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

Melody Bowen
Geol 393
Advisors: Dr. Holtz and Dr. Merck

Abstract

A preliminary evaluation of evolutionary changes in the environmental preferences of Coelacanthiformes is performed, beginning with the included family Latimeriidae, that includes the extant coelacanth *Latimeria*. Coelacanthiformes also includes Whiteiidae, a family of extinct coelacanths from the Triassic, and Mawsoniidae, a family of extinct coelacanths from the Triassic to the Cretaceous, as well as a few genera that will be considered in the fall semester. A database created with resources located with the Paleobiology Database is utilized to reconstruct the evolutionary changes in habitat preferences revealed by changes in depositional environment along Latimeriid lineages, with a focus on the lineage leading to *Latimeria*. In order to assess these changes, the algorithm BayesTraitsV2 is used to reconstruct the evolutionary preferences at internal nodes of the Latimeriid phylogeny using maximum-likelihood methods. The results of this preliminary evaluation indicate a shift to deep water preferences in the clade containing *Macropoma, Swenzia*, and *Latimeria*.

Reconstruction cast of the modern *Latimeria chalumnae*. Triebold, M. 2016. *Latimeria chalumnae* (coelacanth).

Introduction

Coelacanths are part of Sarcopterygii, the lobe-finned fish, a group that also includes Tetrapoda, the land vertebrates. They were thought to have gone extinct at the Cretaceous-Paleogene boundary until 1938, when Latimeria chalumnae was discovered off the coast of South Africa. Subsequently another species was discovered off the coasts of some Indonesian islands in 1997 and was determined to be a different species through genetic testing (Nikaido et al. 2011).

Fossil coelacanth species have been known since the mid-1800s and some have been preserved in great detail. Yet, the morphologies of the fossil species and the environments in which they are discovered vary greatly, including both freshwater and saltwater habitats. In contrast, the two living 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, on opposite ends of the Indian Ocean (Fricke 1988). This study is an attempt to examine the evolutionary trends resulting in this habitat preference are unknown. This study examines the trends within the coelacanth group Latimeriidae, which includes the living species and their closest relatives.

H_0 = Reconstructed habitat preferences of common ancestors of known Latimeriidae taxa reveal no particular trend in habitat preference.

H_1 = Reconstructed habitat preferences of common ancestors of known Latimeriidae taxa reveal an evolutionary trend(s) in habitat preference.

Materials and Methods

- The database of species, their stratigraphic occurrence, and the inferred environment of deposition was collected.
- For genera with multiple species, the most common environments were used to represent each genus.
- BayesTraitsV2 (Pagel et al. 2004) was used to infer the ancestral states at each node of the cladogram.
- The Multistate method was used as the variable "environment of deposition" has more than two discrete states.
- The Maximum-Likelihood protocol was used to determine the relative probability of the different character states at each node, given the observed character states of the rest of the phylogeny.
- Each analysis was one with 1000 simulations.
- The data BayesTraitsV2 returns is in percentages, considering the possibility of each state of habitat preference at the ancestral nodes.
- This data was then modeled in pie-charts to better evaluate the data for a trend in habitat preference along the lineage to Latimeria within Latimeriidae.
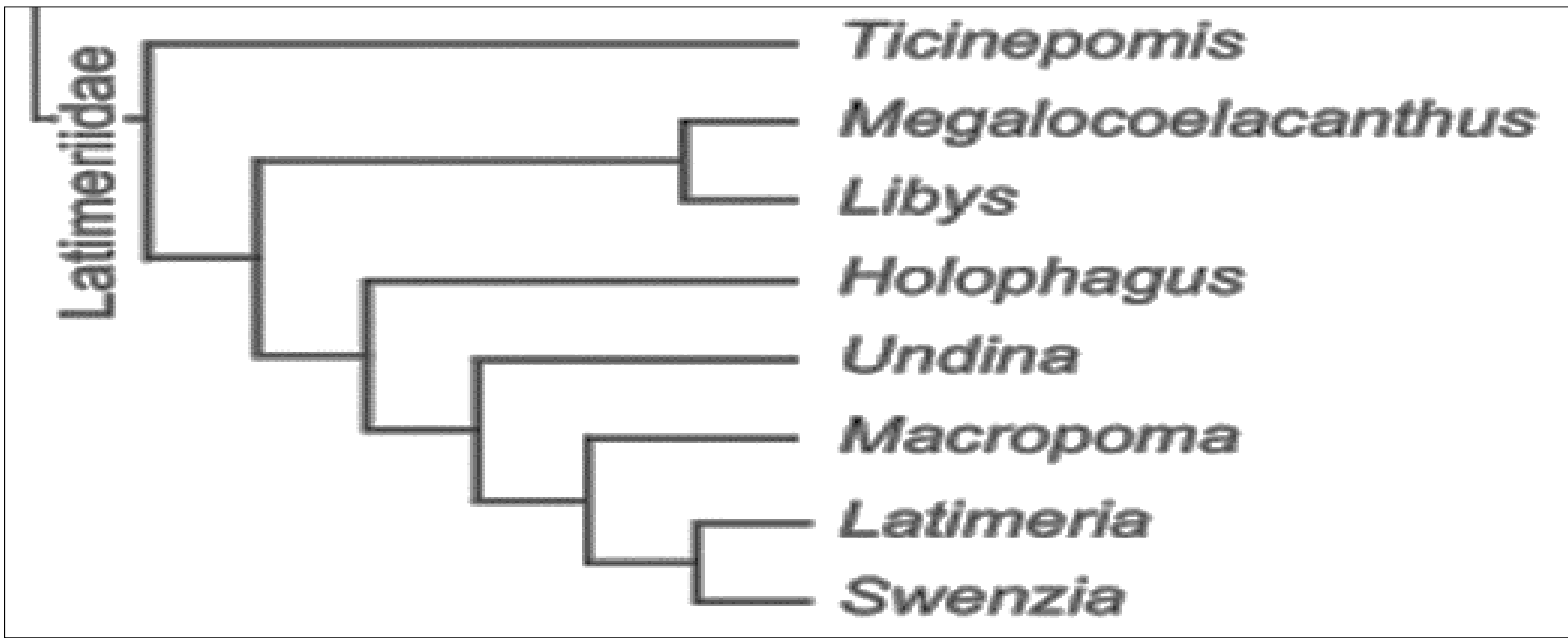
Database

Genus	Species	Depositional Environment	Salinity	Reference
Ticinepomis	peyeri n. gen. n. sp.	Lagoonal	Saline	T. Bürgin. 1992.
Ticinepomis	cf. peyeri	Lagoonal	Hyper/Saline	L. Cavin, H. Furrer, and C. Obrist. 2013.
Ticinepomis	cf. peyeri	Lagoonal	Hyper/Saline	L. Cavin, H. Furrer, and C. Obrist. 2013.
Megalocoelacanthus	dobiei	Pelagic	Saline	W. B. Gallagher, D. C. Parris, and E. E. Spamer. 1986.
Megalocoelacanthus	dobiei	Shallow Marine/Pelagic	Saline	D. R. Schwimmer. 1986
Megalocoelacanthus	dobiei	Subtidal	Saline	D. R. Schwimmer, J. D. Steward, and G. D. Williams. 1994.
Megalocoelacanthus	dobiei n. gen., n. sp.	Subtidal	Saline	D. R. Schwimmer, J. D. Steward, and G. D. Williams. 1994.
Libys	superbus	Lagoonal	Hyper/Saline	K. A. Zittel. 1887.
Libys	polypterus	Lagoonal	Hyper/Saline	G. Münster. 1842.
Holophagus	gulo	Pelagic	Saline	P. M. G. Egerton. 1861.
Holophagus	gulo	Pelagic	Saline	P. M. G. Egerton. 1858.
Holophagus	gulo	Pelagic	Saline	P. Egerton. 1854.
Holophagus	picenus	Lagoonal	Saline	F. Bassani. 1895.
Holophagus	picenus	Lagoonal	Saline	O. Rieppel. 1985.
Holophagus	picenus	Lagoonal	Saline	O. Rieppel. 1985.
Undina	sp.	Pelagic	Saline	E. Andersson. 1916.
Undina	sp.	Lagoonal, Subtidal	Saline	F. Bassani. 1895
Undina	sp.	Lagoonal	Saline	A. Bidar, L. Demay, and G. Thomel. 1972.
Undina	barroviensis	Shallow Marine	Saline	A. S. Woodward. 1890.
Undina	barroviensis	Shallow Marine	Saline	A. S. Woodward. 1890.
Undina	barroviensis	?	?	A. S. Woodward. 1891.
Undina	barroviensis	Pelagic	Saline	A. S. Woodward. 1895.
Undina	penicillata	Lagoonal, Subtidal	Saline	G. Arratia. 2000.
Undina	penicillata	?	?	G. Dietl and G. Schweigert. 2011.
Undina	penicillata	Pelagic	Saline	G. Dietl and G. Schweigert. 2011.
Undina	cf.	Lagoonal	Hyper/Saline	P. L. Forey, O. Monod, and C. Patterson. 1985.
Undina	purbeckensis	Lagoonal	Hyper/Saline	A. S. Woodward. 1916.
Macropoma	sp.	Shallow Marine/Pelagic	Saline	W. J. Kennedy. 1969.
Macropoma	mantelli	Pelagic	Saline	M. Waldman. 1965.
Swenzia	latimerae	Shallow Marine/Pelagic	Saline	G. Clement. 2005.
Latimeria	chalumnae	Shallow Marine	Saline	
Latimeria	menandonesis	Shallow Marine	Saline	

Phylogenetic Analysis by Arratia and Schultze shown focused on Latimeriidae. Arratia, G. and H.-P. Schultze. 2015.

Analysis

- The data collected is simplified into a database with simplified traits to be evaluated.
- Several species were evaluated, and then the most common environments were used to represent each genus.
- BayesTraitsV2 can be used to algorithmically analyze missing traits or characteristics on an ancestral node in the phylogeny.
  - The Multistate method is used as it allows for a finite number of discrete states to be evaluated and reconstructed.
  - The Maximum-Likelihood analysis is used to determine the probability of the character state at each most recent common ancestor node, given the character states of the rest of the phylogeny.
- Environmental habitat preferences were input instead of evaluating physical traits.
- BayesTraitsV2 is given the database information in a format that it could read, and told to run this information 1000 times.
- The data BayesTraitsV2 returns is in percentages, considering the possibility of each state of habitat preference at the missing nodes.
- This data is then modeled in pie-charts to better evaluate the data for a trend in habitat preference along the lineage to *Latimeria* within Latimeriidae.
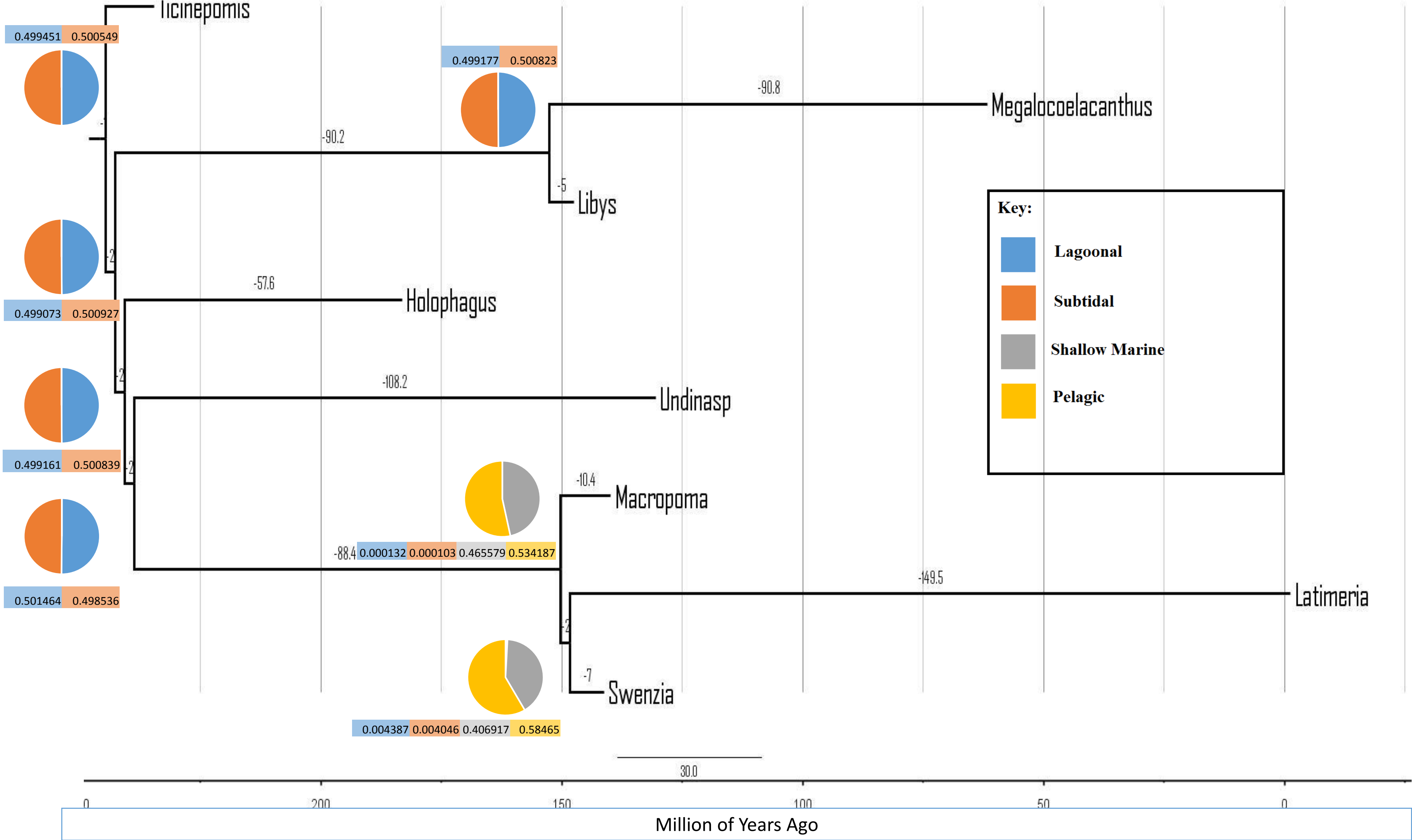
Results & Future Work

This preliminary analysis indicated a noticeable shift in environmental preference within the lineage leading to Latimeria. The preferences evaluated by BayesTraitsV2 revealed an almost 50/50 ratio of lagoonal to subtidal environments within Latimeriidae until the most recent common ancestor of Latimeria, Swenzia, and Macropoma. At this node, there is a complete shift to a ratio between shallow marine and pelagic environments. This shift, although seemingly abrupt at this scale, reveals there is a trend along the lineage to Latimeria within Latimeriidae towards a more deep sea environment.

With this data showing a trend from lagoonal and subtidal to shallow marine and pelagic environments, there is a possibility that this trend extends throughout Coelacanthiformes. Taking this into consideration, I await the evidence of this trend to continue in Coelacanthiformes during the continuation of thesis.

In the future, data collection will continue and eventually include all of the genus and taxa within Coelacanthiformes that have been reported with the appropriate information. The database will then be expanded to include additional clades within Coelacanthiformes. Along with this new information, a more in-depth look at the environmental preferences for each genus will be determined to better evaluate the probabilities at each missing node. To better determine the environmental preferences, salinity conditions will also be determined in the future as well as possibly looking at the tailfins of the different species to determine eating habits and energy. Additionally, the data will be tested to evaluate if any shifts in environmental habitats are associated with Earth system events, such as mass extinctions.

References

Arratia, G. and H-P. Schultze. (2015). "A New Fossil Actinistian from the Early Jurassic of Chile and Its Bearing on the Phylogeny of Actinistia." Journal of Vertebrate Paleontology 35(5):e983524.
Bassani, F. (1895) "La Ittiofauna Della Dolomia Principale Di Giffoni (Provincia Di Salerno)." Palaeontographia Italica 1: 169-210. Print.
Bürgin, T. (1992) "Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland)." Schweizerische Paläontologische Abhandlungen 114:1-164. Web.
Cavin, Lionel, Heinz Furrer, and Christian Obrist. (2013) "New Coelacanth Material from the Middle Triassic of Eastern Switzerland, and Comments on the Taxic Diversity of Actinistians." Swiss J Geosci Swiss Journal of Geosciences 106.2: 161-77. Web.
<http://www.researchgate.net/publication/258847887>.
Clement, Gaël. (2005). "A New Coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the Question of the Closest Relative Fossil to Latimeria." Journal of Vertebrate Paleontology 25.3: 481-91. Web.
Cope, E. D. (1877) "On New Paleozoic Vertebrata from Illinois, Ohio and Pennsylvania." Proceedings of the American Philosophical Society 16.154: 71–91. Web.
Dutel H., Herbin M., Clément G. (2015) "First occurrence of a mawsoniid coelacanth in the Early Jurassic of Europe." Journal of Vertebrate Paleontology: e929581. DOI: 10.1080/02724634.2014.929581
Egerton, P. M. G. (1861) " Holophagus Gulo Decription, in Preliminary Essay upon the Systematic Arrangment of the Fishes of the Devonian Epoch." Memoirs of the Geological Survey of Great Britain, Decade X 23:19. Print.
Egerton, P. De Malpas Grey. (1858) "On Chondrostous, an Extinct Genus of the Sturionidaek, Found in the Lias Formation at Lyme Regis." Philosophical Transactions of the Royal Society of London 148.0: 871-85. Web.
Forey, Peter, Olivier Monod, and Colin Patterson. (1985) "Fishes from the Akkuyu Formation (Tithonian),Western Taurus, Turkey." Geobios 18.2: 195-201. Elsevier: Article Locator. Science Direct, 27 Mar. 2006. Web.
Fricke, H.; Plante, R. (1988). "Habitat requirements of the living coelacanth Latimeria chalumnae at grande comore, Indian Ocean". Naturwissenschaften 75 (3): 149–51.
Furrer, H. (1995) "The Prosanto Formation, a marine Middle Triassic Fossil-Lagerstätte near Davos (Canton Graubunden, Eastern Swiss Alps)." Eclogae Geologicae Helvetiae. 88: 681–683.
Gallagher, W. B., D. C. Paris, and E. E. Spamer. (1986) "Paleontology, Biostratigraphy, and Depositional Environments of the Cretaceous-Tertiary Transition in the New Jersey Coastal Plain." The Mososaur 3: 1-35. Web.
Gess, R. W. and Coates, M. I., (2015) "Fossil juvenile coelacanths from the Devonian of South Africa shed light on the order of character acquisition in actinistians." Zoological Journal of the Linnean Society, 175: 360–383. doi: 10.1111/zoj.12276
Gottfried, Michael D., Raymond R. Rogers, and K Curry Rogers. (2004) "First record of Late Cretaceous coelacanths from Madagascar." Recent advances in the origin and early radiation of vertebrates. Verlag Dr. Friedrich. Pfeil, München: 687-691.
Harris, Rebecca B., Sharon M. Birks, and Adam D. Leaché. (2014) "Incubator Birds: Biogeographical Origins and Evolution of Underground Nesting in Megapodes (Galliformes: Megapodiidae)." Journal of Biogeography J. Biogeogr. 41.11: 2045-056. Web.
<http://onlinelibrary.wiley.com/doi/10.1111/jbi.12357/full>.
Heemstra, Phil. (2001-2016) "What Do We Know about the Coelacanths - Behaviour, Habitat." Science in Africa. Science in Africa CC, Web. <http://www.scienceinafrica.com/what-do-we-know-about-coelacanths-behaviour-habitat>.
Jain, S. L.. (1974) "Indocoelacanthus Robustus N.gen., N.sp. (coelacanthidae, Lower Jurassic), the First Fossil Coelacanth from India". Journal of Paleontology 48.1: 49–62. Web.
Kennedy, W. J. (1969). "The Correlation of the Lower Chalk of South-east England." Proceedings of the Geologists Association 80.4: 459-560. Web.
Lucky, Andrea, Michelle D. Trautwein, Benoit S. Guenard, Michael D Weiser, and Robert R. Dunn. (2013) "Tracing the Rise of Ants – Out of the Ground." PLoS ONE 8.12: n. pag. Web. < http://dx.doi.org/10.1371/journal.pone.0084012>
Musick, John A., M. N. Bruton, and Eugene K. Balon. (1991) The Biology of Latimeria Chalumnae and Evolution of Coelacanths. Dordrecht: Kluwer Academic. Print.
Nikaido, Masato; Sasaki, Takeshi; Emerson, J. J.; Aibara, Mitsuto; Mzighani, Semvua I.; Budeba, Yohana L.; Ngatunga, Benjamin P.; Iwata, Masamitsu; Abe, Yoshitaka (2011). "Genetically distinct coelacanth population off the northern Tanzanian coast." Proceedings of the
National Academy of Sciences 108 (44): 18009–18013.
Pagel, M., Meade, A. and Barker, D. "Bayesian estimation of ancestral character states on phylogenies." Systematic Biology, (2004) 53, 673-684.
Peyer, Karin, Slyvain Charbonnier, Ronan Allain, Emilie Läng, and Renaud Vacant. (2014) "New Look at the Late Jurassic Canjuers Conservation Lagerstätte (Tithonian, Var, France)." Comptes Rendus Palevol July-August 13.5: 403-20. Elsevier: Article Locator. Science Direct.
Web. <http://www.sciencedirect.com/science/article/pii/S1631068314000529>.
Rambaut, Andrew. "Figtree Graphical Phylogeny Viewer." Institute of Evolutionary Biology, University of Edinburgh, n.d. Web. <http://tree.bio.ed.ac.uk/software/figtree/>.
Rieppel, O. (1985) "A Second Actinistian from the Middle Triassic of Monte San Giorgio, Kanton Tessin, Switzerland." Eclogae Geologicae Helvetiae 78: 707-13. Web.
Schwimmer, David R. (1986) "Late Cretaceous Fossils from the Blufftown Formation (Campanian) in Western Georgia." The Mososaur 3 : 109-23. Print.
Schwimmer, David R., J. D. Stewart, and G. Dent Williams. (1994). "Giant Fossil Coelacanths of the Late Cretaceous in the Eastern United States." Geol Geology 22.6: 503-06. Web.
Triebold, Mike. (2016) Latimeria Chalumnae. Digital image. Latimeria Chalumnae (Coelacanth). Association of Applied Paleontological Sciences, Web. <http://www.trieboldpaleontology.com/coelacanth.html>.
Viohl, G. & Zapp, M. (2007): "Schamhaupten, an outstanding Fossil-Lagerstätte in a silicified Plattenkalk around the Kimmeridgian-Tithonian boundary (Southern Franconian Alb, Bavaria)." – N. Jb. Geol. Paläont., Abhandlungen, 245: 127–142; Stuttgart. Print.
Woodward, Arthur Smith, and Paleontographical Society (Great Britain). (1916). The Fossil Fishes of the English Wealden and Purbeck Formations. London: Palaeontographical Society. Print. Web.
Woodward, A. S., (1890). "Notes on some ganoid fishes from the English lower Lias." The Annals and Magazine of natural History, Sixth Series 6:430-436
Woodward, A. S., F.G.S., and F.Z.S. (1891) "I.—Catalogue of the Fossil Fishes in the British Museum (Natural History), Part II." Geological Magazine Geol. Mag. 8.03 : 123. Web.
Zhu, Min, Xiaobo Yu, Jing Lu, Tuo Qiao, Wenjin Zhao, and Liantao Jia. (2012) "Earliest Known Coelacanth Skull Extends the Range of Anatomically Modern Coelacanths to the Early Devonian." Nature Communications 3: 772. Nature Communications.

Phylogenetic tree diagram showing Ticinepomis, Megalocoelacanthus, Libys, Holophagus, Undina sp., Macropoma, Latimeria, and Swenzia with pie charts at nodes.

Key:
- Lagoonal
- Subtidal
- Shallow Marine
- Pelagic

Million of Years Ago