

A phylogenetic comparative analysis of Coelacanthiform environmental
distributions through the fossil record

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Abstract

In order to understand how modern coelacanths came to reside in an isolated open sea environment, a phylogenetic evaluation of environmental habitat preference among the lineage leading to the modern day coelacanth has been completed encompassing the order Coelacanthiformes. Coelacanthiformes includes: Latimeriidae, the Mesozoic-Cenozoic family which contains the living species *Latimeria*; Whiteiidae, a family of extinct coelacanths from the Triassic; Mawsoniidae, a Mesozoic family of extinct; and a few genera that do not belong to these families but are classified among these coelacanthiformes. Using occurrence data from Paleobiology Database, a data set of the environmental preferences among the fossil coelacanth specimens was created. The collected data were then simplified and run through an algorithm named BayesTraits to determine the most probable environments at the internal nodes of the Coelacanthiformes phylogeny from Arratia and Schultze (2015). The hypothesis for this study is that there was a trend towards increasingly deep marine environments along the lineage to the modern *Latimeria*. Results indicate that the environmental preferences along the lineage to *Latimeria* have shifted from open marine environments in the Late Paleozoic towards more inland based habitats during the Early Mesozoic and back to open marine preferences in the Cretaceous and Cenozoic. These results show that coelacanths expanded to many different environments, but that survival may have been more opportunistic.

Introduction

Coelacanths are part of Sarcopterygii, the lobe-finned fish, a group that also includes Tetrapoda, the land vertebrates, and are considered to be “living fossils”. They were thought to have gone extinct during the end of the Cretaceous-Paleogene extinction, and since their rediscovery are commonly thought of as unchanged over millions of years (Weinberg 2000). Actinistian, the subclass in Sarcopterygii that contains all modern and fossil coelacanths, are diagnosed by all species that have lost their maxilla (the upper jaw bone) as well as most species having a diphyccercal tailfin. The order Coelacanthiformes within Actinistia, which represents modern coelacanths and their most recent common ancestor, will be the focus for this analysis.

I am looking at Actinistia, which is broadly defined as all fossil and modern coelacanths. This project focuses on Coelacanthiformes which falls under Actinistia as defined by Arratia and Schultze (2015). Within Coelacanthiformes are 21 taxa that are more closely related to each other than the next taxon with three major families: Whiteiidae, Mawsoniidae, and, Latimeriidae; though Latimeriidae and Mawsoniidae are also defined under Latimerioidei as the clade including *Mawsonia gigas* and *Latimeria chalumnae* (Dutel 2013).

Only the taxa within Coelacanthiformes are evaluated, as evaluating all of Actinistia would be inappropriate and irrelevant to the hypothesis which focuses on the environmental preferences of the closest three families including and related to *Latimeria*.

Though coelacanths are regarded as unchanged through time, they do change drastically in size and preference for environment (Weinberg 2000, Dutel 2013). The Mesozoic coelacanths are good examples of these changes: *Mawsonia* is known from specimens 4 to 6 meters in length in Brazil, and, *Rebellatrix divaricerca* is known especially well for its forked tail, rather than the typically diphyccercal tailfin, both seen in Figure 1 (Mawson 1907, Wendruff 2012). Even with these physical changes, it is also important how they have remained so nearly unchanged over time and survived in this ancestral form.

Modern day coelacanths are peculiar creatures, thought to have been extinct until 1938, when the first species, *Latimeria chalumnae*, was discovered off the coast of South Africa (Weinberg 2000). Since the rediscovery by Marjorie Courtenay-Latimer, another species, *Latimeria menadoensis*, was discovered off the coasts of some Indonesian islands in 1997, which was determined to be a different species through genetic testing (Nikaido 2011). Both species of *Latimeria* dwell in deep sea caves, at depths of around 200 meters during the day and around 50 to 150 meters during the night (Weinberg 2000).

In contrast to the living coelacanth, fossil coelacanth specimens have been recognized since the mid-1800s. These fossils are widespread through time, from their first appearance in the Devonian, to the end of the Cretaceous; excluding the gap in time between the modern and most recent fossil *Latimeria* (Weinberg 2000). Some fossil specimens have been preserved in great detail, though the morphologies of the fossil species and the environments in which they are discovered vary more so than the living *Latimeria*. There is a greater understanding of the environments in which both modern species live, but the selective pressures and evolutionary trends resulting in these habitat preferences are unknown.

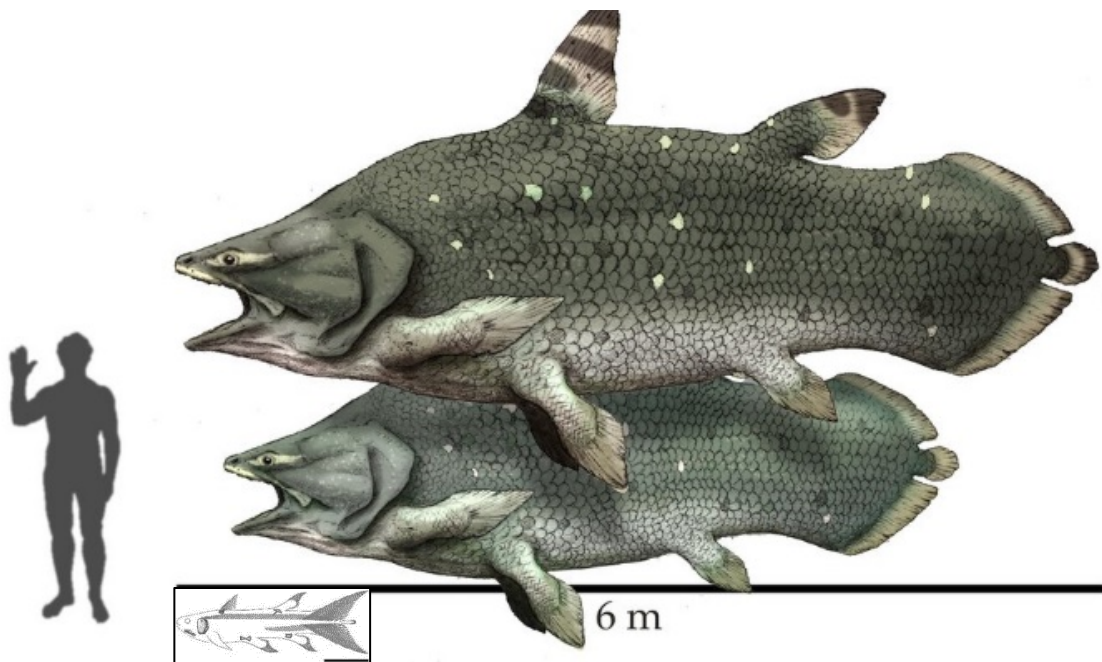


Figure 1: Various coelacanths sized appropriately to a human of 1.9 m. The two larger are *Mawsonia* whereas the smaller is *Rebellatrix*. (Wendruff 2012, Knuppe 2013).

Hypothesis

Coelacanths today inhabit deep sea cave systems during the day, and due to this extreme environment compared to the various environments recorded for the fossil specimens, there may be a trend of variation among fossil coelacanth environmental preferences. To determine this, the lineage leading to *Latimeria* will be evaluated in comparison to the other clades within Coelacanthiformes. The hypothesis for this study is that there is a trend towards increasingly deep marine environmental preferences along the lineage from *Axelia*, *Wimania*, and, *Guizhoucoelacanthus*, to the modern species *Latimeria*. The null hypothesis for this analysis is that there is no trend towards any particular environment along the lineage to *Latimeria*.

Methods and Materials

For this analysis the ancestral state has to be reconstructed to determine the habitat preferences within Coelacanthiformes. In order to reconstruct these environmental preferences, there are three steps required: development of a time-scaled phylogeny, the estimation of the habitats for the individual taxa, and, application of an algorithm to infer the ancestral states.

In order to properly correlate the data that were collected, the phylogeny from Arratia and Schultze's 2015 study of evolutionary characteristic development within Actinistia will be the basis of the phylogeny for this analysis. This phylogeny is based on 37 taxa and 110 characters, on the consensus of the 22 shortest trees, to create an evolutionary consensus of Actinistia, but for this study, it has been restricted to the taxa only within Coelacanthiformes.

A database must be assembled in order to estimate the preferred environments of the taxa within Coelacanthiformes with the phylogeny established. The information required to evaluate these environments depends on information described for each reported specimen. To ensure a time scaled phylogeny, the appearances of the taxa are calibrated alongside the geologic time scale, the age of each deposition, and the formation in which the specimen is found. Both an approximate maximum and minimum age for the lineage duration, from the present, can be concluded from this information. The environment of deposition is determined by the type of sediment and the accompanying non-coelacanth fossil specimens. This also includes the salinity, which can be inferred through the sediment composition, such as the coastal slopes of a marine basin that range from brackish to saline waters. In cases when some information is not preserved, the potential environment may still be deduced.

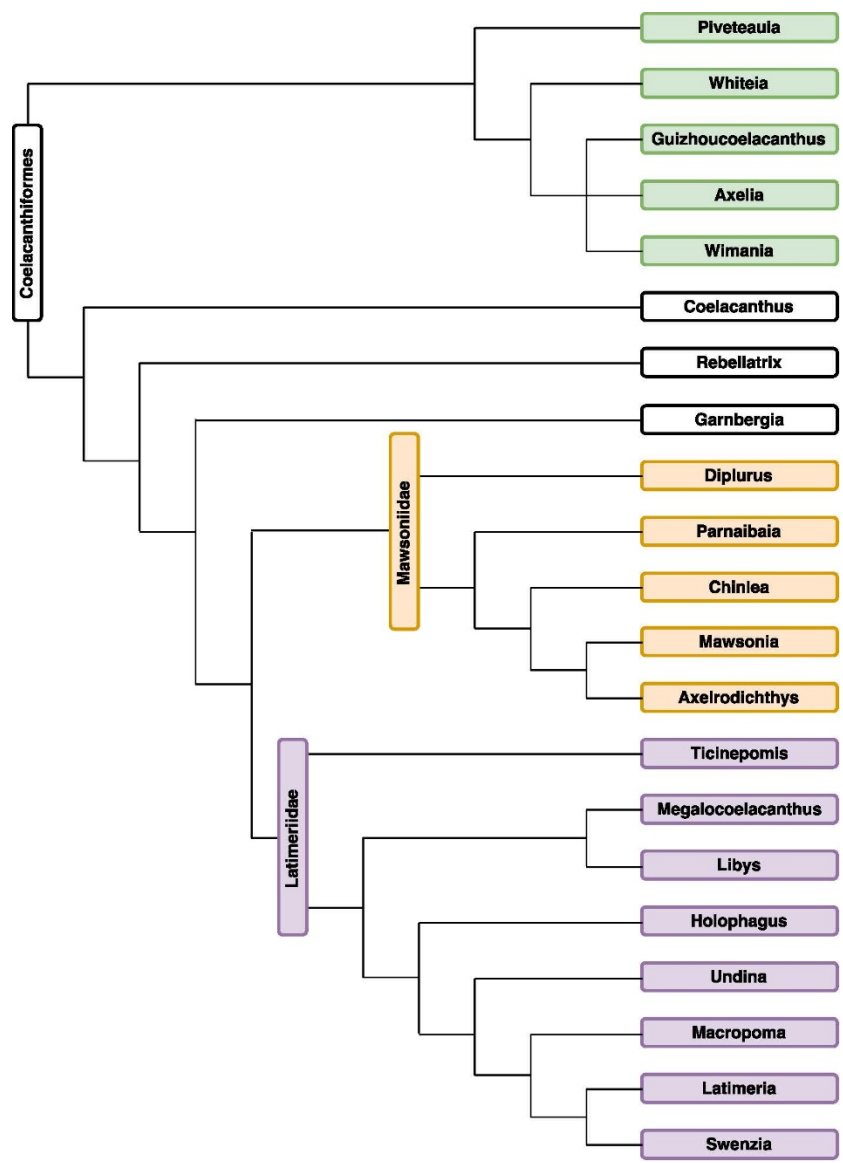


Figure 2: Phylogeny of Coelacanthiformes adapted from Arratia and Schultze 2015.

Paleobiology Database

The data for this analysis were gathered with the help of the Paleobiology Database as a secondary resource, and the original documents describing each fossil specimen as primary resources. This database provides basic information about various different fossils, including: the location of the specimen, the age, the formation, the primary work reporting the specimen, the sister taxa, a list of all taxa identified at this locale, and, occasionally the environment with the lithology. The Paleobiology Database provides the information in the simplest form, but is used to obtain the primary articles so that this information is obtained directly; when the article is unavailable, whether it is in another language and not-translated or very obscure, the information on the Paleobiology Database is used in lieu of the absent article.

Occasionally only the lithology is reported, and as such the environment of preservation has been inferred. Habitat preference was determined using various sedimentary structures, biological structures, relevant salinity information, and, other dating techniques. For example, in Heinz Furrer's 1995 description of the Prosanto Formation, he describes finely laminated limestone and shale which would have formed below wave base which, combined with a lack of bioturbation and rare benthic fossil organisms, represents a small restricted basin with a hypersaline bottom water. The Prosanto Formation is described again in Cavin et al., (2013), suggesting that medium sized fish preying on crustaceans and calcareous algae must have lived along the edge of this basin in shallow oxygenated water. A uranium/lead zircon age of a volcanic ash layer in the upper beds was also determined in Cavin et al., (2013), giving an approximate age range of 237 to 242 mya. This is how information was gathered for the specimens with poorly defined habitats and age ranges.

Once the data were collected, they were organized into a large database incorporating a total of 115 specimens among the 21 taxa within Coelacanthiformes. The information available includes the 21 taxa, their various subtaxa, the maximum and minimum ages, the environments, and, where the information is from (see Appendix III).

In order to appropriately distinguish between the various environments, eight major designations were determined. However, with so many specimens, the data were averaged in order to view the overall trend within the phylogeny, which narrowed the simplified data down to five major environments: fluvial, lagoonal, subtidal, continental shelf, and, pelagic.

BayesTraitsV2

BayesTraitsV2 is utilized in order to algorithmically determine the probability that an ancestral node in the phylogeny would be characterized by a given state. This package can be applied determine the probability of multiple characteristics within a phylogeny (Pagel 2004). BayesMultistate allows for a finite number of discrete states to be evaluated as phylogenetic traits and, will determine the probability of the character state at the root given the character states of the rest of the phylogeny (Pagel 2004). A time calibrated tree file and the states observed in the terminal taxa are required for BayesTraitsV2 to properly determine the probabilities of the states at the internal nodes.

For the data to be readable by BayesTraitsV2, it requires a NEXUS tree format as well as the appropriate characters to evaluate this tree of information (Pagel 2004). The NEXUS tree for this hypothesis is built using a designated number for each species, and then given a respective

length of time for each branch of the tree. The branch lengths were determined using the difference in time between the oldest occurrences of one taxon and that of its closest taxon; for the phylogeny this means there is no separation between the ghost and actual lineage. Some of the specimens shared an oldest occurrence in time, and were therefore given a trivially short branch length of 1 mya in order to prevent creating multiple polytomies and give it a defined separation to visually correlate to the phylogeny properly.

This algorithm has been previously used to determine ancestral environmental preferences, as well as character traits. In Harris et al., (2014), the bird family Megapodiidae was evaluated with BayesTraits to determine their biogeographical origins and to reconstruct their nesting habits. Through this study, Megapodiidae was determined to have ancestrally built mounds for their eggs, in diversification burrow nesting developed, and then switched back once to mound building. In Lucky et al., (2013), this program was used to evaluate the ancestral habitat of ants and where they nest: in soil, in litter, or in a canopy. Utilizing habitat information for each terminal taxa, they determined the ancestral habitat preference began in the soil and later diversified into other habitats.

FigTree

The program FigTree is used to visually depict phylogenetic trees in NEXUS format, and has been utilized to render the phylogeny with the appropriate time-scale (Rambaut 2007). In order for this program to properly orient the phylogeny, the phylogeny had to be built backwards through time with *Latimeria*; using the modern day as the datum, the tree was built moving backwards through geologic history, to connect with each taxa at their respective time intervals. This correlation between the data collected and the time-scale, represent the time-scaled phylogeny as seen in Figure 3.

Results

The completed evaluation of the lineage to *Latimeria* within Coelacanthiformes using BayesTraitsv2 has produced the most likely environmental preferences at the internal nodes, given the information from the database created. The basal most node of Coelacanthiformes, and the internal nodes within the order, have been approximated using the previously mentioned algorithm BayesTraitsv2 and the collected information in the database. There is an overall pattern of open sea preferences which switch to near shore environments, and then shift back to an open sea environments.

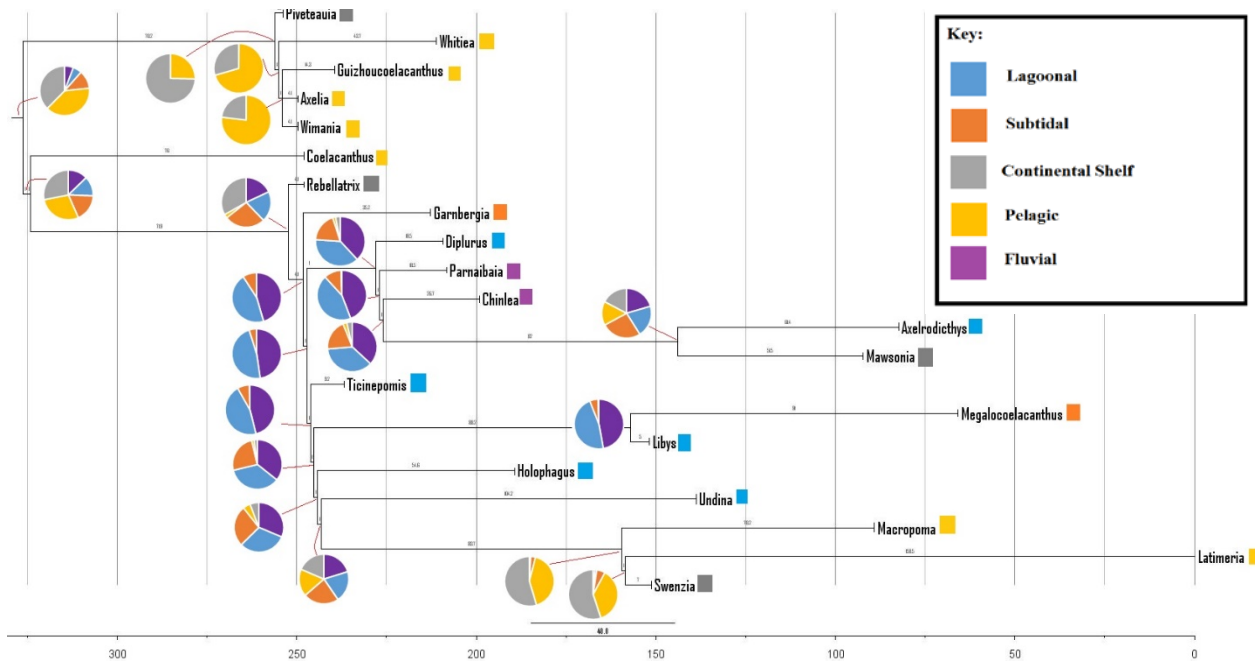


Figure 3: Time-scaled phylogeny (in millions of years from the present) of Coelacanthiformes, with the appropriate probabilities at each internal node.

At the root of Coelacanthiformes, the environmental preference is nearly 40 percent pelagic and 37 percent continental shelf, with the remaining quarter split amongst fluvial, lagoonal, and subtidal environments. This proportion at the root classifies the most basal environmental preference to be primarily deep-sea oriented, with minor possibilities towards the other habitats.

One step up from the base of Coelacanthiformes, often referred to as Whiteiidae, is the basal group of taxa: *Piveteauia*, *Whittea*, *Guizhoucoelacanthus*, *Axelia*, and *Wimania*. All of these taxa share a preference for deeper waters as they have evidence of pelagic environments, other than *Piveteauia* with a preference for continental shelf environments. The internal node between *Axelia*, *Guizhoucoelacanthus*, and *Wimania* shows an overall probable preference for pelagic waters, with a little less than a quarter probability for continental shelf. One step up from that node includes *Whittea*, and the internal node is similar to the previous but with a great probability of continental shelf preference. At the base of this family is *Piveteauia* and with the inclusion of this taxa, the likelihood of environment shifts to almost 75% continental shelf preference and 25% pelagic preference alongside the other environments which are almost negligible. All of these taxa thrived variably in time, most almost to the Triassic, but so far have not been found more recent than 208.5 million years ago.

Before the next family, there are three outlying taxa more closely related to Mawsoniidae and Latimeriidae than the more basal Whiteiidae: *Garnbergia*, *Rebellatrix*, and *Coelacanthus*. *Coelacanthus*' environmental preference is pelagic, whereas *Rebellatrix*'s preference is continental shelf, and *Garnbergia*'s preference is subtidal. The internal node including *Coelacanthus* is 28% pelagic, 28% continental shelf, with between 12-17% for each of the other environments. At the lower node including *Rebellatrix* the probability shifts towards a 33% probability of continental shelf, about two percent for pelagic, and almost 20% for each of the

other environments. With this inclusion, the shift towards more inland environments can be seen but, does not entirely rule out open sea preferences. At the internal node between *Garnbergia* and the rest of the lineage to *Latimeria*, the probable environments have shifted greatly: fluvial and lagoonal environmental preference each have 45%, whereas subtidal preference makes up nearly all of the remaining 10%. This shift in the probabilities is almost drastic in how sudden it seems to switch from being more inclined towards open sea, to more inland environments, but this shift occurred somewhere along nearly 70 million years between just *Coelacanthus* and *Garnbergia* plus the lineage to *Latimeria*.

The following step down the phylogeny is the internal node Latimerioidei, uniting Mawsoniidae and Latimeriidae. This node is influenced by the designated environments within each family, but reveals a greater inclination to lagoonal environments and fluvial environments with 47% each, and the remaining approximate five percent is dominated by a preference for subtidal environments.

The root of Mawsoniidae is the next step down within Coelacanthiformes, which includes five taxa, but is a sister group to Latimeriidae. The five taxa within Mawsoniidae and their environmental preferences from the root down are: *Diplurus* as lagoonal, *Parnaibaia* as fluvial, *Chinlea* as fluvial also, *Axelrodichthys* as lagoonal, and *Mawsonia* as continental shelf. The root node between *Diplurus* and the other taxa within Mawsoniidae is nearly 38% for both fluvial and lagoonal, with 19% subtidal, and, 4% between pelagic and continental shelf environments. This node shows an increased preference for subtidal environments, but changes at the next node within the group. Between *Parnaibaia* and the other mawsoniids, there is a greater probability towards fluvial and lagoonal again at 44% each, with 11% subtidal, and less than 1% for the other two environments together. At the next step down in Mawsoniidae is *Chinlea*, and the internal node between it and the other two taxa is: 36% each for fluvial and lagoonal, 20% for subtidal, nearly 4% continental shelf, and, nearly 3% pelagic. The last internal node within Mawsoniidae is between *Axelrodichthys* and *Mawsonia*, and displays a nearly equal probability for each environmental preference, though subtidal preference is greatest at 26%. This transition within Mawsoniidae reveals an almost continuously split probability between fluvial and lagoonal environments, with minor subtidal preference and almost negligible combination of pelagic and continental shelf probabilities. However, the internal node at the between *Mawsonia* and *Axelrodichthys* shows an equal probability for any environment preference, revealing that the species could have radiated into any environment at that point in the phylogeny.

Following the phylogeny of Coelacanthiformes again, leads to the group Latimeriidae that contains eight taxa and includes the extant *Latimeria*. These taxa and their environmental preferences are: *Ticinepomis* as lagoonal, *Megalocoelacanthus* as subtidal, *Libys* as lagoonal, *Holophagus* as lagoonal, *Undina* as lagoonal, *Macropoma* as pelagic, *Swenzia* as continental shelf, and, *Latimeria* as pelagic. The basal node in Latimeriidae is divided 46% for fluvial, 46% lagoonal, and 8% for subtidal, with less than 0.1% probability for continental shelf and pelagic combined. The internal node between *Libys* and *Megalocoelacanthus* continue this fluvial-lagoonal preference trend with: 47% fluvial, 46% lagoonal, and the remaining 6% with a majority of subtidal probable preference. The next internal node closer to *Latimeria* is the node connecting *Megalocoelacanthus*, *Libys*, and the lineage, which has a greater chance for pelagic, subtidal and, continental shelf environments but it reveals a similar pattern of split majority of fluvial and lagoonal: fluvial is 36%, lagoonal is 36%, subtidal is 25%, and the remaining 3% is pelagic and continental shelf. The next node is *Holophagus* and the lineage to *Latimeria*, which

reveals a greater preference for open sea environments overall: 31% fluvial, 31% lagoonal, 26% subtidal, 6% continental shelf, and 5% pelagic. The following internal node including *Undina*, reveals a change in preference that is nearly split equally among each of the environmental preferences, as they each range from 18% to 23% for each environment. Another step down, is the internal node with *Macropoma* and the lineage to *Latimeria*, reveals a sudden shift to open sea environments entirely: 55% continental shelf, 42% pelagic, 3% subtidal, and the remaining 0.8% is fluvial and lagoonal. The final internal node is between *Swenzia* and *Latimeria*, and continues the probability towards open-sea habitats: 55% continental shelf, 37% pelagic, 6% subtidal, and 1% each for lagoonal and fluvial.

Discussion of Results

This set of results provides a trend within the lineage to *Latimeria* within Coelacanthiformes in which there is a final trend towards deeper marine environments, but also includes an earlier shift towards more in-land based environments. These major transitions in environmental preference occur at major events in time: the Permian-Triassic extinction event, and the Triassic-Jurassic extinction event.

Coelacanthiformes before the Permian-Triassic event included environmental diversity among the various species, habitation in both open sea and near-shore environments. In the time-calibrated phylogeny, at the time of the Permian-Triassic extinction the near-shore preferences increase while the open-sea preferences decrease. Though not primarily affected by the extinction the early coelacanths were most likely affected secondarily, as the benthic fauna in the open-sea that the coelacanths would have preyed upon were marked by extinction of 57% species (Song 2012). With the loss of the benthic species that the coelacanths would have survived on there would be a greater preference towards environments that still included available alternatives, which would be the near-shore environments. This shift towards near-shore environments was likely an effect of the Permian-Triassic extinction, as the open-sea species survive past this event but are less common than those that prefer fluvial and lagoonal environments.

The other major shift in environmental preference within Coelacanthiformes occurs at the Triassic-Jurassic extinction event. The environmental preferences along the time-calibrated Coelacanthiformes phylogeny shift from near-shore environments of lagoons and fluvial systems, to open-sea environments of continental shelf and pelagic waters. However, in comparison the Permian-Triassic was more immediate in time whereas this shift was more gradual; the coelacanths that preferred lagoonal environments survived past this point, but those that preferred more open-sea environments persisted further in time.

These major shifts coincide with physical changes among taxa within the Coelacanthiformes phylogeny. At the branch of Coelacanthus and Latimerioidei, the preorbital bone is absent, and the postorbital bone is reduced to a tube that surrounds the sensory canal (Arratia 2015). These changes describe how the bones that supported the eyes had been restructured to adapt to protect their sensory capabilities more so than before. However, Arratia and Schultze (2015) did not identify a trend of physical changes among the Latimeriidae family, since they were focused on relating the taxa in Coelacanthiformes through development of physical traits.

Conclusion

According to this study, there were two major shifts in preference, including the trend of a preference for increasingly deeper marine environments along the lineage to *Latimeria*. The root of Coelacanthiformes already had a preference for open-sea environments, but with the Permian-Triassic extinction the coelacanths that preferred lagoonal and fluvial environments proliferated, until the Triassic-Jurassic extinction which led to the gradual shift back to the open sea. These various shifts seem to be opportunistic following the extinction events, and support the hypothesis of a trend towards open-sea environments along the lineage to *Latimeria* through Coelacanthiformes.

In the overall scheme of the data, the sudden shift to a fluvial and lagoonal preference appears to be out of place with the data that provides only two fluvial taxa, but in fact is a product of the algorithm BayesTraitsV2. With the shortest length of time being 1 mya for the branches connecting Mawsoniidae and Latimeriidae, BayesTraitsV2 interprets these fluvial preferences with greater emphasis and therefore appear in more than just the Mawsoniidae family. The assumption to put 1 mya between branches of taxa that occur concurrently was to prevent polytomies within the Coelacanthiform phylogeny that would have resulted in shortening this time difference. Expanding the minimum time between these taxa would also have been unreasonable as these taxa occur concurrently in time and would have displaced the other taxa in the time-calibrated phylogeny.

In possible future studies, this hypothesis could be run for further interpretation in which all 115 specimens could be incorporated at polytomies with the taxa they belong to. By assembling all of the data into the information run through BayesTriatsV2, there may be more shifts of environmental preference not seen with this level of simplification. This incorporation could provide more detail on the possible minute shifts of environmental preferences within Coelacanthiformes.

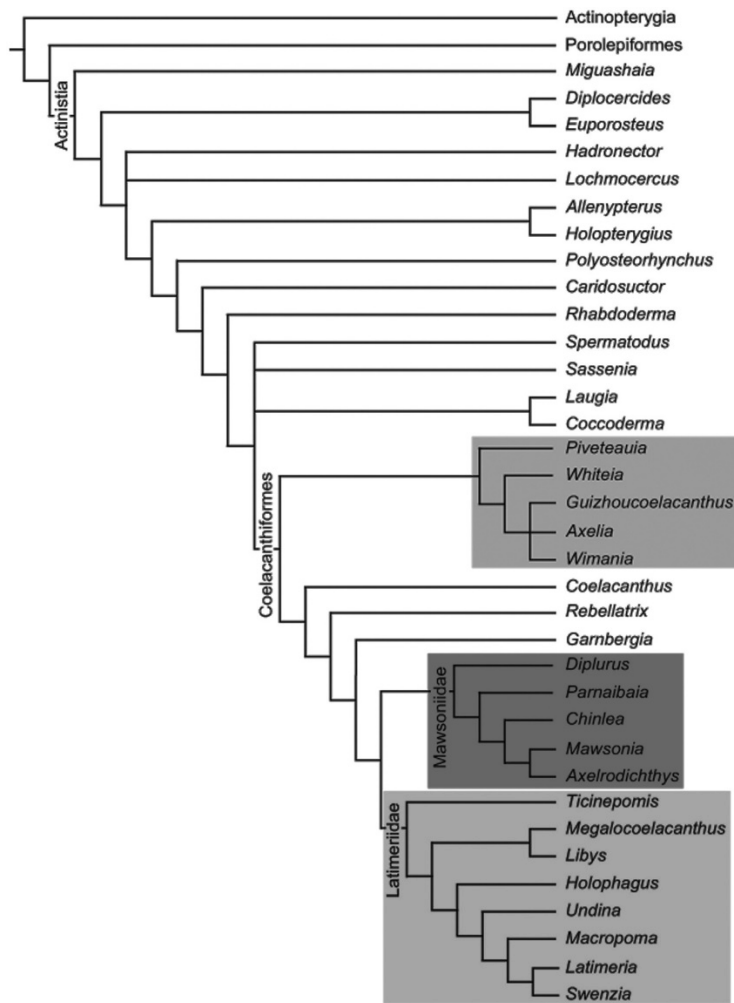
Appendix I

Simplified Data that were run through BayesTraits.

Taxa	Environment
<i>Undina</i>	LAGOONAL
<i>Holophagus</i>	LAGOONAL
<i>Latimeria</i>	PELAGIC
<i>Swenzia</i>	CONTINENTAL SHELF
<i>Megalocoelacanthus</i>	SUBTIDAL
<i>Libys</i>	LAGOONAL
<i>Macropoma</i>	PELAGIC
<i>Ticinepomis</i>	LAGOONAL
<i>Axelrodichthys</i>	LAGOONAL
<i>Mawsonia</i>	CONTINENTAL SHELF
<i>Chinlea</i>	FLUVIAL
<i>Parnaibaia</i>	FLUVIAL
<i>Diplurus</i>	LAGOONAL
<i>Garnbergia</i>	SUBTIDAL
<i>Rebellatrix</i>	CONTINENTAL SHELF
<i>Coelacanthus</i>	PELAGIC
<i>Wimania</i>	PELAGIC
<i>Axelia</i>	PELAGIC
<i>Guizhoucoelacanthus</i>	PELAGIC
<i>Whittea</i>	PELAGIC
<i>Piveteauia</i>	CONTINENTAL SHELF

Appendix II

Phylogeny based on characteristic development from Arratia and Schultze, 2015.



Appendix III

Full data set, built using the Paleobiology Database, which was simplified to run through BayesTraitsv2.

Genus	Species	Environment	Time Max (mya)	Time Min (mya)	Reference
<i>Latimeria</i>					
	<i>chalumnae</i>	Pelagic	<0.01	<0.01	PaleoDB
	<i>menadoensis</i>	Pelagic	<0.01	<0.01	PaleoDB
<i>Swenzia</i>					
	<i>latimerae</i>	Continental shelf	158.5	152	G. Clement. 2005.
<i>Macropoma</i>					
	<i>sp.</i>	Pelagic	99.7	94.3	W. J. Kennedy. 1969.
	<i>Mantelli</i>	Pelagic	94.3	89.3	M. Waldman. 1965.
<i>Undina</i>					
	<i>purbeckensis</i>	Lagoonal	145	139	PaleoDB
	<i>penicillata</i>	N/A	155.7	150.8	PaleoDB
	<i>sp.</i>	Lagoonal	152	145	PaleoDB
	<i>penicillata</i>	Lagoonal	155.7	150.8	PaleoDB
	<i>cf. Undina</i>	Pelagic	152	145	PaleoDB
	<i>barroviensis</i>	Continental shelf	201.6	196.5	PaleoDB
	<i>barroviensis</i>	Continental Shelf	201.6	196.5	PaleoDB
	<i>barroviensis</i>	N/A	203	199.6	A. S. Woodward. 1891.
	<i>barroviensis</i>	Lagoonal	167.7	164.7	PaleoDB
	<i>penicillata</i>	Lagoonal	155.7\152	150.8	PaleoDB
	<i>sp.</i>	Lagoonal	215.6	212	PaleoDB

	<i>sp.</i>	Pelagic	247.2	242	PaleoDB
<i>Holophagus</i>					
	<i>gulo</i>	Pelagic	201.6	189.6	P. M. G. Egerton. 1861.
	<i>gulo</i>	Pelagic	196.5	189.6	P. M. G. Egerton. 1858.
	<i>gulo</i>	Pelagic	196.5	189.6	P. Egerton. 1854.
	<i>picenus</i>	Lagoonal	215.6	212	F. Bassani. 1895.
	<i>picenus</i>	Lagoonal	247.2	242	O. Rieppel. 1985.
	<i>picenus</i>	Lagoonal	247.2	242	O. Rieppel. 1985.
<i>Megalocoelacanthus</i>					
	<i>dobiei</i>	Pelagic	70.6	66	W. B. Gallagher, D. C. Parris, and E. E. Spamer. 1986.
	<i>dobiei</i>	Continental shelf	84.9	70.6	D. R. Schwimmer. 1986.
	<i>dobiei</i>	Subtidal	85.8	84.9	D. R. Schwimmer, J. D. Steward, and G. D. Williams. 1994.
	<i>dobiei n. gen., n. sp.</i>	Subtidal	84.9	70.6	D. R. Schwimmer, J. D. Steward, and G. D. Williams. 1994.
<i>Libys</i>					
	<i>superbus</i>	Lagoonal	157\152	152	PaleoDB
	<i>polypterus</i>	Lagoonal	157\152	152	PaleoDB
<i>Ticinepomis</i>					
	<i>peyeri n. gen. n. sp.</i>	Lagoonal	247.2	242	T. Bürgin. 1992.
	<i>cf. peyeri</i>	Lagoonal	242	237	L. Cavin, H. Furrer, and C. Obrist. 2013.
	<i>cf. peyeri</i>	Lagoonal	242	237	L. Cavin, H. Furrer, and C. Obrist. 2013.
<i>Axelrodichthyes</i>					
	<i>araripensis</i>	Lagoonal	113.0	100.5	S. P. Applegate, L. Espinosa-Arrubarrena, J. Alvarado-Ortega and M. Benammi. 2006.

	<i>sp.</i>	Lagoonal	113.0	100.5	S. P. Applegate, L. Espinosa-Arrubarrena, J. Alvarado-Ortega and M. Benammi. 2006.
	<i>sp.</i>	Lagoonal	122.5	109.0	PaleoDB
	<i>sp.</i>	Fluvial	89.8	83.6	PaleoDB
<i>Mawsonia</i>					
	<i>gigas</i>	Continental Shelf	145.0	130.0	J. Mawson and A. S. Woodward. 1907.
	<i>gigas</i>	Fluvial	145.0	100.5	P. M. Brito, R. J. Bertini, D. M. Martill and L. O. Salles. 1994.
	<i>gigas</i>	Continental Shelf	145.0	100.5	J. Mawson and A. S. Woodward. 1907.
	<i>sp.</i>	Subtidal	105.3	99.6	F. de Broin, C. Grenot, and R. Vernet. 1971.
	<i>sp.</i>	Continental Shelf	105.3	93.5	M. A. Medeiros and C. L. Schultz. 2002.
	<i>sp.</i>	Deltaic	99.6	93.5	J. Mawson and A. S. Woodward. 1907.
	<i>sp.</i>	N/A	113	100.5	F. Fanti, A. Cau, L. Panzarin and L. Cantelli. 2016.
	<i>sp.</i>	N/A	145	100.5	T. Schlüter and W. Schwarzhans. 1978.
	<i>lavocati</i>	Continental Shelf	105.3	93.5	E. Buffetaut. 1994.
<i>Chinlea</i>					
	<i>cf. sp.</i>	Marsh	228	208.5	C. L. Camp and S. P. Welles. 1956.
	<i>sp.</i>	Fluvial	208.5	201.3	R. E. Kirby. 1993.
	<i>sp.</i>	Fluvial	208.5	201.3	R. E. Kirby. 1991.
	<i>cf. sp.</i>	Fluvial	228	208.5	M. J. Polcyn, D. A. Winkler, L. L. Jacobs and K. Newman. 2002.
	<i>sorenseni</i>	Fluvial	228	201.3	B. Schaeffer. 1967.

	<i>sorenseni</i>	Fluvial	228	201.3	B. Schaeffer. 1967.
	<i>sorenseni</i>	Lagoonal	208.5	201.3	E. H. Colbert. 1947.
	<i>sorenseni</i>	Fluvial	228	208.5	P. A. Murry. 1986.
	<i>sorenseni</i>	N/A	228	208.5	P. A. Murry. 1986.
	<i>sorenseni n. gen. n. sp.</i>	Fluvial	228	201.3	B. Schaeffer. 1967.
Parnaibaia					
	<i>maranhaoensis n. gen. n. sp.</i>	Fluvial	163.5	145	Y. Yabumoto. 2007.
Diplurus					
	<i>longicaudatus</i>	Fluvial	228	208.5	C. A. Rizzo. 1999.
	<i>newarki</i>	Fluvial	228	208.5	N. C. Fraser, D. A. Grimaldi, P. E. Olsen and B. Axsmith. 1996.
	<i>longicaudatus</i>	Lagoonal	228	208.5	W. Bock. 1945.
	<i>sp.</i>	N/A	228	208.5	F. Baer and W. Martin. 1949.
	<i>sp.</i>	N/A	228	208.5	R. E. Weems and P. G. Kimmel. 1993.
Garnbergia					
	<i>ommata</i>	Subtidal	215.6	212	E. L. Nicholls and M. Manabe. 2004.
	<i>ommata</i>	Subtidal	247.2	242	M. Martin and S. Wenz. 1984.
Rebellatrix					
	<i>divaricerca</i>	Pelagic	251.3	247.2	A. J. Wendruff and M. V. H. Wilson. 2012.
	<i>divaricerca</i>	Pelagic	251.3	247.2	A. J. Wendruff and M. V. H. Wilson. 2012.
	<i>divaricerca</i>	Pelagic	251.3	247.2	A. J. Wendruff and M. V. H. Wilson. 2012.
	<i>divaricerca</i>	Continental Shelf	251.3	247.2	A. J. Wendruff and M. V. H. Wilson. 2012.
Coelacanthus					
	<i>banffensis</i>	Pelagic	251.3	247.2	L. M. Lambe. 1916.
	<i>madagascariensis</i>	Pelagic	252.2	251.3	A. S. Woodward. 1910.

	<i>madagascariensis</i>	Pelagic	252.2	251.3	E. I. White. 1933.
	<i>evolutus</i>	Pelagic	252.2	251.3	L. Beltan. 1980.
	<i>granulatus</i>	N/A	259.9	254.2	H. W. Holzapfel and E. Malzahn. 1984.
	<i>granulatus</i>	Lagoonal	259.9	254.2	C. G. Diedrich. 2009.
	<i>granulatus</i>	Lagoonal	259.9	254.2	C. G. Diedrich. 2009.
	<i>granulatus</i>	Lagoonal	259.9	254.2	C. G. Diedrich. 2009.
	<i>granulatus</i>	Lagoonal	259.9	254.2	C. G. Diedrich. 2009.
	<i>granulatus</i>	Lagoonal	259.9	254.2	C. G. Diedrich. 2009.
	<i>granulatus</i>	Pelagic	259.9	254.2	A. S. Woodward. 1889.
	<i>granulatus</i>	Pelagic	259.9	254.2	. Schaumberg. 1978.
	<i>granulatus</i>	Pelagic	259.9	254.2	G. Münster. 1842.
	<i>granulatus</i>	Pelagic	259.9	254.2	W. King. 1850.
	<i>granulatus</i>	Pelagic	259.9	254.2	W. King. 1850.
	<i>caudalis</i>	Pelagic	259.9	254.2	W. King. 1850.
	<i>granulatus</i>	N/A	259.9	254.2	A. S. Woodward. 1895.
	<i>sp.</i>	N/A	318.1	306.9	E. D. Cope. 1897.
	<i>lepturus</i>	Pelagic	323.2	315.2	T. Atthey. 1868.
	<i>tingleyensis</i>	N/A	315.2	307	A. S. Woodward. 1889.
	<i>exiguus</i>	Deltaic	311.4	306.9	O. Harger. 1874.
<i>Wimania</i>					
	<i>sinuosa</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>multistriata</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>sp.</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>multistriata</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>sp.</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>multistriata</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>sinuosa</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.

	<i>multistriata</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>multistriata</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
<i>Axelia</i>					
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>elegans</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
	<i>robusta</i>	Pelagic	251.3	247.2	E. A. Stensiö. 1921.
<i>Guizhoucoelacanthus</i>					
	<i>guanlingensis</i>	Pelagic	242	237	B. Geng, M. Zhu, and J. Fan. 2009.
<i>Whittea</i>					
	<i>sp.</i>	Continental Shelf	251.3	247.2	B. Schaeffer and M. Mangus. 1976.
	<i>sp.</i>	Pelagic	251.3	247.2	B. G. Gardiner. 1966.
	<i>oishii</i>	Pelagic	228	208.5	Y. Yabumoto and P. M. Brito. 2016.
	<i>tuberculata</i>	Pelagic	252.2	251.3	J. A. Moy-Thomas. 1935.
	<i>tuberculata</i>	Pelagic	252.2	251.3	J.-P. Lehman. 1952.
	<i>woodwardi</i>	Pelagic	252.2	251.3	J.-P. Lehman. 1952.
	<i>woodwardi</i>	Pelagic	252.2	251.3	J.-P. Lehman. 1952.
	<i>woodwardi</i>	Pelagic	252.2	251.3	E. I. White. 1933.
	<i>woodwardi</i>	Pelagic	252.2	251.3	L. Beltan. 1968.
<i>Piveteauia</i>					
	<i>madgascariensis</i>	Continental Shelf	252.2	251.3	G. Clement. 1999.

Appendix IV

The phylogeny code that was input into BayesTraitsv2 alongside the simplified environmental preference information (Appendix I).

```
#NEXUS
```

```
BEGIN TREES;
```

```
translate
```

```
1    Undina,  
2    Holophagus,  
3    Latimeria,  
4    Swenzia,  
5    Megalocoelacanthus,  
6    Libys,  
7    Macropoma,  
8    Ticinopomis,  
9    Axelrodichthys,  
10   Mawsonia,  
11   Chinlea,  
12   Parnaibaia,  
13   Diplurus,  
14   Garnbergia,  
15   Rebellatrix,  
16   Coelacanthus,  
17   Wimania,  
18   Axelia,  
19   Guizhoucoelacanthus,  
20   Whitiea,  
21   Piveteauia;
```

```
tree tree.3 =
```

```
((21:1.9,(20:43.7,(19:14.3,18:4.1,17:4.1):1):1):70.2,((16:76,(15:4.1,(14:35.2,((13:18.5,(12:18.5,(11:26.7,(9:61.4,10:51.5):82):1):1):18.2):1,(8:9.2,((5:91,6:5):88.2,(2:54.6,(1:104.2,(7:70.2,(3:158.5,4:7):1):83.7):1):1):1):1):4.1):71.9):1):1):1;
```

```
END;
```

Appendix V

BayesTraitsv2 Output						
ENVIRONMENTAL CATEGORIES						
NODE (from root towards <i>Latimeria</i>)	FLUVIAL	LAGOONAL	SUBTIDAL	PELAGIC	CONTINENTAL SHELF	Total
Coelacanthiformes	0.057599	0.058059	0.11774	0.390552	0.376051	1.000001
2	0.000008	0.000017	0.000433	0.253813	0.745729	1
3	0.000082	0.000141	0.001371	0.703345	0.295061	1
4	0	0	0.000039	0.768801	0.231159	0.999999
5	0.127866	0.128296	0.177927	0.284734	0.281178	1.000001
6	0.180509	0.19734	0.266005	0.024551	0.331595	1
7	0.455149	0.453291	0.091153	0.000014	0.000393	1
Latimerioidei	0.477336	0.473265	0.048892	0.000036	0.000471	1
Mawsoniidae	0.381059	0.379723	0.189415	0.018531	0.031273	1.000001
10	0.442237	0.439195	0.113082	0.001659	0.003826	0.999999
11	0.368899	0.36762	0.202452	0.025327	0.035702	1
12	0.205025	0.205916	0.260239	0.155735	0.173085	1
Latimeriidae	0.460532	0.457171	0.080385	0.000395	0.001517	1
14	0.356735	0.355536	0.249719	0.016556	0.021454	1
15	0.471536	0.46829	0.05574	0.000682	0.003752	1
16	0.313527	0.313039	0.266756	0.048396	0.058283	1.000001
17	0.202066	0.202476	0.231793	0.177954	0.185712	1.000001
18	0.004246	0.004538	0.030143	0.41534	0.545732	0.999999
19	0.011525	0.012138	0.055339	0.370444	0.550555	1.000001

Appendix VI

Honor Code

I pledge on my honor that I have not given or received any unauthorized assistance or plagiarized on this assignment/examination.

Melody L Bowen

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