



## Evolutionary relationships of anglerfishes (Lophiiformes) reconstructed using ultraconserved elements

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### ABSTRACT

The macroevolutionary consequences of evolving in the deep-sea remain poorly understood and are compounded by the fact that convergent adaptations for living in this environment makes elucidating phylogenetic relationships difficult. Lophiiform anglerfishes exhibit extreme habitat and predatory specializations, including the use of a fin-spine system as a luring device and unique reproductive strategies where parasitic males attach and fuse to females. Despite their notoriety for these odd characteristics, evolutionary relationships among these fishes remain unclear. We sought to clarify the evolutionary history of Lophiiformes using data from 1000 ultraconserved elements and phylogenomic inference methods with particular interest paid to the Ceratioidei (deep-sea anglerfishes) and Antennarioidei (frogfishes and handfishes). At the suborder level, we recovered similar topologies in separate phylogenomic analyses: The Lophioidei (monkfishes) are the sister group to the rest of the Lophiiformes, Ogcocephaloidei (batfishes) and Antennarioidei (frogfishes) form a sister group, and Chaunacioidei (coffinfishes) and Ceratioidei (deep-sea anglerfishes) form a clade. The relationships we recover within the ceratioids disagree with most previous phylogenetic investigations, which used legacy phylogenetic markers or morphology. We recovered non-monophyletic relationships in the Antennarioidei and proposed three new families based on molecular and morphological evidence: Histiophrynidae, Rhycheridae, and Tathicarpidae. Antennariidae was re-evaluated to include what was known as Antennariinae, but not Histiophryninae. Non-bifurcating signal in splits network analysis indicated reticulations among and within suborders, supporting the complicated history of the Lophiiformes previously found with morphological data. Although we resolve relationships within Antennarioidei, Ceratioidei relationships remain somewhat unclear without better taxonomic sampling.

### 1. Introduction

The Lophiiformes are a group of enigmatic marine teleost fishes that constitute one of the strangest groups of vertebrates on the planet. Colloquially named anglerfishes, these species have been described as “majestic, regal, vaguely terrifying”, “grotesque looking”, and “nightmarish fanged potatoes” (Caryl-Sue, 2013; Broad, 2019; Specktor, 2020). The Lophiiformes come in a variety of shapes and sizes from

dorsoventrally compressed to globose and “football-like” (hence, the footballfishes of Himantolophidae) (Pietsch and Orr, 2007; Miya et al., 2010). Lophiiformes are partially united by their specialized first dorsal fin spine (illicium), which is usually located on the snout and terminates in a fleshy tip that forms a lure (esca) (Pietsch and Orr, 2007). These lures are often bioluminescent and are used for prey capture and interspecific communication and have been implicated in driving the order’s diversification (Herring, 1987; Haddock et al., 2010; Widder, 2010;

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Davis et al., 2014). In addition to their elaborate and glowing lures, this group has a variety of fascinating life history traits, including extreme sexual dimorphism and bizarre reproductive strategies (e.g., parasitic males fusing to females) (Regan, 1925; Bertelsen, 1951; Pietsch, 1976, 2005). These globally distributed fishes span a wide variety of habitat types from shallow water, shelf and slope, to the meso- and bathypelagic ocean. As currently classified, the order Lophiiformes contains five suborders: the Antennarioidei, Ceratioidei, Chaunacoidei, Lophioidei, and Ogocephaloidei.

The Antennarioidei includes the benthic frogfishes and handfishes that inhabit shallow to moderately deep waters (Fig. 1) (Last et al., 1983; Pietsch and Grobecker, 1987; Last et al., 2007; Last and Gledhill, 2009; Arnold and Pietsch, 2012; Arnold et al., 2014). The pectoral fins in antennarioids (as well as some lophioids and ogocephaloids) are modified, creating an elbow-like appearance, allowing these fishes to “walk” along the substrate (Dickson and Pierce, 2018). Species of the Antennarioidei launch some of the fastest predatory strikes in the animal kingdom—members of the genus *Antennarius* are capable of buccal expansion and prey engulfment in less than 4 msec (Grobecker and Pietsch, 1979). This suborder also encompasses some of the most threatened marine teleost fishes in the world, the hand fishes (family Brachionichthyidae) (Edgar et al., 2017; Lynch et al., 2020; Stuart-Smith et al., 2020).

Species within the suborder Ogocephaloidei, or batfishes, are dorsoventrally flattened to such an extent that members of one genus, *Halieutichthys*, are known as the pancake batfishes (Ochiai and Mitani, 1956; Bradbury, 1967, 1988; Endo and Shinohara, 1999; Ho et al., 2010; Derouen et al., 2015). Batfishes typically inhabit the continental shelf and upper slope, though some have been captured or recorded at depths down to 4000 m. In the coronal plane, the shape of ogocephaloids may also be round or triangular (Fig. 1) (Bradbury, 1967, 1988; Ho et al., 2010). In addition, some batfishes have an elongated rostrum, from which their illicium extends (Bradbury, 1967). Experiments have shown that some batfishes actively luring prey emit a chemical attractant from their esca, eliciting the emergence of typically benthic (and thus less visually-stimulated) prey (Nagareda and Shenker, 2009; Alves et al., 2021).

Fishes of Ceratioidei, known commonly as the deep-sea anglerfishes, typically inhabit depths greater than 300 m in the world’s pelagic oceanic regions (Pietsch, 1986; Pietsch and Orr, 2007). The Ceratioidei is the most species-rich of the Lophiiformes suborders with approximately 165 species in 11 families (Fig. 2a–f). The suborder contains the most extreme cases of sexual dimorphism: in terms of mass, females achieve a size of up to 500,000 times greater than males and 60 times longer (Bertelsen, 1951; Pietsch, 1976, 1986). Reproductive strategies within the Ceratioidei are noteworthy as they include males that are facultative or obligate parasites, in many cases fusing to the female to the point where her circulatory system anastomoses with his (Regan, 1925; Bertelsen, 1951; Pietsch, 1976; Munk, 2000; Pietsch, 2005; Swann et al., 2020).

The Chaunacoidei (coffinfishes or sea toads) inhabit moderately deep waters at depths of 90 to more than 2000 m (Caruso, 1989; Caruso et al., 2007). Virtually nothing is known about the biology of coffinfishes, including their reproductive habits; however, ROV footage indicates extreme ontogenetic color change (Lundsten et al., 2012) and a unique respiratory behavior that allows for 30% expansion of the body (Long and Farina, 2019).

The Lophioidei are a group of dorsoventrally compressed, benthic fishes commonly known as goosefishes or monkfishes (Caruso, 1981, 1985; Caruso et al., 2007; Pietsch et al., 2013). Lophioids can be found in temperate, tropical, to subtropical waters globally (except for the eastern Pacific) (Caruso, 1981; Fariña et al., 2008; Gjøstæter, 2009). Goosefishes and monkfishes have extremely oblique mouths and are the only lophiiform fish suborder that are commercially harvested in fisheries for human consumption (Fariña et al., 2008).

Despite the extraordinary biology of anglerfishes, convergent

evolution and evolution in the deep-sea confound the macroevolutionary patterns among these fishes. Evolutionary relationships within the order remain unclear, and phylogenetic incongruence is widespread among datasets (Fig. 3; Pietsch and Grobecker, 1987; Shedlock et al., 2004; Miya et al., 2010; Betancur-R et al., 2013; Near et al., 2013; Derouen et al., 2015; Betancur et al., 2017). Taxonomic and systematic confusion abounds in the order: the extreme sexual dimorphism within ceratioids has led to the description of some free-swimming ceratioid males as separate genera (Regan, 1925; Parr, 1930; Bertelsen, 1951) and attached males had even been described as juveniles of their species (Sædmundsson, 1922).

Phylogenetic tree building is a pillar of evolutionary biology, allowing scientists to reconstruct the history of life on Earth. To examine biological aspects of species, a solid understanding of relationships among those species is necessary. In this study, we sought to clarify the evolutionary relationships among Lophiiformes using a phylogenomic workflow of ultraconserved element loci (UCE). UCES and phylogenomics have recently been used to resolve long-standing phylogenetic problems in fishes (Faircloth et al., 2013; Chakrabarty et al., 2017; Longo et al., 2017; Alfaro et al., 2018; Alda et al., 2019; Friedman et al., 2019; Hart et al., 2020). We inferred Bayesian and multispecies coalescent phylogenetic tree hypotheses, as well as created a phylogenetic network to examine non-bifurcating genetic signal. We chose to examine non-bifurcating signal using a network approach because of suspected complex phylogenetic signal among the order due to unknown hybridization, previous phylogenetic incongruence, and our meager understanding of lophiiform reproductive strategies. We were particularly interested in the relationships among the frogfishes and handfishes of Antennarioidei as well as within deep-sea anglerfishes of Ceratioidei, as there has been a considerable amount of conflict concerning the phylogenetic relationships in these suborders (Alfaro et al., 2018; Arnold, 2014; Arnold and Pietsch, 2012; Betancur et al., 2017; Miya et al., 2010; Near et al., 2013; Pietsch and Grobecker, 1987; Pietsch and Orr, 2007; Shedlock et al., 2004; Pietsch, 1984a). Resolving the relationships among the Lophiiformes will allow for future comparative studies including examinations of locomotion and feeding, diversification rates, and trait histories such as the origin of parasitic males. Additionally, phylogenetic resolution assists conservation efforts by clarifying relationships of groups in need of protection (e.g., the handfishes).

## 2. Materials and methods

### 2.1. Taxon sampling

Our taxon sampling included 131 specimens of Lophiiformes comprising 47 + species and 32 genera from 15 of 18 (85%) families in the order (Table 1; IACUC LSU18-87): 14 genera from 8 of 11 (73%) families of Ceratioidei; 14 genera of Antennarioidei frogfishes, including 11 of 13 genera (85%) and 30 of 47 (64%) species in of Antenariidae; two genera from one family of Ogocephalidae; one genus of Chaunacoidei; and one genus of Lophioidei (Table 1). We also included five species as outgroups from the families Tetraodontidae, Caproidae, Chaetodontidae, and Pomacanthidae. Our outgroups were chosen based on the most closely related taxa from Miya et al. (2010), Near et al. (2013), and Arnold (2014), allowing us to compare results across studies. Samples were collected in the field by the authors, loaned from natural history collections, or data was mined from online repositories (Table 1; Supplementary Table S1).

### 2.2. Molecular sampling and library preparation

Whole genomic DNA was extracted via DNeasy Blood and Tissue kits (Qiagen, Germantown, MD, 20874) from fin clips and tissues stored in 95% ethanol following manufacturer’s protocol. Genomic DNA was quantified with a Qubit 2.0 fluorometer. Library preparation and

Table 1

List of species, family, suborder, and institutional codes for tissue specimens of Lophiiformes used in this study (N = 131).

Genus	Species	Family	Suborder	Antennariidae Group	Museum Collection/Source	SRA Sequence Accession Number
<i>Abantennarius</i>	<i>coccineus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	NSMT-P 68051	SRR18222614
<i>Abantennarius</i>	<i>coccineus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	KU T7143	SRR18222613
<i>Abantennarius</i>	<i>dorehensis</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 157021	SRR18222549
<i>Abantennarius</i>	<i>nummifer</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	RUSI 65251; KU T5049	SRR18222538
<i>Abantennarius</i>	<i>rosaceus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	QS I. 38177	SRR18222583
<i>Abantennarius</i>	<i>sanguineus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118813_1	SRR18222572
<i>Abantennarius</i>	<i>sanguineus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118813_2	SRR18222561
<i>Antennarius</i>	<i>commersoni</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117686	SRR18222522
<i>Antennarius</i>	<i>commersoni</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118986	SRR18222511
<i>Antennarius</i>	<i>hispidus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117828	SRR18222500
<i>Antennarius</i>	<i>indicus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118818	SRR18222612
<i>Antennarius</i>	<i>indicus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118817	SRR18222601
<i>Antennarius</i>	<i>multicellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117826	SRR18222590
<i>Antennarius</i>	<i>multicellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117827	SRR18222556
<i>Antennarius</i>	<i>pardalis</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	CAS 235484; Tissue TI 2010-109	SRR18222555
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	CBM-ZF-10514	SRR18222554
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117694_2	SRR18222553
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117695_2	SRR18222552
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117695_3	SRR18222551
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117696_3	SRR18222550
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117696_4	SRR18222548
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118815	SRR18222547
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118819	SRR18222546
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	CAS 234886; Tissue TI2010-132	SRR18222545
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	CAS 234890; Tissue TI 2012-131	SRR18222544
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	NMNZ P.044669/TS3	SRR18222543
<i>Antennarius</i>	<i>striatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	NMNZ P.057359/TS2	SRR18222542
<i>Antennatus</i>	<i>strigatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	LH05-205	SRR18222541
<i>Antennatus</i>	<i>tuberosus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 118814	SRR18222540
<i>Antennatus</i>	<i>tuberosus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 115750	SRR18222539
<i>Echinophryne</i>	<i>crassispina</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222537
<i>Echinophryne</i>	<i>crassispina</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222536
<i>Echinophryne</i>	<i>crassispina</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222535
<i>Echinophryne</i>	<i>crassispina</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222534
<i>Echinophryne</i>	<i>crassispina</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM P11544	SRR18222533
<i>Fowlerichthys</i>	<i>ocellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 150909	SRR18222532
<i>Fowlerichthys</i>	<i>ocellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 150911	SRR18222586
<i>Fowlerichthys</i>	<i>ocellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 150912	SRR18222585
<i>Fowlerichthys</i>	<i>ocellatus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 150910	SRR18222531
<i>Fowlerichthys</i>	<i>radiusus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	MCZ 144916	SRR18222584
<i>Fowlerichthys</i>	<i>radiusus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	KU T3548	SRR18222582
<i>Fowlerichthys</i>	<i>radiusus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	KU T5131	SRR18222581
<i>Fowlerichthys</i>	<i>scriptissimus</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 112642	SRR18222580
<i>Histiophryne</i>	<i>bougainvilli</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118990_4	SRR18222579
<i>Histiophryne</i>	<i>bougainvilli</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118990_5	SRR18222578
<i>Histiophryne</i>	<i>bougainvilli</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118990_2	SRR18222577
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 117821	SRR18222576
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118816	SRR18222575
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 117816	SRR18222574
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 117820	SRR18222573
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118816**	SRR18222571
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	not cataloged, aquarium trade	SRR18222570
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 117819	SRR18222569
<i>Histiophryne</i>	<i>cryptacanthus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	not cataloged, aquarium trade	SRR18222568
<i>Histiophryne</i>	<i>maggiewalker</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	QS I. 38176	SRR18222567
<i>Histiophryne</i>	<i>pogonius</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 118820	SRR18222566

(continued on next page)

Table 1 (continued)

Genus	Species	Family	Suborder	Antennariidae Group	Museum Collection/Source	SRA Sequence Accession Number
<i>Histiophryne</i>	<i>pogonius</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 119920	SRR18222565
<i>Histiophryne</i>	<i>psychedelica</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	NCIP 6377	SRR18222564
<i>Histiophryne</i>	sp	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	SAM F11719	SRR18222563
<i>Histrio</i>	<i>histrio</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	T3016; KU 29308	SRR18222562
<i>Histrio</i>	<i>histrio</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	KU T5232	SRR18222560
<i>Lophiocharon</i>	<i>lithinostomus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 115749	SRR18222559
<i>Lophiocharon</i>	<i>lithinostomus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	Hsuan-Ching Ho	SRR18222530
<i>Lophiocharon</i>	<i>lithinostomus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	Hsuan-Ching Ho	SRR18222529
<i>Lophiocharon</i>	<i>lithinostomus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	not cataloged, aquarium trade	SRR18222528
<i>Lophiocharon</i>	<i>tresignatus</i>	Antennariidae	Antennarioidei	Group 2 (Histiophrynidae)	UW 115748	SRR18222527
<i>Nudiantennarius</i>	<i>subteres</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 117643	SRR18222526
<i>Nudiantennarius</i>	<i>subteres</i>	Antennariidae	Antennarioidei	Group 4 (Antennariidae)	UW 119524	SRR18222525
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	NMV A29226.005	SRR18222524
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM F17721	SRR18222523
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM 11720	SRR18222521
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222520
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222519
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	Yorke Peninsula, South Australia	SRR18222518
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM 69556	SRR18222517
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM 86337	SRR18222516
<i>Phyllophryne</i>	<i>scortea</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	SAM P11722	SRR18222515
<i>Porophryne</i>	<i>erythroductylus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	UW 118988	SRR18222514
<i>Porophryne</i>	<i>erythroductylus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	AMS I.44699	SRR18222513
<i>Porophryne</i>	<i>erythroductylus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	UW 118988**	SRR18222512
<i>Porophryne</i>	<i>erythroductylus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	AMS I.43749.001	SRR18222510
<i>Rhycherus</i>	<i>filamentosus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	NMV A29238.11	SRR18222509
<i>Rhycherus</i>	<i>filamentosus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	South Australia	SRR18222508
<i>Rhycherus</i>	<i>filamentosus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	NMV 24754	SRR18222507
<i>Rhycherus</i>	<i>filamentosus</i>	Antennariidae	Antennarioidei	Group 1 (Rhycheridae)	NMV A22333	SRR18222506
<i>Tathicarpus</i>	<i>butleri</i>	Antennariidae	Antennarioidei	Group 3 (Tathicarpidae)	WAM 32903.001	SRR18222505
<i>Tathicarpus</i>	<i>butleri</i>	Antennariidae	Antennarioidei	Group 3 (Tathicarpidae)	QS I. 38191	SRR18222504
<i>Tathicarpus</i>	<i>butleri</i>	Antennariidae	Antennarioidei	Group 3 (Tathicarpidae)	QS I. 38227	SRR18222503
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO H 4460-02, GT 1304	SRR18222502
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO H 4465-01, GT 1307	SRR18222501
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO H 4465-02, GT 1308	SRR18222499
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO H 4466-01, GT 1305	SRR18222498
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO	SRR18222497
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO	SRR18222496
<i>Brachionichthys</i>	sp	Brachionichthyidae	Antennarioidei		CSIRO	SRR18222495
<i>Caulophryne</i>	<i>jordani</i>	Caulophrynidae	Ceratioidei		Cajo_99_029 from Miya	SRR18222493
<i>Caulophryne</i>	<i>pelagica</i>	Caulophrynidae	Ceratioidei		NSMT-P 93887(1)	SRR18222492
<i>Ceratias</i>	sp	Ceratiidae	Ceratioidei		UW 042301	SRR18222491
<i>Cryptopsaras</i>	<i>couesii</i>	Ceratiidae	Ceratioidei		YFTC-25185	SRR4432386
<i>Cryptopsaras</i>	<i>couesii</i>	Ceratiidae	Ceratioidei		UW 049299	SRR18222490
<i>Gigantactis</i>	sp	Gigantactinidae	Ceratioidei		CPK104	SRR18222609
<i>Gigantactis</i>	sp	Gigantactinidae	Ceratioidei		CPK108	SRR18222608
<i>Gigantactis</i>	sp	Gigantactinidae	Ceratioidei		G268	SRR18222607
<i>Himantolophus</i>	sp	Himantolophidae	Ceratioidei		CPK105	SRR18222605
<i>Himantolophus</i>	sp	Himantolophidae	Ceratioidei		G169	SRR18222604
<i>Linophryne</i>	sp	Linophrynidae	Ceratioidei		G159	SRR18222603
<i>Linophryne</i>	sp	Linophrynidae	Ceratioidei		G177	SRR18222602
<i>Melanocetus</i>	<i>johnsonii</i>	Melanocetidae	Ceratioidei		Memu_04_068 from Miya	SRR18222599
<i>Melanocetus</i>	<i>murrayi</i>	Melanocetidae	Ceratioidei		00_065	SRR18222598
<i>Bertella</i>	<i>idiomorpha</i>	Oneirodidae	Ceratioidei		NSMT-P 99996(1)	SRR18222595
<i>Chaenophryne</i>	sp	Oneirodidae	Ceratioidei		Crco_00_062 from Miya	SRR18222594
<i>Chaenophryne</i>	sp	Oneirodidae	Ceratioidei		CPK107	SRR18222593
<i>Dolopichthys</i>	sp	Oneirodidae	Ceratioidei		G137	SRR18222592
<i>Oneirodes</i>	<i>thompsoni</i>	Oneirodidae	Ceratioidei		ASIZ-P 0062880	SRR18222591
<i>Oneirodes</i>	<i>thompsoni</i>	Oneirodidae	Ceratioidei		UW 048054	SRR18222606
<i>Puck</i>	<i>pinnata</i>	Oneirodidae	Ceratioidei		SIO-04-35	SRR18222589
<i>Thaumatichthys</i>	<i>pagidostomus</i>	Thaumatichthyidae	Ceratioidei		Thpa_04_083 from Miya	SRR18222587
<i>Thaumatichthys</i>	sp	Thaumatichthyidae	Ceratioidei		G228	SRR18222558

(continued on next page)

Table 1 (continued)

Genus	Species	Family	Suborder	Antennariidae Group	Museum Collection/Source	SRA Sequence Accession Number
<i>Chaunax</i>	<i>pictus</i>	Chaunacidae	Chaunacoidei		Chpi_04_115 from Miya	SRR18222611
<i>Chaunax</i>	sp	Chaunacidae	Chaunacoidei		UW 025870	SRR18222610
<i>Lophiodes</i>	<i>caulinaris</i>	Lophiidae	Lophioidei		Loca_04_078 from Miya	SRR18222600
<i>Dibranchius</i>	<i>atlanticus</i>	Ogcocephalidae	Ogcocephaloidei		UW 025869	SRR18222597
<i>Ogcocephalus</i>	<i>radiatus</i>	Ogcocephalidae	Ogcocephaloidei		Alfaro et al., 2018	SRR4432457
<i>Ogcocephalus</i>	<i>radiatus</i>	Ogcocephalidae	Ogcocephaloidei		UW 118987	SRR18222596
<i>Antigonia</i>	<i>capros</i>	Caproidae			YPM	SRR4432352
<i>Antigonia</i>	<i>capros</i>	Caproidae			Anca_07_078 from Miya	SRR18222494
<i>Chaetodon</i>	<i>kleinii</i>	Chaetodontidae			YFTC-12656	SRR4432408
<i>Chaetodon</i>	<i>ocellatus</i>	Chaetodontidae			CAS-CAC01	SRR4432376
<i>Pomacanthus</i>	<i>paru</i>	Pomacanthidae			CAS	SRR4432415
<i>Tetrabrachium</i>	<i>ocellatum</i>	Tetrabrachiidae			UW 049710C	SRR18222588
<i>Sphoeroides</i>	<i>dorsalis</i>	Tetraodontidae			T3970	SRR18222557

Museum codes follow Sabaj (2016). AMS: Australian Museum, Sydney; ASIZ: Academia Sinica (Chinese Academy of Sciences), Biodiversity Research Museum, Taipei; CAS: California Academy of Sciences; CBM (CMB-ZF): Natural History Museum and Institute, Chiba; CSIRO: Commonwealth Scientific & Industrial Research Organisation, Division of Marine & Atmospheric Research, Australian National Fish Collection; KU: University of Kansas Biodiversity Institute; LH (LHC): Laboratoire d'Hydrobiologie et d'Aquaculture, Faculté des Sciences Agronomiques, Université d'Abomey Calavi, Cotonou; MCZ: Museum of Comparative Zoology, Harvard University; NCIP: Pusat Penelitian dan Pengembangan Oseanologi, Lembaga Ilmu Pengetahuan Indonesia; NMNZ: Museum of New Zealand Te Papa Tongarewa; NMV: Museum Victoria, Melbourne; NSMT: National Museum of Nature and Science, Ueno Park, Tokyo; QS (QSMI): Queen Saovabha Memorial Institute, Thai Red Cross Society; RUSI (SAIAB): South African Institute for Aquatic Biodiversity; SAM: South African Museum, Cape Town; SIO: Scripps Institution of Oceanography, Marine Vertebrate Collection, University of California; UW: University of Washington, Burke Museum of Natural History and Culture, WAM: Western Australian Museum, Perth; YFTC: Yale University, Fish Tissue Collection, Peabody Museum of Natural History (Sabaj, 2016).

sequencing was performed at Louisiana State University and at the RAPiD Genomics Lab (RAPiD Genomics, LLC, Gainesville, FL). Random shearing was performed to obtain DNA fragments around ~600 base pairs using an Episonic Multi-Functional Bioprocessor. The HyperPrep Kit was used for library preparation as well as the MYbaits UCE Acanthomorph target capture kit—1341 UCE loci, 2600 probes—using half reaction volumes and the manufacturer recommended protocols (Arbor Biosciences, Ann Arbor, MI, 48103) (McGee et al., 2016).

DNA sequencing was performed in one lane of an Illumina HiSeq300-PE150 to obtain an expected ~30X sequencing coverage. Our 75% complete data matrix used for phylogenomic analyses was comprised of 1000 UCE loci. The number of UCE loci captured from tissues sequenced in this investigation ranged from 369 (*Antennatus nummifer*, A11) to 1035 (*Phyllophryne scortea*, F2). Number of contigs ranged from 7335 (*Antennatus coccineus*, L2) up to 90,401 (*Histrio histrio*, T5232), and their average length ranged from 1114 to 9158 base pairs (Supplementary Table S1).

### 2.3. Bioinformatics processing

Preprocessing and alignment were completed using the Phyluce pipeline (Phyluce v. 1.6.8) (Faircloth et al., 2012; Faircloth et al., 2013; Faircloth, 2016). We included outgroup sequences from Alfaro et al. (2018) by obtaining the raw sequence read data from Dryad (<https://doi.org/10.5061/dryad.085dd>) (Alfaro et al., 2018) and using adapter sequences obtained from these authors. Adapter trimming and quality control was completed with the *illumiprocessor* (v. 2.10) function in Phyluce using *trimmomatic* (v. 0.39) (Bolger et al., 2014). We used SPAdes (v. 3.12.0) (Prjibelski et al., 2020) for *de novo* assembly on the Louisiana State University High Performance Computing cluster SuperMike-II. Contiguous UCE sequences were extracted using the functions *phyluce\_assembly\_match\_contigs\_to\_probes*, *phyluce\_assembly\_get\_match\_counts*, and *phyluce\_assembly\_get\_fastas\_from\_match\_counts* in Phyluce. We then aligned the UCE loci using *phyluce\_align\_seqcap\_align*. We created a 75% complete data matrix with the Phyluce function *phyluce\_align\_get\_only\_loci\_with\_min\_taxa*. Our 75% complete data matrix contained 1000 UCE alignments and was used for all subsequent analyses. The UCE alignments were entered into PartitionFinder2 (Lanfear et al., 2017) on the CIPRES Science Gateway (v.3.3; <https://www.phylo.org/>) (Miller et al., 2012) to find the best fit models of sequence evolution and partition scheme for each UCE locus. We tested three models of evolution due to ExaBayes model specifications: GTR, GTR + G,

GTR + I + G.

During the target capture process, mitochondrial by-catch is frequently sequenced, and, in some cases, the entire mitochondrial genome can be recovered (Raposo do Amaral et al., 2015; Alda et al., 2017a; Alda et al., 2017b; Zarza et al., 2018; Derkarabetian et al., 2019). As mitochondrial markers are used as barcode markers and since the diversity and amount of available mitochondrial data for Lophiiformes is greater than nuclear, we chose to use mitochondrial data from our sequences to confirm species identities. Thus, cleaned sequence data for some specimens were entered into Geneious (v.10.1.3) and assembled to the most closely related taxon with either a mitochondrial genome or CO1 sequence given the initial species identification and data availability. Assembly was completed with five iterations using the Map to Reference option in Geneious. Following assembly, we generated a consensus sequence using the contigs produced and BLASTed them against the NCBI nucleotide collection database using Megablast.

### 2.4. Phylogenomic analyses

We performed Bayesian phylogenomic reconstruction with the program ExaBayes (v.1.5) (Aberer et al., 2014) on XSEDE (v.2.6.3) on the CIPRES Science Gateway (Miller et al., 2012). We partitioned the dataset following the best scheme from the PartitionFinder2 analysis. The Bayesian analysis was run as two independent runs with four coupled chains for 1,000,000 generations each. Sampling occurred every 1000 generations with 100,000 generations used as burn-in. We set a uniform topological prior, allowing all topologies to have the same prior probability. We used a Dirichlet distribution for our reversible matrix prior as well as our state frequency prior, which allows for change during MCMC sampling. All parameters were left unlinked except for branch lengths, for which we declared a range of partitions linked into one parameter (i. e., 0–3). Convergence of parameters was determined using Tracer (v.1.7.1) (Rambaut et al., 2018). We created a summary maximum clade credibility tree of the posterior distribution of trees using TreeAnnotator (v.2.6.3) from BEAST2 (Bouckaert et al., 2019). For our summary tree, 20% of trees were discarded as burn-in.

In addition to our concatenated Bayesian analysis, we estimated a coalescent-based species tree using the program ASTRAL-II (v.4.1.1) (Mirarab and Warnow, 2015). ASTRAL-II implements a method statistically consistent under the multi-species coalescent model that accommodates gene tree discordance resulting from incomplete lineage sorting. We used individual UCE gene trees as input that we

reconstructed and bootstrapped for 200 replicates using RAxML (v.8.2.11) (Stamatakis, 2014) on the Louisiana State University HPC Cluster SuperMike.

Phylogenetic trees are most often rooted and bifurcating; thus, signs of introgression, hybridization, or horizontal gene transfer, may be lost in the binary tree format (Fitch, 1997; Huson, 1998; Huson and Bryant, 2006; Huson and Scornavacca, 2011; Morrison, 2011; Morrison, 2013). Reproductive strategies and the extent to which hybridization occurs among Lophiiformes overall is not well understood, and previous phylogenetic incongruence suggests complex phylogenetic signal among the order. To visualize non-tree like signal within the Lophiiformes, we created a splits phylogenetic network using the program SplitsTree4 (v.4.15.1) (Huson and Bryant, 2006). We used uncorrected P-distances estimated from sequence data to construct a Neighbor-Net splits network (Bryant and Moulton, 2004). The network was visualized using the Rooted Equal Angle algorithm with *Chaetodon*, *Antigonia*, and *Pomacanthus* as outgroups (Gambette and Huson, 2008). Support for the splits was determined by 1000 bootstrap replicates.

### 3. Results

Both the Bayesian and Multispecies Coalescent Tree (MSC) were created with a 75% complete data matrix equating to 1000 UCE loci. We recovered the Lophioidei as the sister group to the rest of the Lophiiformes with high support (posterior probability  $PP = 1.0$ , and bootstrap support  $BS = 100\%$ , for Bayesian and MSC, respectively), with a clade containing Antennarioidei and Ogocephaloidei as the sister to a clade of Ceratioidei and Chaunacoidei. We found congruent results between the two analyses, with only two family-level relationships in

disagreement. In the phylogenetic network analysis, non-bifurcating relationships were found mainly among suborders using phylogenetic network analysis.

#### 3.1. Bayesian phylogenomic reconstruction

##### 3.1.1. Subordinal relationships

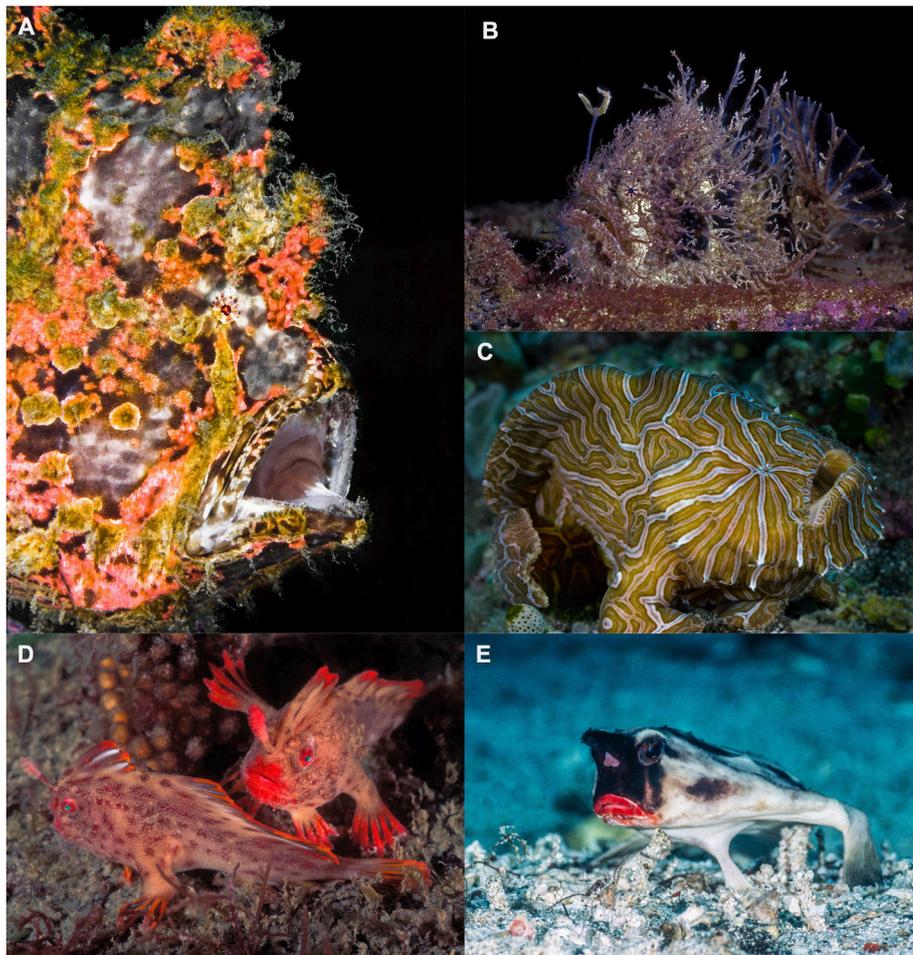
Our Bayesian phylogenetic reconstruction recovered the monophyly of all the suborders of Lophiiformes—except Lophioidei for which we only had one species—with posterior probabilities (PP) of 1.0 (Fig. 4, Fig. 5; ESS = 720). We recovered the Lophioidei as the sister group to the rest of the Lophiiformes. Chaunacoidei was recovered as the sister group to the ceratioidei, and we recovered the Ogocephaloidei as sister to the Antennarioidei (Fig. 4, Fig. 5).

##### 3.1.2. Ceratioidei: family-level relationships

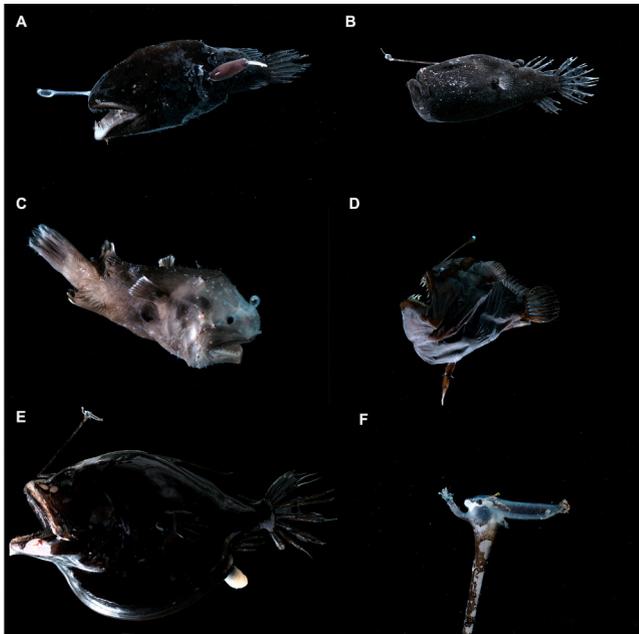
Melanocetidae (black seadevils) was recovered as the basal lineage of the Ceratioidei, followed next in the tree by Gigantactinidae (whipnose anglers) (Fig. 4). Next in the phylogeny included a clade of Lino-phrynidae (leftvents) as the sister group to Ceratiidae (warty seadevils); this clade was the sister group to the remaining ceratioid families. The Oneirodidae (dreamers) were the sister group to a clade formed by Himantolophidae (footballfishes) and Caulophrynidae (fanfins), with Thaumatchthyidae (wolf-trap anglers) as sister to this clade (Oneirodidae + Himantolophidae + Caulophrynidae). All the relationships in this group were supported with  $PP = 1.0$  (Fig. 4).

##### 3.1.3. Antennarioidei: family and subfamily relationships

Antenariidae was recovered as non-monophyletic, with



**Fig. 1.** Select representative photographs of fishes from the suborders Antennarioidei and Ogocephaloidei. (A) Commerson's frogfish, *Antennarius commersoni* (Antennariidae: Antennarioidei); (B) Tasseled frogfish, *Rhycherus filamentosus* (Rhycheridae: Antennarioidei); (C) Psychedelic frogfish, *Histiophryne psychedelica* (Histiophrynidae: Antennarioidei); (D) Handifish, *Brachionichthys politus* (Brachionichthyidae: Antennarioidei); (E) Red-lipped batfish, *Ogocephalus darwini* (Ogocephalidae: Ogocephaloidei). Photographs are not to scale. All photographs are copyright David Hall, [seaphotos.com](http://seaphotos.com). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** Representative photographs of select Ceratioidei fishes. (A) Smooth dreamer, *Chaenophryne draco* (Oneirodidae), (B) Triplewart seadevil, *Cryptosaras couesii* (Ceratiidae), (C) Footballfish, *Himantolophus* sp. (Himatolophidae), (D) Humpback or abyssal anglerfish, *Melanocetus* sp. (Melanocetidae), (E) Bulbous dreamer, *Oneirodes eschrichtii* (Oneirodidae), (F) Close-up of the Bulbous dreamer's esca (*Oneirodes eschrichtii*; Oneirodidae). Photographs are not to scale. All photographs are copyright E. Widder, Ocean Research & Conservation Organization.

Tetrabrachiidae and Brachionichthyidae nested within this group (Fig. 4). We recovered four major clades or groups in this family. The subfamily Histiophryinae was recovered as paraphyletic and included three groups: Groups 1, 2 and 3. Group 1 of histiophrynines (*Echinophryne* + *Phyllophryne* + *Porophryne* + *Rhycherus*) was recovered more closely related to Brachionichthyidae (*Brachionichthys*) than other histiophrynines. Group 2 included genera *Histiophryne*, and *Lophiocharon*, and Group 3 included genus *Tathicarpus* that was sister to

Tetrabrachiidae. These three groups were sister to the subfamily Antennariinae (Group 4) that was recovered as monophyletic and included the genera *Antennarius*, *Antennatus*, *Abantennarius*, *Fowlerichthys*, *Histrio*, and *Nudiantennarius* (Fig. 4).

### 3.2. Multispecies coalescent species tree reconstruction

#### 3.2.1. Subordinal relationships

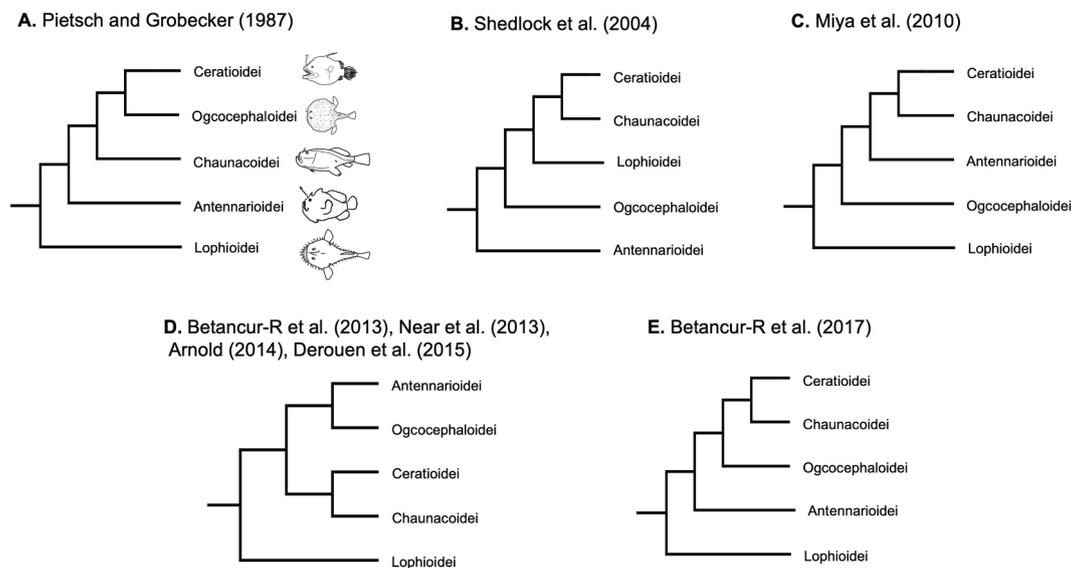
Our multispecies coalescent species tree recovered identical relationships among suborders as our Bayesian phylogeny. We recovered Lophioidei as the sister group to the rest of the Lophiiformes (100% Bootstrap Support; Fig. 5, Supplementary Fig. S1). Ogcocephaloidei was the sister group to Antennarioidei, and this clade in turn was the sister group to Chaunacoidei + Ceratioidei (100% BS; Fig. 5, Supplementary Fig. S1).

#### 3.2.2. Ceratioidei: family-level relationships

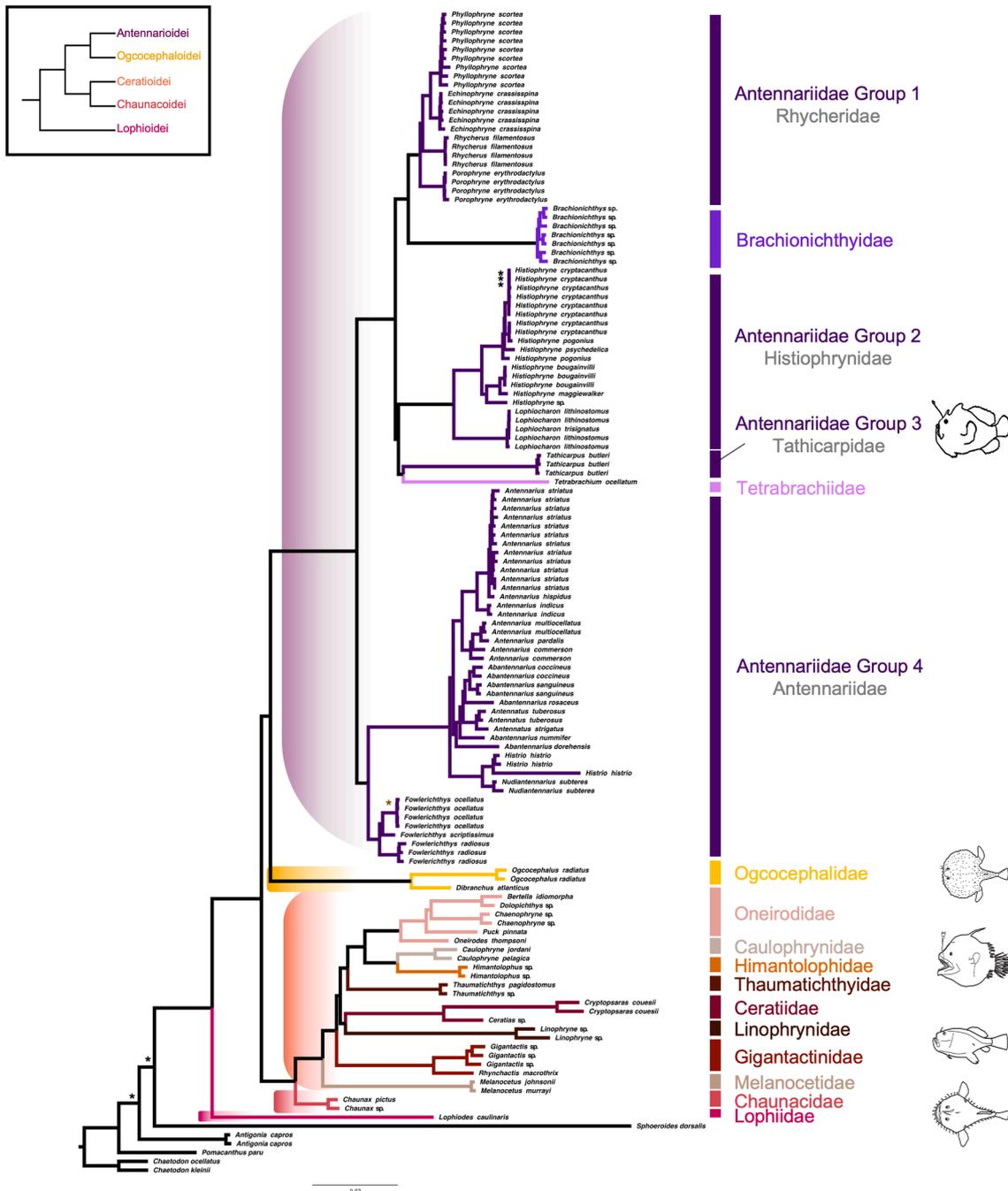
We recovered almost identical relationships between our Bayesian phylogeny and our multispecies coalescent tree with respect to Ceratioidei deep-sea anglerfish families (Fig. 4, Fig. 5), except that we did not find a sister group relationship between Linophrynidae and Ceratiidae within our multispecies coalescent tree (Fig. 5, Supplementary Fig. S1). We found Gigantactinidae was more basal than Linophrynidae, then Ceratiidae followed as the sister group to the remaining ceratioid families; however, the relationship relating to Ceratiidae had <95% BS (92.3%).

#### 3.2.3. Antennarioidei: family-level relationships

Similar to our Bayesian reconstruction, our multispecies coalescent phylogeny recovered Antennariidae as not monophyletic, again with Tetrabrachiidae (*Tetrabrachium*) and Brachionichthyidae (*Brachionichthys*) nested within (Fig. 5). First, we recovered members of histiophrynines (*Echinophryne* + *Phyllophryne* + *Porophryne* + *Rhycherus*) in Group 1 of Antennariidae as the sister group to Brachionichthyidae (*Brachionichthys*). The relationships among these histiophrynines were identical to our Bayesian reconstruction (Fig. 4, Fig. 5). The Group 1 + Brachionichthyidae clade was sister to a group formed by Groups 2 and 3 of Antennariidae and Tetrabrachiidae (*Tetrabrachius*). Group 2 consists of *Histiophryne* and *Lophiocharon*. Unlike in our Bayesian phylogeny, *Tathicarpus* in Group 3 was not sister to Tetrabrachiidae but to



**Fig. 3.** A selection of previously hypothesized subordinal relationships among the Lophiiformes from (A) Pietsch and Grobecker (morphology; 1987), (B) Shedlock et al. (mitochondrial genes; 2004), (C) Miya et al. (mitogenomes; 2010), (D) Betancur-R et al. (nuclear and mitochondrial genes; 2013), Near et al. (nuclear gene supermatrix; 2013), Derouen et al. (nuclear and mitochondrial genes; 2015), (E) Betancur-R et al. (molecular; 2017); Illustrations by T. W. Pietsch are chosen representatives of the suborders.



**Fig. 4.** Family-level relationships among the Lophiiformes constructed with ExaBayes (75% complete data matrix, 1000 UCE loci). Specimen identification can be found in Table 1. Newly proposed families of Antennarioidei are indicated in gray. Asterisks indicate nodes with support PP < 1.0. Black asterisks indicate PP = 0.5 and the brown asterisk indicates PP = 0.99. Inset is the simplified backbone of the phylogeny indicating subordinal relationships. Illustrations by T. W. Pietsch are representative of the suborders.

Group 2 (*Histiophryne* + *Lophiocharon*), although this relationship had extremely weak support (46.56% BS; Fig. 5, Supplementary Fig. S1).

3.3. Splits network analysis

Our splits network showed a substantial amount of non-bifurcating signal (Fig. 6, Supplementary Fig. S2). We recovered reticulate signals from suborder level to within sub-families. Notable reticulate signals existed between *Tathicarpus* and *Tetrabrachium* (*Tetrabrachium*). We found considerable non-tree-like signal within Antennarioidei and within Ceratioidei, as well as between Ogocephaloidei and Ceratioidei (Fig. 6, Supplementary Fig. S2).

4. Discussion

The relationships recovered in our phylogenomic analyses were notably different from previous molecular attempts (e.g., complete mitogenomes, Sanger sequenced loci) (Shedlock et al., 2004; Miya et al., 2010; Near et al., 2013; Betancur et al., 2017) or anatomical/morphological characters (Pietsch and Grobecker, 1987; Pietsch and Orr, 2007). This was the first attempt to elucidate the relationships of anglerfishes using target-capture sequencing methods, and the use of hundreds of ultraconserved elements greatly increased the amount of data available for resolving their evolutionary history.

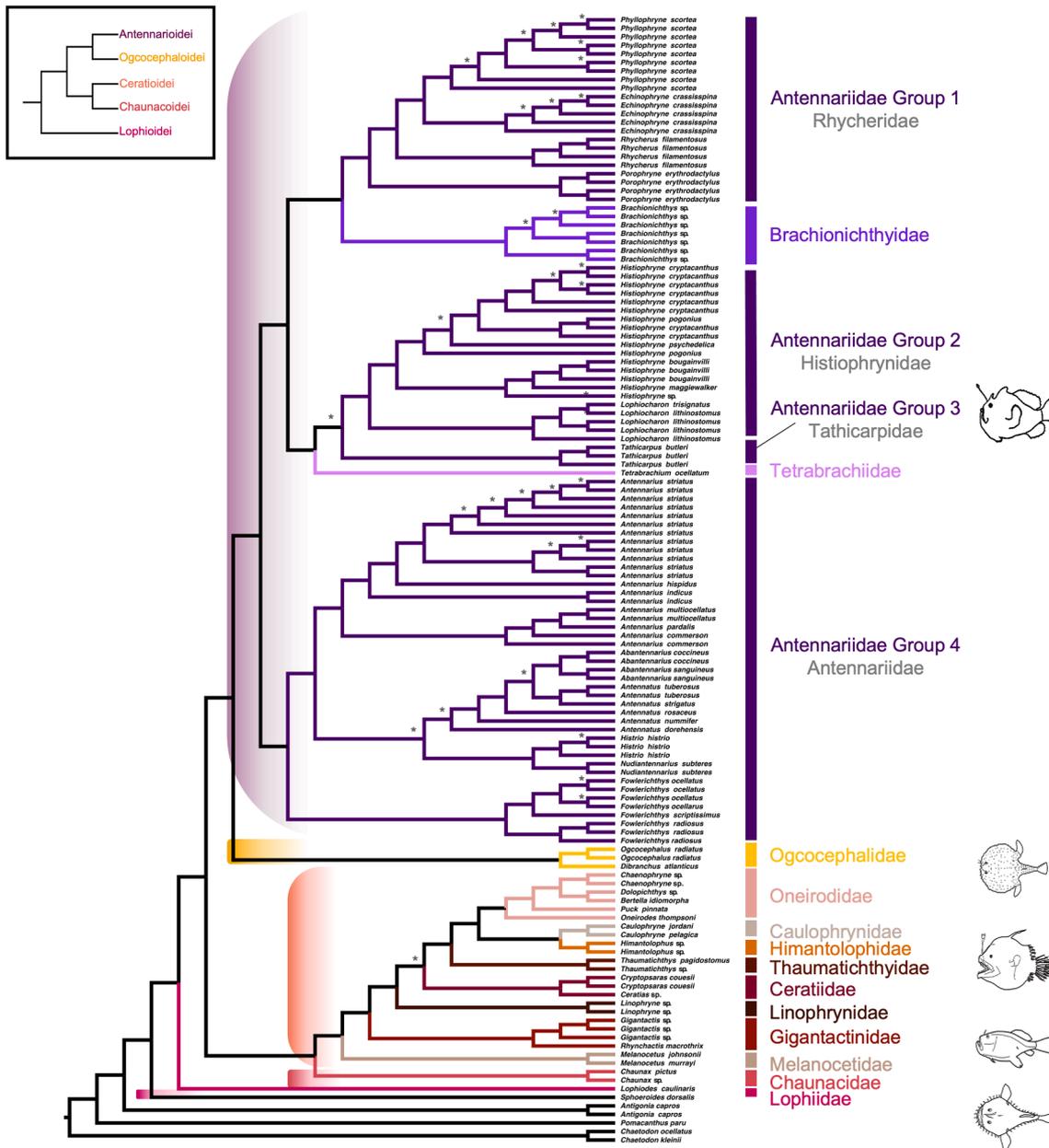


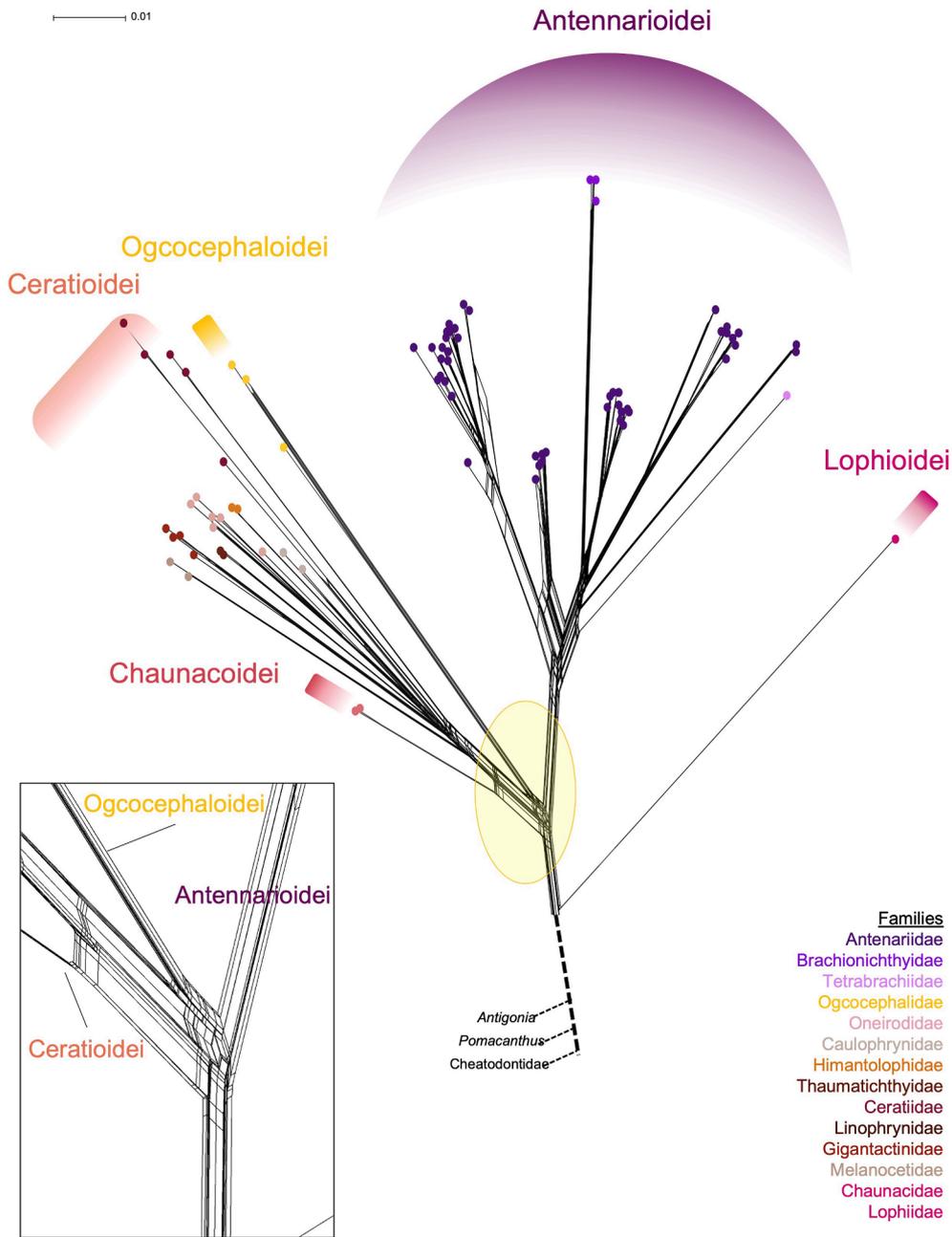
Fig. 5. Family-level relationships among the Lophiiformes constructed with ASTRAL (75% complete data matrix, 1000 UCE loci). Specimen identification can be found in Table 1. Newly proposed families in Antennarioidei are indicated in gray text. Bootstrap replicate support is >95% unless otherwise indicated by an asterisk. See Supplementary Materials for exact support values. Inset is the simplified backbone of the phylogeny indicating subordinal relationships. Illustrations by T. W. Pietsch are representative of the suborders.

#### 4.1. Subordinal relationships

All our phylogenomic analyses recovered the Lophioidei as the sister group to the rest of the Lophiiformes, as was recovered by additional molecular phylogenetic investigations (Miya et al., 2010; Betancur-R et al., 2013; Near et al., 2013; Derouen et al., 2015; Betancur et al., 2017) and supported by six unambiguous synapomorphies from morphological investigation (Pietsch and Orr, 2007). Our phylogenomic hypotheses agreed with one another in relation to subordinal relationships and agreed with the topology found in the molecular phylogenetic investigations of Betancur-R et al. (2013), Near et al. (2013), and Derouen et al. (2015); we found reciprocal sister group relationships between Ogcocephaloidei and Antennarioidei, and between Ceratioidei and Chaunacoidei (Fig. 4, Fig. 5). Among the molecular studies, our hypotheses disagreed with those proposed using partial mitochondrial

sequences (Shedlock et al., 2004), complete mitogenomes (Miya et al., 2010), and a mixture of molecular sequence data (Betancur et al., 2017) (Fig. 3). Arnold and Pietsch (2012) recovered a polytomy at the base of Antennarioidei and Ogcocephaloidei, thus no relationship could be concluded. We also did not recover the subordinal relationships found in morphological phylogenetic investigations (Pietsch and Grobecker, 1987; Pietsch and Orr, 2007); though as discussed by Miya et al. (2010), the unambiguous synapomorphies that unite Ogcocephaloidei and Ceratioidei within Pietsch and Orr (2007) may be simplified or reductive traits perhaps accumulated convergently.

Our splits network showed substantial non-bifurcating signal at the splits of the suborders, including between Ogcocephaloidei and the clade containing Ceratioidei + Chaunacoidei and between Ogcocephaloidei and Antennarioidei (Fig. 6). These relationships indicated historical introgression, potential hybridization, or incomplete lineage



**Fig. 6.** Splits network for the Lophiiformes created using UCE loci. Inset indicates the portion of the network highlighted with a yellow oval to visualize the splits in the network between the Ceratioidei and the Ogcocephaloidei, and among the Ceratioidei. Family colors are denoted in the legend in the bottom right-hand corner. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sorting, which can muddle evolutionary relationships in phylogenetic trees (Bryant and Moulton, 2004; Huson and Scornavacca, 2011; Morrison, 2011; Morrison, 2013). With this particular network analysis, we cannot determine the exact biological events that have led to the non-bifurcating signal. Nevertheless, our concatenated and coalescent-based analyses were largely congruent for most relationships, which may indicate that incomplete lineage sorting was not a major cause for disagreement in our dataset. It is also possible, however, that there was a low signal-to-noise at the deepest nodes of the Lophiiformes tree, and only large phylogenomic datasets like ours resolve these relationships as opposed to previous studies using legacy markers and morphology.

Though the exact biological scenario for the non-bifurcating genetic signal is unknown, interesting questions arise as to hybridization and introgression among the Lophiiformes. An instance does exist of a male from one species attached to a female of another: a male *Melanocetus*

*johnsonii* (Melanocetidae) was partially attached (i.e., attached but without tissue fusion) to a female *Centrophryne spinulosa* (Centrophrynidae) (Pietsch and Nafpaktitis, 1971). Species-specific modes of communication through bioluminescence and chemosensory signals are untestable in laboratory settings due to the nature of deep-sea fishes. Although we know these are important for speciation (Davis et al., 2014), we do not know how often these signals may become confounded. Because finding a mate in the deep-sea can be extremely difficult, perhaps this pressure may lead to more hybridization than previously thought. If hybridization or introgression occurred more frequently in the deep-sea than previously thought, this could reveal itself as conflicting topologies between datasets.

#### 4.2. Familial relationships of the Ceratioidei

The family-level relationships of Ceratioidei that we recovered disagreed with most earlier phylogenetic investigations (Bertelsen, 1984; Pietsch and Orr, 2007; Miya et al., 2010; Near et al., 2013; Arnold, 2014; Betancur et al., 2017). For example, we did not recover a sister group relationship between the Linophryinae and the Thaumatoichthyidae as found in Miya et al. (2010); excluding the paraphyletic *Lasiognathius* sp. as it was not included in the present study). Notably in Miya et al. (2010), relationships of Caulophryinae, Ceratiidae, Gigantactinidae, Thaumatoichthyidae, and Linophryinae were supported with <60% BS, despite their data being obtained from whole mitogenomes. Further, we did not recover a sister group relationship between Oneirodidae and Thaumatoichthyidae, as was found in two morphological investigations (Bertelsen, 1984; Pietsch and Orr, 2007). Near et al. (2013), Betancur et al. (2017), and Alfaro et al. (2018) were large-scale studies and not focused on Lophiiformes, thus they have less sampling from each sub-order and therefore fewer inferences can be made about Lophiiformes evolutionary relationships from these studies. Our phylogenomic hypotheses were the first to recover the Melanocetidae as the first-branching ceratioid group and thus the sister group to the remaining ceratioids. Two molecular phylogenetic investigations recovered a clade containing Melanocetidae and Himantolophidae (Arnold, 2014, Bayesian inference and nuclear genes only; Betancur et al., 2017), a relationship which we did not recover.

It is important to note that all major phylogenetic investigations that include ceratioids proposed a different topology, and no phylogeny, despite the data used, agreed in the evolutionary relationships among ceratioid families (Supplementary Fig. S3). Miya et al. (2010) thoroughly discussed the phylogenetic incongruence that existed between morphological and molecular examinations at the time; however, further molecular investigations were performed, and discordance remained (Near et al., 2013; Arnold, 2014; Betancur et al., 2017; Alfaro et al., 2018).

Representatives of the ceratioid taxa Neoceratiidae, Diceratiidae, and Centrophryinae were not included in our analyses. These families were placed in a variety of different phylogenetic positions by other authors (Bertelsen, 1984; Pietsch and Orr, 2007; Miya et al., 2010; Arnold, 2014). As such, we could not infer where these taxa would be recovered within our own analyses.

Although synapomorphic morphological characters unite most of the ceratioid families, relationships among some of the families, and especially between genera within the Oneirodidae, were less straightforward (Pietsch and Grobecker, 1987; Pietsch and Orr, 2007). Pietsch and Orr (2007) found that only homoplastic characters united the Himantolophidae, Diceratiidae (not included in the current investigation), and Melanocetidae. Additionally, Pietsch and Orr (2007) recovered a clade composed of the Thaumatoichthyidae, Oneirodidae, Caulophryinae, and Linophryinae.

Debate as to the origin of obligate parasitic males in the deep-sea anglerfishes has continued for decades (Pietsch, 1976, 2005; Swann et al., 2020). Our topologies (multispecies coalescent and Bayesian) disagreed on the sister group relationship between Linophryinae and Ceratiidae (Fig. 4, Fig. 5). Our Bayesian phylogeny contained a sister group relationship of Linophryinae and Ceratiidae, which would support the single origin of male parasitism (Fig. S4a). However, in our multispecies coalescent phylogeny, the clade containing Linophryinae and Ceratiidae also contained five other ceratioid lineages that have either temporarily attached males or facultative parasites (Fig. S4b). If a single origin of obligate-parasitic males did occur with the multispecies coalescent topology, there would then need to be reversal back to non-obligate parasitic males in four families. Additionally, we did not include the Neoceratiidae in our study, one of three ceratioid families of Ceratioidei with obligately parasitic males. Thus, no firm conclusions can be drawn as to the origin and evolution of male attachment based on the current study.

#### 4.3. Familial relationships of the Antennarioidei

Within the Antennarioidei, we recovered Antennariidae as paraphyletic with Brachionichthyidae and Tetrabrachiidae nested within (specifically, within the subfamily Histiophryinae; Fig. 4, Fig. 5). Paraphyly of Antennariidae was also recovered previously with both maximum likelihood and Bayesian analyses by Arnold (2014), using a dataset of four concatenated nuclear genes. Between our two analyses (Bayesian and multispecies coalescent), we found disagreement in the relationship of Tetrabrachiidae (*Tetrabrachium*) and antennariids *Tathicarpus*, *Lophiocharon*, and *Histiophryne*. We recovered a sister-group relationship between Tetrabrachiidae (*Tetrabrachium*) and *Tathicarpus* using Bayesian analysis, while multispecies coalescent inference recovered a sister group relationship of *Tathicarpus* and *Lophiocharon* + *Histiophryne*. In a similar, although not identical, fashion, Arnold (2014) recovered differing relationships among these taxa between analyses as well. Our Bayesian analysis and Arnold's (2014) maximum likelihood analysis agreed in topology with a sister-group relationship of Tetrabrachiidae (*Tetrabrachium*) and *Tathicarpus*; however, Arnold (2014) found a novel topology of Tetrabrachiidae (*Tetrabrachium*) as the sister group to *Lophiocharon* + *Histiophryne*, with *Tathicarpus* as the sister group to this clade.

We recovered the Antennariinae clade containing *Histrio*, *Antennatus*, *Abantennarius*, *Antennarius*, and *Folwerichthys* in concordance with Shedlock et al., 2004, Arnold and Pietsch (2012), and Arnold (2014) (Supplementary Fig. S5). Though we did not recover a paraphyletic relationship of *Histrio* as found in Arnold (2014), we did recover *Antennatus* (*tuberosus* and *strigatus*) nested within *Abantennarius*. In additional agreement with previous investigations, we recovered *Lophiocharon*, *Histiophryne*, *Tathicarpus* and Tetrabrachiidae as the sister clade to *Phyllophryne*, *Echinophryne*, *Porophryne*, *Rhycherus*, and Brachionichthyidae (*Allenichthys* and *Kuiterichthys* were not included in our study).

Based on both molecular and morphological evidence, we propose three new families within Antennarioidei: The Histiophryinae (Antennariidae group 2), the Rhycheridae (Antennariidae group 1), and the Tathicarpidae (Antennariidae group 3), and we raise Antennariinae (Antennariidae group 4) to family rank status.

##### 4.3.1. Tathicarpidae new family Hart et al., 2022

Tathicarpidae is diagnosed by a Y-shaped ectopterygoid; epibranchial I with a row of six to 11 teeth borne directly on the bone; proximal end of second pectoral radial reduced, not contributing to articulation of pectoral fin and girdle; all nine rays of caudal fin simple; and only six or seven pectoral-fin rays (Pietsch and Arnold, 2020). Due to their remarkably long fin rays (Pietsch and Arnold, 2020), we recommend the common name of long-fin frogfishes. One genus comprises Tathicarpidae: *Tathicarpus*. The family name was chosen for the singular genus in the family and etymology is as follows: Greek, *tatheis*, *tatheissa*, *teino* = to taughten + Greek, *karpos* = articulation.

##### 4.3.2. Rhycheridae new family Hart et al., 2022

Rhycheridae is defined by the following combination of characters: a pair of simple oval-shaped ovaries (Arnold et al., 2014; Pietsch and Arnold, 2020); lost endopterygoid and epural, T-shaped ectopterygoid; pharyngobranchial present; and all genera are restricted to temperate waters of Australia and Tasmania, below 30° S latitude (Pietsch and Arnold, 2020). Many of these fishes display some amount of red coloration and are often photographed open-mouthed, reminiscent of the Balrog monster from J. R. R. Tolkien's *The Lord of the Rings* novel; thus, we recommend the common name of Balrog frogfishes. Rhycheridae includes *Phyllophryne*, *Echinophryne*, *Rhycherus*, *Porophryne*, and *Kuiterichthys* and *Allenichthys*. Though molecular data was not included in this study for *Allenichthys* or *Kuiterichthys*, the simple ovarian morphology, lack of endopterygoid and epural, and Western and South Australian endemism below 20-30° S latitude suggest *Allenichthys* and *Kuiterichthys*

are members of this clade (Arnold and Pietsch, 2012; Pietsch and Arnold, 2020). All members of this group display parental nest-guarding behavior (except possibly *Kuiterichthys* and *Allenichthys* for which no observations have been made). The family name was chosen based on the oldest genus in the family, *Rhycherus* (Ogilby, 1907).

#### 4.3.3. *Histiophrynidae* new family Hart et al., 2022

Histiophrynidae is contained to *Histiophryne* + *Lophiocharon*. Histiophrynidae is defined by the following characters: the loss of the endopterygoid and epural; the loss of the pharyngobranchial I; and the attachment to the body/carrying of egg masses by females (Pietsch and Arnold, 2020). The attachment and carrying of egg masses by females is reminiscent of the Suriname or Star-Fingered toad: the females of these toads have eggs embedded into their back by male movements during reproduction, and the juveniles emerge from the mother's back following development. We suggest the common name Star-Fingered frogfishes due to the resemblance to the Star-Fingered toad. The genus *Histiophryne* inspired the family name as the etymology could be related to both genera now within the family: Greek, *istion*, *istios* = sail + Greek, *phryne* = toad.

#### 4.3.4. *Antennariidae jarocki* 1822, revised Hart et al., 2022

Antennariidae (Antennariidae group 4) is redefined as *Antennarius*, *Antennatus*, *Fowlerichthys*, *Histrio*, and *Nudiantennarius*. The antennariids are united by having both the mesopterygoid and epural, having double scroll-shaped ovaries (Pietsch and Grobecker, 1987:pl. 10, fig. 161), are broadcast spawners with a distinct larval stage, and have a broad geographic range, with all genera found circumglobally throughout the tropics and subtropics (Arnold, 2014; Pietsch and Arnold, 2020). As the double scroll-shaped ovaries are reminiscent of the graphical visualization of the Golden Ratio Spiral or Fibonacci Sequence Spiral (though described earlier by ancient and medieval Indian mathematicians Virahanka, Gopala, and Hemacandra) (Singh, 1985), we suggest the common name of the Fibonacci frogfishes.

Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae have lost the mesopterygoid and epural, have simple oval-shaped ovaries, undergo direct development, display various degrees of parental care, and are restricted geographically to the Indo-Australian Archipelago (Arnold and Pietsch, 2012; Arnold, 2014). As noted in Arnold (2014), the extremely rare *Lophichthys boschmai*, the only member of the Lophichthyidae, has lost the mesopterygoid and has a greatly reduced or absent epural (Pietsch, 1981, 1984b), has simple, oval-shaped ovaries, and is endemic to the seas between New Guinea and Australia (reproductive modes and behaviors are unknown), and is, therefore, a likely member of this clade as well.

Antennariidae, Tetrabrachiidae, Tathicarpidae, Histiophrynidae, Brachionichthyidae, and Rhycheridae are united by three dorsal fin spines, the first being modified into a lure, and epural absent.

## 5. Conclusions

Anglerfishes (Lophiiformes) are some of the most notorious fishes among the public and scientists alike due to their bizarre morphology and reproductive habits (i.e., parasitic males). Despite this, the evolutionary history among these fishes is still uncertain. We examined the evolutionary relationships among the Lophiiformes using a dataset of 1000 ultraconserved element loci and phylogenomics analyses. We recovered Ogocephaloidei as the sister group to Antennarioidei, and in turn this clade is the sister-group to that of Chaunacoidei and Ceratioidei. In agreement with previous analyses, we recovered Lophioidei as the sister group to the rest of the Lophiiformes suborders. Substantial non-bifurcating signal and disagreement between phylogenies among the deep-sea Ceratioidei anglerfishes suggested a complex evolutionary history that is yet unclear. We diagnosed three new families within Antennarioidei (Histiophrynidae, Tathicarpidae, and Rhycheridae), and re-diagnosed the Antennariidae. The Lophiiformes are as mysterious in

their evolutionary relationships as they are on the physical plane. We have clarified relationships among Antennarioidei; however, relationships among the Ceratioidei remain uncertain.

## Data accessibility statement

Raw sequence data is archived in the NCBI Sequence Repository Archive (PRJNA810755). Supplementary materials are archived on Dryad (<https://doi.org/10.5061/dryad.rbnzs7hd1>). Specimen museum accession number are available in the in-text table.

## CRediT authorship contribution statement

**Pamela B. Hart:** Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Rachel J. Arnold:** Conceptualization, Investigation, Resources, Writing – review & editing, Funding acquisition. **Fernando Alda:** Conceptualization, Investigation, Writing – review & editing. **Christopher P. Kenaley:** Conceptualization, Resources, Writing – review & editing. **Theodore W. Pietsch:** Conceptualization, Resources, Writing – review & editing. **Destinee Hutchinson:** Investigation. **Pro-santa Chakrabarty:** Conceptualization, Resources, Writing – review & editing, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ymp.2022.107459>.

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