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Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations

Matthew P. Davis [a,*], Christopher Fielitz [b]

[a] *Museum of Natural Science, Louisiana State University, 119 Foster Hall, Baton Rouge, LA 70803, USA*
[b] *Department of Biology, Emory & Henry College, Emory, VA 24327, USA*

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A B S T R A C T

The divergence times of lizardfishes (Euteleostei: Aulopiformes) are estimated utilizing a Bayesian approach in combination with knowledge of the fossil record of teleosts and a taxonomic review of fossil aulopiform taxa. These results are integrated with a study of character evolution regarding deep-sea evolutionary adaptations in the clade, including simultaneous hermaphroditism and tubular eyes. Divergence time estimations recover that the stem species of the lizardfishes arose during the Early Cretaceous/Late Jurassic in a marine environment with separate sexes, and laterally directed, round eyes. Tubular eyes have arisen independently at different times in three deep-sea pelagic predatory aulopiform lineages. Simultaneous hermaphroditism evolved a single time in the stem species of the suborder Alepisauroidei, the clade of deep-sea aulopiforms during the Early Cretaceous. This result indicates the oldest known evolutionary event of simultaneous hermaphroditism in vertebrates, with the Alepisauroidei being the largest vertebrate clade with this reproductive strategy.

1. Introduction

The order Aulopiformes (Euteleostei: Cyclosquamata) includes 44 extant genera with approximately 236 species of lizardfishes and their allies (Nelson, 2006). Taxa within the order include predatory marine fishes that range in habitat from inshore coastal systems to the deep sea. Many aulopiform fishes have evolved fascinating deep-sea evolutionary adaptations including a number of highly specialized anatomical eye modifications and a reproductive strategy of simultaneous hermaphroditism, one of the rarest methods of reproduction among vertebrate taxa.

Aulopiformes have been recovered as monophyletic with both morphological (e.g., Rosen, 1973; Baldwin and Johnson, 1996; Sato and Nakabo, 2002) and molecular data (Davis, 2010). Previous studies have recovered them as the sister group to the crown euteleostean clade Ctenosquamata (e.g., Rosen 1973; Davis, 2010), which includes the lanternfishes (Myctophiformes) and the spiny-ray fishes (Acanthomorpha). The fossil record for aulopiform fishes is robust with extinct taxa described from two of the three suborders, the Aulopoidei and the Alepisauroidei. The majority of fossil taxa are associated with the crown aulopiform clade of alepisauroids (Lancetfishes) from Late Cretaceous deposits.

The focus of this work is to explore the divergence times of aulopiform fishes and the character evolution of deep-sea adaptations within a robust molecular phylogenetic framework. Additionally we provide a taxonomic review and synthesis of fossil aulopiform diversity to serve as a resource for future phylogenetic and divergence time studies within this group. In this study we investigate the divergence times of (1) the common ancestor of aulopiforms, (2) the major aulopiform lineages, and (3) the evolutionary history of two aulopiform deep-sea adaptations, eye specializations and simultaneous hermaphroditism. Estimating the divergence times of aulopiform fishes is important to our understanding of the evolutionary history of one of the most diverse deep-sea vertebrate lineages, including the timing and character evolution of deep-sea adaptations.

1.1. Overview of fossil aulopiform taxa and relationships

A listing of the fossil aulopiform fishes is found on Table 1. The oldest complete aulopiform fossil is †*Atolvorator longipectoralis*[1] from the Sergipe-Alagoas basin in northeastern Brazil (Gallo and Coelho, 2008). This formation is dated to the Barremian of the Lower Cretaceous and is estimated to be 125 million years old. Gallo and Coelho (2008) did not conduct a phylogenetic study to explore the relationship of †*A. longipectoralis* to other aulopiform taxa, but hypothesized that the taxon was closely aligned to other extinct

* Corresponding author.
E-mail addresses: matthewdavis@lsu.edu (M.P. Davis), cfielitz@ehc.edu, mpdavis@ku.edu (C. Fielitz).

[1] Throughout this manuscript a † denotes an extinct lineage

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Table 1
Time ranges of fossil aulopiform genera. Subordinal classifications follow Goody (1969) and Davis (2010). A † denotes an extinct lineage.

Taxa	Species	Time range (Ma)	Geologic range (stage age)
†Enchodontoidei			
†*Enchodus*	17	60. 5–99.6	Lower Cenomanian to Paleocene (Danian)
†*Eurypholis*	3	88.5–94.6	Upper Cenomanian to Turonian
†*Palaeolycus*	1	74–83.5	Campanian
†*Parenchodus*	1	93.5–94.6	Upper Cenomanian
†*Rharbichthys*	1	93.5–99.6	Cenomanian
†*Saurorhamphus*	3	93.5–94.6	Upper Cenomanian
†Cimolichthyoidei			
†*Apuliadercitis*	1	65.5–83.5	Coniacian to Early Campanian
†*Brazilodercetis*	1	88.5–90.5	Campanian to Maastrichtian
†*Cimolichthys*	2	65.5–99.6	Turonian
†*Cyranichthys*	1	93.5–99.6	Cenomanian to Maastrichtian
†*Dercetis*	4	70.6–99.6	Cenomanian
†*Dercetoides*	1	96–99.6	Lower Cenomanian to Upper Campanian
†*Hastichthys*	1	94.8–99.6	Lower Cenomanian
†*Leptecodon*	1	65.5–88.6	Lower to mid Cenomanian
†*Nardodercetis*	1	65.5–83.5	Coniacian to early Campanian
†*Nardorex*	1	65.5–83.5	Campanian to Maastrichtian
†*Pelargorhynchus*	1	70.6–76.3	Upper Campanian
†*Prionolepis*	2	94.6–95	Middle Cenomanian
†*Ophidercetis*	1	83.5–65.5	Campanian to Maastrichtian
†*Rhynchodercetis*	6	88.5–99.6	Cenomanian to Turonian
†*Roberticthys*	1	92.1–93.5	Lower Turonian
†*Stratodus*	1	80.6–88.6	Coniacian to Early Campanian
†Ichthyotringoidei			
†*Apateodus*	2	65.5–106.4	Albian to Maastrichtian
†*Apateopholis*	1	93.5–94.8	Upper Cenomanian
†*Ichthyotringa*	3	70.6–99.6	Lower Cenomanian to Campanian
†Halecoidei			
†*Halec*	1	83.5–99.6	Cenomanian to Santonian
†*Hemisaurida*	1	93.5–99.6	Cenomanian
†*Phylactocephalus*	1	93.5–94.6	Upper Cenomanian
†*Serrilepis*	3	93.5–99.6	Lower Cenomanian
Alepisauroidei			
†*Acrognathus*	1	128–130	Hauterivian
†*Drimys*	1	2.5–7.5	Placenzian to Messinian
†*Holosteus*	3	28.4–33.9	Rupelian to Lower Chattian
†*Polymerichthys*	1	5.3–23	Zanclian to Aquitanian
Aulopoidei			
†*Nematonotus*	2	93–96	Upper Cenomanian
Aulopiformes in. sed.			
†*Atolvorator*	1	125–130 (128)	Hauterivian
†*Telepholis*	2	70.6–94.6	Middle Cenomanian to Upper Campanian
†*Yabrudichthys*	1	96–99.6	Lower Cenomanian

alepisauoids (e.g., †Cimolichthyidae, †Serrilepidae). Additionally, isolated tooth elements were suggested to belong to an unidentified alepisauroid taxon which has been described from Barremian deposits of Alcaine in northeastern Spain (Kriwet, 2003). The time range for most of the fossil aulopiforms can be placed between the Lowest Cenomanian to the Maastrichtian.

While there have been many studies focused on the evolutionary relationships of extant aulopiforms (e.g., Rosen, 1973; Johnson, 1982; Baldwin and Johnson, 1996; Sato and Nakabo, 2002; Davis, 2010), relationships within the group including extinct aulopiforms are unclear with the exception of the family †Enchodontidae. Currently, the only phylogenetic study of aulopiform fishes to include both extant and extinct taxa is that of Fielitz (2004), which examined the interrelationships of the family †Enchodontidae. Fielitz (2004) recovered a clade consisting of the extant family Alepisauridae (*Alepisaurus* and *Omosudis*) and the extinct families †Cimolichthyidae and †Enchodontidae, classified under the superfamily Alepisauroidea (Fig. 1; Fielitz, 2004). The oldest specimen analyzed in this study was from the Lower Cenomanian Stage of the Late Cretaceous, approximately 100 million years ago. All other studies examining aulopiform fossils have assigned taxa to extant families based on morphological characteristics with no systematic analysis (e.g., Rosen, 1973), or have left the taxa *incertae sedis* within the order (e.g., Taverne, 2004, 2005).

Hypotheses of aulopiform divergence times have never been explored with molecular data from a robust dataset with comprehensive aulopiform taxonomic sampling. Alfaro et al. (2009) included two aulopiform taxa (*Synodus intermedius* and *Chlorophthalmus* sp.) in their analysis of divergence and diversification rates among vertebrates, and recovered a mean divergence time for the aulopiform clade of 102 Ma (95% HPD 96–138 Ma). Overall, the young mean age recovered for the divergence of the entire clade resulted from their calibration of the aulopiform node. Alfaro et al. (2009) placed a minimum age for the aulopiform clade at 96 Ma, based on fossil representatives †*Nematonotus* spp. (Aulopidae) and †*Acrognathus dodgei* (Chlorophthalmidae), and a soft maximum age of 128–130 Ma based on teeth from an undetermined fossil taxon (Kriwet, 2003). Their calibration scheme for aulopiforms is problematic as the minimum age imposed for the clade is nearly 30 Ma younger than the oldest complete aulopiform fossil †*Atolvorator longipectoralis* (Gallo and Coelho, 2008) and they imposed a soft maximum clade age based on fossil teeth elements from an undetermined taxon that was hypothesized to be closely related to the crown aulopiform lineage of alepisauroids (Kriwet, 2003).