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The Evolution of Fangs Across Ray-Finned Fishes (Actinopterygii)

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The Evolution of Fangs Across Ray-Finned Fishes (Actinopterygii)

by

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A Thesis

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Thesis Committee:
Matthew Davis, Chairperson
Heiko Schoenfuss
Matthew Tornow

Abstract

To date, no study has investigated how many independent evolutions of fangs have occurred across ray-finned fishes. This research addresses this question by focusing on the evolution of fangs across a diversity of marine habitats in the Lizardfishes (Aulopiformes), and then investigating the evolution of fangs across ray-finned fishes (Actinopterygii). Lizardfishes are a diverse order of fishes (~236 species) that are observed to have fang-like teeth and occupy a variety of marine habitats. A taxonomic review of lizardfish specimens representing 35 of 44 genera were examined for the presence of fangs. In addition to assessing the presence of fangs, lizardfish habitat was also evaluated to examine if there is a correlation between fang presence and habitat. I estimated the character evolution of fang presence and habitat across a previously published phylogeny of lizardfish relationships to examine evolutionary patterns. I identified that fangs have independently evolved three times across the lizardfishes. There is also a correlation between the evolution of fangs in lizardfishes and habitat with fangs evolving more frequently in deep-sea pelagic habitats. To further investigate the evolution of fangs, I expanded my research to include a robust hypothesis of relationships among families of ray-finned fishes. Using previously published genetic data, I inferred a phylogeny of 315 species representing 211 families of ray-finned fishes. I again utilized ancestral character-state reconstructions to examine patterns of fang evolution across ray-finned fishes. The results of my analyses indicates that there have been at least 38 independent evolutions of fangs across ray-finned fishes. Generally in families that evolved fangs, when the majority of the species diversity possess fangs they are found in pelagic environments.

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Table of Contents

Chapter Page

III. **Evolution of Fangs Across Ray-finned Fishes**

List of Tables

List of Figures

Chapter 1: INTRODUCTION

What is a Fang?

Fangs are a historically broad term given to enlarged teeth (caniniform) located on the oral jaws of various organisms. Studies that discuss fangs frequently focus on putative functional mechanics (e.g. cutting efficiency) and development (Anderson and LaBarbera, 2006; Feranec, 2008). Moreover, there is an absence of literature with a quantitative or qualitative definition of what constitutes a fang. Several studies have indicated that there is a lack of research into the evolution of fangs (Kardong, 1979; Ernst, 1982; Feranec, 2008). Previous studies that have defined fangs identified them as an organism having teeth that are "elongated and terminate in a sharp point" (Owen, 1840) or simply "fang-like" (Kenaley, 2012).

In order to define a fang for the research presented herein, I am considering the putative functionality of the fangs in the lineages that possess them. The most common hypothesis among studies detailing the functional significance of fangs is that they are used for piercing and capturing prey (Kuch et al, 2006; Folinsbee et al., 2007). However, fangs are also used in certain behavioral aspects. For instance, the sabertooth blenny (*Petroscirtes breviceps*) uses its fangs in a defensive territorial fashion (Smith-Vaniz, 1987). For the purposes of this study, I am defining a fang as a tooth or a bone with tooth-like morphology that is considerably longer and/or larger and fewer in number than other teeth found on the same bones. These fangs also often serve a different functional purpose (e.g. in feeding or behavior) from other teeth on the same bone.

Fish Dentition

Dentition among ray-fined fishes varies widely in regards to morphology and is often associated functionally with the diet of the species. The various types of dentition found in fishes include, but are not limited to, caniniform, molariform, villiform, scraping multi-cuspid teeth, and incisors (Saxena, and Saxena, 2015; Florida Museum of Natural History, 2016). Caniniform teeth are most common in carnivorous fishes (Grubich et al., 2012). They are typically conical in shape and are either straight or curved. These blade-like teeth are used for piercing and restraining prey items. Blade-like teeth are also used to decrease the amount of force needed to pierce or fracture tissues (Anderson and LaBarbera, 2006). Molariform teeth are flattened and are often found in slow benthic predators that crush prey with hard shells such as crustaceans (Lo Galbo et al., 2001). Alternatively, molariform teeth can also be used to crush nuts and berries in frugivorous fishes such as the pacu (*Piaractus mesopotamicus*) (Galetti et al., 2008). Villiform teeth are small slender teeth grouped together resembling that of bristles on a brush. They are used in a similar fashion like canines to control and restrain prey items. Scraping teeth are common among herbivorous and or benthic fishes. These highly modified cuspid teeth are used to scrape algae and vegetation off of stationary objects (Ebeling, 1957).

Predatory fishes that inhabit the deep-sea rely heavily on pelagic prey items (Drazen et al., 2008). Several pelagic species of fishes, such as *Harpadon nehereus* (Bombay duck) and *Scopelarchus analis* (pearleye), possess barbs on the end of their fangs like those of fishing hooks to hold onto their prey. Many species of fishes have also evolved jaw modifications to compensate for such large teeth and can have gapes of greater than 100° when feeding (Kenaley, 2012).

Feeding in Fishes

Fish feeding techniques vary widely among taxa. Suction feeding is the most common technique used by teleost fishes (Wainwright, 2007). Suction feeding involves the rapid expansion of a fish's buccal cavity, which creates negative pressure allowing prey items to be sucked into the mouth. This action must be performed in close vicinity to the prey item to maximize flow velocity on the prey (Norton, 1991). Suction feeding has even expanded into extreme specializations in some fishes. For instance, the sling-jaw wrasse (*Epibulus insidiator*) is able to utilize extreme lower jaw protrusion, so that it may capture prey at a much greater distance. This allows the wrasse to capture more elusive prey items (e.g. small fishes and shrimp) that other fishes are unable to catch (Ferry-Graham et al., 2002).

Another feeding technique found in fishes is "biting" and/or manipulation. Fishes that have a limited gape are unable to create the negative pressure needed to suck prey into their mouths. Instead, these fishes grasp and tear their prey in order to create smaller pieces or simply manipulate their prey through rotation so that it may be swallowed whole (Alfaro et al., 2001; O'connell, (1972). A fish known to tear and rip prey apart is the piranha (Serrasalmidae). Several species of piranha have been documented to shear flesh off of prey using their razor-like teeth (Nico and Taphorn, 1988). These razor-like teeth reduce the amount of force needed to penetrate flesh and make it a quick and effective feeding technique.

A fish that commonly manipulates prey items into its mouth via biting are the true eels (Anguillidae). Anguillids are typically limited to food items that can be swallowed whole. When a prey item is captured and cannot be immediately swallowed, the eel will manipulate the prey into a position where it can then be swallowed whole. Some species of anguillids have adapted to be able to eat larger prey items through a knotting or spinning technique. The eel will hold onto its prey item and then will spin in circles or maneuver itself into a knot (Helfman and Clark, 1986 and Miller, 1987). These techniques allow the eel to apply more force to the prey where large chunks can be removed and subsequently eaten.

Biting is the quintessential feeding strategy for fishes with fangs. The majority of species with fangs lack the premaxillary protrusion abilities found in fishes that employ suction feeding. For instance, an observation of various lestidiid (naked baracudinas) species reveals the anatomy of the skull does not allow for the expansion of the buccal cavity (Harry, 1953). A recent study investigated the functional morphology and ecology of biting in squammapinnes (Konow et al., 2008). The study revealed the repeated evolution of an intermandibular joint (IMJ) plays a major functional role in the enhancement of biting for these fishes. The INJ was also found to exhibit over 35° of flexion which allowed for efficient closing of the jaws. This revelation could indicate a repeated evolution of an INJ in fishes that possess fangs.

In conjunction to both biting techniques, ram feeding is used by fast swimming pelagic fishes and fishes. Ram feeding is the quick propulsion of a predator into an individual or group or prey items (Higham, 2005). The black marlin (*Istiompax indica*) is a well documented ram feeder; it utilizes its large fusiform body and lunate tail to drive itself through the water column. The black marlin has been documented charging prey and using its modified bill to pierce the prey's flesh (Van der Elst and Roxburgh, 1981). Once the prey has been subdued, the marlin shakes it head to dislodge the prey and swallow it.

A fourth feeding technique among fishes is scraping. Scraping is used to remove food items such as algae from stationary objects (e.g. coral, rocks, and wood). Armored catfishes of the family Loricariidae are well documented to utilize scraping as their mechanism for feeding. Armored catfishes have ventral oriented mouths with modified cuspid teeth which they use to scrape food (Adriaens et al., 2009). Another family of fishes known for scraping as their primary method of feeding are the Chaetodontids (butterflyfishes). Butterflyfishes use their small and sometimes elongated jaws for biting or scraping the surfaces of corals.

A fifth feeding technique found in fishes is filter feeding. Filter feeding is the process of intaking water into the oral cavity and then filtering out edible and non edible food items. In fishes, food items are collected in the gill rakers of the fish and any non edible items are expelled with water via the gills. This method is found in both obligate and facultative species of fish such as paddlefish (*Polyodon spatula*), gizzard shads (*Dorosomac epedianum*), alewife (*Alosa pseudoharengus*), and anchovies (Engraulidae) (Drenner et al., 1982).

Diversity of Fangs across Vertebrates

Fangs represent an extreme tooth morphology in regards to comparative size of tooth relative to other teeth on the same bone and occur in the dentition of both terrestrial and aquatic vertebrates. They can be seen in both extinct and extant species (Figure 1.1). There is extensive literature concerning the attachment, development, and placement of teeth within the dentition of vertebrates but little concerning the repeated evolution of fangs. One study found that the enlarged fangs found in *Thylacosmilus*, *Apataelurus*, and machairodonts had independently evolved at least three separate times (Simpson, 1941). Despite this knowledge, it is still widely debated on what the true function of these fangs were. Studies have argued that these fangs were used to transfix prey items while other studies claimed that they were used to strike and rip the flesh of prey in order to cause rapid exsanguination (Matthew, 1901).

Fangs in modern day snakes have also been an evolutionary mystery. While most of the 3000 known species of snakes have teeth, roughly 600 have been identified to possess venomous fangs (World Health Organization, 2010). These fangs are hypothesized to have evolved for extreme functionalities (i.e. rapid venom injection). They are also so long that the tooth bearing bone where they reside has to rotate backwards in order for the mouth to properly close (Cundall, 2009). A recent study was able to pinpoint the source of the evolution of fangs in snakes. The *sonic hedgehog* gene, found within the “gum” flesh, was discovered to be the source of the tooth plan during embryonic development (Maxmen, 2008). This plan revealed that fangs developed in the posterior portion of the mouth. As fangs evolved in snakes, the posterior flesh of the mouth dissociated from the anterior flesh. This allowed fangs to grow in the anterior portion of the mouth while the posterior underwent evolutionary changes.

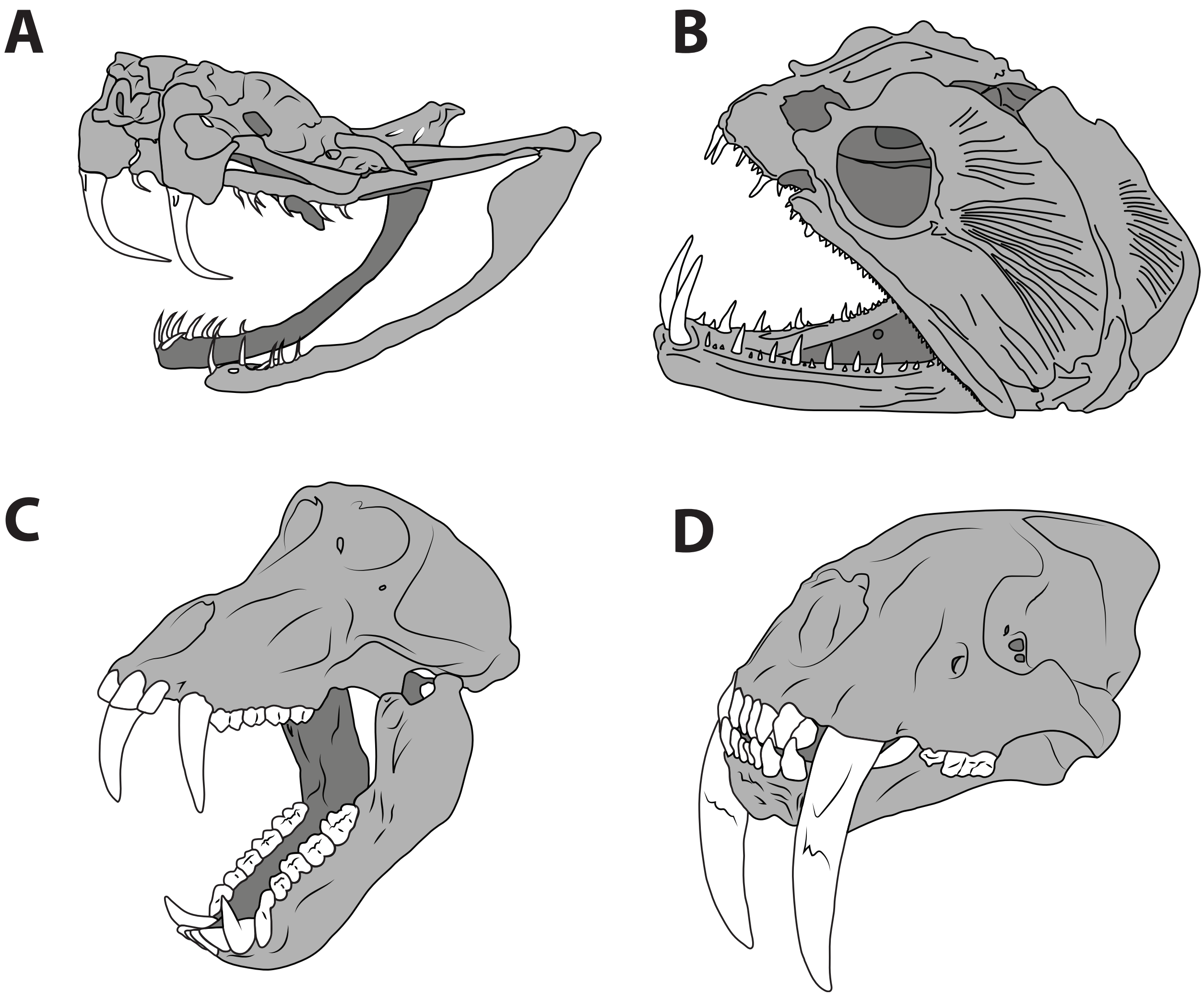

Figure 1.1. Examples of fangs found in extinct and extant vertebrates. A: *Crotalus sp.*, B: *Hydrolycus scomberoides*, C: *Papio sp.*, D: *Smilodon sp.*

Several orders of fishes also possess fangs (Kotrschal and Goldschmid, 1992; Böhlke and Smith, 2002; Kenaley, 2012). These orders include but are not limited to: Aulopiformes (lizardfishes), Stomiiformes (dragonfishes), Beryciformes (fangtooths), and Acanthuriformes (anglerfishes). To date, no study has synthesized the total number of fish species that possess fangs, or investigated the number of times fangs have independently evolved across ray-finned fishes.

One question that arises when surveying fangs across fishes is whether or not to include cartilaginous fishes (class: Chondrichthyes). One might be able to argue that certain species of sharks do possess fangs. The most likely subject would be a recently described species of Squaliform or viper dogfish (Trigonognathus kabeyai). Shirai and Okamura (1992) described the species with noticeably sharp and elongated canines present on the palatoquadrate and Meckel's cartilage. A problem occurs in that the teeth within the dentition of these sharks are largely uniform in size. This immediately excludes the species from this survey based on the definition previously stated. For this study, cartilaginous fishes are not included in this survey of fang presence.

The first goal of this thesis is to examine the anatomy and explore the evolution of fangs across Aulopiformes; an order of fishes that possess fangs on a variety of different bones, with species that occupy a diversity of marine habitats. The second goal of this thesis is to expand this investigation to explore the evolution of fangs across all extant orders of ray-finned fishes.

Chapter 2: EVOLUTION OF FANGS IN LIZARDFISHES (TELEOSTEI: AULOPIFORMES)

Aulopiform Background

The order Aulopiformes includes 44 extant genera with 236 species (Davis and Fielitz, 2010). Members of the order include, but are not limited to, lizardfishes, bombay ducks, cucumber fishes, lancetfishes, green eyes, ice fishes, telescopefishes, and flagfin fishes (Figure 2.1). Aulopiform fishes range in marine habitats from in-shore epipelagic (0-200 meters) waters to the abyssopelagic (4000 – 6000 meters) as either benthic/benthopelagic or pelagic predators (Sweatman, 1984; Thresher et al., 1986). Due to the extreme selective pressures of living in a the deep-sea environment, many species of Aulopiformes have evolved diverse adaptations. Examples of these adaptations include eye modifications, bioluminescence, simultaneous hermaphroditism, and enlarged jaws with dagger-like teeth (Locket, 1971; Davis and Fielitz, 2010).

The dagger-like teeth of some lizardfish species likely assist with the piercing and holding onto prey in the deep sea, a habitat that has been characterized by a lack of prey abundance (Sanders and Hessler, 1969). Some species of mesopelagic deep-sea fishes (e.g. Myctophiformes) perform a nightly vertical migration to shallower waters to prey on zooplankton; pelagic lizardfishes are not known to perform these migrations (Wang, 2001). The first goal of this thesis is to examine the anatomy and explore the repeated evolution of fang-like teeth across Aulopiformes; an order of fishes that possess fangs on a variety of different bones, with species that occupy a diversity of marine habitats. Specifically, this study seeks to

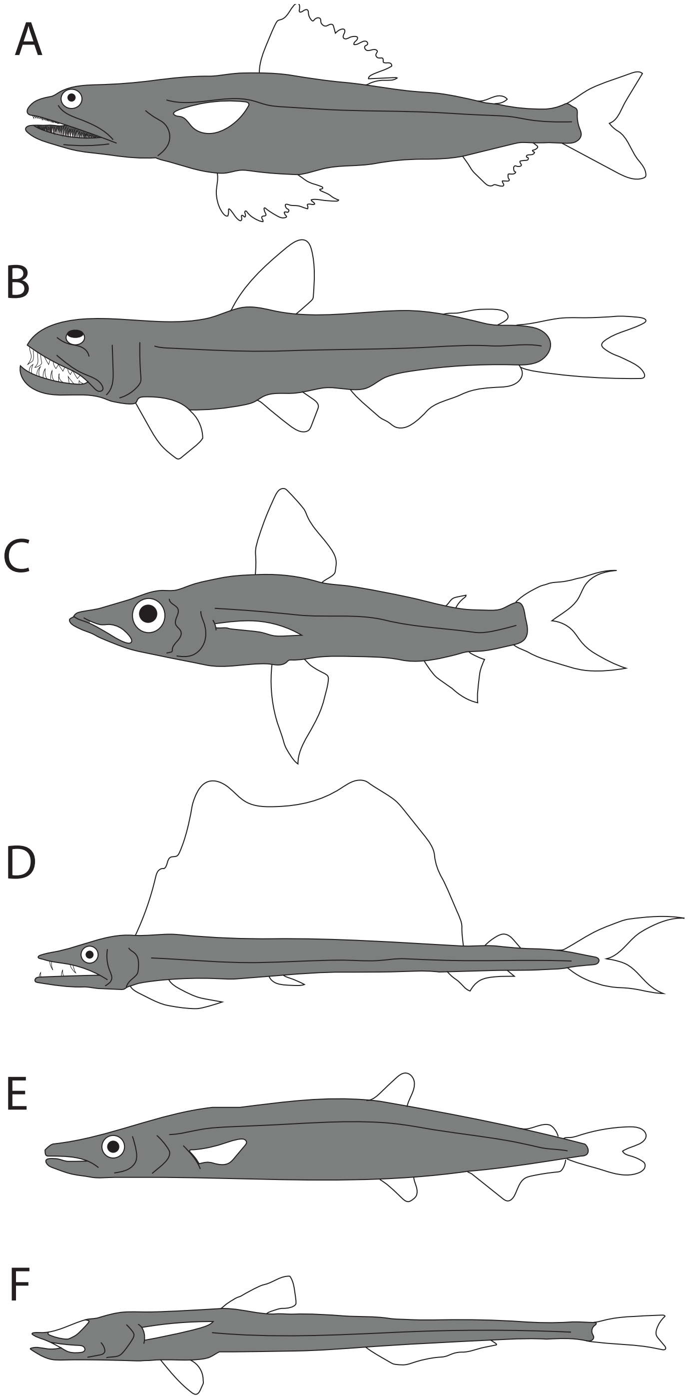

Figure 2.1. Diversity of lizardfish species. A: *Synodus doaki* (Synodontidae), B: *Evermannella indica* (Evermannellidae), C: *Chlorophthalmus truculenta* (Chlorophthalmidae), D: *Alepisaurus ferox* (Alepisauridae), E: *Lestrolepis japonica* (Paralepididae), F: *Ipnops agassizii* (Ipnopidae).

understand how many times fang-like teeth have independently evolved in lizardfishes and if there is any correlation with the habitat these fishes occupy.

Aulopiform Phylogenetic Relationships and Historical Classification

Aulopiform fishes were initially classified within the order Iniomi along with fishes that are currently classified in the Myctophiformes (Lanternfishes) (Regan, 1911; Gregory, 1933). Rosen (1973) was the first to diagnose the order Aulopiformes in which he included 15 extant families and 17 fossil genera. Rosen (1973) classified Aulopiformes as a monophyletic group based on an elongation to the uncinate process on the second epibranchial (EB2) and an elevated cranial condyle on the maxilla (Rosen, 1985; Stiassny, 1986). This elongation of the EB2 bridged the gap between the second and third pharyngobranchials (PB2 and PB3) and is not found within lantern fishes (Myctophiformes). R.K. Johnson (1982) argued that certain paralepidids and neoscopelids share an elongation of the second epibranchial and that a reduction in the EB2 was secondarily derived in myctophids. G. D. Jonhson (1992) countered that Aulopiformes could be classified as a monophyletic group due to similarities among Aulopiform larva and gill arches.

Baldwin and Johnson (1996) were the first to infer an evolutionary tree of Aulopiformes with a parsimony approach (PAUP Version 3.0, ACCTRAN; Swofford, 1991) based on morphological characters. Their findings supported Rosen's (1973) hypothesis of the monophyly of Aulopiformes through seven described characteristics. These characteristics include an enlarged EB2 uncinate process, the absence of a cartilaginous condyle on PB3, the anterior extension of the epipleural series, peritoneal pigmentation of larvae, displacement of one or more anterior epipleurals dorsally into the horizontal septum, absence of a swim bladder, and the fusion of the medial process of the pelvic girdle (Baldwin and Johnson, 1996).

The phylogenetic relationships of Aulopiformes was further investigated by Sato and Nakabo (2002) with the diagnosis of a new family Paraulopidae including the genus *Paraulopus*. Species within *Paraulopus* had previously been classified within *Chlorophthalmus*, with Sato and Nakabo (2002) identifying that *Paraulopus* possesses three diagnostic traits that separate it from other species in *Chlorophthalmus*. These traits include an absence of a gap between the fourth basibranchial (BB4) and the fifth ceratobranchial (CB5), epipleural bones distributed from a posterior portion of the abdominal vertebrae, and the presence of paired olive spots found on the dorsal side of specimens (Sato and Nakabo, 2002). In addition to the creation of *Paraulopus*, Sato and Nakabo (2002) classified *Bathysauroides* to Chlorophthalmoidei elevating it to a familial status along with *Bathysauropsis*.

Recently, Davis (2010) utilized four protein coding gene regions and one mitochondrial gene (*rag1, zic1, enc1, Plagl2, and COI*) to investigate aulopiform evolutionary relationships. With DNA and morphological evidence, Davis (2010) found statistically strong support for the monophyly of Aulopiformes and its status as the sister group to Ctenosquamata (lanternfishes + spiny-rayed fishes). This result conflicts with findings by R.K. Johnson (1982) and Rosen (1985), but supports the findings of Rosen (1973). The monophyly of Aulopiformes was supported by a total of fourteen morphological synapomorphies, some of which include; absence of a swim bladder, presence of a fifth epibranchial (EB5), an enlarged uncinate process on the

EB2, absence of lateral palatine expansion, and an elongated and separated posterior pelvic girdle process.

Davis' (2010) genetic investigation led to a further revision of the classification of Aulopiformes. The monophyly of suborders Chlorophthalmoidei and Alepisauroidei as proposed by Baldwin and Johnson (1996) were not supported. The genus P*araulopus* was not recovered as a member of the suborder Synodonoidei (Figure 2.2) and was, instead, inferred as the sister group to all chloropthalmoid + giganturoid + alepisauroid taxa and is the single member of the suborder Paraulopoidei. Within the superorder Ipnopoidea, taxa of the superorder Giganturoidea were found to be the sister group to Ipnopoidae rather than the suborder Alepisauroidei (Baldwin and Johnson, 1996; Sato and Nakabo, 2002). The family Evermannellidae was recovered as the sister group to taxa in a clade consisting of the families Sudidae, Alepisauridae, and Paralepididae (Davis, 2010). The genus *Sudis* was confirmed as the sister group to a clade consisting of two lineages which include alepisaurid and paralepidid fishes. This allows for the re-elevation of *Sudis* to familial status. The first lineage contains the family Alepisauridae. *Magnisudis* and *Anotopterus* had previously been placed as members of the family Paralepididae; but Davis' (2010) findings recognized both genera as now a part of the family Alepisauridae. The remaining genera of *Paralepis*, *Macroparalepis*, *Arctozenus*, *Lestidiops*, *Lestrolepis*, *Lestidium*, *Stemonosudis*, and *Uncisudis* of the family Paralepididae make up the second lineage.

Baldwin & Johnson (1996)

- Order Aulopiformes
  - Suborder Synodontoidei
    - Family Aulopidae (*Aulopus*)
    - Family Pseudotrichonodontidae (*Pseudotrichonotus*)
    - Family Synodontidae (*Synodus, Trachinocephalus, Harpadon, Saurida*)
  - Suborder Chloropthlamoidei
    - Family Chlorophthalmidae (*Chlorophthalmus, Parasudis*)
    - Bathysauropsis (*B. gracilis, B. malayanus*)
    - Family Ipnopidae (*Ipnops, Bathypterois, Bathytyphlops, Discoverichthys, Bathymicrops*)
  - Suborder Alepisauroidei
    - Family Alepisauridae (*Alepisaurus, Omosudis*)
    - Family Paralepididae (*Anotopterus, Arctozenus, Lestidiops, Lestidium, Lestrolepis, Macroparalepis, Magnisudis, Notolepis, Paralepis, Stemnosudis, Sudis, Uncisudis, Dolichosudis*)
    - Family Evermannellidae (*Coccorella, Evermannella, Odontostomops*)
    - Family Scopelarchidae (*Benthalbella, Rosenblattichthys, Scopelarchoides, Scopelarchus*)
  - Suborder Giganturoidei
    - Bathysauroides gigas
    - Family Bathysauridae (*Bathysaurus*)
    - Family Giganturidae (*Gigantura*)

Sato & Nakabo (2002)

- Order Aulopiformes
  - Suborder Synodontoidei
    - Family Paraulopidae (*Paraulopus*)
    - Family Aulopidae (*Aulopus*)
    - Family Pseudotrichonotidae (*Pseudotrichonotus*)
    - Family Synodontidae (*Synodus, Trachinocephalus, Harpadon, Saurida*)
  - Suborder Chloropthalmoidei
    - Family bathysauroididae (*Bathysauroides*)
    - Family Chlorophthalmidae (*Chlorophthalmus, Parasudis*)
    - Family Bathysauropsidae (*Bathysauropsis*)
    - Family Notosudidae (*Ahliesaurus, Luciosudis, Scopelosaurus*)
    - Family Ipnopidae (*Bathymicrops, Bathypterois, Bathytyphlops, Discoverichthys, Ipnops*)
  - Suborder Alepisauroidei
    - Family Alepisauridae (*Alepisaurus, Omosudis*)
    - Family Paralepididae *(Anotopterus, Arctozenus, Lestidiops, Lestidium, Lestrolepis, Macroparalepis, Magnisudis, Notolepis, Paralepis, Stemnosudis, Sudis, Uncisudis, Dolichosudis*)
    - Family Evermannellidae (*Coccorella, Evermannella, Odontostomops*)
    - Family Scopelarchidae (*Benthalbella, Rosenblattichthys, Scopelarchoides, Scopelarchus*)
  - Suborder Giganturoidei
    - Family Bathysauridae (*Bathysaurus*)
    - Family Giganturidae (*Gigantura*)

Davis (2010)

- Order Aulopiformes
  - Suborder Aulopoidei
    - Family Synodontidae (*Synodus, Trachinocephalus, Harpadon, Saurida*)
    - Family Aulopidae (*Aulopus*)
    - Family Pseudotrichonotidae (*Pseudotrichonotus*)
  - Suborder Paraulopoidei
    - Family Paraulopidae (*Paraulopus*)
  - Suborder Alepisauroidei
    - Superfamily Ipnopoidea
      - Epifamily Giganturoidae
        - Family Giganturidae (*Gigantura*)
        - Family Bathysauridae (*Bathysaurus*)
        - Family Bathysauroididae (*Bathysauroides*)
      - Epifamily Ipnopoidae
        - Family Ipnopidae (*Bathypterois, Ipnops, Bathymicrops, Bathytyphlops, Discoverichthys*)
    - Superfamily Chlorophthalmoidea
      - Family Chlorophthalmidae (*Chlorophthalmus, Parasudis*)
    - Superfamily Notosudoidae
      - Family Notosudidae (*Scopelosaurus, Ahliesaurus, Luciosudis*)
    - Superfamily Alepisauroidea
      - Family Scopelarchidae (*Benthalbella, Rosenblattichthys, Scopelarchus, Scopelarchoides*)
      - Family Evermannellidae (*Odontostomops, Coccorella, Evermannella*)
      - Family Sudidae (*Sudis*)
      - Family Alepisauridae (*Anotopterus, Magnisudis, Omosudis, Alepisaurus*)
      - Family Paralepididae (*Macroparalepis, Paralepis, Arctozenus, Stemonosudis, Lestidiops, Uncisudis, Lestrolepis, Lestidium, Dolichosudis*)

Figure 2.2. Classifications of aulopiform fishes. Genera within each family are listed.

Davis and Fielitz (2010) also investigated the interrelationships of fossil aulopiform species. Davis and Fielitz (2010) classified the extinct family †Enchodontidae as the sister group to the extant family Alepisauridae. †*Enchodus* is an extinct genus of Aulopiformes (lizardfishes) that was prolific during the upper Cretaceous period. (Everhart et al., 2003). The various species of †*Enchodus* were able to survive the Cretaceous-Paleogene mass marine extinction and survived up until the Eocene Epoch (D'Hondt, 2005). †*Enchodus* is notorious for it's well defined palatine and dentary fangs that can been seen in fossilized specimens.

Aulopiform Habitats

Aulopiformes are predatory marine fishes that range from inshore coastal waters to the deep-sea. The family Synodontidae (lizardfishes) is a common inhabitant of coral reef systems around the world and is primarily found in benthic habitats from 0 to 200 meters. Adults can be found among sand flats in inshore bays, reefs, and continental shelves, while juveniles are mainly pelagic (Anderson et al., 1966). Their heads are depressed with a large mouth and gape and have large depressible teeth on their dentary, and lower pharyngeals (Uyeno et al., 1983). Their color variation widely ranges from splotchy browns and greens to vibrant oranges and reds. The majority of inshore lizardfishes are nocturnal hunters and spend the day buried in the sand or perching on rocky outcroppings (Humann and Deloach, 1993). Conversely, the majority of species of Aulopiformes inhabit the deep-sea (Nelson, 2006). Many of these fishes have evolved elaborate evolutionary adaptations to cope with the pressures of living in the mesopelagic and bathypelagic zones. All deep-sea lizardfish including members of the family Bathysauridae (deep-sea lizardfishes) have evolved to be synchronously hermaphroditic (Sulak et al., 1985). Aulopiformes in the family Ipnopidae (deep-sea tripod fishes) have evolved elongated pelvic and caudal fins to elevate themselves off of the sea floor (Jones and Sulak, 1990). Deep-sea benthic Aulopiformes are limited in their colorations being mostly pale, dark brown, or black. Light penetration greatly decreases below 200 meters leaving its inhabitants unable to absorb light. Deep-sea Aulopiformes are also found in pelagic habitats. Open ocean pelagic Aulopiformes have many of the same traits found in benthic species. These traits include synchronous hermaphroditism, absence of a swim bladder, and various eye modifications (Davis and Fielitz, 2010). However, the body morphology of pelagic Aulopiformes greatly differs from their benthic relatives. Benthic Aulopiformes typically have a short cigar shaped body while pelagic species have evolved greatly attenuated ribbon-like body shapes. The lancetfish (*Alepisaurus ferox*) has a maximum total length of two meters with a shallow body depth (Nelson, 1994). Species of Paralepidids (Barracudinas) have been documented to reach total lengths of up to one meter with a similarly reduced body depth (Nelson, 1994).

Aulopiform Dentition

Dentition across the aulopiform radiation varies widely in size, shape, and number (Figure 2.3). The highly predatory genera S*ynodus*, A*ulopus*, and *Saurida*

have several rows of villiform teeth used to capture a wide variety of prey items on reefs (Sweatman, 1984) (Figure 2.3). The only observed shallow benthic species with fangs was

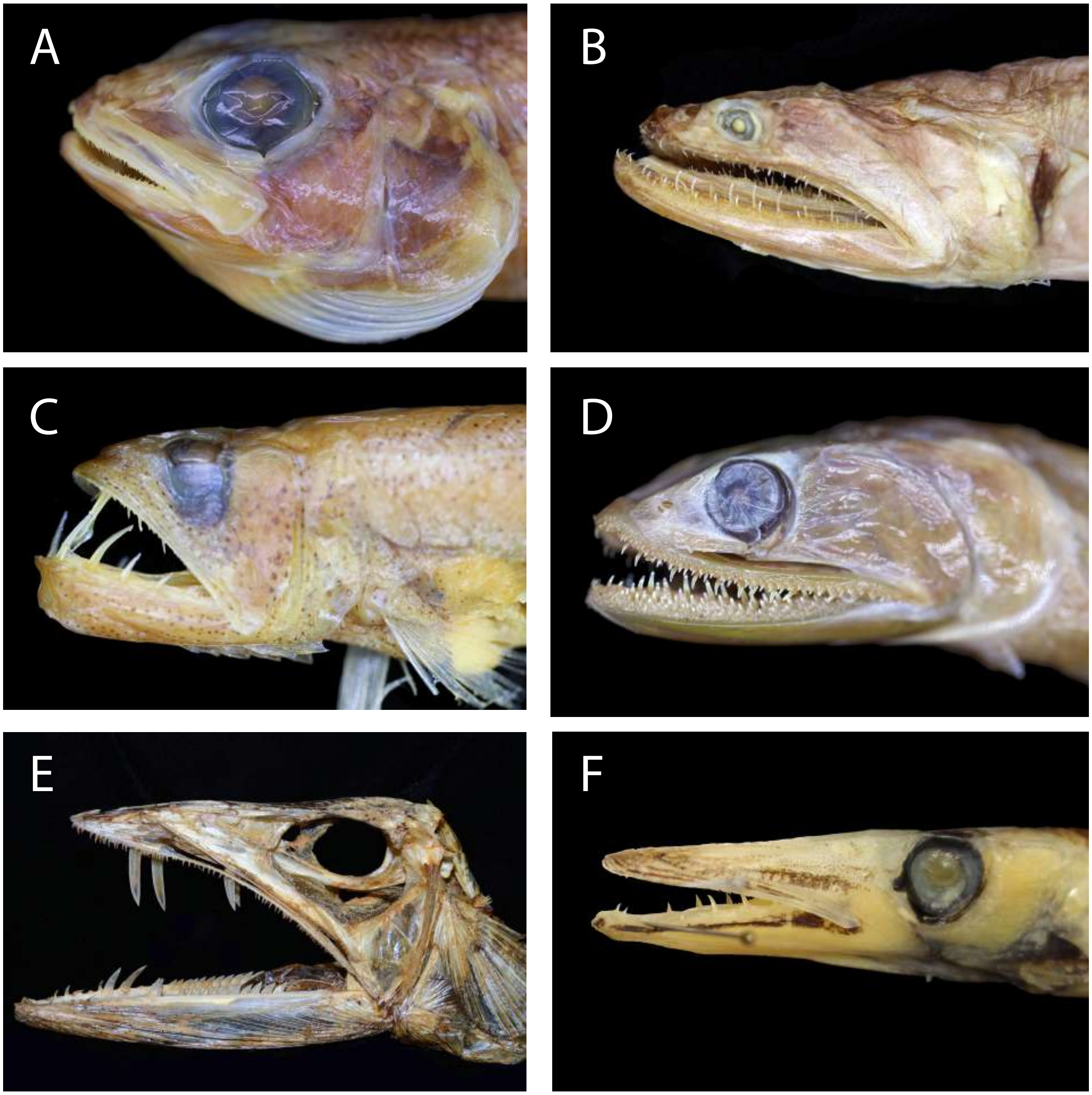

Figure 2.3. Variation in lizardfish dentition. A: *Aulopus sp.* (LACMNH 33649-2), B: *Harpadon microchir* (SU 20714), C: *Evermannella balbo* (MCZ 52329), D: *Saurida tumbil* (BMNH 1966.11.16.1024-1025), E: *Alepisaurus sp.*, F: *Lestrolepis intermedia* (FMNH 117869).

Harpadon microchir (Figure 2.3). These fangs originate on the dentary bone and are recurved towards the posterior portion of the mouth. These fangs also possess large barbs on the end of their fangs much like that of a fishing hook. Pelagic Aulopiformes have evolved long fangs that are compressed and wide similar to razor blades and likely used for catching and restraining prey. Members of the family Evermannellidae (sabertooth fishes) have highly modified palatine teeth which are long, slender, and curve inward slightly (Johnson, 1990). Similarly, Alepisaurids (lancetfishes) are known for possessing two to three distinctively long palatine fangs used for piercing fish, squids, and salps (Post, 1984). An example of these fangs can bee seen in *Alepisaurus* (Figure 2.3). These razor-like fangs originate on both the palatine and dentary bones in *Alepisaurus ferox*. Elongated conical fangs can be seen in species such as *Evermannella balbo* and *Lestrolepis intermedia* (Figure 2.3). These fangs originate on both the palatine and dentary bones in *Evermannella* and solely on the dentary bone in *Lestrolepis*. Short conical fangs can be found in the green eye species, such as *Parasudis truculentus* (Figure 2.4). These fangs are exclusive to the palatine bone and are typically seen in a single pair.

Materials and Methods

Lizardfish specimens from the American Museum of Natural History (AMNH), the Museum of Comparative Zoology (MCZ), The Field Museum of Natural History (FMNH), the Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (LACMNH), Scripps Institution of Oceanography (SIO), the California Academy of Sciences (SU/CAS), the University of Florida - uncatalogued (CI), the Natural History Museum in

Figure 2.4. Palatine fangs in *Parasudis truculentus* FMNH 67146.

London (BMNH), and the Virginia Institute of Marine Science (VIMS) were used in this study. Physical examinations of specimens representing 35 of 44 genera were performed using a Leica MZ8 stereomicroscope Leica MZ16 F fluorescent stereomicroscope. Photographs were taken using a Canon EOS Rebel SL1 Digital SLR camera with a macro lens attachment. Dentition was examined across the aulopiform radiation. Variation in tooth bearing bones (e.g. palatine, dentary, premaxilla, branchial arches, and mesopterygoid), tooth attachment, and tooth anatomy were analyzed on both EtOH and clear and stained specimens. Clear and staining followed standard operating procedure from Taylor (1985).

A previously published phylogeny of aulopiform relationships (Davis and Fielitz, 2010) inferred from one mitochondrial (*COI*) and four nuclear (*enc1, Plagl2, rag1, zic1*) gene fragments is used to reconstruct the evolution of fangs and habitat transitions among lizardfishes. Four character reconstructions were inferred using Mesquite 2.75 (Maddison and Maddison, 2010). The four character states included are:

1. Enlarged fang-like teeth on bones associated with the oral jaws
    (0) Absent
    (1) Present
2. Marine habitat
    (0) Shallow benthic
    (1) Deep-sea benthic
    (2) Deep-sea pelagic

3. Enlarged fang-like teeth on palatine

    (0) Absent

    (1) Present

4. Enlarged fang-like teeth on dentary

    (0) Absent

    (1) Present

Materials Examined

Ahliesaurus berryi: MCZ 161660, 1 of 1

Ahliesaurus berryi: MCZ 163249, 1 of 1

Ahliesaurus berryi: SIO 73-146, 1 of 3

Alepisaurus brevirostris: MCZ 163463, 2 of 3

Alepisaurus ferox: BMNH 2003.11.16.10, 1 of 1

Alepisaurus ferox: FMNH 121671, 1 of 1

Alepisaurus ferox: MCZ 127309, 1 of 1

Alepisaurus sp.: FMNH 8414, 1 of 1

Anotopterus pharao: FMNH 64222, 1 of 1

Anotopterus pharao: MCZ 148409, 1 of 1

Anotopterus pharao: SIO 65-414-25A, 1 of 1

Arctozenus risso: SIO 74-23, 3 of 7

Aulopus bajacali: SIO 84-80, 2 of 2

Aulopus filamentosus: FMNH 63102, 1 of 1

Aulopus parini: LACMNH 32269-9, 2 of 80

Aulopus sp.: LACMNH 33649-2, 2 of 5

Bathypterois atricolor: FMNH 88981, 1 of 3

Bathypterois bigelowi: VIMS 06362, 2 of 6

Bathypterois pectinatus: SIO 72-183, 1 of 1

Bathypterois phenax: MCZ 164528, 1 of 4

Bathysaurus ferox: BMNH 1994.9.19.10, 1 of 1

Bathysaurus ferox: MCZ 138024, 2 of 3

Bathysaurus ferox: MCZ 165208, 1 of 1

Benthalbella dentata: SIO 88-53, 1 of 2

Benthalbella infans: FMNH 79658, 1 of 1

Coccorella atlantica: FMNH 79707, 1 of 1

Coccorella atlantica: SIO 94-38, 1 of 1

Coccorella atrata: SIO 75-157-25, 1 of 1

Chlorophthalmus agassize: BMNH 1939.5.24.445-456, 2 of 11

Chlorophthalmus braziliensis: VIMS 3080, 4 of 55

Chlorophthalmus sp.: FMNH 88989, 2 of 5

Evermannella balbo: MCZ 52329, 1 of 1

Evermannella balbo: MCZ 101362, 1 of 1

Evermannella indica: FMNH 82773, 1 of 1

Evermannella indica: SIO 73-148, 2 of 2

Evermannella indica: SIO 60-239, 1 of 1

Gigantura chuni: BMNH 2002.6.20.426-427, 1 of 1

Gigantura chuni: MCZ 57007, 1 of 1

Harpadon nehereus: CAS 56037, 4 of 7

Harpadon nehereus: BMNH 1986.9.25.21, 1 of 1

Harpadon microchir: SU 20714, 1 of 4

Hime japonicus: LACMNH 42394-1, 1 of 7

Ipnops murrayi: CI 253, 2 of 20

Lagiacrusichthys macropinna: MCZ 125832, 1 of 1

Lestidiops ringens: SIO 79-187, 2 of 2

Lestidiops sp.: FMNH 117866, 1 of 2

Lestidium atlanticum: KU 27946, 1 of 1

Lestidium bigelowi: SIO 75-135, 2 of 3

Lestrolepis intermedia: FMNH 117869, 1 of 1

Macroparalepis brevis: MCZ 68502, 1 of 1

Macroparalepis brevis: MCZ 162097, 1 of 1

Macroparalepis nigra: MCZ 44885, 1 of 1

Macroparalepis sp.: FMNH 49988, 1 of 3

Magnisudis atlantica: MCZ 164296, 2 of 4

Magnisudis atlantica: MCZ 164376, 1 of 2

Notolepis annulata: MCZ 146393, 1 of 1

Notolepis coatsi: MCZ 146397, 1 of 1

Notolepis coatsi: SIO 02-40, 2 of 23

Odontostomops normalops: FMNH 88170, 1 of 2

Odontostomops normalops: MCZ 165564, 1 of 1

Odontostomops normalops: SIO 97-209, 2 of 2

Omosudis lowii: SIO 74-51, 1 of 1

Paralepis elongata: MCZ 43140, 1 of 3

Paralepis hyalina: FMNH 63103, 1 of 1

Paralepis sp.: SIO 61-29, 2 of 2

Parasudis truculentus: VIMS 03261, 2 of 4

Parasudis truculentus: BMNH 1986.4.3.10-13, 1 of 4

Parasudis truculentus: FMNH 67139, 1 of 3

Parasudis truculentus: FMNH 67146, 1 of 1

Rosenblattichthys volucris: SIO 68-582-25, 2 of 2

Saurida tumbil: BMNH 1996.11.16.1024-1025, 2 of 10

Saurida wanieso: SU 60886, 1 of 1

Scopelarchoides danae: MCZ 127125, 1 of 1

Scopelarchus analis: FMNH 79651, 1 of 2

Scopelarchus analis: FMNH 79654, 1 of 1

Scopelarchus analis: MCZ 127130, 1 of 2

Scopelarchus guentheri: SIO 71-386, 1 of 3

Scopelosaurus hubbsi: SIO 75-451, 1 of 1

Scopelosaurus smithii: SIO 69-346, 1 of 1

Stemonosudis macrura: SIO 72-13, 2 of 2

Sudis atrox: MCZ 68329, 1 of 1

Sudis atrox: SIO 97-92, 2 of 2

Sudis hyalina: MCZ 43877, 1 of 1

Synodus lobeli: BMNH 1985.1.16.1, 1 of 1

Synodus saurus: AMNH 29866, 2 of 6

Synodus sp.: AMNH 23079, 2 of 20

Trachicephalus myops: BMNH 1986.11.28.18-21, 2 of 4

Results

The character reconstruction of fang presence indicates most likely there are four independent evolutions of fangs across lizardfishes. These include independent evolutions of fangs in the subfamily Harpadontinae (bombayducks), the family Giganturidae (telescopefishes), the family Parasudidae, and the common ancestor of the Alepisauroidei clade (Figure 2.5). The phylogeny indicates that the common ancestor of Aulopiformes most likely did not have fangs (Figure 2.5).

There were three independent evolutions of palatine fangs across lizardfishes (Figure 2.6). These evolutions are present in the families Giganturidae and Parasudidae and the common ancestor of the Alepisauroidea clade. There was a loss of palatine fangs in the family Sudidae (Figure 2.7). Dentary fangs likely independently evolved three times across the lizardfish radiation (Figure 2.6). These independent evolutions occurred in the the subfamily Harpadontinae, family Giganturidae, and the common ancestor of the Alepisauroidea (Figure 2.6).

In regards to the character reconstruction of habitat across lizardfishes, the common ancestor of the Aulopiformes most likely lived in a benthic inshore environment. The common ancestor of the Alepisauroidei clade indicates the first transition into the deep sea. The phylogeny indicates that there were two independent evolutions of lizardfishes in deep-sea pelagic environments. These evolutions occurred in the common ancestor of the family Giganturidae and the common ancestor of the Chlorophthalmoidea + Notosudoidea + Alepisauroidea clade (Figure 2.5). There were also two independent transitions into deep-sea benthic environments, one in the common ancestor of Ipnopidae, and one in the common ancestor of the Chlorophthalmoidae + Parasudidae.

Discussion

This first objective of this thesis is to explore the evolution of fangs in Aulopiformes (lizardfishes). Overall, the results indicate that large fang-like teeth have independently evolved four times across lizardfishes (Figure 2.5). An anatomical examination of lizardfishes revealed

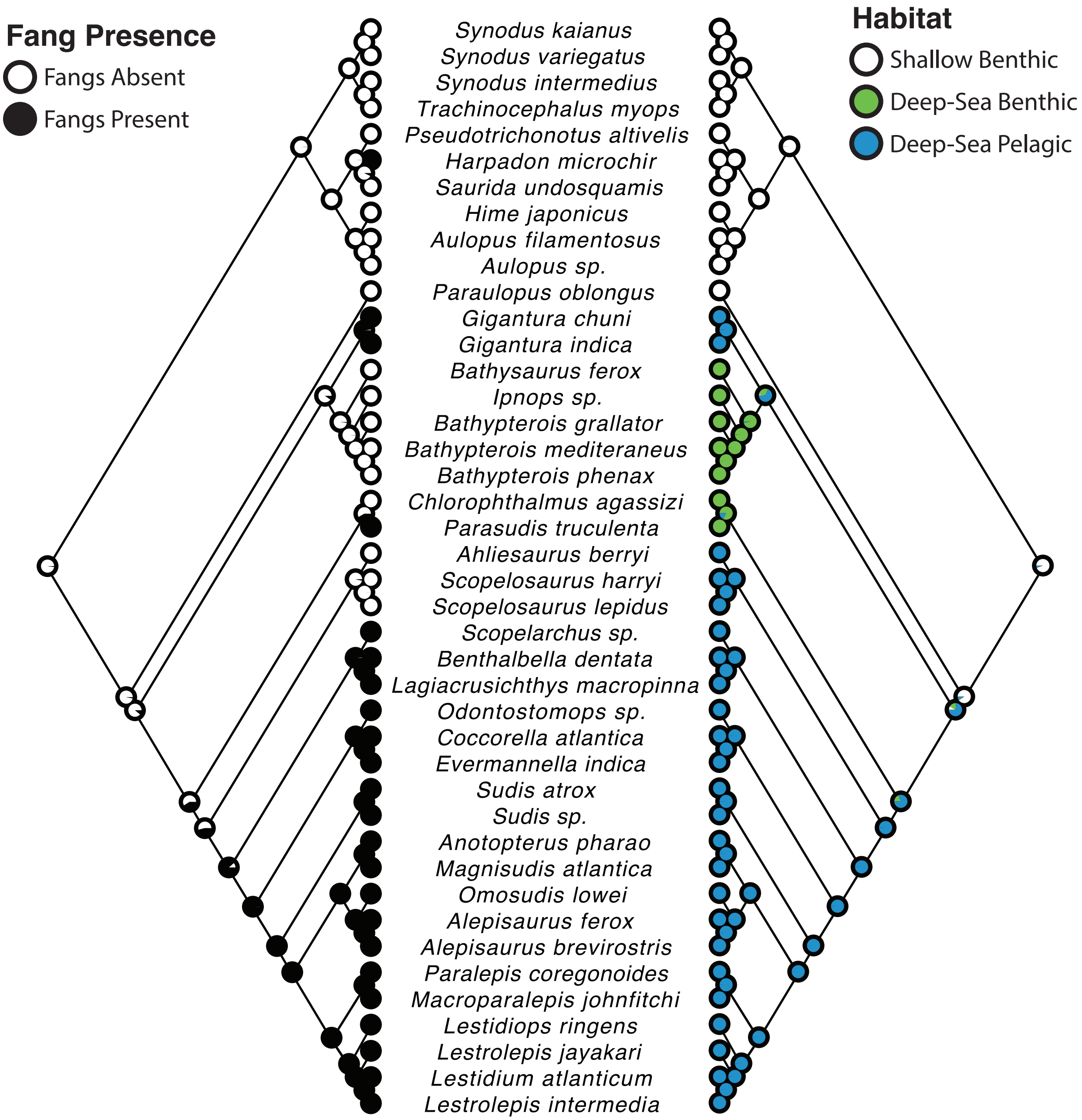

Figure 2.5. Evolutionary relationships of aulopiform fishes based on maximum likelihood estimation from 5 gene fragments with a likelihood ancestral character reconstruction of the evolution of fangs and habitat shifts across the aulopiform radiation. Circles at nodes represent probabilities of character state likelihoods.

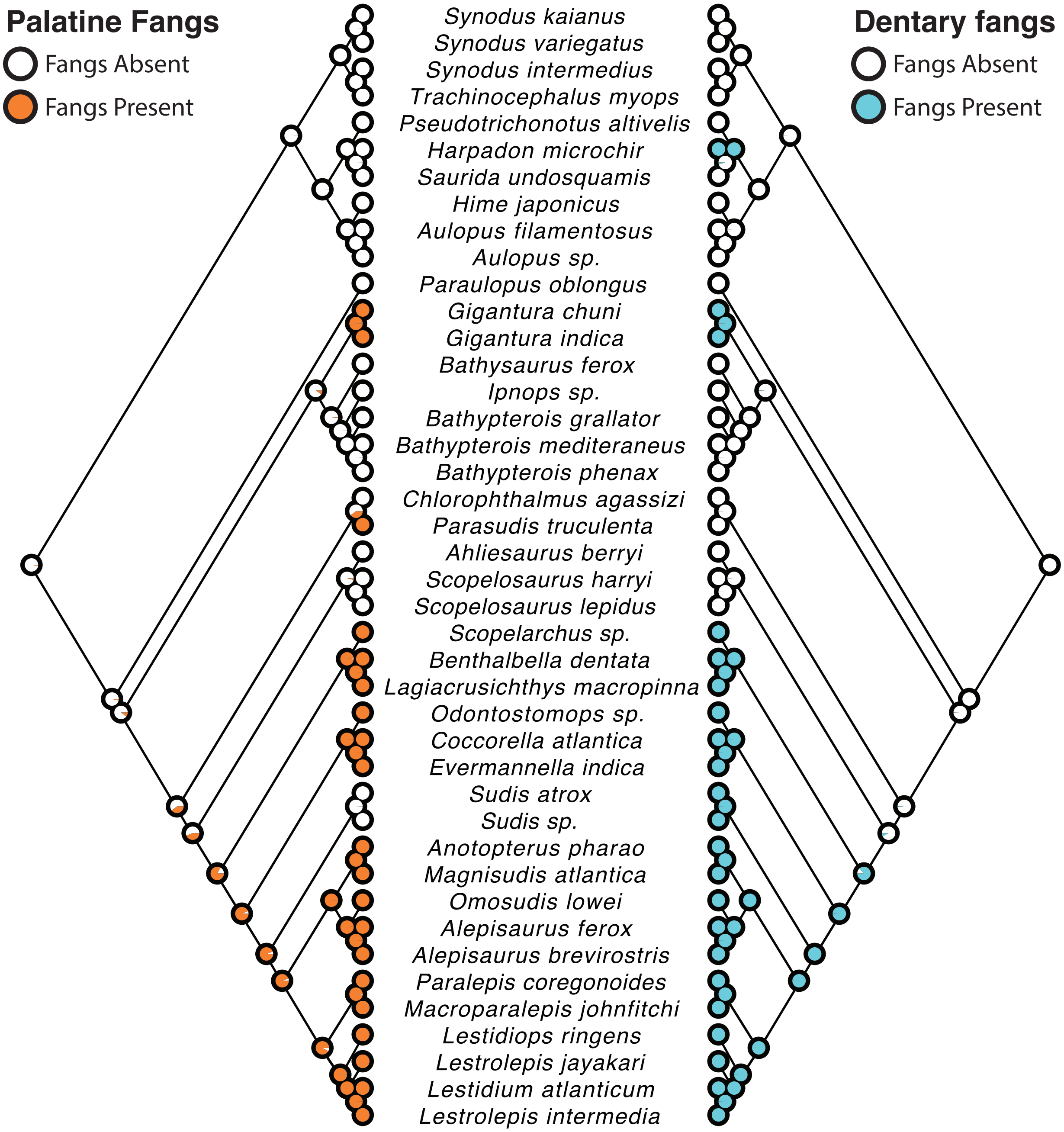

Figure 2.6. Evolutionary relationships of aulopiform fishes based on maximum likelihood estimation from 5 gene fragments with a likelihood ancestral character reconstruction of the evolution of palatine fangs and dentary fangs across the aulopiform radiation. Circles at nodes represent probabilities of character state likelihoods.

Figure 2.7. The highly modified upper jaw of *Sudis hyalina* (FMNH 63103).

that fangs were present on the palatine, dentary, or both bones (Figure 2.6). In reference to palatine fangs, the character state reconstruction indicates that there were three separate evolutions in the families Giganturidae and Parasudidae and most likely in the common ancestor of the Alepisauroidea clade with a loss of palatine fangs in the family Sudidae (Figure 2.7). The lack of palatine fangs in the family Notosudidae (waryfishes) is likely the result of the group having a substantially different diet than other lizardfishes. Species of the genera *Ahliesaurus* and *Scopelosaurus* almost exclusively eat zooplankton, copepods, and euphausiids (Krefft, 1990). The lack of palatine fangs in some species of deep-pelagic lizardfishes could be attributed to the need for more space to accommodate for the evolution of large dentary fangs. For example, *Sudis hyalina* has a highly modified upper jaw that which allows the jaw to properly close around the dentary fangs (Figure 2.7).

When comparing these results to habitat shifts in lizardfishes, there is a correlation between the evolution of fangs and habitat (Figure 2.5). Fangs have predominantly and independently evolved repeatedly in lizardfishes that live in pelagic deep-sea environments, with nearly no species of benthic lizardfishes possessing fangs. Inshore benthic lizardfishes have access to a wide variety and quantity of prey items. A study of the feeding habits of *Synodus englemani* documented attacks on 26 separate species of reef fishes with some individuals fixating on large schools of prey (Sweatman, 1984). The deep-sea benthic lizardfishes also have access to a larger quantity of prey items. Diet analyses have found deep-sea squids, salps, fishes, and decapods in the gut of *Bathysaurus ferox* (Sulak, 1990). It is also hypothesized that these benthic lizardfishes scavenge food from deceased fish or animals that fall to the sea floor (Smith and Baco, 2003). Deep-sea pelagic lizardfishes inhabit an area of the ocean where the variety of prey is great, but the abundance of prey is poor. Marshall (1976) inferred that the average volume of water available for each marine species is one million km^3 and that the frequency of a predator finding a prey item is greatly reduced.

In addition to lizardfishes, numerous lineages of pelagic deep-sea fishes have evolved greatly enlarged fangs (e.g., anglerfishes, dragonfishes) that likely function in assisting with prey capture and retention. Nearly all species of Stomiiformes (dragonfishes) have greatly enlarged fangs (Kenaley, 2009). These fangs, along with their elongated jaws, allow for restraining prey (Kenaley, 2012). Fangtooths (Beryciformes) have also been documented to have greatly enlarged fangs on both their palatine and dentary bones. Their fangs are used to pierce prey items when lunging at rapid speeds (Childress and Meek, 1973).

Chapter 3: EVOLUTION OF FANGS ACROSS RAY-FINNED FISHES

Fangs in Ray-finned Fishes

To date, no study has synthesized the total number of fish lineages that are observed to have fangs, or investigated the number of times fangs have independently evolved across ray-finned fishes. Several species of fishes have been documented to possess what have been described as fangs, fang-like teeth, elongated canines, or teeth that terminate in a sharp point (Haffner, 1952; Fraser, 1971; Olsen, 1971; Shimizu, 1978; Ben-Tuvia and Golani, 1984; Uemura et al., 2000; George et al., 2006; Melo, 2009). For the purposes of this study, a fang is defined as a tooth, or a bone with projections of a tooth-like shape, associated with the oral jaws that is greatly elongated or enlarged and fewer in number relative to the additional teeth found on the same bone.

Ray-finned fishes that possess fangs can be found in both freshwater and marine environments. A preliminary literature review revealed that fangs function in two primary ways. One primary function of fangs is using them as weapons in a territorial dispute (Ros et al., 2004). Species of male sabertooth bennies are known to use their fangs to spar with other males (Bshary and Bshary, 2010). The other primary function of fangs across fishes are to pierce and restrain prey items (Porter and Motta, 2004). For example, predatory piscivorous fishes with fangs, such as the great barracuda (*Sphyraena barracuda*), are able to sever their prey into pieces using their sharp fangs (Habegger et al. 2011). Gregory (1993) noted that in pelagic predatory species such as pikes (Esocidae), barracudas (Sphyraenidae), and hammer jaws (Omosudidae), several, if not all, fang-like teeth are longer and angled anteriorly to function in a way so that prey cannot escape.

Fangs in fishes are historically understudied, with studies that investigate fangs primarily focused on terrestrial vertebrates. Studies of sabertooth cats (e.g. *Smilodon*) often explore the development, growth rates, and replacement of fangs (Rawn-Schatzinger, 1983; Tejada-Flores and Shaw, 1984; Van Valkenburgh and Hertel, 1993; Feranec, 2004). There are a wide breadth of studies that explore the evolution of fangs in snakes due to their ability to inject venom through these teeth (Schaefer, 1976; Ernst, 1982; Kardong, 1993; Hayes et al., 2008). Fangs in fishes have gone understudied in part because the majority of venomous fishes inject venom through spines on their dorsal, anal, and pectoral fins or opercular bones rather than through teeth (Smith et al., 2016). Smith et al. (2016) found that of the roughly 2,500 known venomous fish species, only two genera deliver venom with their fangs, including the one-jawed eel (*Monognathus*), and the the fang-tooth blenny (*Meiacanthus*).

The objective of this study is to answer the following questions: how many families of fishes are observed to have representatives that have fangs, and how many independent evolutions of fangs have occurred across the ray-finned fishes?

Materials and Methods

In order to investigate the evolution of fangs across ray-finned fishes, I used several methods to conduct a survey of fang presence and absence across families of ray-finned fishes. I generated this survey through a combination of three methods; specimen examination, literature search, and online database review.

Ray-finned fish specimens from the Museum of Comparative Zoology (MCZ), The Field Museum of Natural History (FMNH), the Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (LACMNH), Scripps Institution of Oceanography (SIO), and the California Academy of Sciences (SU/CAS) were used in this study. Physical examinations of specimens were performed using a Leica MZ8 stereomicroscope Leica MZ16 F fluorescent stereomicroscope. Presence of fangs was analyzed on both EtOH and clear and stained specimens. Photographs of specimens were taken using a Canon EOS Rebel SL1 Digital SLR camera with a macro lens attachment.

I reviewed online databases (e.g. Digimorph; DigiMorph Staff, 2009; Calacademy; California Academy of Sciences, 2017; FishBase; Froese and Pauly, 2017) for images of ray-finned fishes. These databases often included high resolution photos, illustrations, radiographs, computed tomography scans of fishes which allowed me to accurately conduct a survey for fang presence.

I inferred a phylogeny of ray-finned fishes from ten nuclear (*enc1, Glyt, myh6, Plagl2, Ptr, rag1, SH3PX3, sreb2, tbr, zic1*) and one mitochondrial (*COI*) gene fragments. I utilized previously published gene sequence data from a hypothesis of evolutionary relationships of ray-finned fishes from Davis et al. (2016) in combination with additionally published genetic material (Table 3.1). Additional sequences from GenBank that were not present in Davis et al. (2016) are identified in (Table 3.1).

Sequence data positional homology statements were generated in the alignment program MAFFT (Katoh et al., 2002). A GTR+G model of molecular evolution was used for each partition of the analysis, with the data partitioned by gene and codon for 33 partitions. Evolutionary relationships for the concatenated dataset of eleven gene fragments were reconstructed with a maximum likelihood (RaxML; Stamatakis, 2014) approach following 20 independent independent analysis with the tree with the highest likelihood presented (RaxML; Stamatakis, 2014). A maximum parsimony ancestral state reconstructions of the presence of fangs associated with the oral jaws were performed in Mesquite 2.75 (Maddison and Maddison, 2010). Codings were done with an exemplar of a family. If a family had species possessing and lacking fangs they were coded as polymorphic. The reconstructed character for the evolution of fangs is:

1. Enlarged fang-like teeth on bones associated with the oral jaws
    (0) Absent
    (1) Present

Materials Examined

Acestrorhynchus britskii: FMNH 76404, 1 of 1

Alepisaurus ferox: MCZ 127309, 1 of 1

Anotopterus pharao: FMNH 64222, 1 of 1

Table 3.1 List of additional species added to the previous examined species in Davis et al., (2016) with GenBank accession numbers included.

Taxon	**COI**	**rag1**	**zic1**	**enc1**	**Plagl2**	**Glyt**	**myh6**	**Ptr**	**SH3PX3**	**tbr1**	**sreb2**
Danionella dracula	FJ753509	FJ753520									
Ichthyborus ornatus	HM418226			KF542084	JX985152	KF542179	KF542283		KF542481		JX985216
Schizodon fasciatus	FJ440621	HQ289177					KF569179				
Acestrorhynchus lacustris	HM405050	HQ289157					HQ288960				
Brycon pesu		KX086967			JX190557	JX190269	KX086915	JX190681			
Bagarius yarrelli	EU490855	DQ492446			JN986972	JQ026238	JQ026266	JQ026281			
***Taenioides* sp.**		KF415874	KF416084								
Channa striata	HQ682672	JQ938268	JX189155	JX189000	JQ937572	JX188828	JQ939521	JX190234	JQ940137	JX189304	JX190065
Pseudochromis fridmani		JX189849	JX189075	JX188916	JX189377	JX188750	JX189691	JX190150	JX189607	JX189231	JX189995
Hexagrammos otakii	JF511654	JX189808	JX189037	JX188869	JX189336	JX188702	JX189654		JX189561	JX189189	
Champsodon snyderi	KU944746			KF139578	KF140710	KF139708	KF139962			KF140324	KF140181
Xyrichtys martinicensis	GU225069	JX189893	JX189121	JX188966	JX189413	JX188792	JX189737	JX190200	JX189487	JX189274	JX190037
Lethrinus erythracanthus	KF930046	JX189827	JX189056	JX188893	JX189355	JX188726		JX190126	JX189585	JX189211	JX189978
Lutjanus griseus	HQ162388	KF141274	KF140565	KF139514	KF140778	KF139788	KF140034		KF141512	KF140376	

Arctozenus risso: SIO 74-23, 3 of 7

Argyripnus atlanticus: FMNH 71735, 1 of 1

Astronesthes lucibucca: MCZ 97692, 1 of 1

Chauliodus sloani: FMNH 85128, 1 of 1

Chirocentrus dorab: KU 10518, 1 of 1

Cynoscion nebulosus: KU 29924, 1 of 1

Diplophos maderensis: FMNH 66006, 2 of 2

Evermannella balbo: MCZ 101362, 1 of 1

Gigantura chuni: MCZ 57007, 1 of 1

Gonostoma elongatum: FMNH 71649, 2 of 2

Harpadon nehereus: CAS 56037, 4 of 7

Hoplias trahira: KU 10556, 1 of 1

Hydrolycus scomberoides: FMNH 103657, 1 of 1

Idiacanthus fasciola: MCZ 42390, 2 of 2

Ijimaia antillarum: FMNH 64550, 1 of 1

Lampadena bathyphila: FMNH 49410, 1 of 1

Lestrolepis intermedia: FMNH 117869, 1 of 1

Neoscopelus sp.: FMNH 66735, 2 of 2

Ophiodon elongatus: KU 28443, 1 of 1

Oligosarcus oligolepis: KU 22417, 1 of 1

Osmerus Dentex: FMNH 2684, 2 of 2

Parasudis truculenta: VIMS 03261, 2 of 4

Photostomias guernei: FMNH 49611, 1 of 1

Pseudupeneus maculatus: FMNH 64801, 2 of 11

Scopelarchus analis: MCZ 127130, 1 of 2

Scopelengys tristis: FMNH 71919, 1 of 1

Stomias affinis: FMNH 45733, 1 of 1

Stomias boa ferox: MCZ 128505, 1 of 1

Stomias boa ferox: MCZ 129197. 2 of 2

Sudis atrox: SIO 97-92, 2 of 2

Results

The taxonomic survey of the presence of fangs in ray-finned fishes identified that fangs are present in 62 families (Table 3.2), of which 15 families were unable to be included in the phylogenetic analysis due to a lack of gene sequence data. The phylogenetic relationships of ray-finned fishes inferred from the maximum likelihood analysis (Figure 3.1 - 3.4) are consistent with the previous findings of Davis et al. (2016), with the additional families estimated in consistent phylogenetic position with previous studies on the evolutionary relationships of ray-finned fishes (e.g., Near et al., 2012; Near et al., 2013; Davis et al., 2016; Smith et al., 2016). The ancestral character state reconstruction of the evolution of fangs indicate that there were at least 38 independent evolutions of fangs across ray-finned fishes (Figure 3.1 - 3.4), and likely more

Table 3.2. Comprehensive survey of fang presence across ray-finned fishes.

Survey of Actinopterygian Fishes

Order	Family	Fang Presence	Example Species	Specimen/Reference
Polypteriformes	Polypteridae	No		
Acipenseriformes	Acipenseridae	No		
Acipenseriformes	Polyodontidae	No		
Lepisosteiformes	Lepisosteidae	No		
Amiiformes	Amiidae	No		
Elopiformes	Elopidae	No		
Elopiformes	Megalopidae	No		
Albuliformes	Albulidae	No		
Notacanthiformes	Halosauridae	No		
Notacanthiformes	Notacanthidae	No		
Anguilliformes	Protanguillidae	No		
Anguilliformes	Synaphobranchidae	Yes	*Dysomma gosline*	ANSP 13380 Johnson et al., (2012)
Anguilliformes	Anguillidae	No		
Anguilliformes	Cyematidae	No		
Anguilliformes	Eurypharyngidae	No		
Anguilliformes	Monognathidae	Yes	*Monognathus nigeli*	SIO 87-29 Smith et al., (2016)
Anguilliformes	Moringuidae	No		
Anguilliformes	Nemichthyidae	No		
Anguilliformes	Saccopharyngidae	No		
Anguilliformes	Serrivomeridae	No		
Anguilliformes	Chlopsidae	Yes	*Kaupichthys atlanticum*	ANSP 73687 Böhlke, (1956)

Order	Family	Fang Presence	Example Species	Specimen/Reference
Anguilliformes	Colocongridae	No		
Anguilliformes	Congridae	Yes	Bathyuroconger vicinus	MCZ 74334 Collar et al., (2014)
Anguilliformes	Derichthyidae	No		
Anguilliformes	Muraenesocidae	Yes	Muraenesox cinereus	HUJ-F 9862 Golani and Ben-Tuvia, (1982)
Anguilliformes	Nettastomatidae	Yes	*Hoplunnis macrura*	Smith, (2013)
Anguilliformes	Ophichthidae	Yes	*Aplatophis zorro*	USNM 360118 McCosker and Robertson, (2001)
Anguilliformes	Heterenchelyidae	No		
Anguilliformes	Muraenidae	No		
Anguilliformes	Myrocongridae	Yes	*Myroconger compressus*	ANSP 140308 Smith, (1984)
Osteoglossiformes	Osteoglossidae	No		
Osteoglossiformes	Arapaimidae	No		
Osteoglossiformes	Pantodontidae	No		
Osteoglossiformes	Hiodontidae	No		
Osteoglossiformes	Notopteridae	No		
Osteoglossiformes	Mormyridae	No		
Osteoglossiformes	Gymnarchidae	No		
Clupeiformes	Denticipitidae	No		
Clupeiformes	Clupeidae	Yes	*Chirocentrus dorab*	KU 10518
Clupeiformes	Engraulidae	No		
Alepocephaliformes	Alepocephalidae	No		
Alepocephaliformes	Platytroctidae	No		
Gonorynchiformes	Chanidae	No		

Order	**Family**	**Fang Presence**	**Example Species**	**Specimen/Reference**
Gonorynchiformes	Gonorynchidae	No		
Gonorynchiformes	Kneriidae	No		
Gonorynchiformes	Phractolaemidae	No		
Cypriniformes	Psilorhynchidae	No		
Cypriniformes	Cyprinidae	Yes	*Danionella dracula*	BMNH 2008.1.1.100-119 Britz et al., (2009)
Cypriniformes	Botiidae	No		
Cypriniformes	Cobitidae	No		
Cypriniformes	Balitoridae	No		
Cypriniformes	Nemacheilidae	No		
Cypriniformes	Vaillantellidae	No		
Cypriniformes	Serpenticobitidae	No		
Cypriniformes	Gyrinocheilidae	No		
Cypriniformes	Catostomidae	No		
Characiformes	Citharinidae	No		
Characiformes	Distichodontidae	Yes	*Ichthyborus congolensis*	Daget, (1967)
Characiformes	Alestidae	No		
Characiformes	Hepsetidae	Yes	*Hepsetus odoe*	MNHN 1884-0309 Froese and Pauly, (2017)
Characiformes	Hemiodontidae	No		
Characiformes	Parodontidae	No		
Characiformes	Curimatidae	No		
Characiformes	Prochilodontidae	No		
Characiformes	Anostomidae	Yes	*Gnathodolus bidens*	Myers and De Carvalho, (1959)
Characiformes	Chilodontidae	No		

Order	**Family**	**Fang Presence**	**Example Species**	**Specimen/Reference**
Characiformes	Erythrinidae	Yes	*Hoplias trahira*	KU 10556
Characiformes	Lebiasinidae	No		
Characiformes	Gasteropelecidae	No		
Characiformes	Ctenoluciidae	No		
Characiformes	Acestrorhynchidae	Yes	*Acestrorhynchus britskii*	FMNH 76404
Characiformes	Cynodontidae	Yes	*Hydrolycus scomberoides*	FMNH 103657
Characiformes	Serrasalmidae	No		
Characiformes	Characidae	Yes	*Oligosarcus oligolepis*	KU 22417
Characiformes	Bryconidae	Yes	*Brycon insignis*	CAS 11894 California Academy of Sciences, (2017)
Characiformes	Triportheidae	Yes	*Agoniates halecinus*	MZUSP 92807 Dagosta and Datovo (2013)
Characiformes	Iguanodectidae	No		
Characiformes	Chalceidae	No		
Characiformes	Crenuchidae	No		
Siluriformes	Diplomystidae	No		
Siluriformes	Lacantuniidae	No		
Siluriformes	Ictaluridae	No		
Siluriformes	Horabagridae	No		
Siluriformes	Bagridae	No		
Siluriformes	Cranoglanididae	No		
Siluriformes	Austroglanididae	No		
Siluriformes	Siluridae	No		
Siluriformes	Kryptoglanidae	No		
Siluriformes	Schilbeidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Siluriformes	Pangasiidae	No		
Siluriformes	Amblycipitidae	No		
Siluriformes	Amphiliidae	No		
Siluriformes	Akysidae	No		
Siluriformes	Sisoridae	Yes	*Bagarius yarrelli*	UMMZ 209294 Roberts, (1983)
Siluriformes	Erethistidae	No		
Siluriformes	Clariidae	No		
Siluriformes	Heteropneustidae	No		
Siluriformes	Claroteidae	No		
Siluriformes	Chacidae	No		
Siluriformes	Olyridae	No		
Siluriformes	Malapteruridae	No		
Siluriformes	Ariidae	No		
Siluriformes	Anchariidae	No		
Siluriformes	Plotosidae	No		
Siluriformes	Mochokidae	No		
Siluriformes	Doradidae	No		
Siluriformes	Auchenipteridae	No		
Siluriformes	Pimelodidae	No		
Siluriformes	Pseudopimelodidae	No		
Siluriformes	Heptapteridae	No		
Siluriformes	Cetopsidae	No		
Siluriformes	Aspredinidae	No		
Siluriformes	Nematogenyidae	No		
Siluriformes	Trichomycteridae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Siluriformes	Callichthyidae	No		
Siluriformes	Loricariidae	No		
Siluriformes	Scoloplacidae	No		
Siluriformes	Astroblepidae	No		
Gymnotiformes	Sternopygidae	No		
Gymnotiformes	Apteronotidae	No		
Gymnotiformes	Rhamphichthyidae	No		
Gymnotiformes	Hypopomidae	No		
Gymnotiformes	Gymnotidae	No		
Lepidogalaxiiformes	lepidogalaxiidae	No		
Argentiniformes	Argentinidae	No		
Argentiniformes	Opisthoproctidae	No		
Argentiniformes	Microstomatidae	No		
Argentiniformes	Bathylagidae	No		
Esociformes	Esocidae	No		
Esociformes	Umbridae	No		
Salmoniformes	Salmonidae	No		
Stomiiformes	Diplophidae	No		
Stomiiformes	Gonostomatidae	No		
Stomiiformes	Sternoptychidae	No		
Stomiiformes	Phosichthyidae	No		
Stomiiformes	Stomiidae	Yes	*Chauliodus sloani*	FMNH 85128
Osmeriformes	Osmeridae	Yes	*Osmerus dentex*	FMNH 2684
Osmeriformes	Plecoglossidae	No		
Osmeriformes	Salangidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Osmeriformes	Retropinnidae	No		
Galaxiiformes	Galaxiidae	No		
Ateleopodiformes	Ateleopodidae	No		
Aulopiformes	Aulopidae	No		
Aulopiformes	Harpadontiae	Yes	*Harpadon nehereus*	CAS 56037
Aulopiformes	Synodontidae	No		
Aulopiformes	Pseudotrichonotidae	No		
Aulopiformes	Paraulopidae	No		
Aulopiformes	Giganturidae	Yes	*Gigantura chuni*	MCZ 57007
Aulopiformes	Bathysauridae	No		
Aulopiformes	Bathysauroididae	No		
Aulopiformes	Bathysauropsidae	No		
Aulopiformes	Ipnopidae	No		
Aulopiformes	Parasudidae	Yes	*Parasudis truclenta*	VIMS 03261
Aulopiformes	Chlorophthalmidae	No		
Aulopiformes	Notosudidae	No		
Aulopiformes	Scopelarchidae	Yes	*Scopelarchus analis*	MCZ 127130
Aulopiformes	Evermannellidae	Yes	*Evermannella balbo*	MCZ 101326
Aulopiformes	Sudidae	Yes	*Sudis atrox*	SIO 97-92
Aulopiformes	Alepisauridae	Yes	*Alepisaurus ferox*	MCZ 127309
Aulopiformes	Anotopteridae	Yes	*Anotopterus pharao*	FMNH 64222
Aulopiformes	Paralepididae	Yes	*Arctozenus risso*	SIO 74-23

Order	Family	Fang Presence	Example Species	Specimen/Reference
Aulopiformes	Lestidiidae	Yes	*Lestrolepis intermedia*	FMNH 117869
Myctophiformes	Neoscopelidae	No		
Myctophiformes	Myctophidae	No		
Polymixiiformes	Polymixiidae	No		
Percopsiformes	Percopsidae	No		
Percopsiformes	Aphredoderidae	No		
Percopsiformes	Amblyopsidae	No		
Zeiformes	Cyttidae	No		
Zeiformes	Oreosomatidae	No		
Zeiformes	Parazenidae	No		
Zeiformes	Zenionidae	No		
Zeiformes	Grammicolepididae	No		
Zeiformes	Zeidae	No		
Stylephoriformes	Stylephoridae	No		
Gadiformes	Muraenolepididae	No		
Gadiformes	Bregmacerotidae	No		
Gadiformes	Euclichthyidae	No		
Gadiformes	Macrouridae	No		
Gadiformes	Moridae	No		
Gadiformes	Melanonidae	No		
Gadiformes	Gadidae	No		
Gadiformes	Lotidae	No		
Gadiformes	Phycidae	No		
Gadiformes	Merlucciidae	Yes	*Merluccius merluccius*	MNHN 1996-1401 Froese and Pauly, (2017)
Lampriformes	Lampridae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Lampriformes	Veliferidae	No		
Lampriformes	Lophotidae	No		
Lampriformes	Radiicephalidae	No		
Lampriformes	Trachipteridae	No		
Lampriformes	Regalecidae	No		
Beryciformes	Monocentridae	No		
Beryciformes	Trachichthyidae	No		
Beryciformes	Anomalopidae	No		
Beryciformes	Diretmidae	No		
Beryciformes	Anoplogastridae	Yes	*Anoplogaster cornuta*	HUMZ 64191 Shimizu, (1978)
Beryciformes	Holocentridae	No		
Beryciformes	Stephanoberycidae	No		
Beryciformes	Hispidoberycidae	No		
Beryciformes	Melamphaidae	No		
Beryciformes	Gibberichthyidae	No		
Beryciformes	Berycidae	No		
Beryciformes	Rondeletiidae	No		
Beryciformes	Barbourisiidae	No		
Beryciformes	Cetomimidae	No		
Ophidiiformes	Ophidiidae	No		
Ophidiiformes	Carapidae	No		
Ophidiiformes	Bythitidae	No		
Ophidiiformes	Aphyonidae	No		
Ophidiiformes	Parabrotulidae	No		
Batrachoidiformes	Batrachoididae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Gobiiformes	Apogonidae	No		
Gobiiformes	Kurtidae	No		
Gobiiformes	Rhyacichthyidae	No		
Gobiiformes	Odontobutidae	No		
Gobiiformes	Eleotridae	No		
Gobiiformes	Thalasseleotrididae	No		
Gobiiformes	Butidae	No		
Gobiiformes	Gobiidae	Yes	*Taenioides purpurascens*	AMS I.46350-001 Australian Museum, (2014)
Gobiiformes	Trichonotidae	No		
Scombriformes	Gempylidae	Yes	*Thyristoides marleyi*	Froese and Pauly, (2017)
Scombriformes	Trichiuridae	Yes	*Trichiurus lepturus*	Olsen, (1971)
Scombriformes	Scombridae	No		
Scombriformes	Scombrolabracidae	No		
Scombriformes	Amarsipidae	No		
Scombriformes	Centrolophidae	No		
Scombriformes	Nomeidae	No		
Scombriformes	Ariommatidae	No		
Scombriformes	Tetragonuridae	No		
Scombriformes	Stromateidae	No		
Scombriformes	Pomatomidae	No		
Scombriformes	Bramidae	No		
Scombriformes	Caristiidae	No		
Scombriformes	Icosteidae	No		
Scombriformes	Arripidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Scombriformes	Chiasmodontidae	Yes	*Chiasmodon niger*	BMNH 1863.12.12.4 Melo, (2009)
Syngnathiformes	Aulostomidae	No		
Syngnathiformes	Fistulariidae	No		
Syngnathiformes	Centriscidae	No		
Syngnathiformes	Solenostomidae	No		
Syngnathiformes	Syngnathidae	No		
Syngnathiformes	Dactylopteridae	No		
Syngnathiformes	Pegasidae	No		
Syngnathiformes	Mullidae	No		
Syngnathiformes	Callionymidae	No		
Syngnathiformes	Draconettidae	No		
Synbranchiformes	Nandidae	No		
Synbranchiformes	Anabantidae	No		
Synbranchiformes	Osphronemidae	No		
Synbranchiformes	Helostomatidae	No		
Synbranchiformes	Channidae	Yes	*Channa argus*	ANSP Uncatalogued DidgiMorph Staff (2009)
Synbranchiformes	Synbranchidae	No		
Synbranchiformes	Mastacembelidae	No		
Synbranchiformes	Chaudhuriidae	No		
Synbranchiformes	Indostomidae	No		
Carangiformes	Centropomidae	No		
Carangiformes	Latidae	No		
Carangiformes	Lactariidae	No		
Carangiformes	Rachycentridae	No		
Carangiformes	Echeneidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Carangiformes	Carangidae	No		
Carangiformes	Nematistiidae	No		
Carangiformes	Coryphaenidae	No		
Carangiformes	Menidae	No		
Carangiformes	Leptobramidae	No		
Carangiformes	Istiophoridae	No		
Carangiformes	Polynemidae	No		
Carangiformes	Sphyraenidae	Yes	*Sphyraena barracuda*	USNM 14978 De Sylva, (1963)
Carangiformes	Toxotidae	No		
Carangiformes	Psettodidae	No		
Carangiformes	Citharidae	No		
Carangiformes	Scophthalmidae	No		
Carangiformes	Paralichthyidae	No		
Carangiformes	Bothidae	No		
Carangiformes	Achiropsettidae	No		
Carangiformes	Pleuronectidae	No		
Carangiformes	Samaridae	No		
Carangiformes	Achiridae	No		
Carangiformes	Soleidae	No		
Carangiformes	Cynoglossidae	No		
Atheriniformes	Atherinidae	No		
Atheriniformes	Bedotiidae	No		
Atheriniformes	Melanotaeniidae	No		
Atheriniformes	Pseudomugilidae	No		
Atheriniformes	Atherinopsidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Atheriniformes	Notocheiridae	No		
Atheriniformes	Isonidae	No		
Atheriniformes	Phallostethidae	No		
Cyprinodontiformes	Aplocheilidae	No		
Cyprinodontiformes	Notobranchiidae	No		
Cyprinodontiformes	Rivulidae	No		
Cyprinodontiformes	Profundulidae	No		
Cyprinodontiformes	Fundulidae	No		
Cyprinodontiformes	Valenciidae	No		
Cyprinodontiformes	Goodeidae	No		
Cyprinodontiformes	Poeciliidae	No		
Cyprinodontiformes	Cyprinodontidae	No		
Cyprinodontiformes	Anablepidae	No		
Beloniformes	Scomberesocidae	No		
Beloniformes	Belonidae	No		
Beloniformes	Hemiramphidae	No		
Beloniformes	Zenarchopteridae	No		
Beloniformes	Exocoetidae	No		
Beloniformes	Adrianichthyidae	No		
Blenniiformes	Gobiesocidae	No		
Blenniiformes	Tripterygiidae	No		
Blenniiformes	Labrisomidae	No		
Blenniiformes	Clinidae	No		
Blenniiformes	Chaenopsidae	No		
Blenniiformes	Dactyloscopidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Blenniiformes	Blenniidae	Yes	*Petroscirtes breviceps*	Froese and Pauly, (2017)
Blenniiformes	Opistognathidae	No		
Blenniiformes	Grammatidae	No		
Blenniiformes	Plesiopidae	No		
Blenniiformes	Pseudochromidae	Yes	*Pseudochromis moorei*	Froese and Pauly, (2017)
Blenniiformes	Congrogadidae	No		
Blenniiformes	Pomacentridae	No		
Blenniiformes	Embiotocidae	No		
Blenniiformes	Ambassidae	No		
Blenniiformes	Mugilidae	No		
Cichliformes	Polycentridae	No		
Cichliformes	Pholidichthyidae	No		
Cichliformes	Cichlidae	No		
Scorpaeniformes	Serranidae	Yes	*Mycteroperca tigris*	Froese and Pauly, (2017)
Scorpaeniformes	Epinephelidae	No		
Scorpaeniformes	Anthiidae	No		
Scorpaeniformes	Niphonidae	No		
Scorpaeniformes	Trachinidae	No		
Scorpaeniformes	Bembropidae	No		
Scorpaeniformes	Percophidae	No		
Scorpaeniformes	Bovichtidae	No		
Scorpaeniformes	Pseudaphritidae	No		
Scorpaeniformes	Eleginopsidae	No		
Scorpaeniformes	Nototheniidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Scorpaeniformes	Harpagiferidae	No		
Scorpaeniformes	Artedidraconidae	No		
Scorpaeniformes	Bathydraconidae	No		
Scorpaeniformes	Channichthyidae	No		
Scorpaeniformes	Percidae	Yes	*Sander lucioperca*	Froese and Pauly, (2017)
Scorpaeniformes	Hoplichthyidae	No		
Scorpaeniformes	Platycephalidae	No		
Scorpaeniformes	Bembridae	No		
Scorpaeniformes	Triglidae	No		
Scorpaeniformes	Congiopodidae	No		
Scorpaeniformes	Neosebastidae	No		
Scorpaeniformes	Synanceiidae	No		
Scorpaeniformes	Scorpaenidae	No		
Scorpaeniformes	Normanichthyidae	No		
Scorpaeniformes	Hypoptychidae	No		
Scorpaeniformes	Gasterosteidae	No		
Scorpaeniformes	Aulorhynchidae	No		
Scorpaeniformes	Anoplopomatidae	No		
Scorpaeniformes	Bathymasteridae	No		
Scorpaeniformes	Stichaeidae	No		
Scorpaeniformes	Cryptacanthodidae	No		
Scorpaeniformes	Pholidae	No		
Scorpaeniformes	Ptilichthyidae	No		
Scorpaeniformes	Zaproridae	No		
Scorpaeniformes	Scytalinidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Scorpaeniformes	Anarhichadidae	No		
Scorpaeniformes	Zoarcidae	No		
Scorpaeniformes	Zaniolepididae	No		
Scorpaeniformes	Hexagrammidae	Yes	*Ophiodon elongatus*	KU 28443
Scorpaeniformes	Trichodontidae	No		
Scorpaeniformes	Cyclopteridae	No		
Scorpaeniformes	Liparidae	No		
Scorpaeniformes	Rhamphocottidae	No		
Scorpaeniformes	Scorpaenichthyidae	No		
Scorpaeniformes	Jordaniidae	No		
Scorpaeniformes	Agonidae	No		
Scorpaeniformes	Cottidae	No		
Scorpaeniformes	Psychrolutidae	No		
Acropomatiformes	Epigonidae	No		
Acropomatiformes	Banjosidae	No		
Acropomatiformes	Pentacerotidae	No		
Acropomatiformes	Polyprionidae	No		
Acropomatiformes	Acropomatidae	Yes	*Synagrops japonicus*	Froese and Pauly, (2017)
Acropomatiformes	Howellidae	No		
Acropomatiformes	Pempheridae	No		
Acropomatiformes	Glaucosomatidae	No		
Acropomatiformes	Ostracoberycidae	No		
Acropomatiformes	Lateolabracidae	No		
Acropomatiformes	Bathyclupeidae	No		
Acropomatiformes	Dinolestidae	Yes	*Dinolestes lewini*	Fraser, (1971)

Order	Family	Fang Presence	Example Species	Specimen/Reference
Acropomatiformes	Hemerocoetidae	No		
Acropomatiformes	Creediidae	No		
Acropomatiformes	Champsodontidae	Yes	*Champsodon guentheri*	Froese and Pauly, (2017)
Acropomatiformes	Scombropidae	Yes	*Scombrops oculatus*	Froese and Pauly, (2017)
Acropomatiformes	Symphysanodontidae	No		
Labriformes	Gerreidae	No		
Labriformes	Labridae	Yes	*Iniistius pavo*	Wainwright et al., (2004)
Uranoscopiformes	Centrogenyidae	No		
Uranoscopiformes	Leptoscopidae	No		
Uranoscopiformes	Pinguipedidae	No		
Uranoscopiformes	Cheimarrichthyidae	No		
Uranoscopiformes	Ammodytidae	No		
Uranoscopiformes	Uranoscopidae	No		
Centrarchiformes	Centrarchidae	No		
Centrarchiformes	Sinipercidae	No		
Centrarchiformes	Cirrhitidae	No		
Centrarchiformes	Chironemidae	No		
Centrarchiformes	Aplodactylidae	No		
Centrarchiformes	Cheilodactylidae	No		
Centrarchiformes	Latridae	No		
Centrarchiformes	Percichthyidae	No		
Centrarchiformes	Perciliidae	No		
Centrarchiformes	Enoplosidae	No		
Centrarchiformes	Terapontidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Centrarchiformes	Kuhliidae	No		
Centrarchiformes	Kyphosidae	No		
Centrarchiformes	Parascorpididae	No		
Centrarchiformes	Oplegnathidae	No		
Centrarchiformes	Dichistiidae	No		
Acanthuriformes	Callanthiidae	No		
Acanthuriformes	Sillaginidae	No		
Acanthuriformes	Dinopercidae	No		
Acanthuriformes	Lethrinidae	No		
Acanthuriformes	Nemipteridae	No		
Acanthuriformes	Sparidae	No		
Acanthuriformes	Centracanthidae	No		
Acanthuriformes	Emmelichthyidae	No		
Acanthuriformes	Luvaridae	No		
Acanthuriformes	Zanclidae	No		
Acanthuriformes	Acanthuridae	No		
Acanthuriformes	Malacanthidae	No		
Acanthuriformes	Hapalogenyidae	No		
Acanthuriformes	Haemulidae	No		
Acanthuriformes	Lutjanidae	Yes	*Lutjanus cyanopterus*	Froese and Pauly, (2017)
Acanthuriformes	Sciaenidae	Yes	*Cynoscion nebulosus*	KU 29924
Acanthuriformes	Leiognathidae	No		
Acanthuriformes	Chaetodontidae	No		
Acanthuriformes	Pomacanthidae	No		
Acanthuriformes	Monodactylidae	No		

Order	Family	Fang Presence	Example Species	Specimen/Reference
Acanthuriformes	Drepaneidae	No		
Acanthuriformes	Ephippidae	No		
Acanthuriformes	Lobotidae	No		
Acanthuriformes	Datnioididae	No		
Acanthuriformes	Moronidae	No		
Acanthuriformes	Siganidae	No		
Acanthuriformes	Cepolidae	No		
Acanthuriformes	Scatophagidae	No		
Acanthuriformes	Priacanthidae	No		
Acanthuriformes	Caproidae	No		
Acanthuriformes	Lophiidae	No		
Acanthuriformes	Antennariidae	No		
Acanthuriformes	Tetrabrachiidae	No		
Acanthuriformes	Lophichthyidae	No		
Acanthuriformes	Brachionichthyidae	No		
Acanthuriformes	Chaunacidae	No		
Acanthuriformes	Ogcocephalidae	No		
Acanthuriformes	Caulophrynidae	Yes	*Caulophryne pelagica*	BMNH 2000.1.14.106 Miya et al., (2010)
Acanthuriformes	Neoceratiidae	Yes	*Neoceratias spinifer*	ZMUC P921726 Miya et al., (2010)
Acanthuriformes	Melanocetidae	Yes	*Melanocetus eustales*	SIO 55-229 Miya et al., (2010)
Acanthuriformes	Himantolophidae	Yes	*Himantolophus appelii*	CSIRO H.5652-01 Miya et al., (2010)
Acanthuriformes	Diceratiidae	Yes	*Bufoceratias shaoi*	ASIZP 61796 Miya et al., (2010)
Acanthuriformes	Oneirodidae	Yes	*Chaenophryne quasiramifera*	SIO 72-180 Miya et al., (2010)

Order	Family	Fang Presence	Example Species	Specimen/Reference
Acanthuriformes	Thaumatichthyidae	Yes	*Lasiognathus saccostoma*	ZMUC P92121 Bertelsen and Pietsch, (1996)
Acanthuriformes	Centrophrynidae	No		
Acanthuriformes	Ceratiidae	Yes	*Ceratias uranoscopus*	BMNH 1887.12.7.15 Pietsch, (1986)
Acanthuriformes	Gigantactinidae	Yes	*Gigantactis gargantua*	LACM 9748-028 Miya et al., (2010)
Acanthuriformes	Linophrynidae	Yes	*Linophryne polypogon*	BMNH 2004.9.12.167 Miya et al., (2010)
Acanthuriformes	Triacanthodidae	No		
Acanthuriformes	Triacanthidae	No		
Acanthuriformes	Balistidae	No		
Acanthuriformes	Monacanthidae	No		
Acanthuriformes	Aracanidae	No		
Acanthuriformes	Ostraciidae	No		
Acanthuriformes	Triodontidae	No		
Acanthuriformes	Tetraodontidae	No		
Acanthuriformes	Diodontidae	No		
Acanthuriformes	Molidae	No		

given not all families of fishes that been observed to have evolved fangs are included in the phylogenetic analysis due to data availability (Table 3.1).

Discussion

The second objective of this thesis was to investigate the evolution of fangs across ray-finned fishes (Actinopterygii). Based on the results of the ancestral character reconstruction, large fangs are inferred to have evolved at least 38 times across ray-finned fishes (Figures 3.1-3.5). These fangs evolved in a variety of different lineages across the fish tree of life, with fangs not concentrated in any particular taxonomic area. The evolution of fangs across fishes are discussed further herein, including likely functional purposes in some cases, and the association of fang evolution and life history.

Evolution of Fangs Among Lower Teleost Fishes

Fangs are not present in any extant lower actinopterygian fishes, including the bichirs (Polypteriformes), the sturgeons (Acipenseriformes), or the holostean fishes (gars and bowfin). Fangs are first observed among actinopterygians within lineages of lower teleost fishes, including eels, clupeids, and even minnows which traditionally lack any teeth on the oral jaws. Overall, fangs have evolved at least 12 independent times among lower teleost fishes.

Within the Anguiliformes (eels), fangs are observed in the conger eels (Congridae), cutthroat eels (Synaphobranchidae), and duckbilled eels (Nettastomatidae) (Figure 3.1). The species of eels that have evolved fangs within these families are all found in pelagic marine environments and predate small fishes on coral reefs and the deep sea (Karmovskaya and Merrett, 1998). One

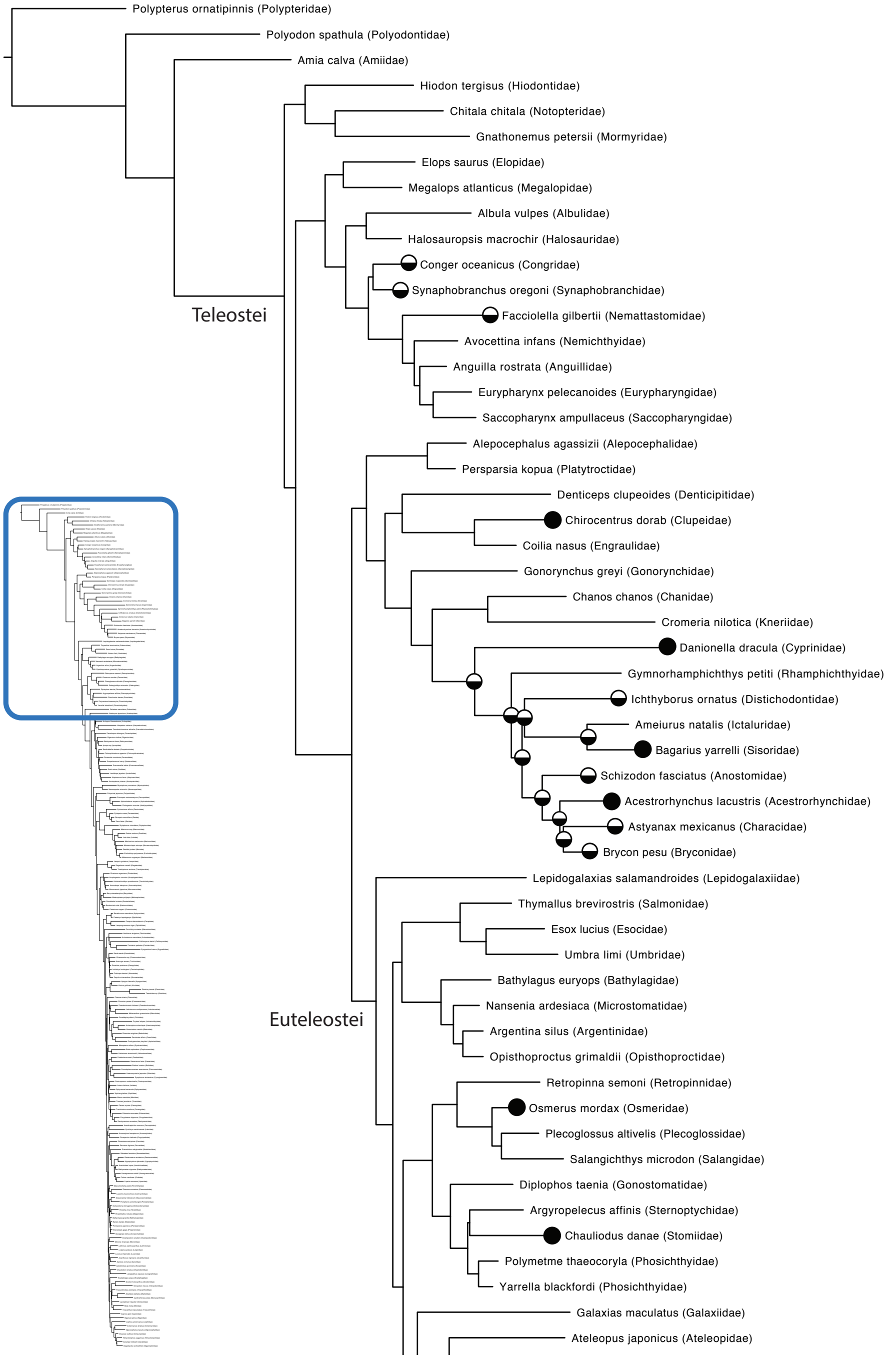

Figure 3.1. Evolutionary relationships of ray-finned fishes based on likelihood estimations from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs. Circles at nodes represent probabilities of character states. Black circles indicate a presence of fangs. Polymorphic families are indicated by a black and white circle at the tip. Equally parsimonious reconstructions of fang presence or absence are indicated by black and white circles at nodes.

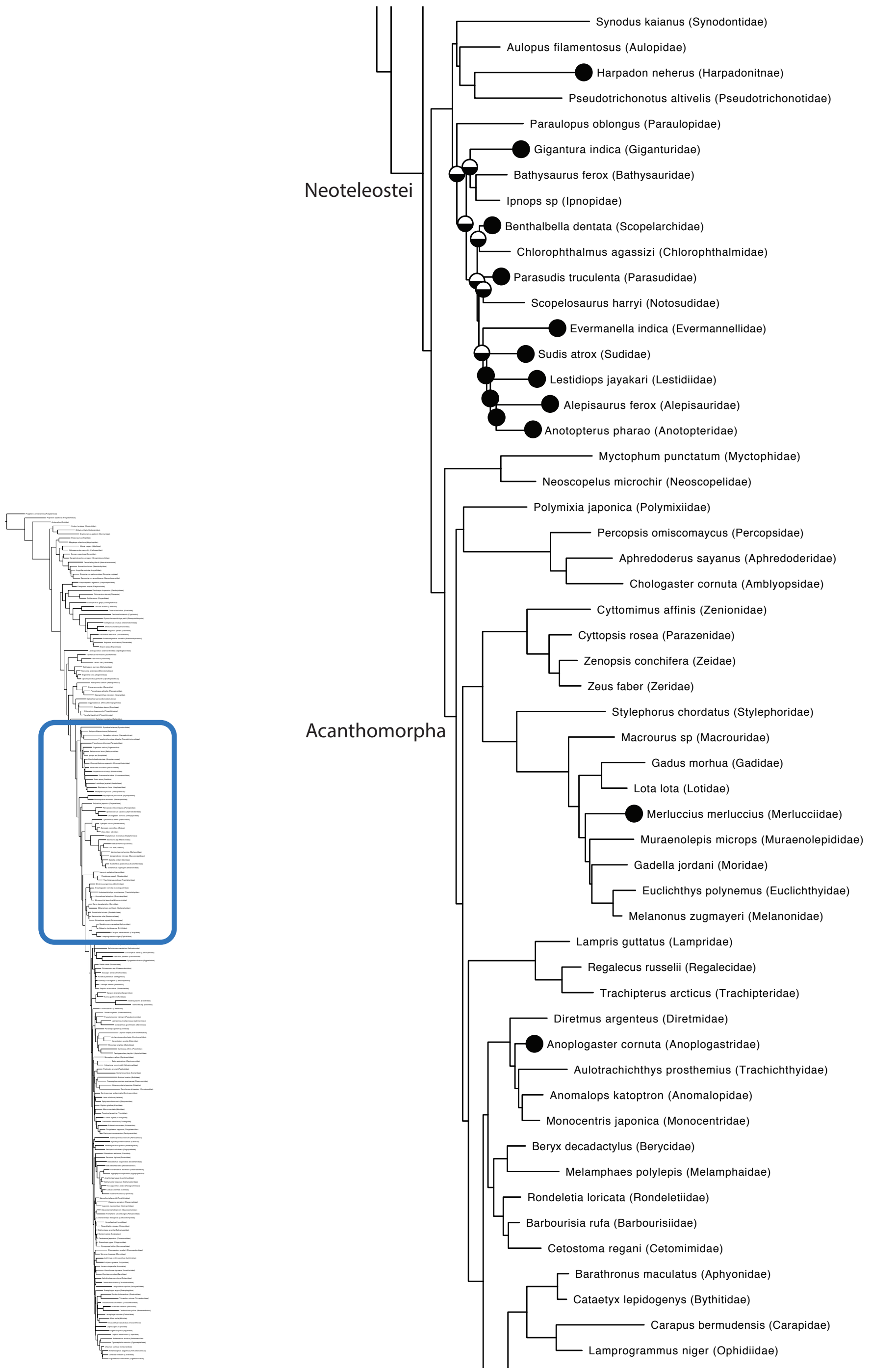

Figure 3.2. Continuation of tree of evolutionary relationships of ray-finned fishes based on likelihood estimations from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs. Circles at nodes represent probabilities of character states. Black circles indicate a presence of fangs. Polymorphic families are indicated by a black and white circle at the tip. Equally parsimonious reconstructions of fang presence or absence are indicated by black and white circles at nodes.

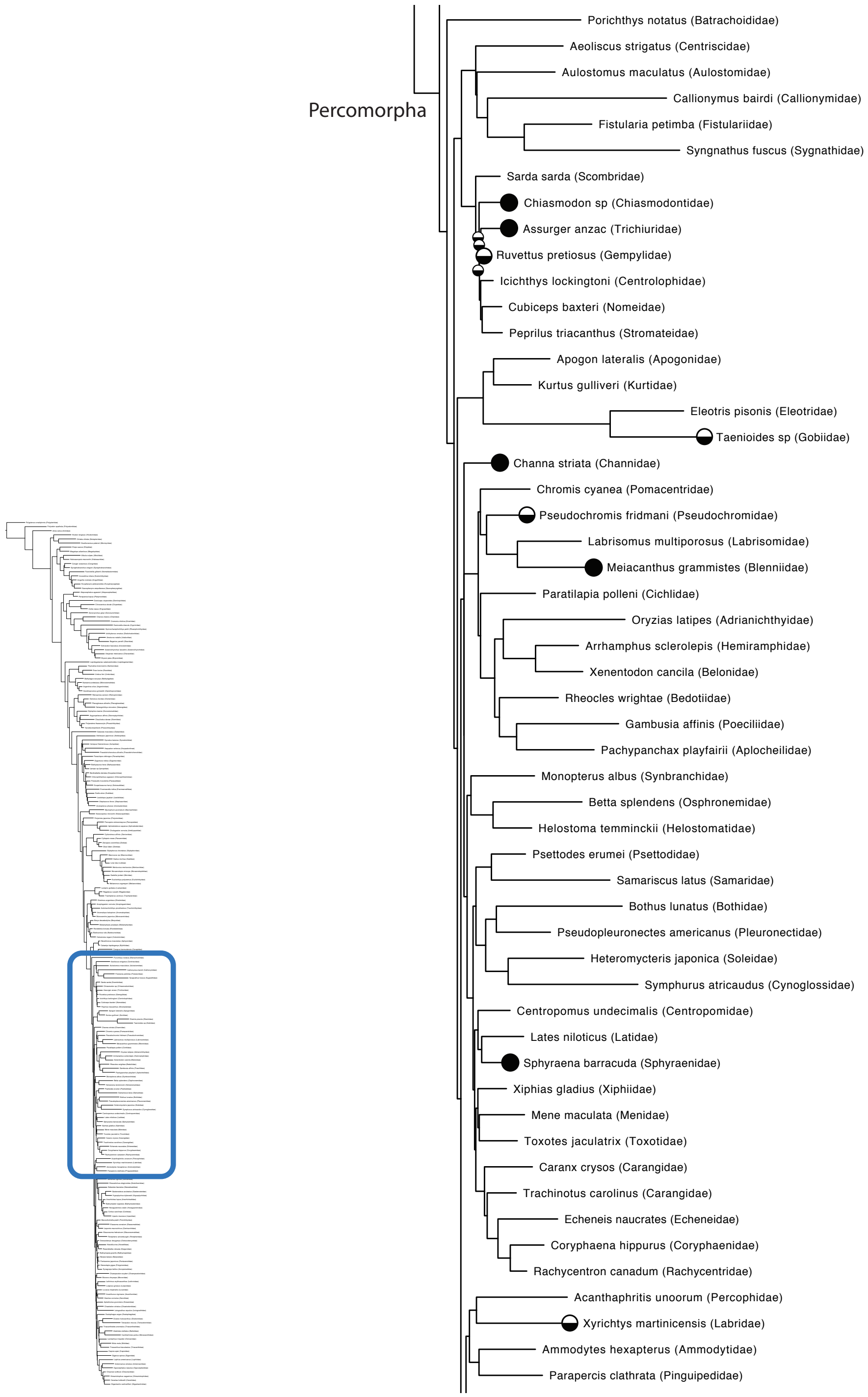

Figure 3.3. Continuation of tree of evolutionary relationships of ray-finned fishes based on likelihood estimations from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs. Circles at nodes represent probabilities of character states. Black circles indicate a presence of fangs. Polymorphic families are indicated by a black and white circle at the tip. Equally parsimonious reconstructions of fang presence or absence are indicated by black and white circles at nodes.

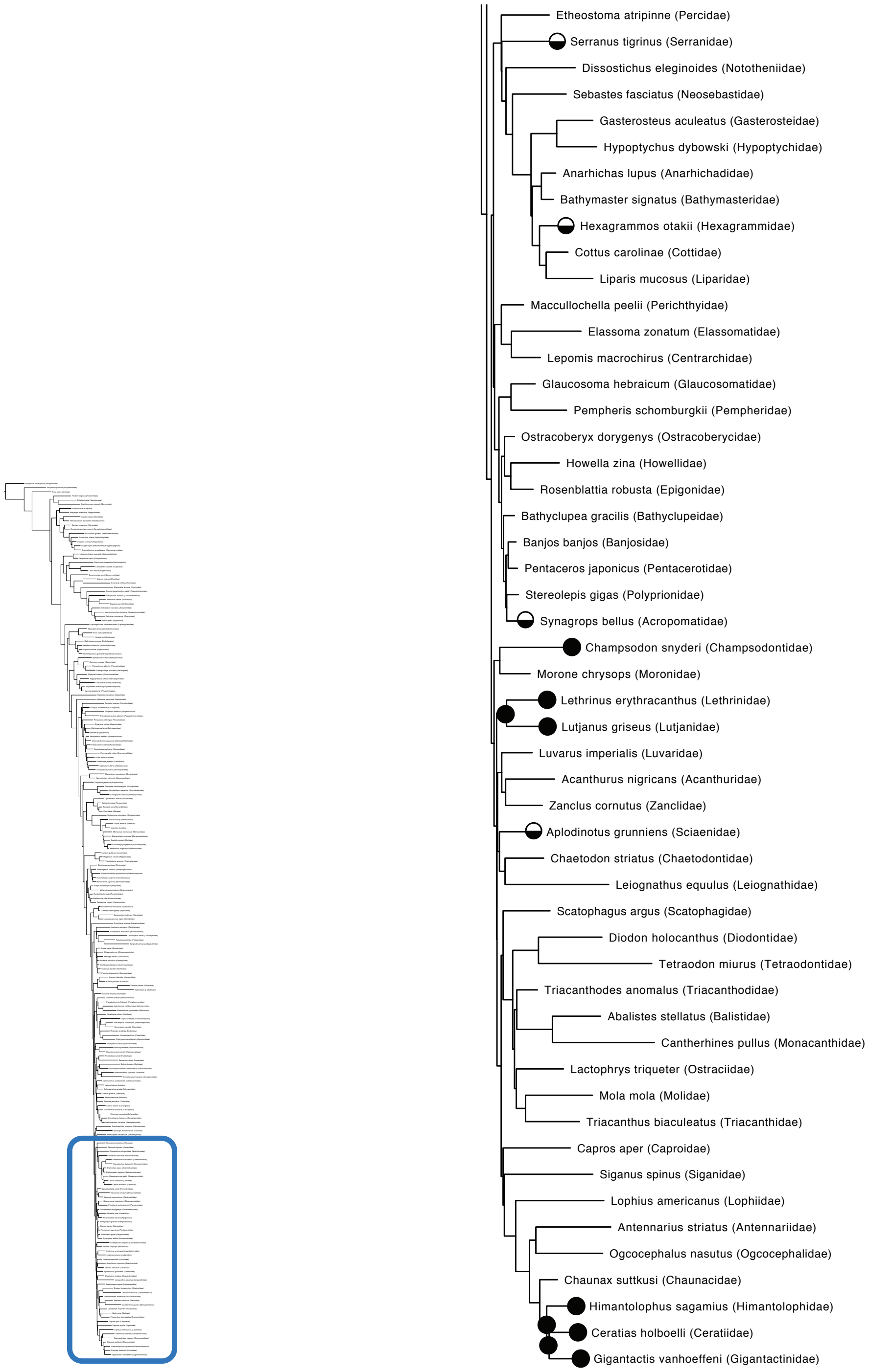

Figure 3.4. Continuation of tree of evolutionary relationships of ray-finned fishes based on likelihood estimations from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs. Circles at nodes represent probabilities of character states. Black circles indicate a presence of fangs. Polymorphic families are indicated by a black and white circle at the tip. Equally parsimonious reconstructions of fang presence or absence are indicated by black and white circles at nodes.

species of deep-sea eel, *Monognathus nigeli,* has been documented to use its singular fang to inject venom into prey items, and it is the only species of the 2,500 known venomous fishes to inject venom through its fangs for the purpose of predation (Smith et al., 2016).

Within the Otocephala, fangs have evolved in four orders of fishes, including the Clupeiformes (herrings), Cypriniformes (minnows), Siluriformes (catfishes), and Characiformes (tetras). In Clupeiformes (herrings), the pelagic predatory wolf herring (*Chirocentrus dorab*) is observed to posses large fangs (Chacko, 1949) (Figure 3.1). This is an interesting change in the feeding strategy for a clupeiform fish, as the majority of species in this order are filter feeders (Huse and Toreson, 1996).

One of the most interesting evolutionary events of fangs in fishes is in the Cypriniformes (minnows), one of largest radiations of freshwater fishes (Figure 3.1). The dracula minnow (*Danionella dracula*) is a miniaturized minnow species with fang-like projections on the upper and lower jaws (Britz et al., 2009). These fangs are particularly interesting because all other species of Cypriniformes lack any teeth within their oral jaws (Britz et al., 2009). These fangs are not true teeth and are osteological projections that originate on the upper jaw and dentary bone. Britz et al. (2009) noted that the source of the upper fangs cannot be definitively pinpointed due to a reduction in ossification in miniaturized fishes. The source of the upper fangs are hypothesized to originate on the maxilla, premaxilla, or a combination of the latter (Brizt et al., 2009).

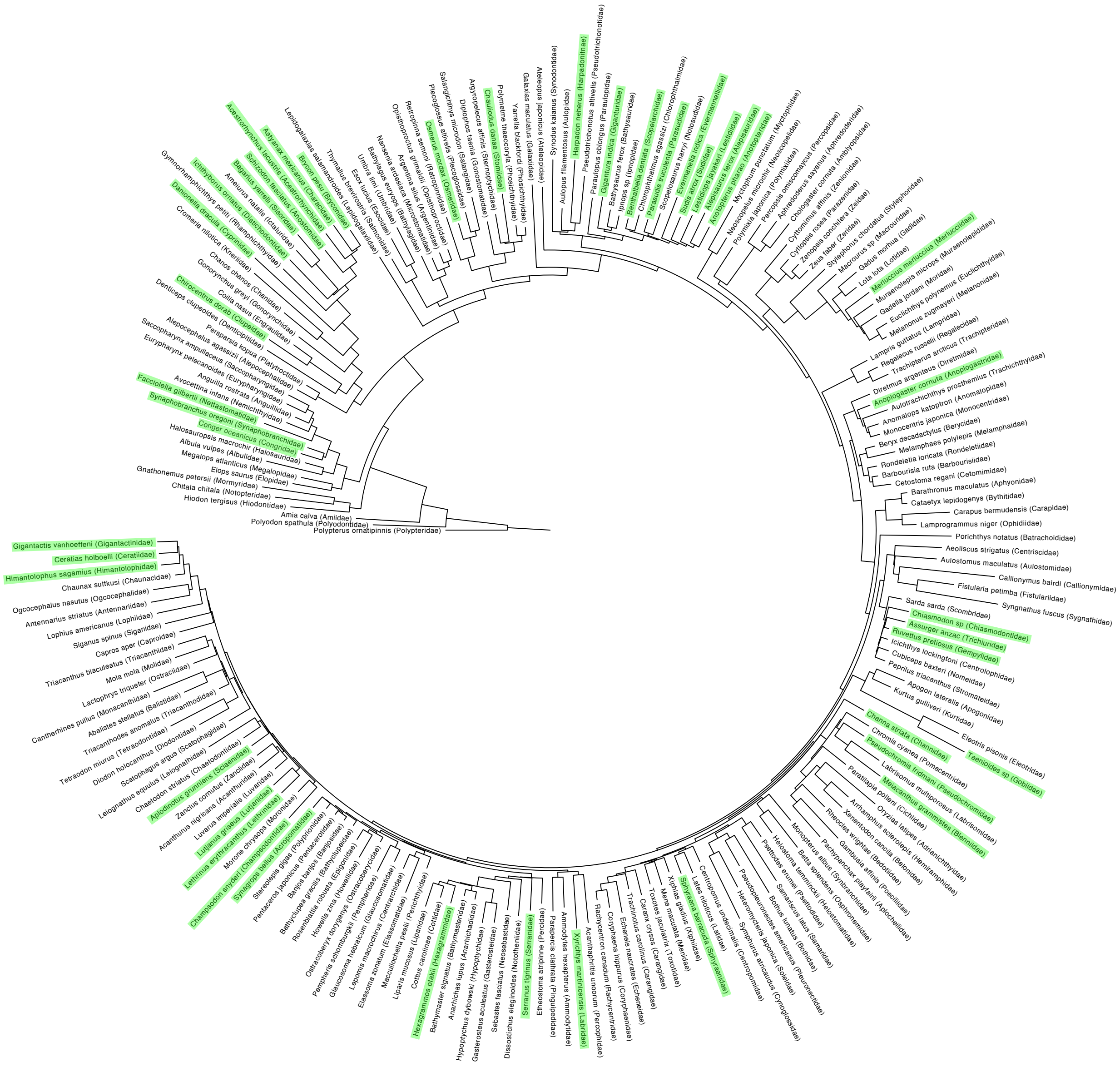

Figure 3.5. Evolutionary relationships of ray-finned fishes based on maximum likelihood estimation from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs actinopterygian radiation. Highlighted branches indicate the presence of fangs within the family.

Among lower teleost fishes, fangs have also evolved in various catfish (Siluriformes) families, including the sisorid catfishes (Sisoridae) (Figure 3.1). *Bagarius yarrelli,* or the giant devil catfish, is well documented to posses large fang-like teeth (Roberts, 1973). These fish can grow to lengths up to 6.6 feet and can weigh upwards of 200 pounds which make them prized game fish (Kottelat et al., 1993). There are several unsubstantiated cases of these catfishes attacking and even killing people (Cockcroft, 2008). Finally, fangs also evolved in several characiform families (Anostomidae, Acestrorhynchidae, Characidae, Bryconidae) (Figure 3.1). Characins (Mattox and Toledo-Piza, 2012) and are typically found in pelagic freshwater environments (Nelson, 1994).

Evolution of Fangs Across Lower Euteleost Fishes

There were six independent evolutions of fangs among the lower euteleost fishes in three orders, including the Osmeriformes (smelts), Stomiiformes (dragonfishes), and Aulopiformes (lizardfishes). Fangs evolved in the family Osmeridae (smelts) (Figure 3.1), within the Osmeriformes. Species within the Osmeridae are circumpolar in distribution and are anadromous spawners (Mecklenburd et al., 2011). These fishes primarily feed on copepods, euphasiids, and amphipods, but will also use their large fangs to predate fishes (Rooney and Paterson, 2009).

Some of the most anatomically extraordinary fangs in fishes have evolved within the Stomiiformes in the family Stomiidae (dragonfishes) (Figure 3.1), which includes over 300 species. The dragonfishes are a entirely pelagic deep-sea lineage of fishes which possess greatly enlarged fangs on both their upper and lower jaws (Kenaley, 2012). The fangs found within these fishes are so large that many species cannot fully close their jaws (Kenaley, 2012).

Finally, within the Aulopiformes (lizardfishes), there were 4 independent evolutions of fangs (Figure 3.2). Lizardfishes are a highly predatory group of fishes found in a wide variety of marine habitats (Davis and Fielitz, 2010). Fangs evolved in several of the deep-sea pelagic species of aulopiforms, including the telescopefishes (Giganturidae), lancetfishes (Alepisauridae), daggertooths (Anotopteridae), barracudinas (Paralepididae), pearleyes (Scopelarchidae), and sabretooth fishes (Evermannellidae) (Gregory, 1933; Harry, 1953; Johnson, 1982; Baldwin and Johnson, 1996; Davis, 2015).

Evolution of Fangs Across Spiny-rayed Fishes (Acanthomorpha)

Fangs have independently evolved at least 20 times across the acanthomorph spiny-rayed fishes (Figure 3.3-3.4), with the bulk of the evolutionary events occurring in the Percomorpha. Two independent evolutions of fangs occurred in the lower acanthomorph fishes within the Gadiformes (cods) and Beryciformes (squirelfishes) (Figure 3.2). The first of these two independent evolutions is observed in the gadiform family Merlucciidae (herring hakes) (Figure 3.2). Members of the family Merlucciidae feed mainly on Atlantic herrings (Cohen et al., 1990), and are found in marine pelagic habitats in the Eastern Atlantic Ocean, Mediterranean Sea, and North Sea. These fishes spend their days resting on sandy bottoms of the mesopelagic zone (200 - 1000 meters) until night when they swim into open water looking for food (Cohen et al., 1990).

The second independent evolution of fangs in the lower Acanthomorpha is within the beryciform family Anoplogastridae (fangtooths) (Figure 3.2). Fangtooths, as their name implies, possess disproportionately long fangs on their upper and lower jaws. Their fangs are so long that fangtooths have evolved sockets on both sides of their brain to accommodate their fangs when their mouth is closed (Post, 1986). Fangtooths are a pelagic marine species that inhabit the deep sea at depths of up to 5,000 meters (Coad and Reist, 2004). Young fangtooths feed on zooplankton and crustaceans and gradually switch to eating other fishes as they become larger (Post, 1986).

Among the percomorphs, which includes over 18,000 species of fishes, there have been at least 18 independent evolutions of fangs across 5 orders. Three independent evolutions occurred in the Scombriformes (tunas) in the families Chiasmodontidae, Trichiuridae, and Gempylidae (Figure 3.3). The deep-sea swallowers (Chiasmodontidae), are predatory fishes found in the mesopelagic and bathypelagic habitats worldwide (Melo, 2009). The swallowers derive their name from their ability to swallow prey items many times larger than themselves. The cutlassfishes (Trichiuridae), are benthopelagic predators found in marine and brackish habitats (Muus and Nielsen, 1999). Adults perform vertical diurnal migrations to the surface where they prey on other fishes with the occasional crustacean or squid (Nakamura and Parin, 1993). The snake mackerels (Gempylidae), are similar to swallowers and cutlassfishes in that they are pelagic predators (Nakamura and Parin, 1993). Snake mackerels are fished commercially and used in various cuisines. The flesh of the snake mackerels are very oily and can have purgative properties if large amounts are consumed (Roche et al., 2002).

Another notable evolution of fangs in percomorphs occurs in the Gobiiformes (gobies) (Figure 3.3). The purple eel goby (*Taenioides purpurascens*) is a benthopelagic cave goby endemic to the East coast of Australia (Hoese et al., 2006). These fishes are hypothesized to eat invertebrates, crustaceans, and small fishes (Hoese et al., 2006).

The only other venomous fangs in fishes, other than the one-jawed eel, are found in the family Blenniidae (blennies) in the fang-tooth blennies (Smith et al., 2016). However, this venom is not used in a predatory manner. Instead, the venom is used for defense against predators. Their venom rapidly decreases the blood pressure of its attackers causing dizziness and disorientation (Casewell et al., 2017).

Wrasses (Labridae) were also observed to have evolved fangs (Figure 3.3). The evolution of fangs in wrasses is unique in that their diets are quite different from other pelagic predators. Wrasses posses large conical fangs which they use to pull soft bodied prey items (e.g. sea stars, sea urchins, sea cucumbers, and small fishes) out of tight spaces in coral reefs (Clifton and Motta, 1998). Their diet is also primarily composed of hard bodied prey, such as crustaceans, which they crush with large molariform teeth (Clifton and Motta, 1998). Additional independent evolutions of fangs have evolved in pelagic inshore fishes such as the groupers (Serranidae), snappers (Lutjanidae), emperors (Lethrinidae), and drums (Sciaenidae) (Figure 3.4). These fishes use their large jaws and well defined fangs to predate smaller reef fishes, squids, octopi, and crustaceans (Chao, 1978; Allen, 1985; Lieske and Myers, 1994).

Finally, fangs evolved in the common ancestor of deep pelagic anglerfishes, and are observed in the football fishes (Himantolophidae), warty seadevils (Ceratiidae), and the whipnose anglerfishes (Gigantactinidae) (Figure 3.4). The anglerfishes are well known for using a bioluminescent lure, a modified first dorsal fin called an esca, to attract prey (O'Day, 1974). These fishes are highly predatory and have well developed fangs on both their dentary and upper jaws (Pietsch, 2009).

Conclusions

As the phylogeny presented in this study includes exemplars in some cases of a family of fishes that may not have fangs, I highlighted on the phylogenetic hypothesis families where the vast majority or all documented species in the family possess fangs on their oral jaws (Figure 3.6). In general, all of the families where all species in the family possess fangs are pelagic fishes in predominantly marine habitats. As is the case with most lineages that have evolved fangs, fishes in these families are predatory, and include such groups as the barracudas, dragonfishes, and fangtooths. This pattern of repeated fang evolution across fishes (>38 times), and predominantly in pelagic fishes, indicates that fangs may be an important adaptation for predatory fishes in these environments, and the repeated evolution of these fangs may be the result of of selective pressures in these pelagic environments.

Figure 3.6. Evolutionary relationships of ray-finned fishes based on maximum likelihood estimation from 11 gene fragments with a parsimony ancestral character reconstruction of the evolution of fangs actinopterygian radiation. Green branches indicate families where the majority of species are observed to have fangs. Blue branches indicate families where the majority of species are not observed to have fangs.

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