryne* + *Leptacanthichthys*). *Microlopichthys* has a sister group relationship with *Lasiognathus* that was recovered in Oneirodidae rather than Thaumatichthyidae. *Lasiognathus* is sister group to *Puck*, which is sister group to *Chirophryne* and *Leptacanthichthys*.

Discussion

Interrelationships of Lophioidei within Acanthuriformes

Our total evidence analysis combining morphological data from (Pietsch and Orr, 2007), mitochondrial genomes, and UCE nuclear data inferred a monophyletic Lophioidei (see Figures 1.3, 1.4 and 1.5) is consistent with the following recent phylogenetic studies that included molecular data (Yamanoue et al., 2007; Yagishita et al., 2009; Miya et al., 2010; Near et al., 2012; Davis et al., 2016; Mirande, 2016; Rabosky et al., 2018; Hart et al., 2022). The suborder Lophioidei was inferred to be the sister group to the Tetraodontoidei (pufferfishes and allies) nested in the order Acanthuriformes.

Intrarelationships of Lophiodei

The total evidence phylogenetic analysis included taxonomic representatives from all 5 infraorders of Lophioidei (see Figure 1.5). This stem placement of the monkfishes (Lophiodeo) within Lophioidei in our analyses (see Figures 1.3, 1.4, and 1.5) is convergent with morphological studies including Pietsch and Orr (2007). Research utilizing genetic data including Miya et al. (2010), Mirande (2016), Rabosky et al. (2018), and Hart et al. (2022) recovered this placement as well. Shedlock et al. (2004) in their usage of rRNA 16s genes did not recover this placement but instead recovered Antennariidae as the stem lineage of Lophioidei. The recovery of a direct sister group relationship between (Antennaroideo) and the batfishes (Ogcocephaloideo) (see Figure 1.5) is only convergent with Hart et al. (2022) that also used UCE datasets. Typically, the relationship between (Antennarioideo) and the batfishes (Ogcocephaloideo) is recovered in a stepwise fashion (Shedlock et al., 2004; Miya et al, 2010). The clade consisting of Antennarioideo and Ogcocephaloideo is sister group to a clade of coffinfishes (Chaunacoideo) and deep-sea anglerfishes (Ceratoideo). The clade of coffinfishes (Chaunacoideo) and deep-sea anglerfishes (Ceratoideo) has also been recovered by Shedlock et al. (2004), Miya et al. (2010), Rabosky et al. (2018), and Hart et al., 2022.

The following morphological character support of Lophioideo infraorders is derived from Pietsch and Orr (2007). All morphological character descriptions and numbers are directly associated with the morphological matrix as examined by Pietsch and Orr (2007) but with optimizations on the most likely tree from the total evidence analysis in this study. Our analysis indicates Lophioideo as the stem infraorder of Lophioidei as found in Pietsch and Grobecker (1987), Pietsch and Orr (2007), Miya et al. (2010), Mirande (2016), Rabosky et al. (2018) (see Figure 1.2) which is inferred across all three analyses (see Figure 1.3, 1.4, and 1.5). The monophyly of Lophioideo is supported by morphological characters including: the absence of a well-developed supraethmoid **(1)**, also convergent in Gigantactinidae, Thaumatichthyidae, and *Lasognathus*; eight caudal-fin rays **(52)** also convergent in *Caulophryne* and *Cryptopsaras*. Our taxonomic sampling included all recognized genera in Lophiidae and we inferred a monophyletic family. *Lophiodes* was found to be paraphyletic which could result from a lack of taxon coverage for the genus and requires further investigation.

We recovered a monophyletic Antennarioideo with the taxa coverage of 20 out of 21 genera which includes family representatives from Antennariidae, Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, Rhycheridae Tetrabrachiidae, and Brachionichthyidae. Hart et al. (2022) recently described Tathicarpidae, Histiophrynidae, and Rhycheridae as new families of the Antennarioideo and the results of our total evidence analysis and the combined UCE and mitochondrial genome data analysis support the monophyly of these families. Hart et al. (2022) recovered Antennariidae as sister group to Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae (see Figure 1.2). The total evidence analysis and the combined UCE and mitochondrial genome data analysis recovered a sister group relationship between Brachionichthyidae and Rhycheridae as recovered by Hart et al. (2022), but our analyses did not recover Tetrabrachiidae as sister group to Tathicarpidae, instead *Fowlerichthys* (Antennariidae Group 2) and was instead recovered as the sistergroup to Tetrabrachiidae (see Figure 1.4 and 1.5) indicating a paraphyletic Antennariidae. It is likely that *Fowlerichthys* will be placed in its own family. In the total evidence analysis and the combined UCE and mitochondrial genome data analysis Tathicarpidae was recovered as the sister group to Histiophrynidae (see Figure 1.4 and 1.5) The monophyly of Antennarioideo in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: the moderately inflated skin of the larvae **(85)** also convergent in Ceratoidei excluding Chaunacoidei, Caulophryne Gigantactinidae, *Thaumatichthys*, and Himantolophidae; small larval pectoral fins **(87)** also convergent in Ceratoidei excluding Chaunax, Caulophryne, Gigantactinidae, Thaumatichthys, and Himantolophidae.

Ogcocephaloideo was inferred to be monophyletic in all three analyses with coverage of all genera (see Figures 1.3, 1.4, and 1.5). This is consistent with prior morphological, genetic, and combined studies in Shedlock et al. (2004), Pietsch and Orr (2007), Miya et al. (2010), Robosky et al. (2018), and Hart et al. (2022) (see Figure 1.2) The clade consisting of Antennaroideio and Ococephaloideo is the sister group to Chaunacoideo and Ceratoideo as also recovered by Hart et al. (2022) (see Figure 1.2). Regan's (1912) classification indicated a high affinity between Antennarioideo families and Ogcocephaloideo included under a single suborder, but this classification also included Chaunacoideo and Pietsch (1981) tested this arrangement and couldn't find substantial evidence to support it. Frogfishes (Antennarioideo) and batfishes (Ogcocephaloideo) are captivating in their locomotion, using their pectoral fins that have analogously evolved into feet which is an interesting trait of this newfound clade. An insight on any morphological characters that produce a synapomorphy for the clade would help support this relationship. All genera of Ogcocephalidae were found to be monophyletic. The monophyly of Ogcocephaloideo in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: the absence of the first epibrachial also convergent in Ceratoidei **(43)**; a tiny opening of the escal pore leading from the central cavity to the outside **(57)** also found in Ceratoidei, but with no opening in *Caulophryne*, *Rhynchactis*, and Neoceratidae.

Chaunacoideo was recovered as the sister group to deep-sea anglers (Ceratoideo) in all three analyses with a coverage of all genera in our analyses (see Figures 1.3, 1.4, and 1.5). This relationship was also recovered in Shedlock et al. (2004), Miya et al. (2010), Robosky et al.

(2018), and Hart et al. (2022) (see Figure 1.2). The single family Chaunacidae was found to be monophyletic with two genera which was also recovered in prior morphological, genetic, and combined studies in Shedlock et al. (2004), Pietsch and Orr (2007), Miya et al. (2010), Lundsten et al. (2012), Robosky et al. (2018), and Hart et al. (2022) (see Figure 1.2). The monophyly of Chaunacoideo in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: the expanded and squared off posteroventral margin of the articular **(35)** which is also convergent in Ceratiidae.

Ceratoideo was recovered as the crown infraorder of Lophioidei in all three analyses with a coverage of 31 out of 35 genera. The resolution of the Ceratoideo that encompasses all families recovers new relationships that are unique and have been unseen in prior arrangements. This is also the transition to the evolution of bioluminescent escae and barbels (as found in Linophrynidae), the extreme dimorphism, and parasitic reproductive behavior found in Ceratoid fishes. Linophrynidae, the sole family in possession of bioluminescent barbels, is sister group to the rest of the clade as recovered in Shedlock et al., 2004. *Lasiognathus* was recovered in the family Oneirodidae rather than Thaumatichthyidae, as also found in Miya et al. (2010), and is now considered a taxon in Oneirodidae. This infraorder is the most diverse clade within the order and raises the question of why these fishes diversified substantially quicker than the other clades in the order. Bioluminescence has been hypothesized in promoting higher speciation rates in deep-sea environment even with the lack of genetic isolating barriers (Davis et al., 2014) and is more than likely responsible for this suborder’s high speciation and success in deep-sea habitats. The evolution of their bioluminescent escae is an understudied topic and could yield supporting evidence for these relationships, as well as give an insight into the success of these horrors of the deep. The monophyly of Linophrynidae in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: the pterotic is tapered and distally pointed in overlapping the sphenotic (**13)**; has series of four to six short spines along the anterior, lateral, and posterior margins of the preopercle **(20)**, tubular eyes in the males **(74)**. The monophyly of in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: the supraoccipital is displaced anteriorly in metamorphosed females with a majority of the dorsal surface lying in the vertical plane allowing for abutment for the pterygiophore of the illicium **(14)**; the intropercle is reduced to a small triangular bone also convergent in Neoceratidae **(23)**; the caudal fin is emarginate in females **(51)**; five pectoral radials **(65)**; olfactory organs that are greater than 30% of head length **(75)**. The monophyly of Caulophrynidae in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: extremely long dorsal and anal fin rays in metamorphosed fanfin anglers **(61)**. The monophyly of Ceratiidae in the total evidence approach analysis is supported by these morphological characters from Pietsch and Orr (2007) including: concealed distal light organ in the larvae also convergent in Diceratiidae **(59)**; present caruncles **(62)**; oval and conical shaped eyes of the males **(74)**; hump-backed shaped larvae **(84)**. The monophyly of Melanocetidae is supported by the morphological characters including: fused dermal spinules to form a medial ridge on the snout which is also convergent in *Microlophichthys* in Oneirodidae **(80)**. The monophyly of the families Neoceratidae, Centrophrynidae, Diceratiidae, Himantolophidae, and Oneiroidae are supported by UCE and mitochondrial DNA data. Within the family Oneiroidae, *Oneirodes* was recovered as paraphyletic with *Spiniphryne*. This genus requires further study to resolve this relationship.

Conclusions

The morphologically bizarre lineage of the anglerfishes (Lophioideo) and their evolutionary relationships have been examined through a total evidence phylogenetic analysis that encompasses ultraconserved gene elements, whole mitochondrial genomes, and morphological characters resulting in the most data-rich hypothesis of relationships of Lophioidei to date (see Figure 1.5). Two other analyses consisting of UCE data (see Figure 1.3) and UCE data and mitochondrial genomic data (see Figure 1.4) were also produced. A clade that produces a sister group relationship of the frogfishes (Antennarioideo) and the batfishes (Ogcocephaloideo) and a sister group relationship between the coffinfishes (Chaunacoideo) and the deep-sea anglerfishes (Ceratoideo) has only been described in one other study (Hart et al., 2022) using similar ultraconserved gene elements. The stem infraorder of the anglerfishes was found to be the monkfishes (Lophioideo) and the stem family of the remarkably unusual lineage of the deep-sea anglerfishes (Ceratoideo) was the leftvents (Linophrynidae), a lineage with elaborate bioluminescent hyoid barbels found in no other anglerfish lineage. This unique hypothesis of anglerfish evolutionary relationships will serve as a road path to explore the evolutionary characteristics of this lineage for the continuation of this thesis.

Chapter II

Habitat Occurrences and the Evolution of Luring Strategies in Lophioidei

Introduction

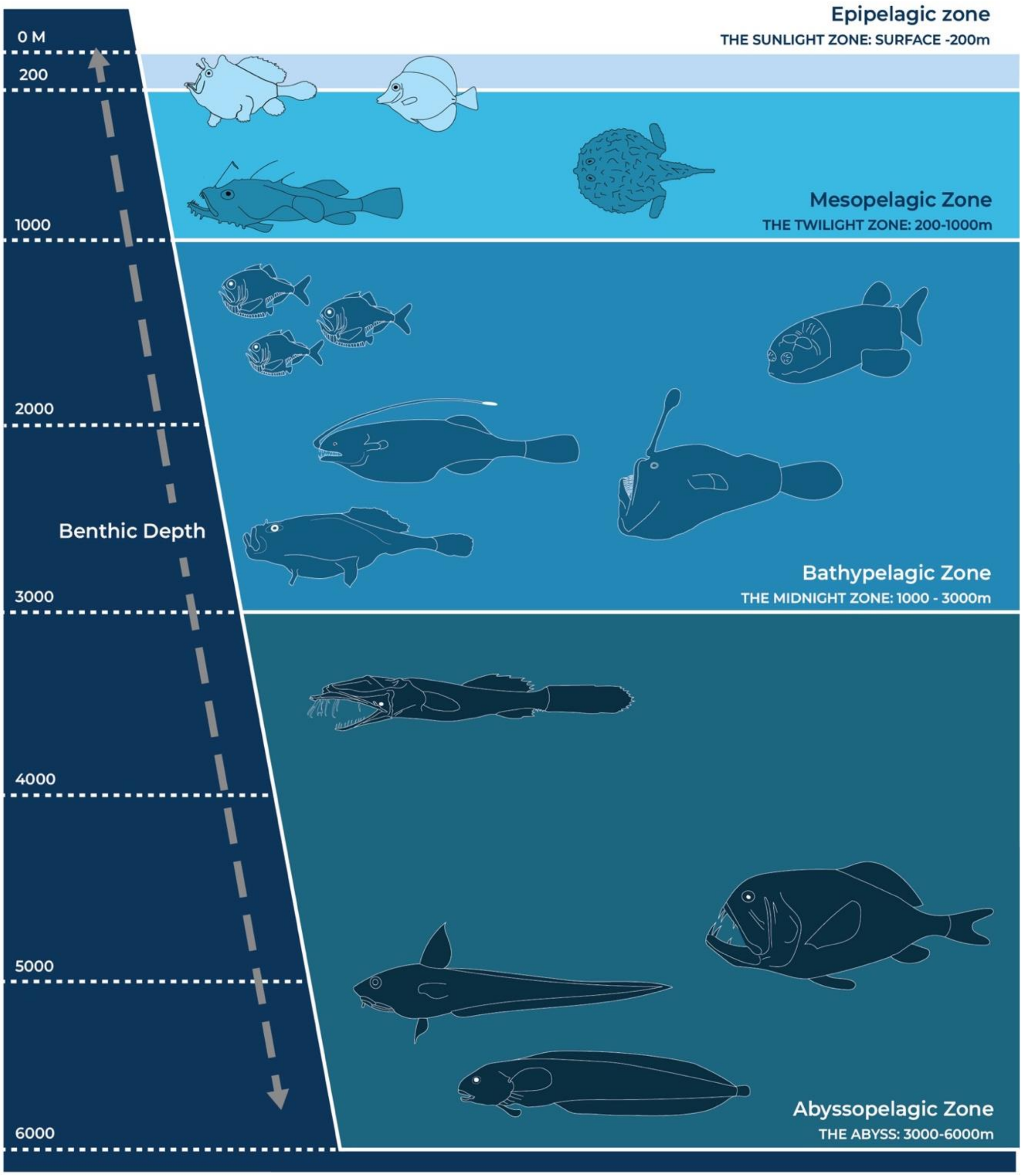
Anglerfish Habitats

The oceanic water column is described by several layers each with its own characteristics with respect to depth, abiotic, and biotic factors. These layers are divided into the epipelagic zone (0 – 200 m), mesopelagic zone (200 – 1000 m), bathypelagic zone (1000 – 3000m), and the abyssopelagic zone (3000 – 6000m) (see Figure 2.1). The photic zone, where natural sunlight occurs and facilitates photosynthesis (Giner et al., 2020) typically occurs in the epipelagic zone where depths beyond 200m are described as the aphotic zone where sunlight can no longer be found resulting in dark habitats. Once beyond 200 m, the heat of the epipelagic zone begins to drop drastically once beyond the thermocline. Waters found in deep-water habitats are found at near-freezing temperatures and pressures increase linearly (around 1 bar per 10 meters of water depth) resulting in the extreme oceanic habitat, the deep sea. Though these conditions are alien-like to humans and inhospitable, numerous oceanic lineages have successfully thrived in these habitats. One lineage of actinopterygian fishes that occupy habitats across these oceanic layers is the infraorder Lophioidei (the anglerfishes). Several lineages of actinopterygian fishes have made transitions into deep-sea habitats that have facilitated in the evolution of astounding biological mechanisms.

Lophioideo (monkfishes) are found in benthic, shallow to midwater depths in the on the outer continental shelf and upper continental slope and occur typically in tropical and temperate seas with limited or no occurrences in the Southern Ocean, ranges in the northern Atlantic between northern California and the Sea of Okhotsk, the southern point of South America, and several accounts in the Artic (see Figure 2.2). These fishes lay on muddy, sandy, or rocky substrates to conceal their dorsoventrally compressed bodies typically on continental shelfs or the continental slope. Fishes in Lophioideo are significantly larger in size compared to the rest of Lophioidei and are the only commercially caught anglerfishes. Fisheries frequently conduct studies to investigate the abundance and distribution of the monkfishes and have noticed increased population abundance and recruitment because of raising ocean temperatures in Icelandic waters (Solmundsson et al., 2009).

Figure 2.1.

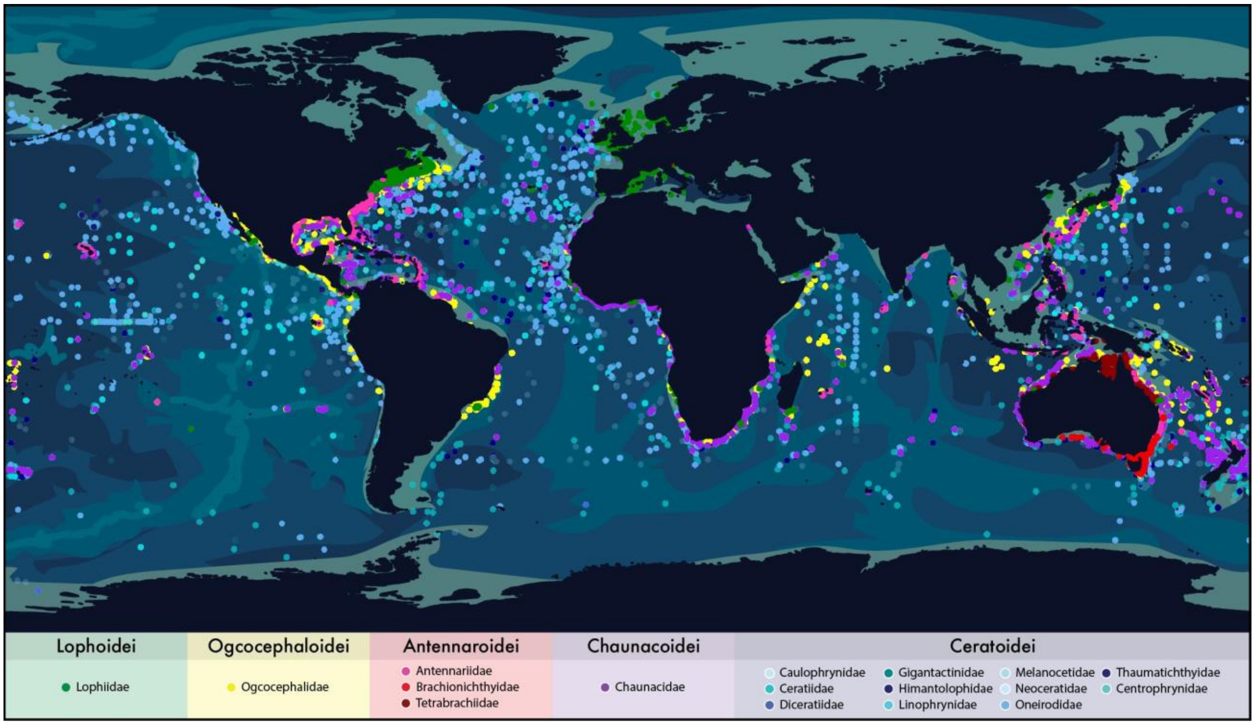
Oceanic Depth Map



Note. Oceanic layers comprised of the Epipelagic Zone (0 – 200m), Mesopelagic Zone (200 – 1000m), Bathypelagic Zone (1000 – 3000m), and Abyssopelagic Zone (3000 – 6000 m)

Figure 2.2.

Global distribution of anglerfishes.



Note. Global distribution occurrences of ~2500 anglerfishes (Lophioidei) distributed by infraorders from Gbif.org (2023) museum collection occurrence data.

Antennarioideo (frogfishes) are found primarily in benthic shallow depths in the Epipelagic Zone, apart from *Histrio histrio* which is a pseudo-pelagic frogfish found in floating sargassum seaweed (Pietsch and Grobecker, 1987). These fishes are found in tropical to subtropical waters. There are no occurrences in the Southern, Artic, or Mediterranean oceans with several species able to tolerate brackish and freshwater (see Figure 2.2). Frogfishes can be found in coral reef habitats, muddy, sandy, or rocky benthic substrates, and are typically cryptically camouflaged with several extreme examples of mimicry such as the Psychedelic Frogfish (*Histiophryne psychedelica*) which resembles hermatypic coral (Pietsch and Arnold, 2020). Modifications to the pectoral fins of these fishes allow them to pseudo-walk on the seafloor, a bizarre fin modification found in monkfishes, frogfishes, batfishes, and coffinfishes.

Ogcocephaloideo (batfishes) are found primarily in shallow to deep-water benthic habitats and occur typically in tropical and subtropical waters like Antennarioideo (see Figure 2.2). The dorsoventrally compressed bodies of the batfishes allow them to lie and walk across the seafloor. Habitat shifts in batfishes have been explored in prior studies (Derouen et al., 2014) and ancestral state reconstructions indicate batfishes originated on the lower continental shelf in the disphotic zone as preference in these habitats.

Chaunacoideo (coffinfishes) are found in deep-water benthic habitats on the outer continental shelf and the upper continental slope. They are found in tropical and temperate oceanic waters in the Pacific, Atlantic, and Indian Oceans (see Figure 2.2). The gill ventilatory system of these fishes has been explored to discover a breath-holding behavior, used to increase the body volume of these fishes by 30%, presumably to increase buoyancy and reduce the energy needed to travel (Long and Farina, 2019).

Ceratoideo (deep-sea anglerfishes) are found in deep-water habitats between the Mesopelagic Zone and the Abyssopelagic zone. Except for *Thaumatichthys*, these fishes occupy pelagic habitats. Spread across the Atlantic, Indian, and Pacific Oceans, these fishes have the widest global distribution (see Figure 2.2), but the exact depths these fishes occupy are unknown. Because of the practice of using deep-sea nets that cover a large range to collect ceratoid anglers, it's unclear at what specific depths these fishes are found. *Thaumatichthys* the only truly benthic ceratoid of the infraorder can be found using only benthic deep-sea trawls, indicating its preference near the sea floor. Deep-sea anglers undergo a variety of vertical migrations associated with larval and metamorphosed development (Bertelsen, 1951; Pietsch, 1974; Pietsch and Grobecker, 1980).

The Esca, Illicium, and Pterygiophore Apparatus

The denoting feature of the anglerfish is the modified first dorsal fin-spine that is broken into three components: the esca, illicium, and associated pterygiophore (Pietsch and Grobecker, 1987; Shimazaki and Nakaya, 2004; Pietsch and Orr, 2007). This apparatus is widespread throughout the order apart from *Neoceratias*, and what gives the group its name: the anglerfishes.

Acanthomorpha is comprised of fishes that have evolved spiny rays that are most often found in the first dorsal fin and anterior most fin-rays of the anal fin. These spiny rays can be used as a deterrent towards predation and even facilitate venomous pathways as found in lineages such as Scorpeaniformes (Smith et al., 2016).

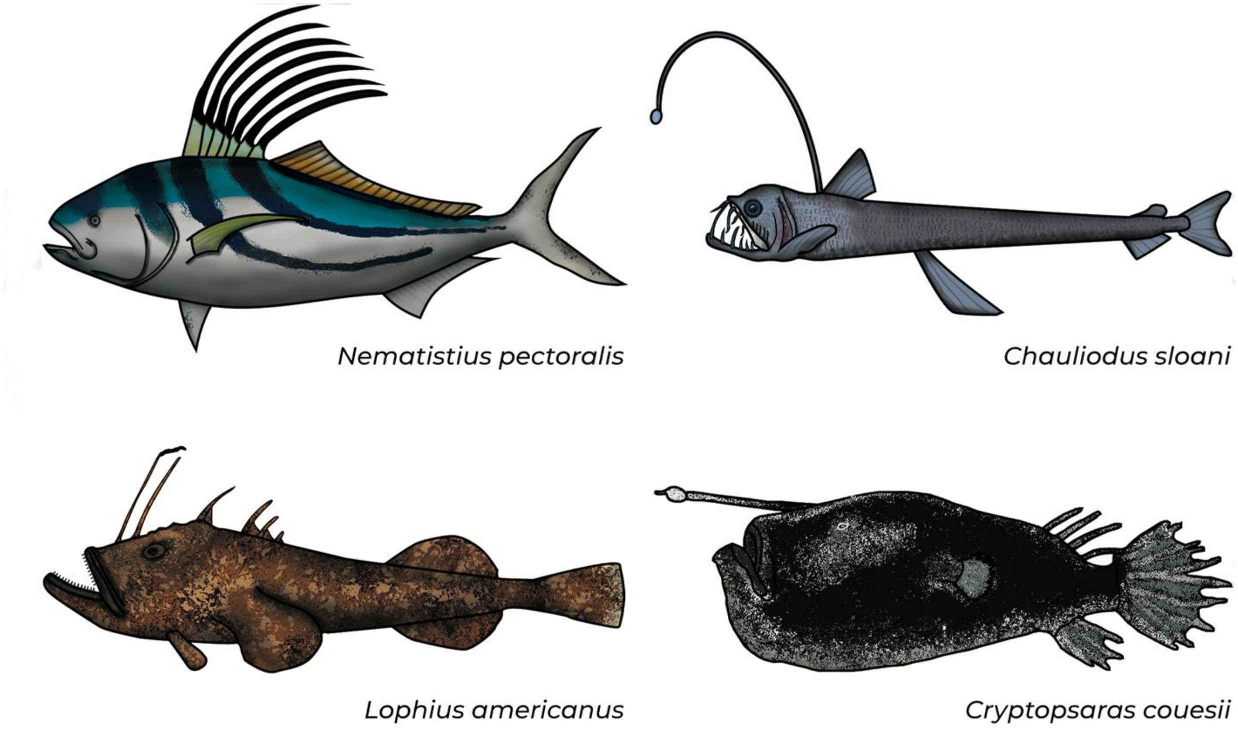
Few fishes use the dorsal fin as a luring apparatus and this adaptation is distinctly found in Lophioidei and *Chauliodus* (Stomiidae). *Chauliodus* has a similar modification to its dorsal fin-spine anatomy, where a luminous organ on the distal tip of an elongated first dorsal-fin spine is hypothesized to be used as a lure (Battaglia et al., 2018). In Lophioidei, the esca, illicium, and associated pterygiophore comprise the distinct lure found in the group (see Figure 2.3). The pterygiophore is the associated bones or cartilage connected to the base of the dorsal and anal fins. Typically positioned under the dermis as a connecting point to the dorsal fins in other fishes, the pterygiophore associated with the first dorsal-fin ray of Lophioidei can either be encompassed by tissue held beneath the dermis or protrude and extend laterally.

The associated pterygiophore can range in length from being relatively short or long in length with variation across the order. Connected to the associated pterygiophore is the modified dorsal-fin spine; the illicium. (Pietsch and Grobecker, 1987; Pietsch and Orr, 2007). This bone can similarly be short or long in length and varies throughout the order (Regan, 1912; Shimazaki and Nakaya, 2004; Pietsch, 2009; Pietsch and Arnold, 2020). Attached to the illicium is the fleshy tissue used as bait, the esca. The esca is the key component of the luring strategy as it acts as “bait” while the illicium and associated pterygiophore act as the “rod”. This evolutionary marvel aids in the hunting of these ambush predators found across the world’s oceans (Regan, 1912; Pietsch and Grobecker, 1987, Pietsch, 2009; Pietsch and Arnold, 2020).

Lophioideo (monkfishes) are found on benthic habitats are highly carnivorous with a dorsoventrally compressed body plane. The lures of the monkfishes are simplistic with extremely thin lures with variation in the escae and pairs with the large gaping-mouth oriented dorsally to catch prey (Caruso, 1981; Caruso, 1983; Matsunuma and Muto, 2020) . The first dorsal fin-spine used as a lure is followed by several mobile dorsal fin-spines located posteriorly and these separated individual dorsal-fin spines are described as cephalic spines and can vary in quantity (Caruso and Suttkus, 1979; Ho et al., 2014). These cephalic spines are not used in the luring behavior of monkfishes like the first dorsal-fin spine. The escae of monkfishes can vary in morphology and length (see Figure 2.4) from being slender and naked, being covered in dermal spinules that give it a feather-like appearance, containing a pennant-like flap, being covered in cutaneous filaments (cirri), or even absent in some species (Caruso, 1981; Caruso, 1983; Ho et al., 2014). Monkfishes will move their lure in a forward and backwards motion, while vibrating, flicking, and posing their lures to imitate moving bait for suspecting prey. The lures of Lophioideo have not been identified in being bioluminescent or glandular to excrete chemical attractants to aid in the luring behavior of these fishes.

Figure 2.3.

Drawings depicting dorsal-fin modifications to fishes.

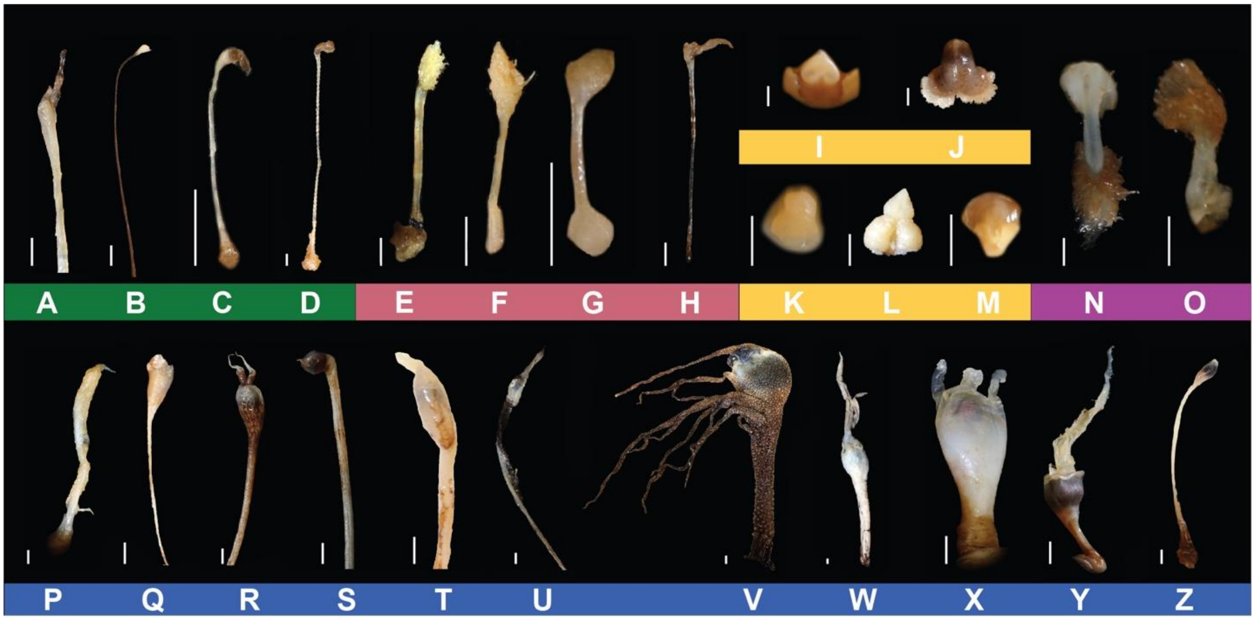


Note. Top left: *Nematistius pectoralis* (roosterfish), top right: *Chauliodus sloani* (viperfish), bottom left: *Lophius americanus* (monkfish), bottom right: *Cryptopsaras couesii* (triplewart seadevil).

Antennarioideo (frogfishes) are found on benthic habitats and in pelagic habitats (*Histrio histrio*) and have a robust, laterally compressed build with a forward-facing mouth (Pietsch and Grobecker, 1987; Pietsch and Arnold, 2020). These fishes have extremely modified pectoral fins that can allow them to walk across the seafloor. Frogfishes have two distinct enlarged cephalic spines positioned posteriorly to the first modified dorsal-fin spine lure (Pietsch and Grobecker, 1987; Last and Gledhill, 2009; Pietsch and Arnold, 2020). These cephalic spines like monkfishes, serve no part in the luring behavior of these fishes. The first dorsal-fin spine of frogfishes is thin and can be equipped with a variety of escae that range in morphology. The escae of frogfishes (see Figure 2.4) can be slender and naked, covered in cutaneous filaments (cirri), encompassed by various folds of tissue, can have various appendages both singular, bifid, or trifid, can have club-like extremities, can have a variation of escal swellings, or any variation or combination of those listed or even absent (Pietsch and Grobecker, 1987; Last and Gledhill, 2009; Pietsch et al., 2009; Pietsch and Arnold, 2020). Frogfishes will move their lure in a forward and backwards motion, while vibrating, flicking, and posing their lures to imitate moving bait for suspecting prey. The lures of Antennarioideo typically don’t rely on chemical or bioluminescent aids, except for *Antennarius striatus* (Pietsch and Grobecker, 1987).

Figure 2.4.

Anglerfish escae portrayed by multiple family and genus representatives.



Note. Colors associated with phylogenetic tree (see Figure 2). Scale bars = 2 mm (A) *Lophiodes caulinaris*, LACM 8836-10. (B) *Lophiodes miacanthus*, LACM 46040-3. (C) *Lophiomus setigerus*, LACM 44743-7. (D) *Lophius americanus*, LACM 34328-1. (E) *Antennarius avalonis*, LACM 49991-1. (F) *Histrio*, LACM 8975-1. (G) *Kuiterichthys* sp., LACM 11537-1. (H) *Lophiocharon trisignatus*, LACM 54171-1. (I) *Dibranchus erinaceus*, LACM 33699-2. (J) *Halieutaea fitzsimonsi*, 44745-6. (K) *Malthopsis mitrigera*, LACM 56294-1. (L) *Ogcocephalus darwini*, LACM 43975-2. (M) *Zalieutes elater*, LACM 6552-2. (N) *Chaunax* sp., LACM 44750-3. (O) *Chaunax* sp., LACM 35843-1. (P) *Caulophryne polynema*, LACM 33923-1. (Q) *Centrophryne spinulosa*, LACM 31105-24. (R) *Ceratias tentaculatus*, LACM 11025-7. (S) *Cryptopsaras couesii*, LACM 11231-1. (T) *Bufoceratias wedli*, 34272-1. (U) *Gigantactis vanhoeffeni*, LACM 45001-1. (V) *Himantolophus sagamius*, LACM 43760-1. (W) *Himantolophus albinares*, LACM 57239-2. (X) *Borophryne apogon*, LACM 30053-10. (Y) *Linophryne densiramus*, LACM 38440-1. (Z) *Melanocetus murrayi*, LACM 36113-1.

Ogcocephaloideo (batfishes) are found on only benthic habitats and have extremely dorsoventrally compressed body planes, with odd variation in their shape from a dorsally directed point of view ranging from being circular, triangular, spade-like, and ovular. The mouths of these fishes are directed downwards and are the only infraorder of fishes that are not primary piscivores. The main diet of these fishes includes gastropods and other benthic invertebrates (Nagareda and Shenker, 2009). The lures of batfishes are typically retracted within an illicial cavity where the lure is housed entirely. Some batfishes can extend this lure beyond the illicial cavity as part of its luring behavior. The escae (see Figure 2.4) are typically glandular and can range in morphologies including symmetric lateral bulbs, single spade-like or heart-like bulbs, and/or added fringe or filaments. The escae of batfishes have been hypothesized of being capable of excreting chemical attractants during luring behaviors (Combs, 1973; Nagareda and Shenker, 2009) and are more than likely using this chemical attractant aimed at benthic invertebrates buried in the substrate.

Chaunacoideo (coffinfishes) are found on benthic habitats and have globular bodies. The lures of the coffinfishes are extremely short and are housed in a wide and shallow illicial cavity. The cavity is not enclosed like those found in batfishes and allows for the lure to rotate in a forward position and backwards. The length of the lure is typically stout and equal in length compared to the escae, which are typically covered in dense cutaneous filaments (cirri) (see Figure 2.4). Due to the deep-water habitats these fishes reside, observations of the luring behaviors of these fishes are hard to come by, but there is no evidence that these fishes have bioluminescent or chemical attractant lure capabilities.

Ceratoideo (deep-sea anglerfishes) are predominantly found in deep-sea pelagic habitats apart from *Thaumatichthys* being a benthic angler (Pietsch, 2009). Ceratoideo has some of the most vibrant and unique lures in the order and is the only infraorder of Lophioidei with widespread bioluminescent capabilities (Haygood and Distel, 1993; Pietsch, 2009; Davis et al., 2014; Davis et al., 2016) apart from Caulophrynidae, and Neoceratiidae (Bertelsen, 1951). The length of the lures in the deep-sea anglerfishes can be highly variable and the length of the illicium and pterygiophore can also be highly variable. In some taxa, the illicium and exposed pterygiophore can have small to relatively large dermal spinules along the surface. Escae morphology in the deep-sea anglerfishes can vary greatly and has some of the most diversity found within the Lophioidei (see Figure 2.4). Combinations of bulbs, distal appendages, single/paired/ or multiple tassels, club-like extremities, long or short attached filaments, small or large dermal spinule, and a variety of escae distal appendages (Pietsch et al., 2006; Ho et al., 2016; Rajeeshkumar et al., 2016; Bañon et al., 2019; Ho and Shao, 2019). The bioluminescent escae consist of a variety of modifications to direct, redirect, and limit light including light absorbing tissue layers that typically includes heavily pigmented and light reflecting tissue layers typically silvery or mirror-like in appearance, and tubular channels designed to reflect light throughout the structure (Bertelsen, 1951; Munk, 1999; Pietsch, 2009). In addition to these mechanisms, there are associated nervous and blood vessel networks, escal glands, and smooth muscle fibers associated with the bioluminescent escae. The bioluminescence is produced by symbiotic bacteria (Davis et al., 2016; Haygood and Distel, 1993) to produce a luminous effect used in luring and the symbionts that have been identified are related to the genus *Vibrio* (Haygood and Distel, 1993). ROV and aquatic submersibles have allowed these fishes to be viewed in their natural habitats, but the luring behaviors of these fishes are still rarely seen. *Caulophryne* uses its non-bioluminescent esca to lure prey into a network of elongated dorsal, anal, and caudal ray fins creating a spiderweb-like sensory array. *Thaumatichthys* has an esca that originates in its mouth, so as the fish opens its mouth, a dangling lure serves as bait as these fishes swim across abyssobenthic landscapes.

Luring Strategies

Anglerfishes that use their escae without the aid of bioluminescence or the excretion of chemical pheromones can be classified as having a mechanical luring strategy. These lures as far as we know only rely on their ability to be viewed as a potential prey item or bait by a prey item targeted by the anglerfish to be enticed into the proximity of the strike zone. *Macroclemys* the Alligator Snapping Turtle exhibits a similar behavior involving motions of the tongue shaped like an annelid while its mouth is held opened and this behavior is initiated by a visual stimulus to start the behavior (Drummond and Gordon, 1979). The motions associated with this strategy as well as the following strategies to be described can involve waving the lure in a forward and backward vertical motions, slight horizontal motions, or strategic vibrations or lack of motion used to simulate live bait. Prey attraction luring strategies of *Antennarius hispidus, A. maculatus,* and *A. Striatus* have been observed in controlled studies (Grobecker and Pietsch, 1979) that describe the behaviors of these fishes when presented with prey, the timing and motions used in the luring behavior, and descriptions of the strike zone and feeding behavior. This strategy is typically found in shallow or midwater anglers in Lophioideo, Antennaroideo, and Chaunacoideo. A unique deep-sea mechanical luring behavior found in *Gigantactis,* a Ceratoid angler, occurs where they invert their body in a downward facing fashion while extending a lure towards the benthic substrate while drifting with the ocean currents to entice prey (Moore, 2002). Monkfishes will place themselves close to the benthic substrate to wave their lures with a variety of movements and their mouths are oriented upwards to feed on lured prey items directly above.

The addition of the excretion of chemical attractants or pheromones to the esca can be describing as a chemical luring strategy. Chemical pheromones and attractants can be found in a variety of permutations and combinations for their specific use and can be used in alarm signaling to danger stimuli (Verheggen et al., 2010), sexual communication, and baiting found in insects (Tan et al., 2014). Ogcocephaloideo and the single Antennaroideo species *Antennarius striatus* have been documented in emitting a chemical attractant (Nagareda and Shenker, 2009; Pietsch and Grobecker, 1987). Histological examination of the escae in *Dibranchus, Halieutaea, Haliemetus, Halieutopsis, Malthopsis, Ogcocephalus,* and *Zalieutues* performed by Combs (1973) described glandular systems consisting of follicles of secretory cells with a series of ducts allowing for an external release of chemical attractants through pores. Nagareda and Shenker (2009) demonstrated *Ogcocephalus cubifrons* ability to use chemical attractants to increase the response stimuli of a common gastropod *Nassarius vibex*, of which the diet of *O. cubifrons* includes as well as other benthic invertebrates. It is unclear if the chemical attractants used by the batfishes of Ogcocephaloideo are specifically tailored towards luring gastropods, but dietary analysis of batfishes has shown a variation in the diet with a preference of benthic invertebrates rather than other fishes as found in other anglerfishes (Nagareda and Shenker, 2008). The esca of *Antennarius striatus* has numerous secretory cells in the epidermal layer of the esca whereas matured granules approaching a centrally located lumen release the chemical attractant. This behavior was demonstrated in (Pietsch and Grobecker, 1987) by collecting the surrounding water near a luring *A. striatus* and using an artificial lure that would excrete the hypothesized chemical attractant and showed a higher prey approach proportion compared to the artificial lure used without the harvested chemical attractant from *A. striatus*. It is also noted that *A. striatus* was found in various positions where its strike zone was aimed downstream of ocean currents.

Bioluminescence is the result of an oxidized luciferin, a molecule that emits photons, while catalyzed by a luciferase. This biological phenomenon is found widespread across the tree of life in single-celled bacteria, dinoflagellates, fungi, cnidarians, insects, and fishes (Herring, 1987; Haddock et al., 2010; Widder, 2010; Davis et al., 2014; Davis et al., 2016). In deep-sea habitats, bioluminescence facilitates speciation in species-specific bioluminescent organs (Davis et al., 2016) as found in Stomiiformes and Myctophiformes and are hypothesized in communication, prey attraction, predator deterrence, and camouflage. Blue luminescence (450-500) travels the furthest in seawater, as the color has the highest frequency of any color in the visible spectra and occurs in most bioluminescent organisms. Bioluminescence in the anglerfishes originates from symbiotic bacteria housed in the escae and studies have indicated that these bacteria can be species specific (Haygood and Distel, 1993) indicating a reliance on the ceratoid escae for the bacteria to survive. It's unknown how deep-sea anglerfishes acquire these bacteria and at what point in their lifecycle they begin to house the bacteria, as the escae of newly metamorphosed ceratoids contain little to no bacteria to produce the luminous effect (Munk et al., 1998). There is no evidence indicating that ceratoid males or larvae of females have bioluminescent capabilities, and it could serve to lure prey as well as communicate or lure males for mating.

Biofluorescence in the escae of anglerfishes has been surveyed in multiple instances in *Antennarius striatus* eliciting a reddish-orange fluorescence response (De Brauwer and Hobbs, 2016) and *Himantolophus sagamius* eliciting a green fluorescence response (Ludt and Clardy, 2022) as well as biofluorescence found on the whole body of *Antennarius maculatus* eliciting a reddish-orange fluorescence response (Sparks et al., 2014). It is hypothesized that biofluorescence in fishes can serve a variety of roles including communication, camouflage, and prey attraction and some fishes including catsharks can visualize these patterns (Gruber et al., 2016). Further work is needed to investigate the variation of biofluorescence in anglerfishes and its potential role in the luring strategy of these fishes.

The focus of this study is to investigate the depth and habitat preferences of anglerfishes and the luring strategies used by these fishes using a character state reconstruction analysis. In addition, a morphometric analysis of the luring apparatus (pterygiophore, illicium, and escae) will be conducted to compared to the lure length ratios across the radiation and across the depth and habitat preferences of the anglerfishes. In this study we address the following questions: (1) What are the habitat and depth preferences of the anglerfishes (Lophioidei)? (2) What types of lures have evolved in the Lophioidei? (3) Are there any trends of lures associated with habitat and/or depth preferences of anglerfishes?

Materials and Methods

Taxonomic Sampling

Physical examinations of adult anglerfish species used in this study include material from the Natural History Museum of Los Angeles County (LACM). Additional photographs of anglerfish specimens were provided by request from the Museum für Naturkunde (ZMB), Muséum national d'Histoire naturelle (MNHN), and the Australian Museum (AMS). Additional photographs of anglerfish species were included in analyses from GBIF.org (2023), Sketchfab.com (2023), *Oceanic Anglerfishes Extraordinary Diversity in the Deep Sea*, *Frogfishes: Biodiversity, Zoogeography, and Behavioral Ecology*, Fishbase (Froese and Pauly, 2018), *Fishes: A guide to their Diversity*, and peer review publications which are listed in the Material Examined section. Any specimens with missing or highly damaged lures due to preservation were excluded from this study. Males of Ceratoideo were also excluded from this study due to their extreme physical sexual dimorphisms across some taxa. Museum acronyms follow Sabaj (2020). In total, 111 specimens representing 102 species, 51 of 68 genera, and all families are included in this chapter. Specimens physically examined were photographed under white lighting conditions using a Canon EOS Rebel T7i DSLR camera equipped with a macro lens while positioned on their lateral side facing left. Additionally, photographs of the escae with scales were photographed under the same white light conditions using a 100 mm Canon macro lenses.

Digital Mensural Data Collection

Photographs were resized to fit a W: 5000 px by H: 4000 px without alteration to photo ratio using the Image Processor in Adobe Photoshop (2019). The photograph of *Thaumatichthys binghami* UW 47537 was the only photo straightened using Adobe Photoshop while preserving body shape and length. Mensural measurements of all photos were performed using ImageJ (Schneider et al., 2012) using the "Analyze: Set Scale" function based on scale bars followed by using the "Analyze: Measure" function to measure standard lengths (SL), illicium and exposed pterygiophore length, and escae length. Due to the physiology of the extendable lures in Ogcocephaloideo and the difficulty in measuring lures in formalin-fixed specimens, lure morphometrics of this infraorder were excluded in this study.

Standard lengths (SL) were measured from the tip of the snout to the last vertebra. The luring apparatus of anglerfishes were straightened for measuring. Lure total lengths (TLL) were measured from the insertion of the illicium or exposed pterygiophore to the start of the fleshy distal appendage, the esca. Esca lengths (ES) were measured from the base of the illicium to the tip of the esca or the furthest distal appendage present.

Biogeographic Map

Global distributions of 2489 occurrences of Lophiodei representing 17 families were mapped using the rgbif package (Chamberlain et al., 2023) and terra package (Shifaw, 2021) on R. Lophiodei occurrences were sourced from Gbif.org (2023) using the occ_data function. Occurrences were digitally colored using Adobe Illustrator according based on color scheme found in Chapter 1.

Character State Coding

The total-evidence phylogeny consisting of ultraconserved gene fragments, mitochondrial genomes, and morphological characters were used to infer character evolution of depth preferences followed by benthic or pelagic preferences and luring strategies. Depth data for each genus was procured from museum collection data uploaded on Fishnet2 (2014) to find mode values for depth. Character states for depth preferences included: (0) found in both fresh and marine habitats, (1) predominantly found in the Epipelagic Zone (Surface - 200m), (2) predominantly found in the Mesopelagic Zone (200m - 1000m), (3) predominantly found in the Bathypelagic Zone (1000m - 3000m), and (4) predominantly found in the Abyssopelagic Zone (3000m - 6000m) (see Figure 2.1 for depth map). Character states for benthic or pelagic preferences included: (0) predominantly found on benthic surfaces and (1) predominantly found in pelagic habitats. Character states for luring strategy included: (0) no luring strategy used and/or absent, (1) mechanical, (2) chemical, and (3) bioluminescent. Character evolution analyses included maximum parsimony optimizations using the program Mesquite (Maddison and Maddison, 2023).

Results

Depth Preferences of Lophiodei

A parsimony character state analysis inferred depth preferences of the common ancestors of anglerfish lineages (Lophioidei, Figure 2.5). The outgroup of Tetraodontoidei was inferred to occupy epipelagic depths. The Lophioidei common ancestor was inferred to be found in epipelagic depths and is found in the frogfishes (Antennarioideo) and some batfishes (Ogcocephaloideo) including the genera *Malthopsis, Ogcocephalus, Zalieutes,* and *Halieutichthys* (see Figure 2.5). Three independent transitions to mesopelagic depths from epipelagic depths were found in (1) Lophoideo, (2) Ogcocephaloideo genera including *Coelophrys*, *Solocisquama*, *Halicmetus*, and *Dibranchus*, (3) the Ogcocephaloideo genus *Halieutaea* (see Figure 2.5). Four independent transitions to mesopelagic depths from bathypelagic depths were found in (1) the Chaunacoideo genus *Chaunax*, (2) the Linophrynidae genus *Haplophryne*, (3) the family Diceratiidae, and (4) the Oneirodidae genus *Chaenophryne* (see Figure 2.5). Two independent transitions to bathypelagic depths from epipelagic depths were found in (1) the Ogcocephaloideo genus *Halieutopsis* and (2) the Chaunacoideo and Ceratoideo sister group clade (see Figure 2.5). A single transition to abyssopelagic depths from bathypelagic depths occurred in Thaumatichthyidae (see Figure 2.5).

Table 2.1.

Morphological Data Matrix.

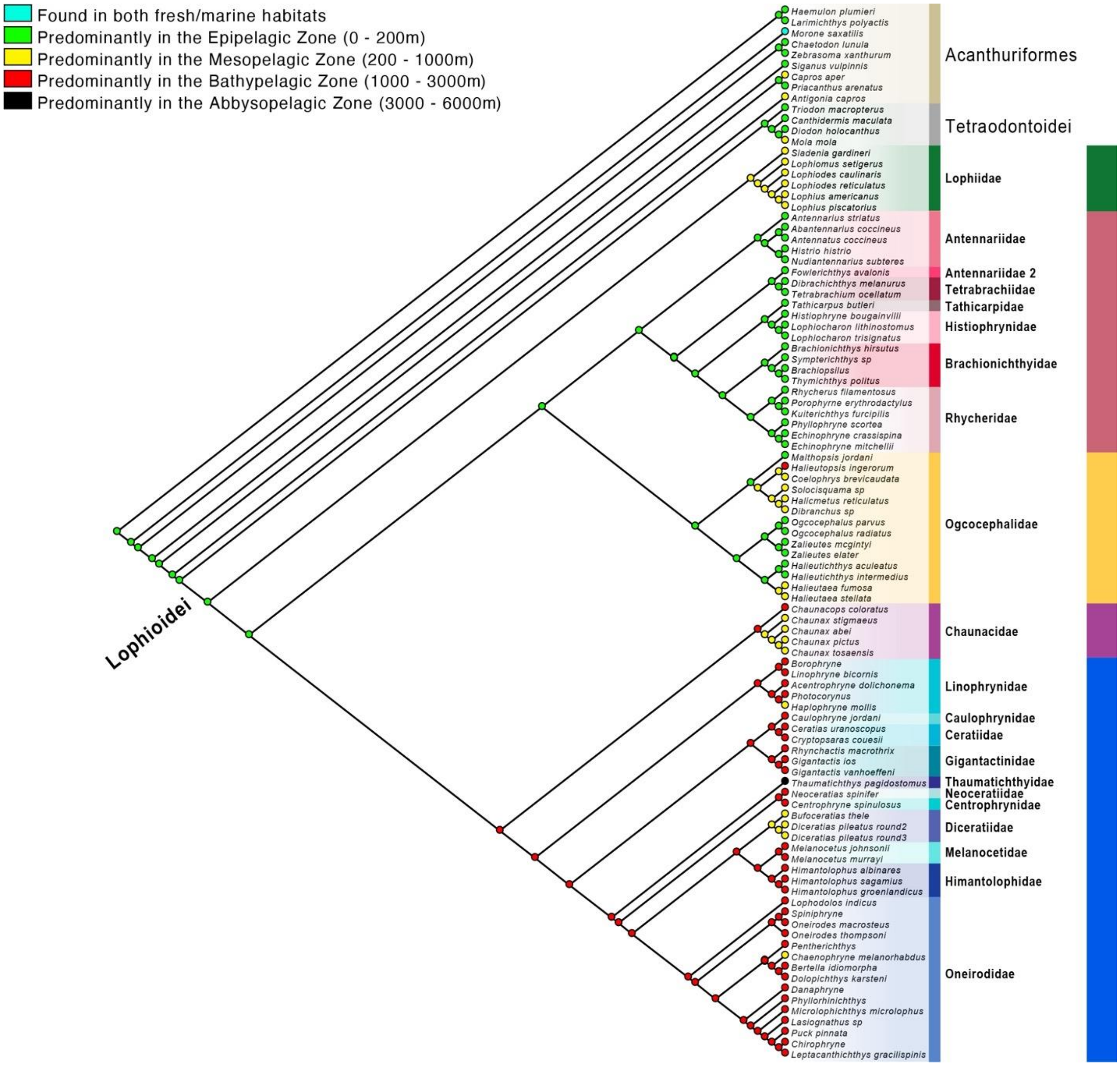
Outgroups	01	02	03	**Lophioidei**	01	02	03
Antigonia capros	3	1	0	*Halieutichthys aculeatus*	2	0	2
Canthidermis maculata	2	1	0	*Halieutichthys intermedius*	2	0	2
Capros aper	3	1	0	*Halieutopsis ingerorum*	4	0	2
Chaetodon lunula	2	1	0	*Haplophryne mollis*	3	1	3
Diodon holocanthus	2	1	0	*Himantolophus albinares*	4	1	3
Haemulon plumieri	2	1	0	*Himantolophus groenlandicus*	4	1	3
Larimichthys polyactis	2	1	0	*Himantolophus sagamius*	4	1	3
Mola mola	3	1	0	*Histiophryne bougainvilli*	2	0	1
Morone saxatilis	1	1	0	*Histrio histrio*	2	1	1
Priacanthus arenatus	2	1	0	*Kuiterichthys furcipilis*	2	0	1
Siganus vulpinnis	2	1	0	*Lasiognathus* sp.	4	1	3
Triodon macropterus	2	1	0	*Leptacanthichthys gracilispinis*	4	1	3
Zebrasoma xanthurum	2	1	0	*Linophryne bicornis*	4	1	3
Lophioidei				*Lophiocharon lithinostomus*	2	0	1
Abantennarius coccineus	2	0	1	*Lophiocharon trisignatus*	2	0	1
Acentrophryne dolichonema	4	1	3	*Lophiodes caulinaris*	3	0	1
Antennarius striatus	2	0	1&2	*Lophiodes reticulatus*	3	0	1
Antennatus coccineus	2	0	1	*Lophiomus setigerus*	3	0	1
Bertella idiomorpha	4	1	3	*Lophius americanus*	3	0	1
Borophryne sp.	4	1	3	*Lophius piscatorius*	3	0	1
Brachionichthys hirsutus	2	0	1	*Lophodolos indicus*	4	1	3
Brachiopsilus sp.	2	0	1	*Malthopsis jordani*	2	0	2
Bufoceratias thele	3	1	3	*Melanocetus johnsonii*	4	1	3
Caulophryne jordani	4	1	1	*Melanocetus murrayi*	4	1	3
Centrophryne spinulosus	4	1	3	*Microlophichthys microlophus*	4	1	3
Ceratias uranoscopus	4	1	3	*Neoceratias spinifer*	4	1	0
Chaenophryne melanorhabdus	3	1	3	*Nudiantennarius subteres*	2	0	1
Chaunacops coloratus	4	0	1	*Ogcocephalus parvus*	2	0	2
Chaunax abei	3	0	1	*Ogcocephalus radiatus*	2	0	2

Chaunax pictus	3	0	1	*Oneirodes macrosteus*	4	1	3
Chaunax stigmaeus	3	0	1	*Oneirodes thompsoni*	4	1	3
Chaunax tosaensis	3	0	1	*Pentherichthys* sp.	4	1	3
Chirophryne sp.	4	1	3	*Photocorynus* sp.	4	1	3
Coelophrys brevicaudata	3	0	2	*Phyllophryne scortea*	2	0	1
Cryptopsaras couesii	4	1	3	*Phyllorhinichthys*	4	1	3
Danaphryne sp.	4	1	3	*Porophyrne erythrodactylus*	2	0	1
Dibrachichthys melanurus	2	0	1	*Puck pinnata*	4	1	3
Dibranchus sp.	3	0	2	*Rhycherus filamentosus*	2	0	1
Diceratias pileatus round2	3	1	3	*Rhynchactis macrothrix*	4	1	3
Diceratias pileatus round3	3	1	3	*Sladenia gardineri*	3	0	1
Dolopichthys karsteni	4	1	3	*Solocisquama* sp.	3	0	2
Echinophryne crassispina	2	0	1	*Spiniphryne*	4	1	3
Echinophryne mitchellii	2	0	1	*Sympterichthys* sp.	2	0	1
Fowlerichthys avalonis	2	0	1	*Tathicarpus butleri*	2	0	1
Gigantactis ios	4	1	3	*Tetrabrachium ocellatum*	2	0	1
Gigantactis vanhoeffeni	4	1	3	*Thaumatichthys pagidostomus*	5	0	3
Halicmetus reticulatus	3	0	2	*Thymichthys politus*	2	0	1
Halieutaea fumosa	3	0	2	*Zalieutes elater*	2	0	2
Halieutaea stellata	3	0	2	*Zalieutes mcgintyi*	2	0	2

Note. Character 1 describes depth preferences with states: (0) found in both fresh and marine habitats, (1) predominantly found in the Epipelagic Zone (Surface - 200m), (2) predominantly found in the Mesopelagic Zone (200m - 1000m), (3) predominantly found in the Bathypelagic Zone (1000m - 3000m), and (4) predominantly found in the Abyssopelagic Zone (3000m - 6000m). Character 2 describes habitat with states: (0) predominantly found on benthic surfaces and (1) predominantly found in pelagic habitats. Character 3 describes luring strategy with states: (0) no luring strategy used and/or absent, (1) mechanical, (2) chemical, and (3) bioluminescent.

Figure 2.5.

Parsimony character state analysis of habitat transitions of anglerfishes



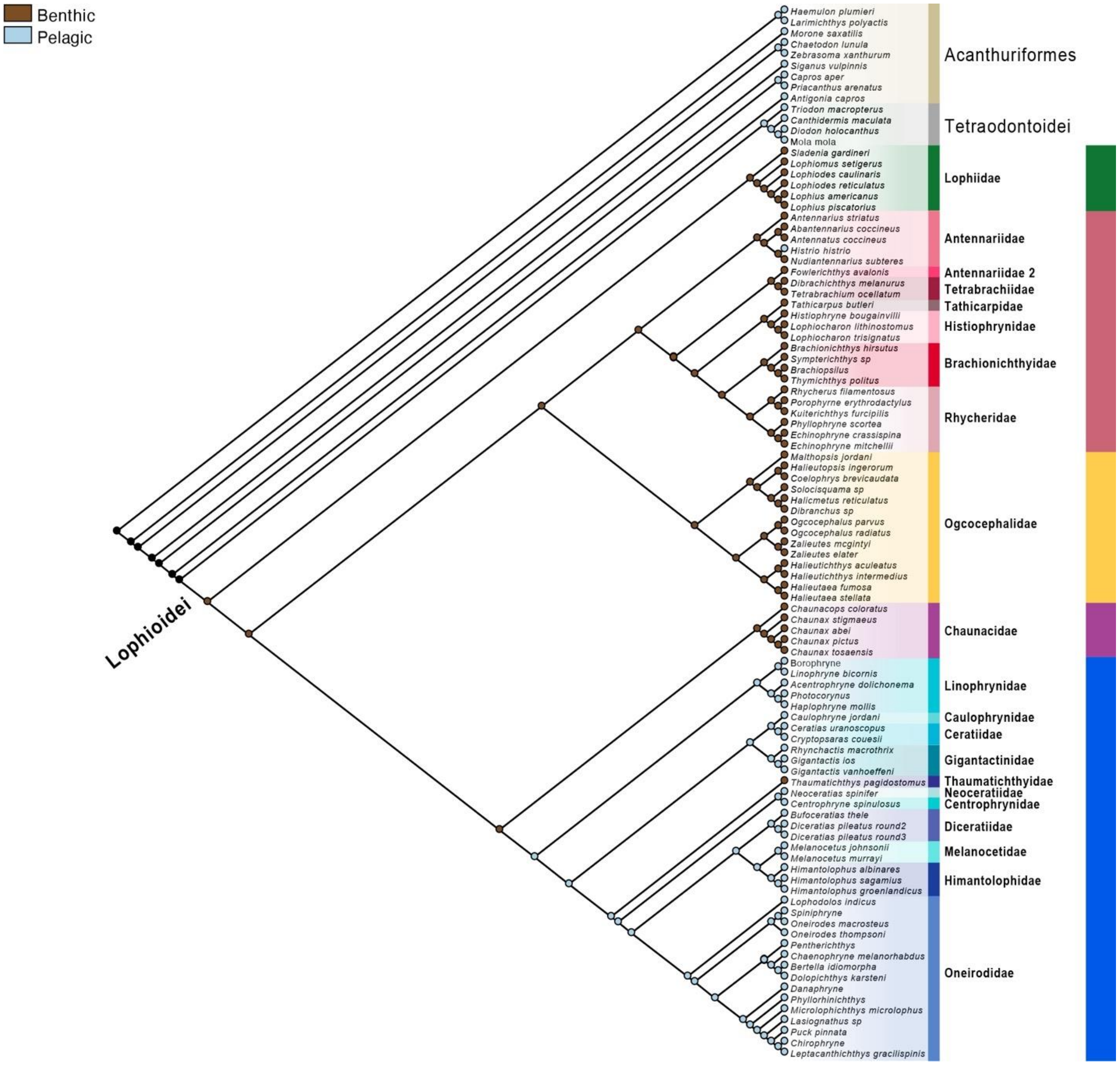
Note. Parsimony character state analysis of habitat transitions of anglerfishes based on Total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data.

Habitat Distributions and Preferences of Lophioidei

A parsimony character state analysis inferred benthic and pelagic preferences of anglerfishes (Lophioidei) (see Figure 2.6). The outgroup of Tetraodontoidei was inferred to occupy pelagic habitats. The Lophioidei common ancestor was inferred to be found in benthic habitats (see Figure 2.6). A single transition to benthic habitats from pelagic habitats was found in Thaumatichthyidae (see Figure 2.6). Two independent transitions to pelagic habitats from benthic habitats were found in (1) the Antennariidae genus *Histrio* and (2) the deep-sea anglerfishes (Ceratoideo) (see Figure 2.6).

Figure 2.6.

Parsimony character state analysis of benthic or pelagic preferences of anglerfishes



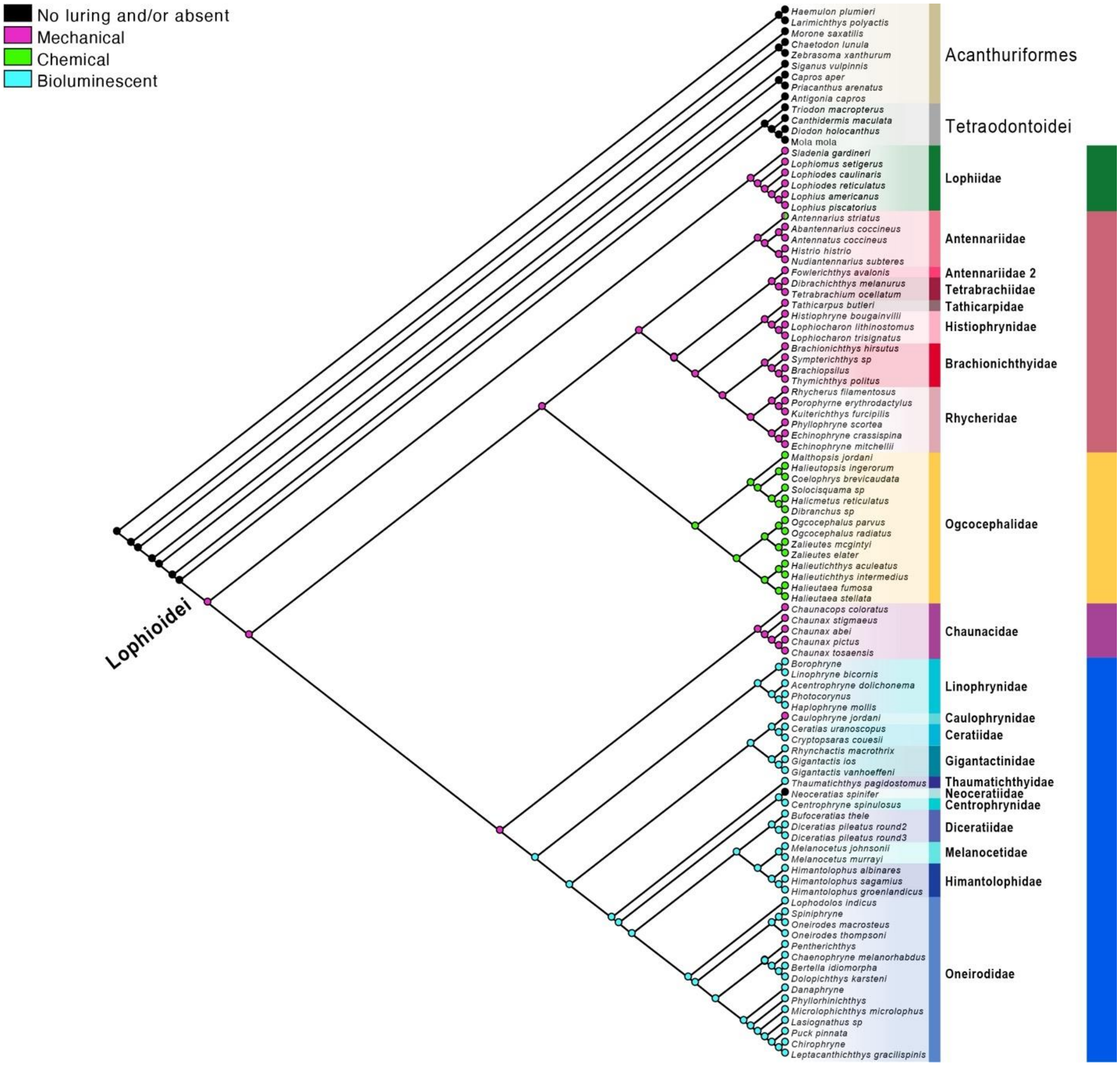
Note. Parsimony character state analysis of benthic or pelagic preferences of anglerfishes based on Total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data.

Luring Strategies of Lophiodei

A parsimony character state analysis inferred the luring strategies of anglerfishes (Lophioidei) (see Figure 2.7). The outgroup of Tetraodontoidei was inferred to lack a first dorsal fin-spine luring apparatus. The Lophioidei common ancestor was inferred to use a mechanical luring strategy and is found in Lophioideo, Antennarioideo, Chaunacoideo, and independently evolved in the Ceratoideo family Caulophrynidae (see Figure 2.7). Chemical luring evolved two independent times found in (1) Ogcocephaloideo and (2) the Antennariidae species *Antennarius striatus* which exhibits both mechanical and chemical luring strategies (see Figure 2.7). There is a single evolutionary event of bioluminescence found in the deep-sea anglerfishes (Ceratoideo) (see Figure 2.7). Bioluminescence has been lost in Caulophrynidae. The luring apparatus used by anglerfishes was lost entirely in the deep-sea anglerfish family Neoceratiidae) (see Figure 2.7).

Figure 2.7.

Parsimony character state analysis of luring strategies of anglerfishes



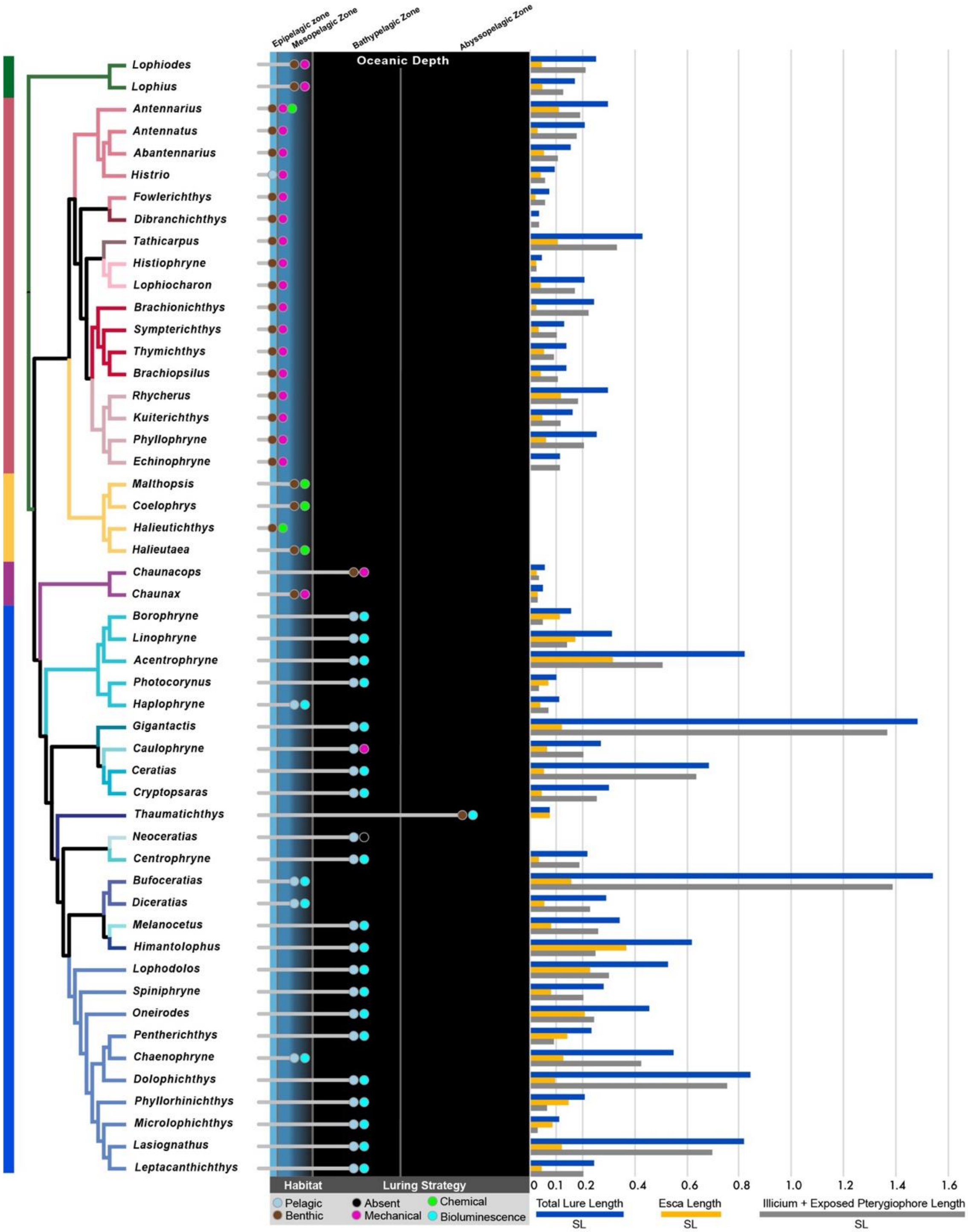
Note. Parsimony character state analysis of luring strategies of anglerfishes based on Total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data.

Lure Lengths of Lophiodei

A genus level total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data was used to lure lengths found in the anglerfishes (Lophioidei) in contrast to depth preferences, habitat preferences, and luring strategies (see Figure 2.8). The deep-sea anglerfishes had an average TTL / SL ratio ~2x (44.3%) compared to the monkfishes (Lophioideo) (20.8%) and the frogfishes (Antenarioideo) (18.6%) (see Table 2.2 and 2.3). The deep-sea anglerfishes had an average TTL / SL ratio ~10x compared to the coffinfishes (Chaunacoideo) (4.7%) (see Table 2.2 and 2.3). The highest TTL / SL ratios were found in the deep-sea anglerfish genera *Giganactis* (148%) and *Bufoceratias* (154%) (see Figure 2.8 and Table 2.2). In epipelagic habitats, anglerfishes in benthic habitats (19.2%) were nearly ~2x in length compared to pelagic lures (8.9%) (see Figure 2.8 and Table 2.4). The lowest luring lengths were found in bathypelagic benthic habitats (5.1%) compared to the highest luring lengths found in meso- and bathypelagic anglers in pelagic habitats (61.9% and 43.3%) (see Figure 2.8 and Table 2.4). Bioluminescent lures (46%) were found to be nearly ~2x in length compared to mechanical lures (19.2%) (see Figure 2.8).

Figure 2.8.

A genus-level phylogeny of anglerfishes (Lophioidei)



Note. A genus-level phylogeny of anglerfishes (Lophioidei) based on Total evidence maximum likelihood tree derived from UCE, mitochondrial genome, and morphological data.

Table 2.2.

Lure mensural value comparisons

Suborder	Family	Genus	TLL / SL	ES % of TLL
Lophoidei	Lophiidae	*Lophiodes*	25%	16%
		Lophius	17%	27%
Antennarioidei	Antennariidae	*Antennarius*	29%	36%
		Antennatus	20%	11%
		Abantennarius	15%	32%
		Histrio	9%	39%
		Fowlerichthys	7%	21%
	Tetrabrachiidae	*Dibrachichthys*	3%	0%
	Tathicarpidae	*Tathicarpus*	43%	23%
	Histiophrynidae	*Histiophryne*	4%	54%
		Lophiocharon	20%	18%
	Brachionichthyidae	*Brachionichthys*	24%	8%
		Sympterichthys	13%	22%
		Thymichthys	13%	35%
		Brachiopsilus	13%	26%
	Rhycheridae	*Rhycherus*	29%	39%
		Kuiterichthys	16%	28%
		Phyllophryne	25%	22%
	Rhycheridae	*Echinophryne*	11%	0%
Chaunacoidei	Chaunacidae	*Chaunacops*	5%	35%
		Chaunax	4%	53%
Ceratoidei	Linophrynidae	*Borophryne*	16%	71%
		Linophryne	31%	56%
		Acentrophryne	82%	38%
		Photocorynus	10%	69%

	Haplophryne	11%	35%
Gigantactinidae	*Gigantactis*	148%	8%
Caulophrynidae	*Caulophryne*	26%	23%
Ceratiidae	*Ceratias*	68%	7%
	Cryptopsaras	30%	14%
Thaumatichthyidae	*Thaumatichthys*	7%	100%
Neoceratiidae	*Neoceratias*	0%	0%
Centrophrynidae	*Centrophryne*	22%	14%
Diceratiidae	*Bufoceratias*	154%	10%
	Diceratias	28%	19%
Melanocetidae	*Melanocetus*	34%	23%
Himantolophus	*Himantolophus*	62%	59%
Oneirodidae	*Lophodolos*	53%	43%
	Spiniphryne	28%	28%
	Oneirodes	45%	46%
	Pentherichthys	23%	61%
	Chaenophryne	55%	23%
	Dolopichthys	84%	11%
	Phyllorhinichthys	21%	71%
	Microlophichthys	11%	75%
	Lasiognathus	82%	15%
	Leptacanthichthys	24%	17%

Note. Total Lure Lengths (TLL) and Escae (ES) lengths in comparison to Standard Lengths (SL).

Table 2.3.

Infraorder comparisons of Total Lure Length (TL) / Standard Length (SL).

	Average TLL / SL	Standard Deviation
Lopioideo	20.8%	0.058
Antennarioideo	18.6%	0.098
Ogcocephaloideo		
Chaunacoideo	4.7%	0.006
Ceratoideo	44.3%	0.396

Table 2.4.

Depth and habitat comparisons of Total Lure Length (TL) / Standard Length (SL).

		Average TLL / SL	Standard Deviation
Epipelagic Zone			
	Benthic	19.2%	0.098
	Pelagic	8.9%	0
Mesopelagic Zone			
	Benthic	15.3%	0.104
	Pelagic	61.9%	0.640
Bathypelagic Zone			
	Benthic	5.1%	0
	Pelagic	43.3%	0.342
Abyssopelagic Zone			
	Benthic	7.1%	0

Discussion

Evolutionary Patterns of Depth Preferences, Habitat Transitions, and Lure Type

This study aims to understand the evolutionary patterns associated with habitat transitions of anglerfishes (Lophioidei) and the impact on their lure lengths and types. In Epipelagic habitats (Surface – 200m), frogfishes (Antennaroideo) and some batfishes (Ogcocephaloideo), have been successful in their diversification and luring strategies (see Figure 2.2.5 and 2.8). The sargassum frogfish *Histrio* is the only pelagic anglerfish found in this oceanic layer (see Figure 2.6 and 2.8), hunting within the ecosystem of sargassum algae floating near the surface (Pietsch and Arnold, 2020). Other frogfishes found in benthic habitats are ambush predators and use their cryptic patterns enhanced by attached sponges, algae, and detritus to stalk their prey on both muddy, sandy, and rocky landscapes. Frogfishes wave their lures in a variety of ways to entice their prey to enter their strike zone and this is predominantly mechanical, a physical lure except in *Antennarius striatus* (Pietsch and Grobecker, 1987) where chemical luring has independently evolved in the infraorder (see Figure 2.7 and 2.8).

In Mesopelagic habitats (200m – 1000m), monkfishes (Lophioideo), some batfishes (Ogcocephaloideo), some coffinfishes (Chaunacoideo), and some deep-sea anglerfishes have depth preferences on the continental shelves or the continental slope (see Figure 2.5, 2.6 and 2.8). The Mesopelagic Zone is the beginning of the aphotic zone where daylight penetrating through the water column begins to dissipate. The stem lineage of Lophioidei, the monkfishes, is found with a mechanical luring strategy which occurs throughout the frogfishes, coffinfishes, and *Caulophryne* (see Figures 2.7 and 2.8). In batfishes, there is a single widespread evolutionary development of chemical attractant lures (Combs, 1973; Nagareda and Shenker, 2009) (see Figures 2.7 and 2.8) found throughout the family and in conjuncture with their benthic lifestyle with downward facing mouths, more than likely serves in luring invertebrates found in the substrate. In this zone, the monkfishes, batfishes, and coffinfishes are benthic and have evolved numerous evolutionary adaptations to help thrive in this habitat including dorsoventrally flattened bodies, modified pectorals for seafloor locomotion, and modifications to increase buoyancy to reduce energy for locomotion (Long and Farina, 2019). Several deep-sea anglerfishes including Diceratidae and *Chaenoophryne* (Oneiroidae) were caught frequently at these depths in pelagic habitats.

The Bathypelagic zone (1000m - 3000m) is dominated by the deep-sea anglerfishes (Ceratoideo) (see Figures 2.5, 2.6, and 2.8) and is where bioluminescence as an aid in luring is predominantly found There is a single evolutionary event of bioluminescent lures found in the anglerfishes at Ceratoideo with a loss of bioluminescence found in the fanfin anglerfishes (Caulophrynidae) which uses a mechanical luring strategy (see Figures 2.7 and 2.8). Linophrynidae also has evolved bioluminescent barbels, which may aid in luring and communication. There is also a loss of the luring apparatus altogether in Neoceratiidae (see Figure 2.7 and 2.8), which has enlarged teeth for gripping prey and lacks any other adaptations used for prey attraction.

The Abyssopelagic Zone (3000m - 6000m) only encounters a single family of ceratoid angler, the wolftrap anglerfish (Thaumatichthyidae). This family is also the only benthic ceratoid angler found in deep-sea benthic trawls (see Figures 2.5, 2.6, and 2.8). The lures of this family have migrated so far anteriorly that the luring apparatus is housed in the mouth of the wolftrap angler.

Evolution of Lure Length

The components of the luring apparatus (pterygiophore, illicium, esca) vary in length and their function with notable examples found in the batfishes that can protrude their lures from an illicial cavity and *Gigantactis* a ceratoid angler that can orient themselves upside-down to pose their lure towards the seafloor in a trolling behavior (Moore, 2002). This study investigated the standard lengths of anglerfishes in comparison to their lure lengths to study evolutionary patterns associated with the depth of taxa (see Figures 2.5 and 2.8, Tables 2.2, 2.3, and 2.3). The extendable lures in Ogcocephaloideo were difficult to measure due to their formalin fixation and photographs of these fishes typically do not illustrate the extension of these lures, therefore lure measurements of batfishes were not included in this study. Overall, I found that Ceratoideo has the largest total lure length compared to standard lengths of 44%, double that of Lophioideo and Antennaroideo, and nearly ten times longer than Chaunacoideo indicating deep-sea pelagic habitats have facilitated longer lures in the anglerfishes (see Table 2.1). The longest lure to standard body length is found in *Gigantactis* (148%) and *Bufoceratias (*154%). By comparison, anglerfishes Meso and Bathypelagic depths had higher TLL/SL lengths in pelagic anglers compared to benthic anglers (see Table 2.2). Benthic lures found in Epipelagic depths were found to be nearly twice as large as the pelagic lures of *Histrio*. The lures of Abyssopelagic *Thaumatichtys* were found to be only 7.1% of the standard length, more than likely due to the lure being fixed within the mouth of the wolftrap to prevent self-biting or choking on a long lure.

Bioluminescent lures were also found to be quantifiably longer in comparison to body lengths (46%) compared to mechanical non-chemical/bioluminescent lures (19.2%). This elongation in bioluminescent lures in ceratoid fishes raises the question if the lures serve a more communication-oriented role in addition to luring rather than a lure-oriented role. Though not described in this study, the escae of the ceratoid anglers are by far more complex in both their anatomy and morphology (Bertelsen, 1951; Munk et al., 1998, Pietsch, 2009) compared to the mechanical lures found in monkfishes (Lophiidae) and frogfishes (Antennaroiodeo) and would benefit from a morphological character state study to investigate the homology and evolution of those lures. Nonetheless, the lures of the Lophoidei are extremely successful in speciation of the lineage, only being lost in one genus *Neoceratias* and the reduction or loss of the lure would've otherwise been more widespread. The evolutionary modifications to the lures of these fishes are astounding, and though this study covered three luring types: mechanical, chemical attractant, and bioluminescent, the role of understudied phenomenon such as biofluorescence and mimicry still raise further questions in their role in luring and communication in the anglerfishes.

The escae of anglerfishes indicate signs that mimicry aids the lures of these fishes to be successful in their hunting behaviors. Lütken (1871) was the first to suggest that the escae of ceratoid fishes could be mimicking to aid in luring prey. My examinations of the lures of anglerfishes at the Natural History Museum of Los Angeles County (LACM) did leave me to believe that the lures of these fishes did resemble other organisms that could be used as bait for the anglerfish prey (see Figure 2.5). *Lophiocharon trisignatus* (LACM 54171-1) resembled a flatworm or swimming ribbonworm, *Centrophryne spinulosa* (LACM 31105-24) and *Ceratias tentaculatus* (LACM 11025-7) resemble small species of Decapodiformes (squids), and the cutaneous filaments of the esca of *Antennarius avalonis* (LACM 49991-1) resembled krill and their paired swimming legs used for locomotion.

Conclusions

The fascinating lineage of anglerfishes makes for an excellent case study in studying the effects on the impacts on the evolution of a group when found widespread across oceanic depths, and curcumin to different extreme and different oceanic conditions. Overall, it was found that the anglerfishes (Lophioidei) are found widespread across benthic and pelagic habitats from inshore to deep-sea depths (6000m). The luring apparatus of the anglerfish which is comprised of the exposed pterygiophore (in some taxa), the illicium, and the escae is found to have three luring strategies: mechanical, chemical, and bioluminescent. There were two independent evolutionary events of developing a mechanical luring strategy, two independent evolutionary events of developing a chemical luring strategy, and a single event found widespread through the deep-sea anglerfishes of bioluminescent luring strategies. The overall lure lengths of the anglerfishes are highly variable throughout the suborder and predominantly serve in deceiving prey with a unique morphological component (escae) with/without the aid of chemical attractants or bioluminescence into being enticed into the feeding zones of these horrors of the ocean.

Chapter III

Evolution of Anglerfish Body Shape and Luring Capabilities

Introduction

Movement range in Lophioidei and luring behavior

Anglerfishes are renowned for their ability to entice prey using anatomical modifications to the first dorsal-fin spine (pterygiophore, illicium, and esca). This modification is found across the radiation and has only been lost in Neoceratidae. Anglerfishes and their allies are found in benthic and pelagic habitats ranging from inshore epipelagic to abyssopelagic depths (6000 m), resulting in numerous modifications to the luring apparatus including and not limited to chemical attractants, bioluminescence, biofluorescence, and mimicry. The evolution of mechanical, chemical, and bioluminescent lures was explored in Chapter 2, but the behaviors of how the lures are applied in luring and feeding strategies at different depths are not fully understood. A handful of prior studies have described in full detail the luring patterns of anglerfishes, predominantly in epi- and meso- pelagic frogfishes (Antennarioideo) Pietsch and Grobecker (1987) and batfishes (Ogcocephaloideo) (Nagareda and Shenker, 2009).

To attract prey into the strike zone of the anglerfish, the lure must (1) compel the prey item to believe the escae is a form of food or potential prey and (2) must direct the enticed prey towards the anglerfish and/or the strike zone. Anglerfishes located in benthic habitats may have their prey located near the substrate, as found in batfishes (Ogcocephaloideo) who feed primarily on benthic invertebrates found on or beneath the benthic substrate or may be located superiorly, laterally, or anteriorly. The behavior of using a dorsal-fin modification for luring is found in one other fish lineage *Chauliodus* (Stomiidae) which has independently evolved a modification to its first dorsal fin-ray, with luminous tissue on the distal tip hypothesized for luring in deep-sea habitats. In the anglerfishes (Lophioidei), the combination of cryptic camouflage patterns, the slow and steady movements of these sit-and-wait ambush predators, and the lures of these fishes' aid in the feeding success of these oceanic predators, and the bioluminescent lures of the deep-sea anglerfishes have potentially aided in the increased speciation of this lineage (Davis et al., 2016).

Geometric morphometrics is a powerful tool in quantifying body shape variation across lineages of fishes that have evolved in response to different and varying habitats (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; Maile et al., 2020; Martin et al., 2022). 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; Farr´e et al., 2016; Tuset et al., 2018; Martin et al., 2022; Martinez et al., 2022), 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; Maile et al., 2020; Martin et al., 2022). The Lophioidei is an ideal lineage for studying the evolution of body shape in marine environments, as they are found from inshore to deep-sea depths both in benthic and pelagic habitats and exhibit a variety of body shape morphologies.

The focus of this study is to quantitatively investigate the body shapes of anglerfish taxa using a geometric-morphometric approach to infer body shape changes across habitat transitions in the anglerfish lineage while also examining the rotational motions of the lures of these fishes. In this study we address the following questions: (1) Are there quantifiable differences in body shapes found in Lophioidei? (2) What are the luring ranges of anglerfishes associated with lure types and habitat preferences? (3) Do anglerfish body shapes have a significant impact on their luring ranges and types?

Materials and Methods

Taxonomic Sampling

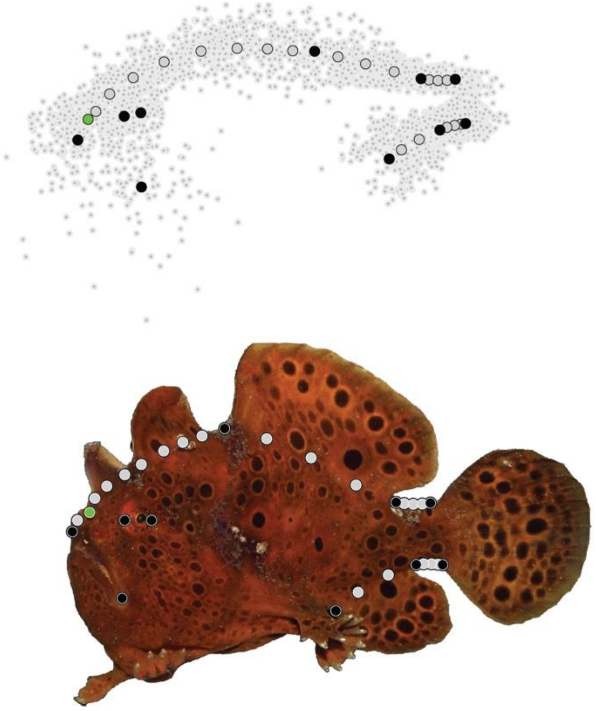
Physical examinations of adult anglerfish species used in this study include material from the Natural History Museum of Los Angeles County (LACM). Additional photographs of anglerfish specimens were provided by request from the Museum für Naturkunde (ZMB), Muséum national d'Histoire naturelle (MNHN), and the Australian Museum (AMS). Additional photographs of anglerfish species were included in analyses from GBIF.org (2023), Sketchfab.com (2023), *Oceanic Anglerfishes Extraordinary Diversity in the Deep Sea*, *Frogfishes: Biodiversity, Zoogeography, and Behavioral Ecology*, Fishbase (Froese and Pauly, 2018), *Fishes: A guide to their Diversity*, and peer review publications which are are listed in the Material Examined section. Any specimens with missing or highly damaged lures due to preservation were excluded from this study. Males of Ceratoideo were also excluded from this study due to their extreme physical sexual dimorphisms across some taxa. Museum acronyms follow Sabaj (2020). In total, 111 specimens representing 102 species, 51 of 68 genera, and all families are included in this chapter. Specimens physically examined were photographed under white lighting conditions using a Canon EOS Rebel T7i DSLR camera equipped with a macro lens while positioned on their lateral side facing left. Additionally, photographs of the escae with scales were photographed under the same white light conditions using a 100 mm macro lenses.

Geometric Morphometrics and Statistical Analyses

A landmark-based geometric morphometric approach was used to quantify Lophioidei body shapes. Using the R package steromorph (Olsen and Westneat, 2015), 11 homologous landmarks (black circles in Figure 3.1) were placed at the (1) anterior-most tip of the upper premaxilla, (2) posterior-most tip of the lower maxilla (3) anterior margin of the eye (4) posterior margin of the eye (5) anterior insertion of the dorsal fin (6) posterior insertion of the dorsal fin (7) dorsal insertion of the caudal peduncle (8) ventral insertion of the caudal peduncle (9) posterior insertion of the anal fin (10) posterior insertion of the anal fin (11) margin insertion of illicium or pterygiophore (green circle in Figure 3.1), followed by 16 sliding semi-landmarks were distributed across five defined curves along anglerfish body margins (see Figure 3.1) as used in prior studies (McMahan et al., 2011; Maile et al., 2020; Martin et al., 2022). To prevent the inclusion of shape variation due to stomach fullness (Martinez and Sparks, 2017) or stomachs altered due to dissections, we excluded semi-landmarks around the stomach area in our analyses (see Figure 3.1).

Figure 3.1.

Geometric morphometric landmark placement



Note. Position of fixed homologous landmark (black and green) and sliding semi-landmarks (grey) locations used in this study.

Body shape analyses follow Maile et al. (2020) and Martin et al. (2022). The R package geomorph v. 4.0.5 (Adams et al., 2019) was used to perform a generalized Procrustes analysis (GPA) using bending energy for semilandmark alignment. Specimen shape values and centroid sizes were averaged by genera. The total evidence phylogenetic analysis of Lophioidei from Chapter 1 was used to incorporate averaged Procrustes variables in a phylogenetic regression consisting of 10,0000 iterations using the geomorph function 'procD.pgls' (Adams et al., 2019)to test the allometric effect between body shape and specimen size. Under residual randomization, regression resampling was calculated using residual shape values that were obtained from a reduced model and then randomly assigned to the original linear model. After removing the observed variation in shape caused by differences in specimen size and phylogenetic influence using residuals from this technique, a principal component analysis (PCA) was plotted to visualize the shape data of anglerfishes. We calculated morphological disparity using the geomorph function 'morphol.disparity' (Adams et al., 2019)to compare potential differences in the amount of body-shape variability among anglerfishes, infraorders, depth preferences, pelagic/benthic preferences, and lure types.

Anglerfish Luring Degrees of Range

Luring ranges were measured based on rotational motions degrees from between 0 and 360 degrees and were measured between a forward-stop position and a backward/resting-stop position. Forward-stop positions indicate the potential position of the tip of the esca or tip of the illicium (in escae lacking taxa) when in a forward extension. Backward/resting-stop positions indicate the potential position of the esca or illicium (in escae lacking taxa) when in a backward luring extension and/or a position of rest laying on the forehead or dorsal surface of the body. The point of rotation was positioned on the insertion point of the illicium and/or exposed pterygiophore. The forward-stop positions were restricted based on a series of parallel and nonparallel transverse lines. Parameters of luring forward-stop and backward/resting-stop positions were based on photographs and videos of live and deceased specimens and from physical lure examinations of anglerfish taxa to create a set of infraorder and family parameters. Batfishes (Ogcocephaloideo) exhibit a rectilinear luring motion and were excluded from this analysis. Parameters for the forward-stop lure positions are described below and backward/rest-stop lure positions do not extend below the dorsal margin of the body unless defined below.

Lophioideo:

(1) Forward-stop position does not extend below a parallel transverse line intersecting at the uppermost tip of the premaxilla (see Figures 3.4 and 3.5, Lophiidae).

Antennarioideo:

(1) Forward-stop position does not extend below a transverse line between the lure insertion point and uppermost tip of the premaxilla (see Figures 3.4 and 3.5, Antennariidae).

Chaunacoideo:

(1) Forward-stop position does not extend beyond a transverse line, perpendicular to the body margin with an insertion at the base of the illicium (see Figures 3.4 and 3.5, Chaunicidae).

Ceratoideo:

Linophrynidae:

(1) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the lure (see Figures 3.4 and 3.6, Linophrynidae: *Acentrophryne*, *Borophryne*, and *Linophryne*)

(2) Forward-stop and backward/resting-stop positions are symmetric, both defined by a transverse line between the insertion of the lure and the lateral-most marginal sides of the esca (see Figures 3.4 and 3.6, Linophrynidae: *Haplophryne* and *Photocorynus*)

Gigantactinidae:

(1) Forward-stop position does not extend below a transverse line originating at the insertion of the uppermost tip of the premaxilla and extends at 150 radial degrees upward (see Figures 3.4 and 3.6, Gigantactinidae)

Caulophrynidae:

(1) Forward-stop position does not extend below a transverse line originating at the insertion of the lure and extends at 210 radial degrees downward (see Figures 3.4 and 3.6, Caulophrynidae)

Ceratiidae:

(1) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the lure (see Figures 3.4 and 3.6, Ceratiidae: *Ceratias*)

(2) Forward-stop and backward/resting-stop positions are symmetric, forward-stop position is defined by a transverse line between the insertion of the lure and the uppermost tip of the premaxilla (see Figures 3.4 and 3.6, Ceratiidae: *Cryptopsaras*)

Thaumatichthyidae:

(1) Forward-stop and backward/resting-stop positions are symmetric, both defined by a transverse line between the insertion of the lure and the lateral-most marginal sides of the esca (see Figures 3.4 and 3.6, Thaumatichthyidae)

Centrophrynidae:

(1) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the lure (see Figures 3.4 and 3.6, Centrophrynidae)

Diceratiidae:

(1) Forward-stop position does not extend below a transverse line between the lure insertion point and the uppermost tip of the premaxilla (see Figures 3.4 and 3.6, Diceratiidae: *Diceratias*).

(2) Forward-stop position does not extend beyond a transverse line, perpendicular to the body margin with an insertion at the base of the illicium (see Figures 3.4 and 3.6, Diceratiidae: *Bufoceratias*).

Melanocetidae:

(1) Forward-stop position does not extend below a transverse line between the lure insertion point and uppermost tip of the premaxilla (see Figures 3.4 and 3.6, Melanocetidae)

Himantolophidae:

(1) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the lure (see Figures 3.4 and 3.6, Himantolophidae)

Oneirodidae:

(1) Forward-stop and backward/resting-stop positions are symmetric, both defined by a transverse line between the insertion of the lure and the lateral-most marginal sides of the esca (see Figures 3.4 and 3.6, Oneirodidae: *Microlophichthys* and *Phyllorhinichthys*)

(2) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the illicium (see Figures 3.4 and 3.6, Oneirodidae: *Lophodolos*)

(3) Forward-stop position does not extend below a parallel transverse line intersecting at the insertion of the upper premaxilla (see Figures 3.4 and 3.6, Oneirodidae: *Chaenophryne*, *Dolophichthys*, *Lasiognathus*, *Leptacanthichthys*, *Oneirodes*, *Pentherichthys*, and *Spiniphryne*).

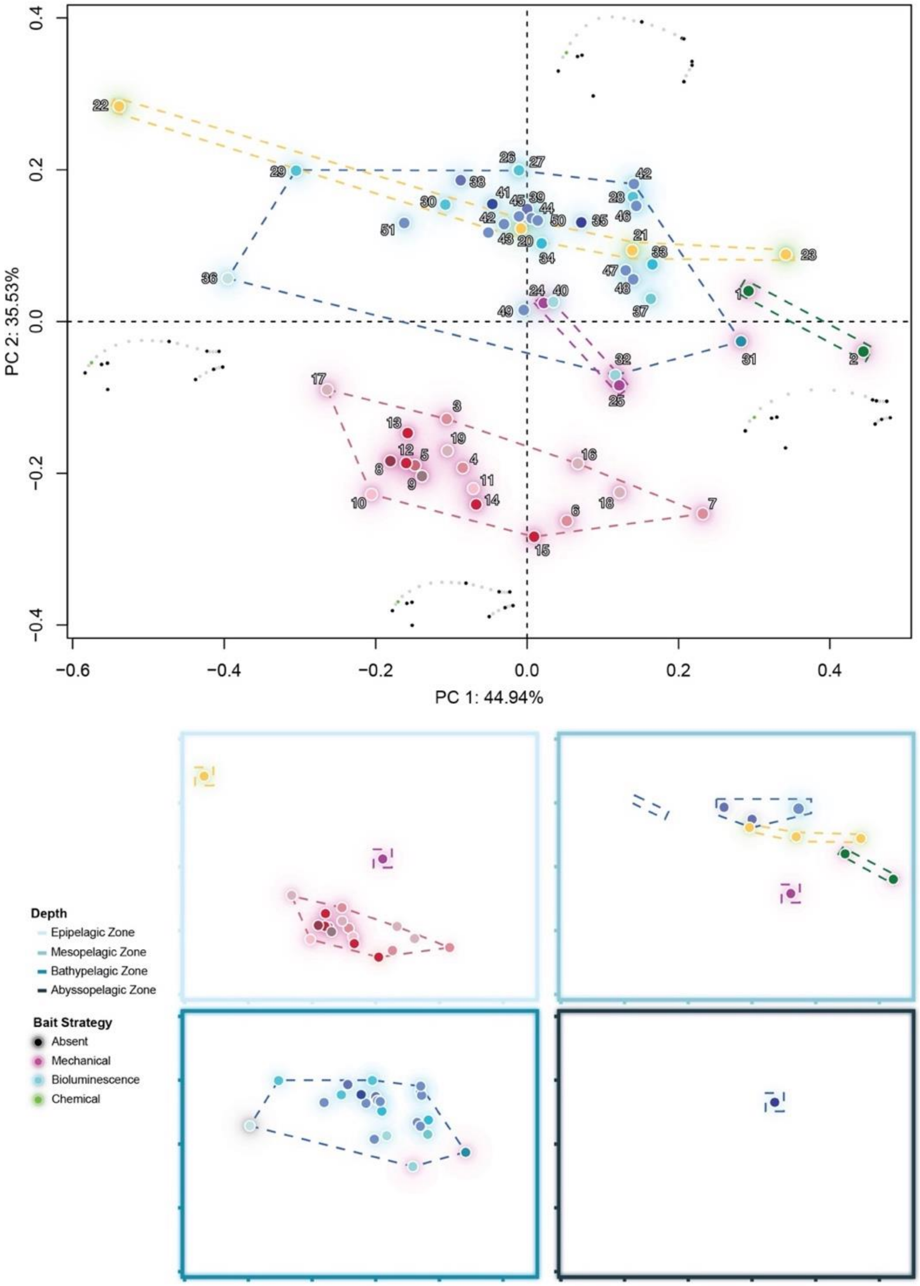
Results

Variation and Body Shape Disparity Across Anglerfishes

The consensus configuration of the relative warp analysis infers the average Lophioidei body shape as compressiform, with an insertion of the luring apparatus near the uppermost tip of the premaxilla. The dorsal fin is positioned posteriorly near the caudal peduncle and the anal fin is almost half in length compared to the dorsal fin. The results of the principal component analysis indicate variation in body shape among anglerfishes (see Figure 3.1, 3.2, 3.3, 3.5, and 3.6) with principal components (PC) 1 and 2 describing 78.47% of the overall variation. The first two principal components describe body-shape variation associated with the length and position of median fins and depth and elongation in anglerfish body shape. The morphospace on the low score extreme along PC1 includes taxa with a slightly elongated compressed compressiform body, with the dorsal fin located posteriorly, closer to the caudal peduncle (see Figure 3.2). The morphospace on the high score extreme of PC1 includes taxa with an elongated compressiform body, with the dorsal fin more posteriorly positioned to the midpoint of the body and compressed. The morphospace on the low score extreme along PC2 describes a compressiform body, with the dorsal fin located posteriorly, closer the caudal peduncle. The morphospace on the high score extreme of PC2 describes a globular and round body shape with the dorsal fin located posteriorly and the gaps between the dorsal/anal fin and caudal fin is highly reduced.

Figure 3.2.

Relative warp analysis of anglerfish body shape depicting PC1 + PC2



Note. Relative warp analysis consisting of 11 homologous landmarks and 19 sliding landmarks. Circle positions represent the average location in the morphospace for each genus. See Table 3.6 for genera labels.

Table 3.1.

Lophioidei disparity values from the morphological disparity test by Lophioidei depth preference.

	Abyssopelagic	Bathypelagic	Epipelagic	Mesopelagic
Procrustes Variance	0.0000	0.0245	0.0182	0.0201
P-Values				
Abyssopelagic	-	0.048*	0.165	0.146
Bathypelagic		-	0.459	0.632
Epipelagic			-	0.827
Mesopelagic				-

Note. Asterisks denote significant values.

Table 3.2.

Lophioidei disparity values from the morphological disparity test by Lophioidei habitat preferences.

	Benthic	Pelagic
Procrustes Variance	-	0.00681
P-Values		
Benthic	-	0.328
Pelagic		-

Note. Asterisks denote significant values.

Table 3.3.

Lophioidei disparity values from the morphological disparity test by Lophioidei luring strategies.

	Absent	Bioluminescent	Chemical Attractant	Mechanical
Procrustes Variance	0.0000	0.0208	0.00623	0.0209
P-Values				
Absent	-	0.119	0.682	0.12
Bioluminescent		-	0.064*	0.976
Chemical Attractant			-	0.069*
Mechanical				-

Note. Asterisks denote significant values.

Table 3.4.

Lophioidei disparity values from the morphological disparity test by Lophioidei infraorders.

	Antennarioideo	Ceratoideo	Chaunacoideo	Lophioideo	Ogcocephaloideo
Procrustes Variance	0.009	0.023	0.003	0.001	0.006
P-Values					
Antennarioideo	-	0.001*	0.597	0.449	0.668
Ceratoideo		-	0.052	0.034*	0.020*
Chaunacoideo			-	0.870	0.830
Lophioideo				-	0.690
Ogcocephaloideo					-

Note. Asterisks denote significant values.

Taxa within the Lophioidei generally display a dorsoflattened compressiform body shape and cluster near the high score extreme of PC1 and the middle of PC2 with a dorsal fin located posteriorly. Monkfishes had the lowest disparity in body shape (Procrustes variance 0.001) and were found to be significantly different compared to deep-sea anglerfishes (P = 0.034). The family Lophiidae was found to be tightly clustered and have compressed compressiform body shapes with reduced dorsal fins located posteriorly to the midpoint of the body (see Figure 3.2 and 3.5).

Taxa within Antennarioideo generally display a compressiform body shape and cluster near the middle of PC1 and the lower score of PC2 with wider dorsal fins located posteriorly and a moderate gap between the dorsal fin and caudal fin. Frogfishes had the second highest disparity in body shape (Procrustes variance 0.009) and were found to be significantly different compared to deep-sea anglerfishes (P = 0.001). The frogfishes displayed a wide range of quantified body shapes. Frogfishes found on the lower score of PC1 (Tetrabrachiidae, Tathicarpidae, Brachionichthyidae, Histiophryne, Rhycheriidae) had longer dorsal fins located posteriorly to the midpoint of the body. Frogfishes found on the higher score of PC1 (*Fowerichthys, Phyllophryne, Histrio, Brachiopsilus, Rhycherus*) had slightly reduced dorsal fins located posteriorly to the midpoint of the body

Taxa found in the Ogcocephaloideo generally display a slightly compressed compressiform body shape and spread between the low and high scores of PC1 across the higher score of PC2. The dorsal fins are reduced and located posteriorly to the midpoint of the body. Batfishes had the third highest disparity in body shape (Procrustes variance 0.006) and were found to be significantly different compared to deep-sea anglerfishes (P = 0.02). The family Ogcocephaloideo have a variation in body shapes ranging from compressed compressiform with longer dorsal fins located posteriorly to the midline of the body to compressiform body shapes with reduced dorsal fins located posteriorly to the midline of the body (see Figure 3.23.2 and 3.5).

Taxa found in the Chaunacoideo generally display a compressiform body shape and are found near the consensus shape of the Lophioidei. The coffinfishes had the second lowest disparity in body shape (Procrustes variance 0.003) and were not found to be significantly different compared to other anglerfish infraorders. The family Chaunacidae were found to be tightly clustered and have compressiform body shapes with wide dorsal fins located posteriorly to the midpoint of the body (see Figures 3.2 and 3.5).

In general, taxa within the deep-sea anglerfish infraorder Ceratoideo exhibit a globular compressiform body shape and were located on or around the censuses shape of the Lophioidei with dorsal fins located posteriorly to the midpoint of the body and a highly reduced caudal peduncle. Overall, anglerfishes in Ceratoideo had a higher disparity in body shape (Procrustes variance 0.023) compared to the monkfishes (Lophioideo) (P = 0.034), frogfishes (Antennarioideo) (P = 0.001), and the batfishes (Ogcocephaloideo) (P = 0.02) as seen in Table 3.4). The deep-sea anglerfishes displayed a wide range of quantified body shapes. Body shapes found on the low score of PC1 have slightly elongated compressiform bodies as found in *Photocorynus*, *Neoceratias*, *Lasiognathus*, and *Thaumatichthys*. Other deep-sea anglerfishes have slightly globular compressiform body shapes with a reduction in the caudal peduncle and a dorsal fin located posteriorly to the midline of the body.

Phylomorphospace

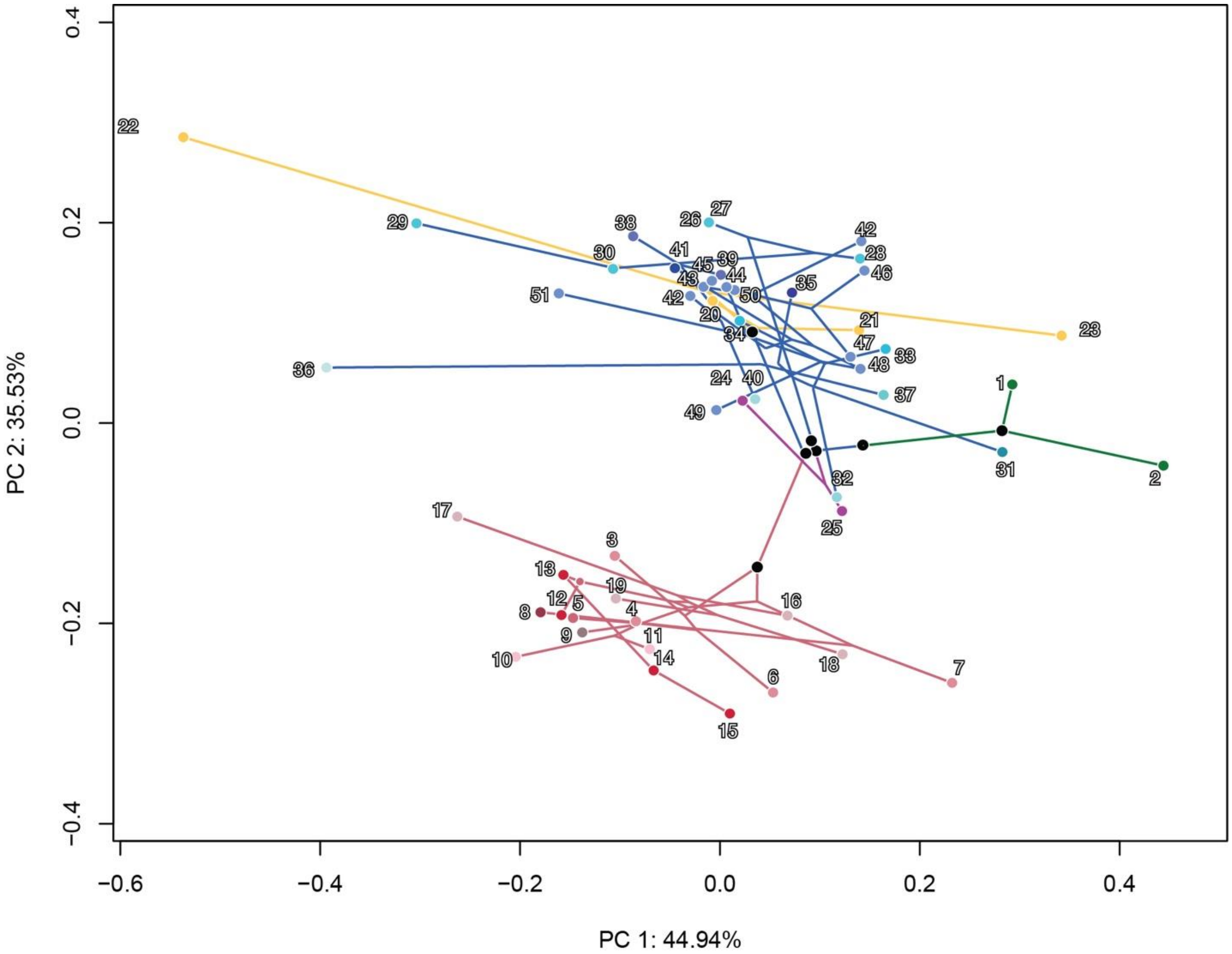
In most instances, closely related genera within infraorders tended to cluster nearer to each other in shape space with less closely related taxa being more morphologically different (see Figure 3.3). For example, in some taxa in the deep-sea anglerfishes (Ceratoideo), similar body shapes of slight globular compressiform bodies were found in Diceratiidae, Himantolophidae, and Melanocetidae. Still in the deep-sea Ceratoideo, there are closely related lineages that are significantly different (e.g. *Gigantactis, Thaumatichthys, Caulophryne, Borophryne,* and *Himantolophus*).

Variation of Body Shape Across Marine Habitats

The relative warp and disparity analysis indicate a quantitative differentiation in body shape across different depth preferences and habitats. Epipelagic anglerfishes in the infraorders Antennaroideo, Ogcocephaloideo (*Halieutichthys*), and Chaunacoideo (*Chaunax)* are found in two distinct clusters. Antennaroideo and Chaunax possess compressiform bodies and reside in a single cluster found near the low score of PC2 and have a slight spread between the low and high scores of PC1. *Halieutichthys* is found on the low score of PC1 and the high score of PC2 which has a similar slightly extended compressiform body (see Figure 3.2 and 3.5). Epipelagic anglerfishes had the second lowest overall Procrustes variance of the four depth preferences and showed no significant differences in comparison (see Table 3.1). Mesopelagic anglerfishes in the infraorders Lophoideo, Ogcocephaloideo (*Coelophrys*, *Halieutaea*, and *Malthopsis*), Chaunacoideo (*Chaunacops*), and Ceratoideo (*Bufoceratias*, *Diceratias*, and *Chaenophryne*) are found in multiple clusters near the high scores of PC1 and PC2 (see Figure 3.2, 3.5, and 3.6). The Lophoideo and Ogcocephaloideo (Coelophrys and *Halieutaea*) in these depths have dorsoflattened compressiform bodies (see Figures 3.2 and 3.5). *Chaunacops* is found between a cluster of Lophoideo and the Antennaroideo with a slightly compressed-dorsoflattened compressiform body (see Figures 3.2 and 3.5). The deep-sea anglerfishes (Ceratoideo) at these depths have a globular compressiform body (see Figures 3.2 and 3.6). Mesopelagic anglerfishes had the second-highest overall Procrustes variance of the four depth preferences and showed no significant differences in comparison (see Table 3.1). Anglerfishes in bathypelagic depths consist only of deep-sea anglerfishes (Ceratoideo) and possess a range of globular compressiform bodies to slightly elongated compressiform bodies (*Photocorynus*, *Neoceratias*, *Lasiognathus*) found near the consensus configuration (see Figure 3.2 and 3.6). The bathypelagic anglerfishes had the highest overall Procrustes variance of the four depth preferences and showed no significant differences in comparison (see Table 3.1). The only abyssopelagic genus *Thaumatichthys* was recovered near the dorsoflattened compressiform bodies found near the Lophoideo, Ogcocephaloideo, and some deep-sea anglerfishes (Ceratoideo) (see Figure 3.2 and 3.6). Abyssopelagic anglers had the lowest overall Procrustes variance in body shape (0.000) due to a single genus occupying this depth.

Figure 3.3.

Phylomorphospace visualization



Note. Phylomorphospace plot of principal component 1 and principal component 2 incorporating total evidence phylogeny of Lophioidei. Circle positions represent the average location in the morphospace for each genus. See Table 3.6 for genera labels.

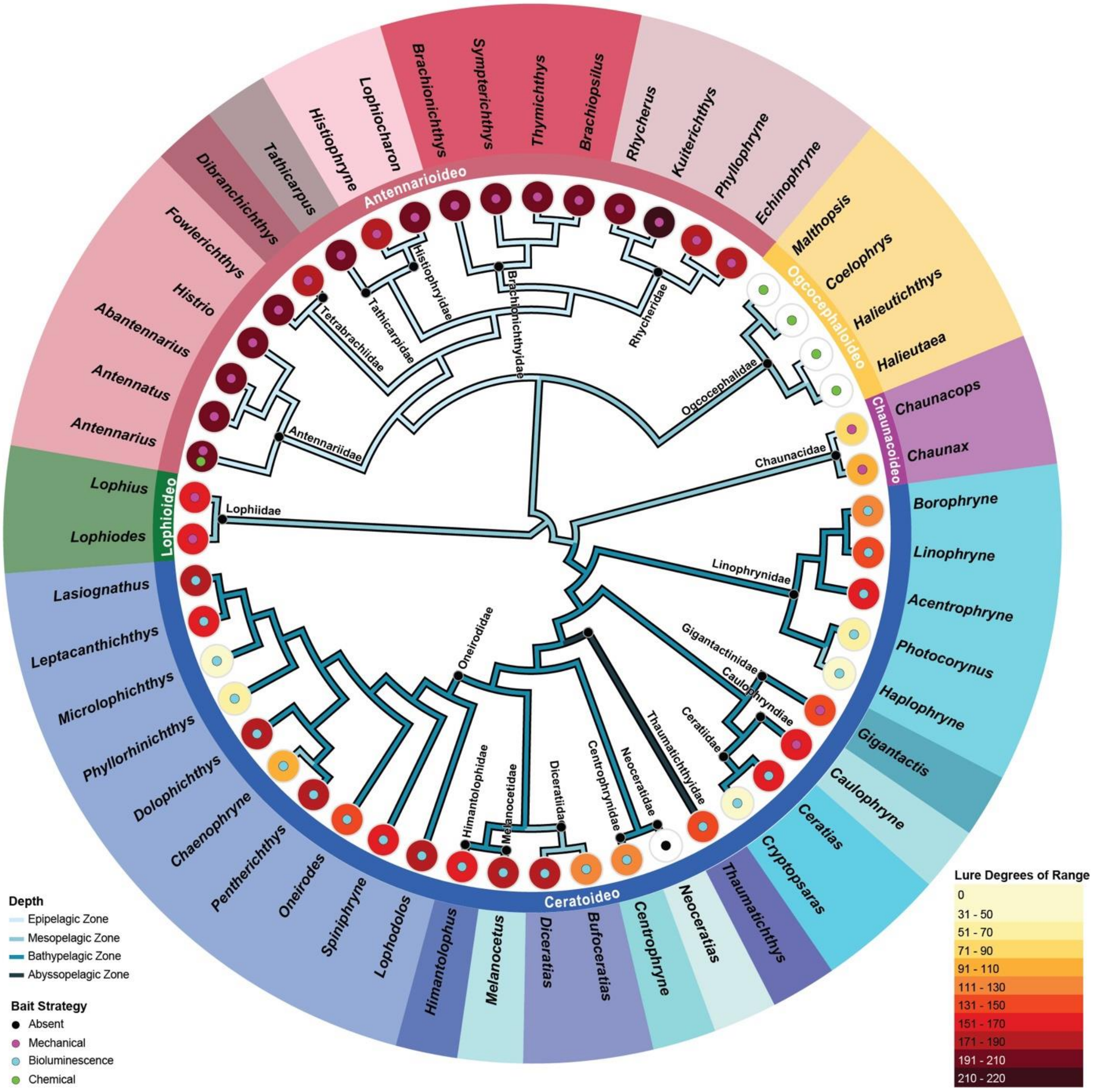
Variation in the Luring Ranges of Anglerfishes

The luring ranges of the anglerfishes (Lophioidei) were found to range between 34.15 degrees and 217 degrees in a rotational motion. The highest luring ranges were found in the Antennarioideo families Antennariidae (197.2 degrees), Tathicarpidae (197.6 degrees, Brachionichthyidae (198.6 degrees), Histiophrynidae (195.4 degrees), and Rhycheridae (196.5 degrees) (see Figures 3.4 and 3.5 and Table 3.5). The smallest lures were found in Ceratiidae (*Cryptopsaras* 34.15 degrees) and Oneirodidae (*Microlophichthys* 40.4 degrees) (see Figures 3.4 and 3.6 and Table 3.5) but on average Chaunacoideo had the lowest family average of 87.3 degrees (see Figures 3.4 and 3.5 and Table 3.5). Mechanical luring ranges (180.8 degrees) were greater than bioluminescent luring ranges (133.1 degrees). Lure ranges found in Epipelagic depths were greater in pelagic habitats (198.4 degrees) compared to benthic habitats (198.4 degrees) (see Table 3.6). Mesopelagic and bathypelagic depths both had higher luring ranges found in pelagic habitats (Mesopelagic: 126.6 degrees; Bathypelagic: 128.2 degrees) compared to benthic habitats (Mesopelagic: 70.93 degrees; Bathypelagic: 79.15 degrees) (see Table 3.6). Abyssopelagic benthic lures were on average 132.5 degrees (see Table 3.6).

In Lophioideo, the family Lophiidae on average had a luring range of 165.0 degrees. This luring range was higher by comparison to other benthic anglerfish families including Chaunacoideo: Chaunacidae (87.3 degrees) and Ceratoidoeo: Thaumatichthyidae (132.5 degrees) (see Table 3.6). This luring range was lower by comparison to all benthic families found in Antennarioideo including Antennariidae (197.2 degrees),

Figure 3.4.

A genus-level phylogeny of lure range evolution



Note. A genus-level phylogeny from the total evidence phylogeny of Lophioidei depicting the evolution of luring lengths of anglerfishes.

Table 3.5

Averaged habitat and depth preference luring degree ranges.

Depth Zone	Luring Degree Range
Epipelagic Zone	185.5768519
Benthic	184.822549
Pelagic	198.4
Mesopelagic Zone	98.77194444
Benthic	70.93
Pelagic	126.6138889
Bathypelagic Zone	125.7545
Benthic	79.15
Pelagic	128.2073684
Abyssopelagic	132.5
Benthic	132.5

Tathicarpidae (197.8 degrees), Tetrabrachiidae (185.8 degrees), Brachionichthidae (198.6 degrees), Histiophrynidae (195.4 degrees) (see Table 3.6). The luring ranges of Lophioideo are found in mesopelagic depths in both benthic and pelagic habitats. The monkfishes (Lophioideo) with these lure lengths are in general dorsoflattened compressiform body shape and cluster near the high score extreme of PC1 and the middle of PC2 with a dorsal fin located posteriorly (see Figures 3.4 and 3.5 and Table 3.6).

In Antennarioideo, the infraorder had the highest lure ranges of all anglerfishes found in Antennariidae (197.2 degrees), Tathicarpidae (197.8 degrees), Tetrabrachiidae (185.8 degrees), Brachionichthidae (198.6 degrees), Histiophrynidae (195.4 degrees). This is higher than other benthic anglerfish families including Chaunacoideo: Chaunacidae (87.3 degrees), Ceratoidoeo: Thaumatichthyidae (132.5 degrees), and Lophioideo: Lophiidae (165.0 degrees) (see Table 3.6).

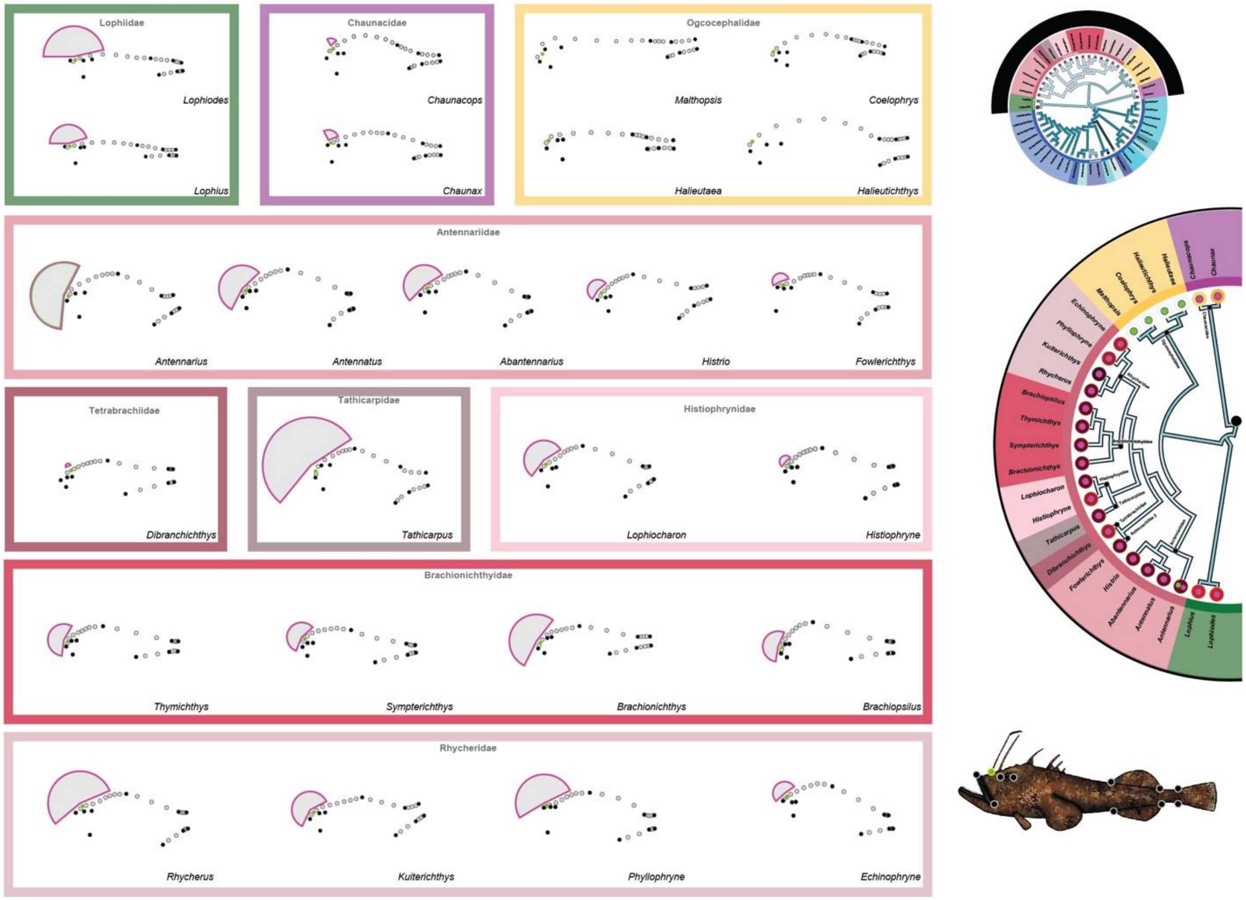
The pelagic frogofish, *Histrio histrio* had a luring range of 198.4 degrees) (see Table 3.6). The luring ranges of Antennarioideo are found in epipelagic depths in both benthic and pelagic habitats. The frogfishes (Antennarioideo) with these high lure lengths are in general a compressiform body shape and cluster near the middle of PC1 and the lower score of PC2 with wider dorsal fins located posteriorly and a moderate gap between the dorsal fin and caudal fin (see Figures 3.4 and 3.5 and Table 3.6).

In Chaunacoideo, the infraorder had the lowest average lure ranges compared to other benthic anglerfish families including Antennarioideo: Antennariidae (197.2 degrees), Tathicarpidae (197.8 degrees), Tetrabrachiidae (185.8 degrees), Brachionichthidae (198.6 degrees), Histiophrynidae (195.4 degrees), Lophioideo: Lophiidae (165.0 degrees), and Ceratoidoeo: Thaumatichthyidae (132.5 degrees) (see Table 3.6). The luring ranges of Chaunacoideo are found in meso- and bathypelagic depths in benthic habitats. The coffinfishes (Chaunacoideo) with these lure lengths are in general a compressiform body shape and are found near the consensus shape of the Lophioidei (see Figures 3.4 and 3.5 and Table 3.6).

In Ceratoideo, the infraorder had variable pelagic and benthic luring ranges. The benthic Thaumatichthyidae (132.5 degrees) had a higher luring range compared to Chaunacoideo: Chaunacidae (87.3 degrees) and had a lower luring range compared to Antennarioideo: Antennariidae (197.2 degrees), Tathicarpidae (197.8 degrees), Tetrabrachiidae (185.8 degrees), Brachionichthidae (198.6 degrees), Histiophrynidae (195.4 degrees) and Lophioideo: Lophiidae (165.0 degrees) (see Table 3.6). The highest luring ranges in pelagic deep-sea anglerfishes (Ceratoideo) were found in Melanocetidae (183.4 degrees), Caulophrynidae (183.3 degrees), Himantolophidae (167.1 degrees), Diceratiidae (141.3 degrees), and Oneiroodidae (140.47) (see Table 3.6). These luring ranges are lower than the infraorder Antennarioideo: Antennariidae (197.2 degrees), Tathicarpidae (197.8 degrees), Tetrabrachiidae (185.8 degrees), Brachionichthidae (198.6 degrees), Histiophrynidae (195.4 degrees) and except for Melanoocetidae, Caulophrynidae, and Himantolophidae, Lophioideo: Lophiidae (165.0 degrees) (see Table 3.6). The lowest luring ranges in pelagic deep-sea anglerfishes (Ceratoideo) were found in Ceratiidae (102.0 degrees), Linophrynidae (103.7 degrees), Centrophrynidae 118.5 degrees), and Gigantactinidae (133.55). These luring ranges are higher than Chaunacoideo: Chaunacidae (87.3 degrees) (see Table 3.6). The luring ranges of Ceratoideo are found across meso-, bathy-, and abyssopelagic depths in both benthic and pelagic habitats. The deep-sea anglerfishes (Ceratoideo) with these lure lengths are in general a globular compressiform body shape and were located on or around the censuses shape of the Lophioidei with dorsal fins located posteriorly to the midpoint of the body and a highly reduced caudal peduncle (see Figures 3.4 and 3.6 and Table 3.6).

Figures 3.5.

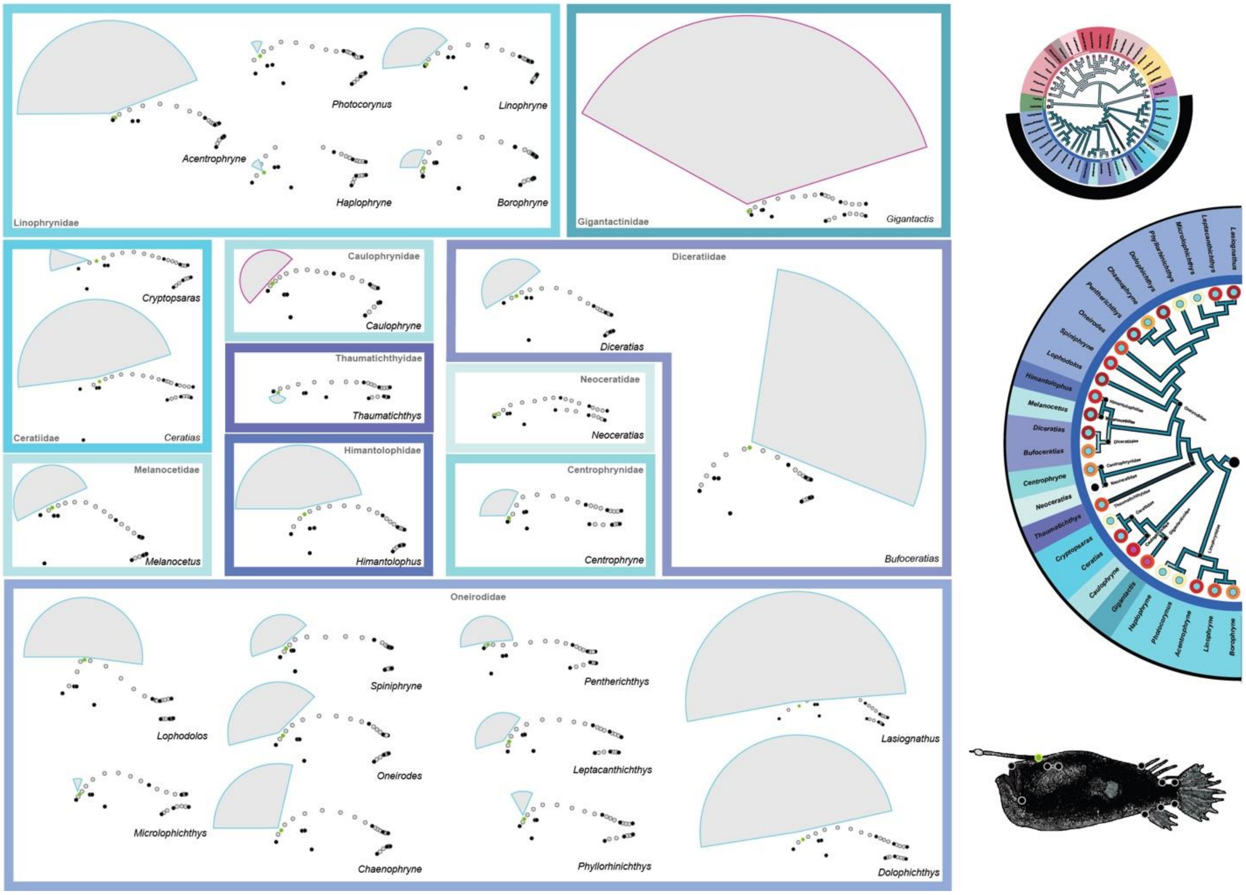
Body shapes and luring range depictions part 1



Note. Body shapes and luring range depiction of genera of Lophioideo, Chaunacoideo, and Antennarioideo. Fixed homologous landmark (black and green) and sliding semi-landmarks (grey). Colors of luring ranges associated with luring strategy.

Figures 3.6.

Body shapes and luring range depictions part 2



Note. Body shapes and luring range depiction of genera of Ceratoideo. Fixed homologous landmark (black and green) and sliding semi-landmarks (grey). Colors of luring ranges associated with luring strategy.

Table 3.6

Luring degree ranges of anglerfishes (Lophioidei).

Genera #	Suborder	Family	Genus	Luring Degree Range
1	Lophoidei	**Lophiidae**	*Lophiodes*	167.2
2			*Lophius*	162.9
3	Antennarioidei	**Antennariidae**	*Antennarius*	202.3
4			*Antennatus*	199.7
5			*Abantennarius*	194.0
6			*Histrio*	198.4
7			*Fowlerichthys*	191.7
8		**Tetrabrachiidae**	*Dibrachichthys*	185.8
9		**Tathicarpidae**	*Tathicarpus*	197.8
10		**Histiophrynidae**	*Histiophryne*	189.6
11			*Lophiocharon*	201.2
12		**Brachionichthyidae**	*Brachionichthys*	191.3
13			*Sympterichthys*	205.7
14			*Thymichthys*	202.7
15			*Brachiopsilus*	194.6
16		**Rhycheridae**	*Rhycherus*	196.95
17			*Kuiterichthys*	217
18			*Phyllophryne*	184.9
19			*Echinophryne*	187
20	Ogcocephaloidei	**Ogcocephalidae**	*Malthopsis*	0
21			*Coelophrys*	0
22			*Halieutichthys*	0
23			*Halieutaea*	0
24	Chaunacoidei	**Chaunacidae**	*Chaunacops*	79.2
25			*Chaunax*	95.5
26	Ceratoidei	**Linophrynidae**	*Borophryne*	114
27			*Linophryne*	143.8
28			*Acentrophryne*	159.4
29			*Photocorynus*	53.8
30			*Haplophryne*	47.35

31	**Gigantactinidae**	*Gigantactis*	133.5
32	**Caulophrynidae**	*Caulophryne*	183.3
33	**Ceratiidae**	*Ceratias*	169.9
34		*Cryptopsaras*	34.15
35	**Thaumatichthyidae**	*Thaumatichthys*	132.5
36	**Neoceratiidae**	*Neoceratias*	0
37	**Centrophrynidae**	*Centrophryne*	118.5
38	**Diceratiidae**	*Bufoceratias*	111.3
39	**Diceratiidae**	*Diceratias*	171.4
40	**Melanocetidae**	*Melanocetus*	183.4
41	**Himantolophus**	*Himantolophus*	167.1
42	**Oneirodidae**	*Lophodolos*	187.3
43		*Spiniphryne*	158.5
44		*Oneirodes*	149.3
45		*Pentherichthys*	186.6
46		*Chaenophryne*	103.2
47		*Dolopichthys*	176.4
48		*Phyllorhinichthys*	53.1
49		*Microlophichthys*	40.4
50		*Leptacanthichthys*	163.8
51		*Lasiognathus*	186.1

Discussion

Variation of Body Shape

This chapter aims to understand the evolution of body shape in anglerfishes (Lophioidei) that have evolved in different marine depths and habitats and that have evolved different luring strategies used by the first modified dorsal-fin luring apparatus. There is significant quantitative evidence of body-shape change among the radiation of anglerfishes and that there is distinct clustering of body shape-patterns associated with marine depth preferences and habitats (see Figure 3.2). The character state reconstruction analysis performed in Chapter 2 (see Figure 2.6 and 2.7) indicates the common ancestor of the anglerfishes (Lophioidei) was an epipelagic anglerfish found in benthic habitats with seven independent invasions into mesopelagic habitats, two independent invasions into bathypelagic habitats, and one invasion into abyssopelagic habitats and the body shapes of taxa found in these differing habitats occupy different regions of morphospace (see Figure 3.2). Anglerfishes found in epi-, meso-, and bathypelagic habitats exhibit similar body shape disparity and variance and the deep-sea anglerfish infraorder Ceratoideo exhibits a higher variance and disparity compared to other infraorders. We hypothesize that deep-sea anglerfishes (Ceratoideo) exhibit a wide range of body shapes to facilitate the transition to deep-sea depths while evolving adaptations to help broaden their evolutionary ecology into new niche spaces. The body shapes of the deep-sea anglerfishes is considerably more globular compared to other anglerfishes (Lophioideo, Antennarioideo, and Ogcocephaloideo) presumably due to the dominance these fishes have in pelagic deep-sea habitats.

The common ancestor of anglerfishes (Lophioidei) was inferred to live in epipelagic benthic habitats, and we identify those epipelagic benthic anglerfishes have a similar spread of body shape morphologies compared to meso- and bathypelagic anglerfishes indicating that these habitats have had similar impacts on the facilitation of the diversification of body shapes. The body shapes of the anglerfishes can broadly be described as a compressiform shape, with dorsal fins located posteriorly to the midline of the body. The compressiform body shape facilitates short bursts of speeds while reducing unnecessary body length (Pettersson and Hedenström, 2000; Fisher and Hogan, 2007), which would aid these ambush predators that typically are waiting patiently for prey to be enticed by their lures. Maile et al., 2020 use a geometric morphometric approach on Aulopiformes (lizardfishes), that exhibit similar habitat and depth occupations from inshore to deep-sea habitats and found that deep-sea pelagic lizardfishes had long and thin body shapes compared to cigar-shaped inshore benthic lizardfishes. In a lineage with similar depth spreads, it's fascinating to see how both the body shapes of anglerfishes and lizardfishes have evolved differently when exposed to similar extreme conditions (lack of natural sunlight, increased pressure, near freezing temperatures, etc). These results, in the scope of Martinez et al., 2021 which found higher disparities in body shapes in deep-sea habitats compared to shallow water habitats, highlight the variability and complexity of the ecological factors that drive the evolution in differing oceanic habitats.

The frogfishes (Antennarioideo) exhibit compressiform body shapes with wider dorsal fins located posteriorly and a moderate gap between the dorsal fin and caudal fin. These fishes spend a vast majority of their time on benthic surfaces on muddy, rocky, coraline, or algae surfaces biding their time waiting for prey to ambush (Arnold and Pietsch, 2012) and use their modified pectorals for “pseudo-walking” across these habitats to maintain their stealth. Rarely do these fishes swim for long periods in comparison to being perched on benthic substrates, indicating the compressiform body shape aids in the body shape reduction while still allowing for quick burst to evade predators. The deep-sea anglers that exhibit a similar breadth of body morphologies are typically found in pelagic habitats (apart from Thaumatichthyidae) and can range from globular compressiform to slightly elongated compressiform bodies (*Photocorynus*, *Neoceratias*, *Lasiognathus*). Deep-sea anglerfishes have indicated a sit-and-wait ambush predation lifestyle as observed in situ videos of *Gigantactis* and *Caulophryne*, and metamorphosed females typically have larger bodies by comparison of their caudal fin, indicating a weak caudal-power output (Pietsch, 2009) in combination with weak bone ossification and muscle development to reduce the effects of deep-sea pressures. Martinez et al., 2021 found that deep-sea fishes displayed a more frequent adoption of body shapes that facilitated reduced locomotion, as found in the globular bodies of the deep-sea anglerfishes.

Variation of Luring Degree Ranges

There are a handful of studies that investigate the luring behaviors in full timing detail predominantly in fishes that can be kept in aquaria predominantly in Antennarioideo (Pietsch and Grobecker, 1987) and Ogcocephaloideo (Nagareda and Shenker, 2009). The observations of deep-sea anglerfishes (Chaunacoideo and Ceratoideo) typically rely on remote submersibles to capture this behavior on film. This study found the frogfishes (Antennarioideo) to display the greatest luring degree ranges of the anglerfishes (see Table 3.6). From observations from video photoage, frogfishes generally move their lures in very fast motions and generally have less tissue growth constricting the illicum and its movements. The luring motion can rotate back and forth orientated in a forward direction and in combination with the "pseudo-feet" as a result of the modified pectorals of these fishes, allow them to orient their bodies to aim this lure in a multitude of directions. Mechanical luring strategies are closely associated with this infraorder indicating a need for mechanical lures to move further degree ranges to convince prey that the morphology of these mechanical escae are bait and/or prey. By comparison, the bioluminescent lures have ~47 degrees less in rotational motion capabilities than mechanical ones, with some genera (*Photocorynus*, *Microlophichthys*, and *Phyllorhinichthys*) having dense tissue coverage around the lure, limiting the degree range. The lures of the deep-sea anglerfishes typically have higher tissue coverage encompassing the exposed pterygiophore and illicium which may serve in reducing the effects of deep-sea pressures, but it needs to be emphasized that a majority of these deep-sea anglerfishes have not been observed alive in their natural habitats, even less so while performing these luring behaviors. This is both unsettling and extremely exciting, as it further drives the mystifying reputation these fishes have and serves as a driver to continue deep-sea investigations. It's also hypothesized in deep-sea anglerfishes, the bioluminescent lure aids in communication directed towards the males for mating purposes (Pietsch, 2009; Davis et al., 2014; Davis et al., 2016) and may have aided in the speciation of this rich infraorder of anglerfishes that encompasses nearly a third of the recognized taxa of the suborder. It should also be highlighted that the nervous systems of the bioluminescent escae in conjuncture with the soft muscles that encapsulate the lures have led to the hypothecation that these luminous displays can be shuttered to reduce the light display. It may be the case with deep-sea anglerfishes, that rather than using a luring rotational motion to lure, luminous intensity patterns may be used to entice prey. Batfishes were excluded from this study due to their directional and immobile lures housed in illicial cavities, but the infraorder itself is an understudied group and the luring behaviors of these fishes have only been observed in aquaria conditions (Drum and Croaker, 2016), and would serve as an interesting case in the utilization of chemical attractions in relation to lure motion and kinematics.

Conclusions

The findings of this study indicate that there has been considerable evolution in the body shape associated with the depth and habitat preferences and luring strategies associated with the anglerfishes. The transitions into different depths and habitats have facilitated the evolution of the body shape of these fishes and have resulted in a varying range of body shapes and luring degree ranges. The average body shape of the anglerfishes was found to be a compressiform body shape that aids in the sit-and-wait ambush behaviors these fishes exhibit and the morphospace is dominated by two large clusters that include Lophoideo, Chaunacoideo, Ogcocephaloideo, and Ceratoideo and another that consists of Antennaroideo. Both the Antennaroideo and Ceratoideo have larger trends of body morphologies found in inshore and deep-sea depths. The only significant body shape disparity between habitats was found between the bathypelagic and abyssopelagic anglers while the Ceratoideo had the highest body shape variance and disparity in contrast to monkfishes, frogfishes, and batfishes. The degrees of rotational motion of the luring apparatus of these fishes were also investigated, finding that mechanical lures had higher ranges of rotational motions motion compared to bioluminescent lures. Frogfishes (Antennarioideo) have by far the longest luring ranges of all Lophioidei resulting in epipelagic depths where these fishes reside in having the furthest rotational motions range in comparison to other depths.

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Appendix A: Material Examined

Material Examined Personally Examined

Antennarius coccineus LACM 9383-2

Antennatus strigatus: LACM 20677

Borophryne apogon LACM 30053-10

Bufoceratias wedli LACM 34272

Caulophryne polynema LACM 33923-1

Centrophryne spinulosa LACM 31105-24

Ceratias tentaculatus LACM 11025-7

Chaenophryne melanorhabdus LACM 9810-21

Chaunax sp. LACM 44750-3

Cryptopsaras couesii LACM 11231-1

Dolopichthys longicornis LACM 9612-49

Gigantactis gargantua LACM 30996-16

Gigantactis vanhoeffeni LACM 45001-1

Haplophryne mollis LACM 11235-25

Himantolophus cornifer LACM 33325-1

Himantolophus sagamius LACM 43760-1

Himantolophus albinares LACM 57239-2

Himantolophus sagamius LACM 60082-1

Histrio histrio LACM 8975-1

Kuiterichthys sp. LACM 11537-1

Leptacanthichthys gracilspinis LACM 33625-2

Linophryne indica LACM 36046-11

Linophryne densiramus LACM 38440-1

Linophryne coronata LACM 9254-34

Lophiocharon trisignatus LACM 54171-1

Melanocetus murrayi LACM 36113-1

Melanocetus johnsonii LACM 57236-2

Microlophichthys microlophus LACM 33607-1

Oneirodes notius LACM 10716-6

Oneirodes luetkeni LACM 33628-1

Oneirodes eschrichtii LACM 6697-5

Oneirodes acanthias LACM 9100-1

Phyllorhinichthys micractis LACM 57238-7

Spiniphryne gladisfenae LACM 10970-2

Photos Requested from Collections

Coelophrys micropa MNHN-IC-2002-3660

Phyllophryne scortea I.17614-028

Neoceratias spinifer ZMB 19383

Rhycherus filamentosus I.41560-001

GBIF

Diceratias trilobus AMS I.31144-004

Echinophryne reynoldsi NMV A3212

Halieutichthys aculeatus USNM 447444

Lophiodes beroe FMNH 77275

Lophiodes reticulatus FMNH 77265

Lophiodes caulinaris MCZ 28737

Lophiodes insidiator MNHN-IC-1973-0024

Pentherichthys venustus MCZ 161002

Rhycherus filamentosus NMV A521

Sketchfab.com

Chaunax abei QUYK 11588

Gigantactis paxtoni I.20314-018

Halieutaea stellata QUYK 11912

Lophius litulon QUYK 11894

"Oceanic Anglerfishes Extraordinary Diversity in the Deep Sea"

Cryptopsaras couesii BMNH 2006.10.19.1

Melanocetus johnsonii BMNH 2004.6.3.2-3

Photocorynus spiniceps UW 116975

"Frogfishes: Biodiversity, Zoogeography, and Behavioral Ecology"

Abantennarius coccineus BPBM 18246

Abantennarius analis UW 20874

Abantennarius coccineus BPBM 29214

Abantennarius drombus BPBM 8471

Abantennarius nummifer BPBM 21512

Abantennarius rosaceus BPBM 17497

Acentrophryne dolichonema HUMZ 175257

Antennarius maculatus LACM 42731-1

Antennatus linearis USNM 38704

Dibrachichthys melanurus QM I.37271

Histiophryne maggiewalker QMB I.37621

Kuiterichthys pietschi AMS I.33555-004

Lophiocharon hutschinsi WAM P.27673-002

"Fishes: A guide to their Diversity"

Antennatus sanguineus SIO 65-342

Arnold and Pietsch, 2011

Histiophryne maggiewalker QM I.37621

Bray, 2020

Sympterichthys unipennis MNHN A4630

Caruso, 1983

Lophius piscatorius RMNH 2036

Han et al., 2017

Fowlerichthys scriptissimus JNU 637

Hartel et al., 2008

Dolopichthys danae MCZ 164089

Ho et al., 2014

Lophiodes triradiatus ZSI 2246

Ho and McGrouther, 2015

Chaunacops spinosus I.24355-004

Chaunacops melostomus I.31151-004

Ho and Shao, 2010

Malthopsis gigas MNHN IC-2003-1247

Ho and Shao, 2019

Oneirodes formosanus sp.nov ASIZP 59950

Gigantactis cheni sp.nov. ASIZP 62947

Ho 2016

Himantolophus danae HUMZ 194700

Ho et al., 2013

Chaunax flavomaculatus sp.nov NMNZ P.032620

Chaunax mulleus sp.nov NMNZ P.039650

Chaunax penicillatus NMNZ p.032640

Ho et al., 2013 (Revision of Batfishes)

Malthopsis asperata NMNZ P.035177

Malthopsis parva NMNZ P.017180

Last and Gledhill, 2009

Brachionichthys australis CSIRO H 4451-01

Brachiopsilus dianthus sp.nov CSIRO H4995-01

Brachiopsilus ziebelli sp.nov CSIRO T1993-01

Brachiopsilus dossenus sp.nov NMV A29405-002

Sympterichthys moultoni sp.nov CSIRO H3773-03

Thymichthys politus CSIRO H 4118-01

Thymichthys verrucosus CSIRO H 4453-03

Miya et al., 2010

Diceratias pileatus FMNH 64543

Himantolophus appelii CSIRO H.5652-01

Lasiognathus amphirhamphus BMNH 2003.11.16.12

Melanocetus eustalus SIO 55-229

Thaumatichthys binghami UW 47537

Moore et al., 2003

Lasiognathus intermedius MCZ 57778

Ohnishi et al., 1997

Antennatus flagellatus NSMT-P 49487

Pietsch, 2004

Lophiocharon hutschinsi WAM P.27673-002

Pietsch and Orr

Chaenophryne quasiramifera SIO 72-180

Pietsch and Shimazaki, 2005

Acentrophryne dolichonema HUMZ 175257

Pietsch et al., 2009

Dibrachichthys melanurus QM I.37271

Rajeeshkumar et al., 2016

Ceratias uranoscopus CMLRE 3341210

Rafael Bañón et al., 2019

Caulophryne polynema MNCN ICTIO 291.461

Ceratias holboelli MNCN ICTIO 291.456

Dolopichthys karsteni MNCN ICTIO 291.453

Haplophryne mollis MNCN ICTIO 291.464

Linophryne brevibarbata MNCN ICTIO 291.462

Linophryne bicornis MNCN ICTIO 291.463

Lophodolos acanthognathus MNCN ICTIO 291.448

Oneirodes eschrichtii MNCN ICTIO 291.449

Robertson et al., 2017

Fowlerichthys avalonis USNM 422343

Sainsbury et al., 1985

Tathicarpus butleri (Fishbase)