THE TELEOST ICHTHYOFAUNA FROM THE LATE CRETACEOUS OF MADAGASCAR: SYSTEMATICS, DISTRIBUTIONS, AND IMPLICATIONS FOR GONDWANAN BIOGOEGRAPHY

By

Summer A. Ostrowski

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Geological Sciences

2012

ABSTRACT

THE TELEOST ICHTHYOFAUNA FROM THE LATE CRETACEOUS OF MADAGASCAR: SYSTEMATICS, DISTRIBTUTIONS, AND IMPLICATIONS FOR GONDWANAN BIOGEOGRAPHY

By

Summer A. Ostrowski

Madagascar is known for its highly endemic Recent fauna. However, the full deep-time temporal context of Madagascar's endemicity is not completely understood, due to the patchy fossil record of the island. The Upper Cretaceous deposits of the Maevarano Formation in northwestern Madagascar provide insight into this issue due to their rich vertebrate fauna, including dinosaurs, crocodylians, frogs, turtles, snakes, mammals, and fishes. The Maevarano Formation consists of fluvial and alluvial deposits and accompanying debris flows, and exhibits excellent fossil preservation. Fossil fishes from the formation represent coastal marine and freshwater taxa, some of which have been identified in earlier reports.

This study focuses on identifying teleosts present within the Maevarano Formation, and the resulting implications for Gondwanan biogeography. The teleosts are first identified to the most precise taxonomic unit possible, and their distributions during the Late Cretaceous are analyzed. Several of the fish taxa present extend the known temporal and/or geographic ranges of significant teleost clades (e.g. Elopomorpha, Characiformes, and Cypriniformes). Parsimony Analysis of Endemism and Simpson's and Jaccard's similarity indices showed some fossil fish taxa (e.g. elopomorphs) as rather cosmopolitan and less affected by continental geographical relationships. The presence of the identified fishes from the Late Cretaceous of

Madagascar fishes shows major turnover in fish diversity in Madagascar from the Triassic to the Recent, and how the faunal composition changed with the progressive isolation of Madagascar. Comparison at the ordinal level between the Triassic, Late Cretaceous, and Recent fish faunas show that the dramatic change in fish diversity is comparable with what has occurred in the strictly terrestrial vertebrate taxa over the last 200 million years of Madagascar's history. This information supports the likelihood of successive waves of immigrations of vertebrate taxa after the isolation of the island, some of which presumably would have had large enough establishing populations to persist on the island and diversify. These waves have resulted in a higher degree of endemicity in the island's fauna today, relative to the fauna which existed on Madagascar throughout its geological history. These results highlight the complexities of deciphering fish biogeography, due to their transient nature and their ability to disperse across marine environments that act as barriers to fully terrestrial groups.

This dissertation is dedicated to my parents, Rodney & Charlotte Ostrowski, for their unwavering love and support all of these years.

ACKNOWLEDGEMENTS

I would like to acknowledge the following for help and support:

My major advisor, Dr. Michael D. Gottfried, for guidance, along with fieldwork and teaching opportunities that are unparalleled.

My guidance committee: Dr. Michael D. Gottfried, Dr. Robert L. Anstey, Dr. Danita S. Brandt, and Dr. Brian A. Hampton. Their assistance on this project has been greatly appreciated.

My family: Dad, Mom, Paul, Renee, Eric, Cris, Dave, Heather, Alayna, Walker, Ethan, Connor, Sawyer, Mya, Kennedy, Aiden, and The Notos for their continued love and encouragement.

My husband, Dr. Chris Noto, for his sacrifices, influence, and inspiration.

Dr. David W. Krause (PI) for the Mahajanga Basin Project and fossil preparator Joe Groenke of Stony Brook University.

Museum personnel who helped me access collections: Field Museum of Natural History (William Simpson in Geology, and Leo Smith in Ichthyology); British Museum of Natural History (Martha Richter); Royal Museum for Central Africa (Daniel Baudet); and University of Michigan Museum of Zoology (Gerry Smith).

Many thanks to Variance, Leo, and Mona for their fuzzy bellies.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: INTRODUCTION

Problem being studied

Higher teleost fishes are known for their rapid evolutionary diversification as members of the most diverse vertebrate clade (Rojo, 1991), and therefore are sensitive indicators of evolutionary dispersal mechanisms. The "higher" teleost fossil fish faunas of Madagascar from the Late Cretaceous are largely undescribed, but they have the potential to increase our understanding of Gondwanan biogeography during this crucial interval. Late Cretaceous Madagascar terrestrial faunas have been described and put into a biogeographic context, but the higher teleosts have not been comprehensively analyzed or placed in a large biogeographic framework. This dissertation identifies new fish material from the Late Cretaceous of Madagascar and addresses hypotheses relating to teleost systematics and clade dispersal that are relevant to Gondwanan biogeography.

Objectives and Format

This research serves the following purposes: 1) Identify fossil fish material from the Late Cretaceous of Madagascar to the most precise taxonomic level possible, using comparative specimens and literature. 2) Determine how this newly identified material increases the understanding of the taxa ecologically and evolutionarily based on the literature. 3) Use the newly identified material in a Parsimony Analysis of Endemism (PAE) and Cluster Analysis of Similarity Indices to compare the Maastrichtian fishes of Madagascar to other Maastrichtian fossil fish assemblages. These analyses are used to examine vicariance and marine dispersal hypotheses regarding the Late Cretaceous fish fauna of Madagascar. 4) Compare and comment on how the Late Cretaceous fishes from Madagascar affect the understanding of Madagascar’s faunal endemicity through geologic time and Gondwanan fish biogeography.

This dissertation is set forth in several sections. The “Introduction” provides a historical account of the Mahajanga Basin Project (which this work is a component of) and introduces the geology of the Late Cretaceous of Madagascar. Chapter 2 “Distribution and Systematics of Teleost Fishes of the Late Cretaceous of Madagascar” will address the identification, systematics, and distribution of the fossil ichthyofauna, and Chapter 3 “The Albuloid Fishes (Teleostei: Elopomorpha) of the Late Cretaceous of Madagascar” provides identification, systematics, and distribution of a particular group of teleosts, the elopomorpha. Chapters 2 and 3 discuss the significance of these new fossils to our broader understanding of fish distribution during the Late Cretaceous. Chapter 4 is titled “Implications for Gondwanan Biogeography from New Teleosts described from the Late Cretaceous of Madagascar and general comments on changes in the ichthyofauna on Madagascar over geologic time.” Chapter 4 includes a brief review of Madagascar’s biogeographic hypotheses and tests fish biogeography using Parsimony Analysis of Endemism and similarity indices with Maastrichtian fossil fish localities and the newly identified taxa in Chapters 2 and 3. Chapter 4 also discusses the turnover that has occurred in the fish fauna over the past 200 million years of Madagascar’s history. The final section, “Conclusions and Future Directions” summarizes and synthesizes the conclusions from the previous chapters and discusses further avenues of research involving this project.

History of Research on Madagascar

The Upper Cretaceous strata of northwestern Madagascar, in the Mahajanga Basin, have long been known to contain very rich terrestrial fossil assemblages (Figure 1). Some exploratory work was done during the late nineteenth and early twentieth centuries in the Mahajanga Basin, and terrestrial vertebrate fossils were discovered and described (Depéret, 1886a, b). A number of papers throughout the first 80 years of the 20th century, described the geology (Collignon, 1968; Perrier de la Bathie, 1919; Piveteau, 1926) and dinosaur, crocodilian, or snake fossils (Asama et al., 1981; Buffetaut and Taquet, 1979; Hoffstetter, 1961; Lavocat, 1955a, b; Obata and Kanie, 1977; Ravoavy, 1991; Russel et al., 1976; Sues, 1980; Sues and Taquet, 1979; Thévenin, 1907).

The Mahajanga Basin Project started in 1993 and is run jointly by Dr. David W. Krause of Stony Brook University and the University of Antananarivo. There have been expeditions to Mahajanga approximately every-other-year since its inception. The author participated during the 2010 expedition as a collaborator on the project.

Geology of the Late Cretaceous of Madagascar

Northwestern Madagascar is characterized by a Senonian (specifically, Coniacian, Santonian, Campanian, and Maastrichtian) continental interval followed by a Maastrichtian-Eocene marine interval (Boast and Nairn, 1982). The Coniacian exhibits a mixture of lagoonal-continental beds with some marine incursions. The Santonian contains cross-bedded sandstones and dinosaur remains. The ?Santonian-?Campanian of the Marovoay beds and the Maastrichtian of the Maevarano Formation are mostly continental sandstones with pronounced cross-bedding and make up the majority of the rock record during this time (Boast and Nairn, 1982; Rogers, 2005). The majority of the vertebrate taxa occur within the Maevarano Formation, including dinosaurs, crocodilians, frogs, snakes, mammals, birds, and fishes (Krause et al., 2006). There is a continuous section of fossiliferous, marine limestone extending from the Maastrichtian into the lower Cenozoic (Boast and Nairn, 1982). This limestone is interpreted to be the marine Berivotra Formation, which is the marine temporal equivalent to the continental Anembalemba Member during the Maastrichtian as described by Rogers et al. (2000).

There are four described Upper Cretaceous sedimentary units in the Mahajanga Basin which occur above the Coniacian flood basalts dated at 88 million years old (Besairie, 1972; Perrier de la Bathie, 1919). However, these sedimentary units were more recently redescribed in detail by Rogers and placed into a regional framework. This research uses the interpretation of Rogers et al. (2000) and the geologic map from Rogers et al. (2007) for the geological context of these Late Cretaceous deposits, as displayed in Figure 1, (Rogers et al., 2007).

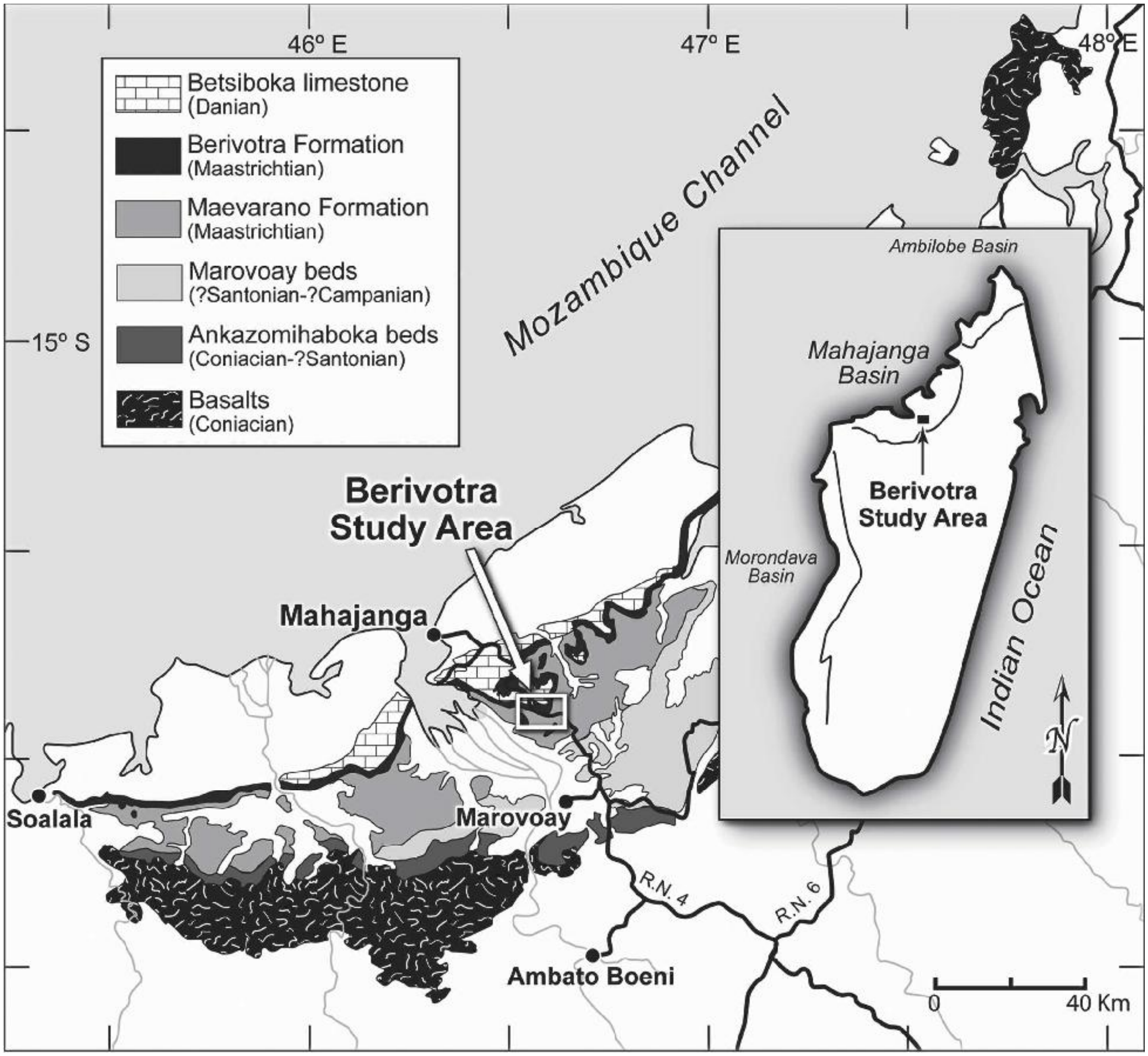
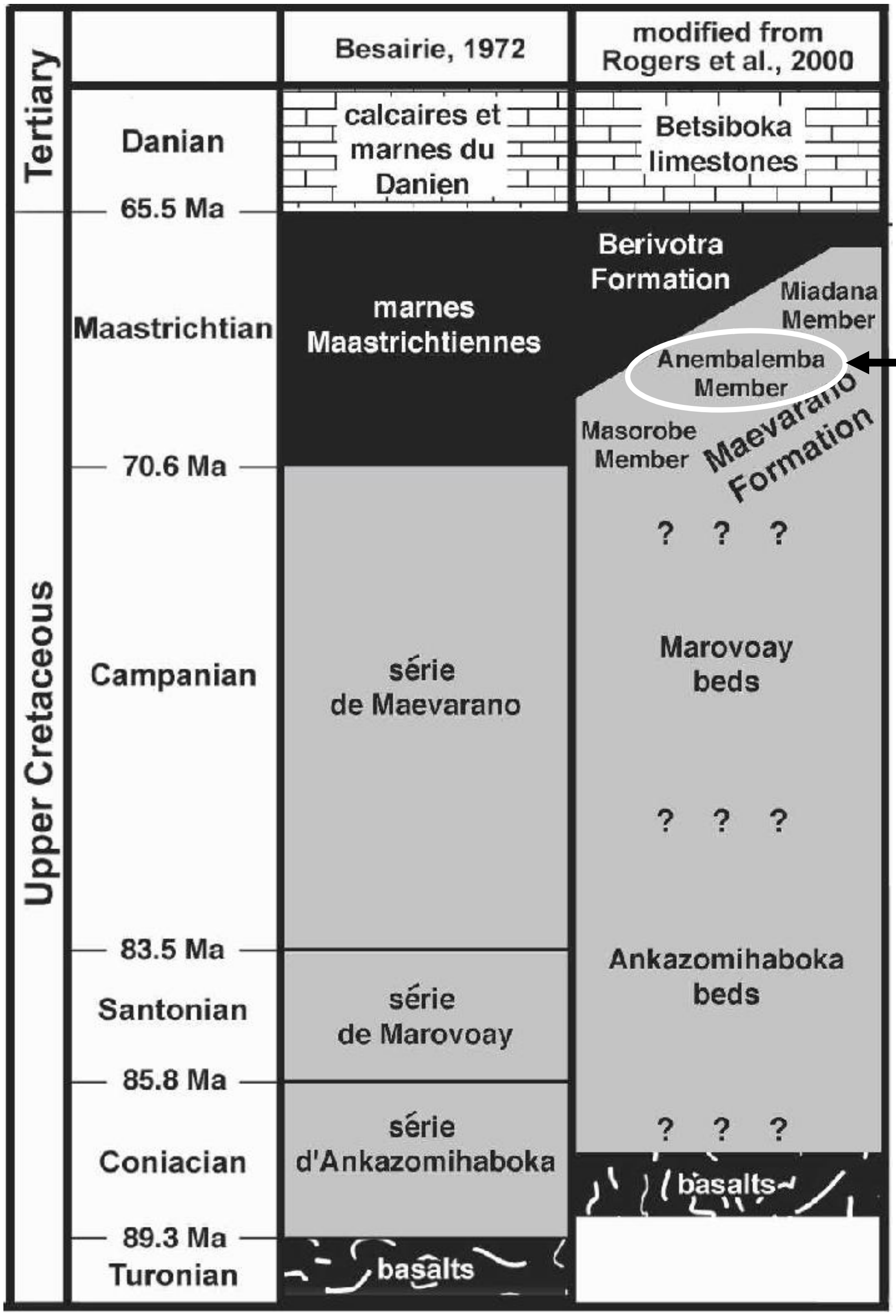


FIGURE 1: Geologic Map of the Mahajanga Basin field area, highlighting the sedimentary rock units of the Late Cretaceous (Rogers, 2005; Rogers et al., 2007).

Maevarano Formation: The type section is described from an outcrop near Berivotra, Madagascar, and is equivalent to the “serie de Maevarano” of Besairie (1972). The contact between the Maevarano Formation and the underlying Marovoay beds is unknown (Rogers et al., 2000). The upper contact between the Maevarano formation and the Berivotra Formation is easily recognizable by a disconformity with a succession from sandstones (Maevarano) to shales (Berivotra). A revised stratigraphy of the relationships of these rock units is shown in Figure 2. The Berivotra Formation is well-cemented with calcite and contains well-rounded chert and polished bone and selachian teeth (Gottfried and Rabarison, 1997; Gottfried et al., 1998)



Main fossil bearing member; Kinkony not pictured

FIGURE 2: The Upper Cretaceous and Paleogene stratigraphy of the Mahajanga Basin, Northwestern Madagascar (Rogers et al., 2000; Rogers et al., 2007).

The Maevarano Formation (~76 Ma to ~65.5 Ma) is acknowledged to be primarily terrestrial (Rogers et al., 2000) or coastal, and interfingers with the marine Berivotra Formation. The paleoenvironmental setting of the Maevarano formation is interpreted to be a low-relief alluvial plain, with the crystalline highlands to the southeast, and the Mozambique Channel to the northwest (Rogers et al., 2000). The three members described within the Maevarano Formation are the Masorobe Member, Anembalemba Member, and the Miadana Member. Another more recently discovered member within the Maevarano Formation, is informally known as the “Lac Kinkony Member”, and was referred to as an “unnamed member” in a paper describing a new turtle species (Gaffney et al., 2009). In that turtle paper, the “unnamed member” lies above the Anembalemba Member, and is coeval with the Miadana member. This newly recognized stratigraphic unit is still to be formally described and put into regional context with the other stratigraphic units. To date, the Kinkony has produced a large amount of fossil material (crocodilians, actinopterygians, and turtles) (Gaffney et al., 2009). The fossil fishes present in the “Lac Kinkony Member” will be discussed in subsequent chapters; however, the fishes’ geographical and environmental context is somewhat speculative.

Description of members within the Maevarano Formation:

Masorobe member (~77 Ma to 70 Ma; Late Campanian): This member is mostly reddish, coarse-grained poorly-sorted sandstone, siltstone, and claystone (Rogers et al., 2000). The Masorobe contains well-preserved paleosols with 36 pedogenic layers throughout the section. Evidence for pedogenesis includes color banding, root casts, root mottling, and rare slickensides (Rogers et al., 2000). The

Masorobe shows some primary stratification in the form of small- to large-scale tabular and trough cross-bedding. No invertebrate fossils have been found in this member, and vertebrate fossils are singular, poorly preserved pieces (Rogers et al., 2000). None of the fossils identified in this research occur within the Masorobe. The depositional environment of Masorobe is interpreted to be broad and shallow low-sinuosity channel belts, intercalated with floodplain deposits (Rogers et al., 2000). The pedogenic features are evidence for well-adapted vegetation on the floodplain in a dry climate.

Anembalemba Member (70 Ma to ~ 67.5 Ma, Maastrichtian): The Anembalemba member consists of two facies. Facies 1 is a fine- to coarse-grained, poorly sorted sandstone with a significant amount of clay, and is light gray to white in color (Rogers et al., 2000). This facies has small- to medium-scale tabular and trough cross stratification. Facies 2 is an olive green, fine- to coarse-grained, poorly sorted, clay-rich, massive sandstone. These facies are interbedded with one another with evidence of erosional contacts. The Anembalemba member contains abundant, well-preserved fossils. Facies 1 contains relatively abundant bone and teeth, but it is Facies 2 that contains the majority of the well-preserved (and articulated) vertebrate fossil material (Rogers et al., 2000). Invertebrates occur within the Anembalemba member, but they are rare (Krause and Hartman, 1996). The environment of Facies 1 is interpreted as the product of downstream migration of fluvial bedforms (Rogers et al., 2000). The poorly-sorted nature of sediments in Facies 2 is interpreted as the result of rapid sediment dumping (e.g. floods) (Rogers et al., 2000). The majority of the fishes addressed in this research are from the Anembalemba Member.

"Lac Kinkony Member" (Maastrichtian): This still-informal member was recently recognized on the coast of northwestern Madagascar and the geology is currently being described by R. Rogers. It has been suggested that this deposit lies above the Anembalemba Member and contains abundant fish material along with crocodyliforms, turtles and non-avian dinosaurs (Gaffney et al., 2009). This mixture of taxa does not give a clear view of depositional environment.

Miadana Member (~67.5 Ma to 66 Ma): The lithology of the Miadana Member is fine- to coarse-grained sandstone, siltstone, and claystone that ranges in color from white, to greenish gray to red (Rogers et al., 2000). The only evidence for primary stratification is faint cross-bedding (Rogers et al., 2000). The lower contact of the Miadana Member with the Anembalemba Member is unknown due to dense vegetation. The upper contact is a disconformity marked by olive-yellow claystone of the Berivotra Formation (Rogers et al., 2000). The smaller grain size of the Miadana relative to other members within the Maevarano Formation is interpreted as a result of the decrease in stream gradient in a lower coastal plain setting (Rogers et al., 2000).

REFERENCES

REFERENCES

Asama, Y., Obata, I., and Kanie, Y., 1981, Paleontological investigations of Madagascar by the National Science Museum Team, Recent Progress in National Science, Japan, Volume 6: Tokyo, p. 163-174.

Besairie, H., 1972, Géologie de Madagascar. I. Les terrains sédimentaires, 1-463 p.

Boast, J., and Nairn, A., 1982, An outline of the geology of Madagascar. , *in* Nairn, A., and Stehli, FG, ed., The ocean basins and Margins. Vol. 6. The Indian Ocean, Volume 6: New York, Plenum, p. 649-696.

Buffetaut, E., and Taquet, P., 1979, Un nouveau Crocodilien me´sosuchien dans le Campanien de Madagascar: Trematochampsa oblita, n. sp.: Bull. Soc. Ge´ol. France, v. 21, p. 183-188.

Collignon, M., 1968, Le Crétacé supérieur de Madagascar dans l'etat actuel de nos connaissances. Son passage au Paleocene. Essai de comparaison avec l'Indie: Geological Society of India Memoir, v. 2, p. 320-334.

Depéret, C., 1886a, Note sur les Dinosauiens Sauropodes et Théropodes du Crétacé supérieur de Madagascar: Bulletin de la Société Géologique de France, v. 21, p. 176-194.

—, 1886b, Sur l'existence de Dinosauriens, Sauropodes et Théropodes dans le Crétacé supérieur de Madagascar.: C R Séances Acad. Sci. Paris Ser II, v. 122, p. 483-485.

Gaffney, E., Krause, D., and Zalmout, I., 2009, Kinkonychelys, A New Side-Necked Turtle (Pelomedusoides: Bothremydidae) from the Late Cretaceous of Madagascar: American Museum Novitates, p. 1-25.

Gottfried, M., and Rabarison, A., 1997, First Mesozoic Gondwanan record of a sawshark (Chondrichthyes, Pristiophoriformes) from the Late Cretaceous of Madagascar: Journal of Vertebrate Paleontology, v. 17, p. 750-751.

Gottfried, M., Randriamiaramanana, L., Rabarison, J., and Krause, D., 1998, Late Creatceous fish from Madagascar: implications for Gondwanan biogeography: Journal of African Earth Sciences, v. 27, p. 91-92.

Hoffstetter, R., 1961, Noveaux restes d'un serpent Boidé (*Madtsoia madagascariensis* nov. sp. dans le Crétacé supérieur de Madagascar, Bulletin du Muséum National d'Histoire Naturelle, Volume 33: Paris, p. 152-160.

Krause, D., and Hartman, J., 1996, Late Cretaceous fossils from Madagascar and Their Implications for Biogeographic Relationships with the Indian Subcontinent, *in* Sahni, A., ed., Cretaceous Stratigraphy and paleaeoenvironments, Memoir Geological Society of India, p. 135-154.

Krause, D., O'Connor, P., Curry Rogers, K., Sampson, S., Buckley, G., and Rogers, R., 2006, Late Cretaceous Terrestrial Vertebrates from Madagascar: Implications for Latin American Biogeography: Annals of the Missouri Botanical Garden, v. 93, p. 178-208.

Lavocat, R., 1955a, Etude des gisements de Dinosauriens de la région de Majunga (Madagascar): Trav. Bur. Geol. , v. 69, p. 1-19.

—, 1955b, Sur une portion de andibule de Théropode provenant du Crétacé supérieur de Madagascar, Bulletin du Muséum National d'Histoire Naturelle, Volume 27: Paris, p. 256-259.

Obata, L., and Kanie, Y., 1977, Upper Cretaceous dinosaur-bearing sediments in Majunga region, northwestern Madagascar, Bulletin of the National Science Museum Series C Geology, Volume 3, p. 161-172.

Perrier de la Bathie, M., 1919, Les terrains postérieurs au Crétacé moyen de la région de Majunga: Bull. Acad. Malgache, v. 4, p. 205-212.

Piveteau, J., 1926, Contribution de l'étude des formations lagunaires du Nord-Ouest de Madagascar: Bulletin de la Societe Geologique de France, v. 26, p. 33-38.

Ravoavy, F., 1991, Identification et mise en catalogue des vertébrés fossiles récoltes dan le Crétacé supérieur continental de la région de Berivotra (Majunga) fouille 1987, University Antananarivo Mem. Rech., Volume 2, p. 55-104.

Rogers, R., 2005, Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar: Geology, v. 33, p. 297-300.

Rogers, R., Hartman, J., and Krause, D., 2000, Stratigraphic Analysis of Upper Cretaceous Rocks in the Mahajanga Basin, Northwestern Madagascar: Implications for Ancient and Modern Faunas: Journal of Geology, v. 108, p. 275-301.

Rogers, R., Krause, D., Rogers, K., Rasoamiaramanana, A., and Rahantarisoa, L., 2007, Paleoenvironment and paleoecology of Majungasaurus crenatissimus (Theropoda : Abelisauridae) from the Late Cretaceous of Madagascar: Journal of Vertebrate Paleontology, v. 27, p. 21-31.

Rojo, A., 1991, Dictionary of evolutionary fish osteology: Boca Raton, CRC Press, 273 p.

Russel, D., Taquet, P., and Thomas, H., 1976, Nouvelles récoltes de Vertébrés dans les terrains continentaux du Crétace supérieur de la région de Majunga (Madagascar). C R Sommaire Seances Bulletin de la Societe Geologique de France Volume 5, p. 205-208.

Sues, H.-D., 1980, A pachycephalosaurid dinosaur from the Upper Cretaceous of Madagascar and its paleobiogeographical implications: Journal of Paleontology, v. 54, p. 954-962.

Sues, H.-D., and Taquet, P., 1979, A pachycephalosaurid dinosaur from Madagascar and a Laurasia-Gondwanaland connection in the Cretaceous: Nature, v. 279, p. 633-635.

Thévenin, A., 1907, Dinosauriens (Paléontologie de Madagascar IV): Anneles de Paléontologie, v. 2, p. 121-136.

CHAPTER 2: SYSTEMATICS AND DISTRIBUTIONS OF TELEOST FISHES FROM THE LATE CRETACEOUS OF MADAGASCAR

INTRODUCTION

Fishes previously described from the Late Cretaceous of Madagascar include those from the older (Santonian/Coniacian) Ankazomihaboka sandstones --- a coelacanth resembling *Axelrodichthys* and *Mawsonia* (Gottfried et al., 2004), and the amiid *Melvius* (Gottfried and Ostrowski, 2009). From the marine Berivotra Formation (concurrent deposition with Anembalemba member), a moderately diverse elasmobranch fauna has been reported including: *Pristiophorus* sp. (Pristiophoriformes, Pristiophoridae); *Parapalaeobates* sp. (Rajiformes, Rhinobatidae); cf. *Brachyrhizodus* sp. (Rajiformes, Myliobatoidea); *Carcharias* sp. (Lamniformes, Odontaspididae); *Squalicorax kaupi* and *S. pristodontus* (Lamniformes, Anacoracidae); and *Serratolamna serrata, Cretolamna appendiculata,* and *C. maroccana* (Lamniformes, Cretoxyrhinidae) (Gottfried and Rabarison, 1997; Gottfried et al., 2001). Within the Maevarano formation, there have been accounts of gars (Lepisosteidae, Actinopterygii) *Lepisosteus* sp. (Gottfried and Krause, 1998), and an ariid catfish (Gottfried and Ostrowski, 2008).

This chapter describes the identifiable teleost fish fossils from the late Cretaceous deposits of Madagascar. The description and subsequent identification to the most precise taxonomic level possible leads to a discussion of the significance of the occurrence of these fossils spatially and temporally. The fossil material, though relatively well-preserved, consists of disarticulated elements which are not associated, and often fragmentary. Identifications are possible down to generic level for some specimens, but only to order or family level for others. Even at the taxonomic level of family, the presence of some of these families during the Late Cretaceous is significant because they are considered “advanced” teleosts and rarely occur during that time interval. Identifications from otoliths alone were not included, unless associated with fossil bones.

The fishes described here are all actinopterygians, and primarily teleosts. The only non-teleost described is a pycnodont, which is in a group Pycnodontiformes and considered a sister group to teleosts (Nursall, 1996b). The teleosts described herein fall within Elopiformes, Albuliformes, Aulopiformes, Perciformes (within Neoteleostei), Cypriniformes, Characiformes, and Siluriformes. Their phylogenetic relationships within Teleostei are shown in Figure 3.

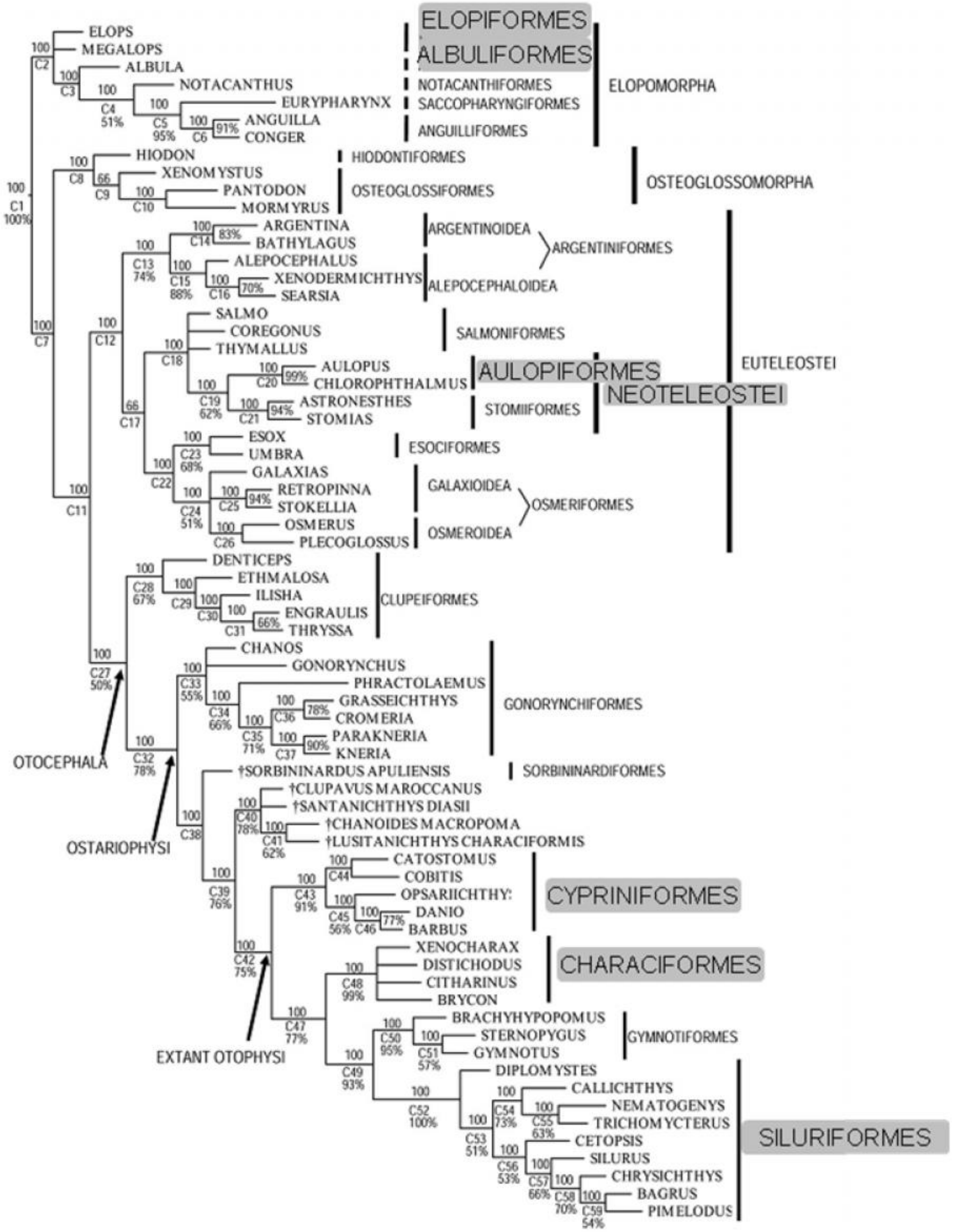


FIGURE 3: Phylogenetic relationships between teleostean groups from Diogo et al, 2008. See Diogo et al. for a full description of their methods and results. Circled groups are discussed herein.

MATERIALS AND METHODS

Institutional abbreviations

R.G. - Royal Museum for Central Africa, Tervuren, Belgium; **UALVP** – University of Alberta Vertebrate Paleontology Collection, Edmonton, Alberta, Canada; **MAD** – Mahajanga Basin Project field number. Madagascar specimens were compared to identified museum specimens and literature descriptions with photographs.

Field Collection and Image Capture

The fish material from the Late Cretaceous of Madagascar was collected by the Mahajanga Basin Project by standard surface collection methods at microsite localities during field seasons ranging from 1993 – 2010. The specimens herein from Madagascar have a prefix of “MAD” followed by a field number. When the specimens are accessioned upon publication, they will be housed in the University of Antananarivo in Antananarivo, Madagascar (UA prefix), or in the Field Museum of Natural History in Chicago, Illinois (FMNH prefix). All images were captured using a Nikon Coolpix L18. The Characiformes element and Siluriformes vertebra were photographed using an Olympus SZ61-ILST microscope with attached Luminera Infinity 2-2C color camera and Infinity Capture version 4.4.0 software.

Systematic paleontology

Anembalemba Member:

ACTINOPTERYGII Cope, 1887

PYCNODONTIFORMES Berg, 1937

PYCNODONTIDAE *sensu* Nursall, 1996b

Coelodus Heckel, 1854

Identification of material and *Coelodus* osteology: MAD 96326 is an incomplete vomerine toothplate (Figure 4) approximately three centimeters long and increases along this length from 1 centimeter in width to 2.5 centimeters in width. There are 22 teeth of varying size (2 millimeters to 1 centimeter in diameter) across the entire toothplate. The teeth are smaller anteriorly than posteriorly, and the vomer tapers anteriorly. The three lateral-most rows are preserved of the usual five rows that are typical on *Coelodus*. The largest teeth would be the middle row on a complete specimen. On MAD 93236, these largest teeth are well rounded and oval in shape with a slightly punctacted surface. The middle row teeth are approximately one-half the size of the more medial teeth and are well worn from the action of grinding with the opposing crushing toothplate, resulting in depressions in the center of the teeth. The teeth of the most lateral row are smaller, more circular, and pedestaled on the vomer. This tooth row is also well-worn from the durophagus lifestyle of crushing benthic prey. The labial side (Figure 4B) is heavily weathered and little surface texture remains. The caudal cross-sectional view (Figure 4C) shows the teeth in profile (teeth on top of image), exhibiting their low, well-rounded shape, and elongate proportions. Figure 4C also shows the thickness of the vomer, which is characteristic of the durophagus lifestyle.

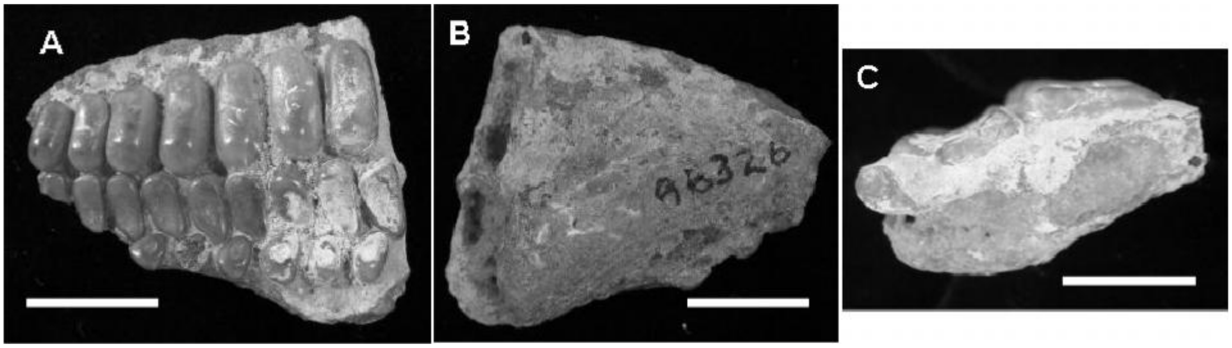


FIGURE 4: MAD 06326, *Coelodus* toothplate from the Late Cretaceous of Madagascar pictured in lingual view (A), labial view (B), and posterior cross-sectional view (C). Scale bar = 1 centimeter.

Pycnodontiforms have crushing teeth that are characteristic of their durophagus feeding mode. Superficially, there are many similarities in pycnodont teeth, but *Coelodus* teeth have distinctive characteristics (Kriwet et al., 1999). *Coelodus* crushing teeth in are usually highly rounded and laterally flattened, and located on the vomer. There are five longitudinal rows of teeth which decrease in size from poster to anterior. The teeth are approximately twice as broad as long and oval in outline. No lateral teeth are inserted into smaller spaces between main teeth. The teeth have an apical indentation with crenulated margins (Kriwet et al., 1999).

***Coelodus* paleoecology and distributions:** Paleoecologically, *Coelodus* is durophagus with a laterally-compressed body, and lived in reef and lagoon environments (Nursall, 1996a). The fossil record extends from the Late Triassic of Italy (Tintori, 1981) through the Paleogene of Europe (Blot, 1987) and mainland Africa (Longbottom, 1984). The genus is found primarily within the margins of the Tethys Sea and into the widening Atlantic Ocean (Nursall, 1996a). *Coelodus* is a relatively common fossil within Cretaceous deposits (Table 1), and their Cretaceous distribution is shown in Figure 5.

TABLE 1: Geographic and stratigraphic distribution of *Coelodus* during the Cretaceous.

COUNTRY	FORMATION/LOCALITY	REFERENCE
Argentina	Yacoraite	Gasparini and Buffetaut, 1980
Bolivia	El Molino	Gayet et al., 2001
Egypt	Bahaije	Slaughter and Thurmond, 1974
Germany	Ahlen	Giers, 1964
India	Nimar Sandstone	Chiplonker and Ghare, 1977
Niger	Niger Basin Locality	Arambourg and Joleaud, 1943
Romania	Cochirleni	Simionescu, 1913
Spain	La Cabana	Vullo et al., 2009
	Lerida Province	Wenz, 1989
Syria	Unnamed limestone	Hussakof, 1916
United Kingdom	Tunbridge Wells	Naish and Sweetman, 2011
United States	Kiowa (Kansas)	Everhart, 2009
	Twin Mountains (Texas)	Slaughter, 1969

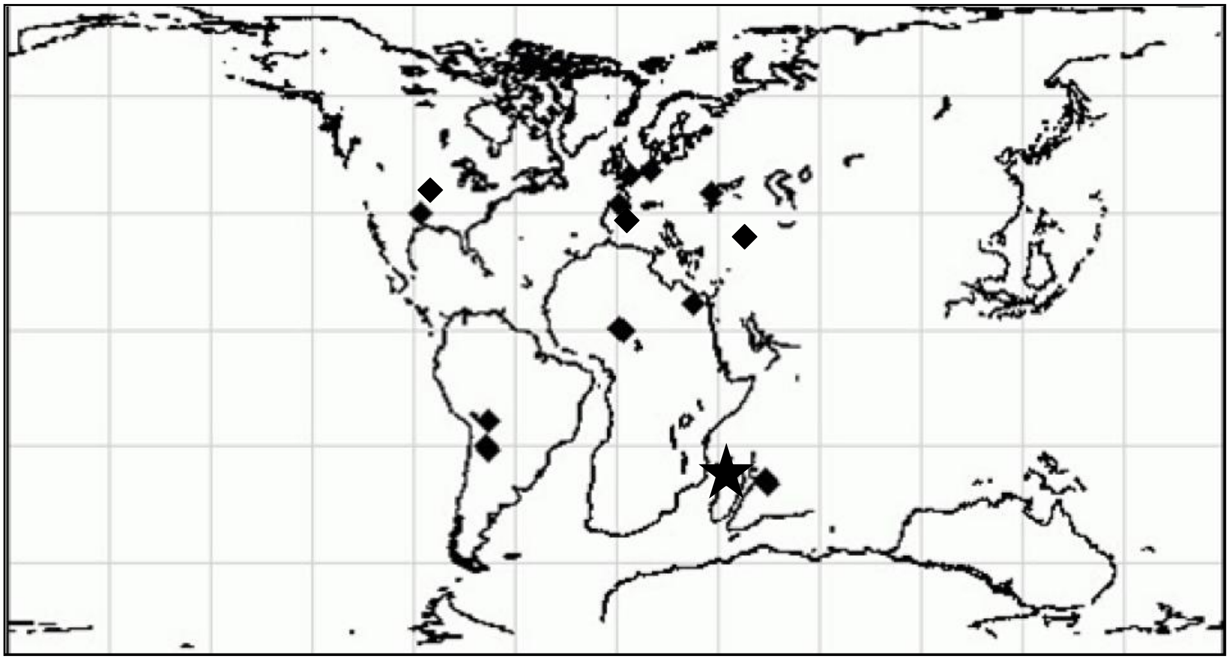


FIGURE 5: Location and distribution of *Coelodus* during the Cretaceous (diamonds), plus the addition of the Late Cretaceous of Madagascar (star) Map modified from Alroy, 2012.

The presence of *Coelodus* during the Late Cretaceous in Madagascar is close to the southern most occurrence of this genus during that time and near the specimens from India (Chiplonker and Ghare, 1977). It is not surprising that this genus, or that pycnodonts in general, would be found in Madagascar at this time due to the coastal marine environment suggested by the Anembalemba Member fishes. The occurrence in Madagascar shows this genus is more widespread than the general assumption that it was associated with the Tethys and Atlantic. Similar to other genera described by teeth only (e.g. *Enchodus*), the taxonomy of pycnodonts is muddled. Over 450 species of pycnodont exist and were originally described by tooth morphology and jaw fragments (Nursall, 1996b). Suspect "species" will likely be called into question as more complete fossils are discovered (Nursall, 1996b).

TELEOSTEI Müller, 1846

AULOPIFORMES Rosen, 1973

ENCHODONTIDAE Lydekker, 1889

Enchodus Agassiz, 1833-1844

Comparative material: R.G. 3596 - *Enchodus* cf. *lemonnieri* tooth; UALVP 22956 – *Enchodus* cf. *shumardi* tooth.

Referred material: MAD 93014-17, *Enchodus* tooth without enamel; MAD 98470, *Enchodus* tooth with enamel.

Identification of material and *Enchodus* osteology: The comparative specimens (Figure 6) exhibit distinctive enchodontid tooth features, the two asymmetrical cutting edges and an overall slight curvature. The specimens within the Madagascar fauna are known from teeth alone, without enamel (Figure 7) and with enamel (Figure 8). The tooth without enamel does not have a complete tip and is just over 2 centimeters in length and 0.75 centimeters at the widest point. The tooth with enamel is also missing the tip and is 1.5 centimeters long and 0.3 centimeters at the widest point. The bases are complete, slightly flared, and taper towards the tip. Each tooth has 2 cutting edges and is slightly laterally flattened and has a slight curvature. The cross section of the teeth is slightly asymmetrical in that the labial side of the tooth has a stronger curved arc in the tooth outline, than does the lingual side (Figures 7C, 8C). Because the teeth have a naturally rounded base, without enamel, it indicates these teeth naturally weathered out of the jaw bones and were not broken.

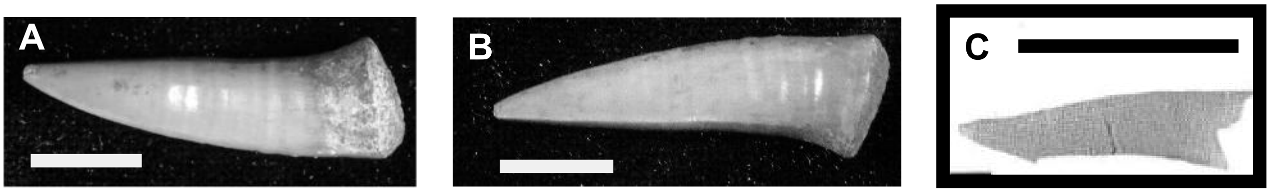


FIGURE 6: R.G. 3596 - *Enchodus* cf. *lemonnieri* tooth (A and B, 2 lateral views of the same tooth) and UALVP 22956 – *Enchodus* cf. *shumardi* tooth (C). Scale bar = 1 centimeter.

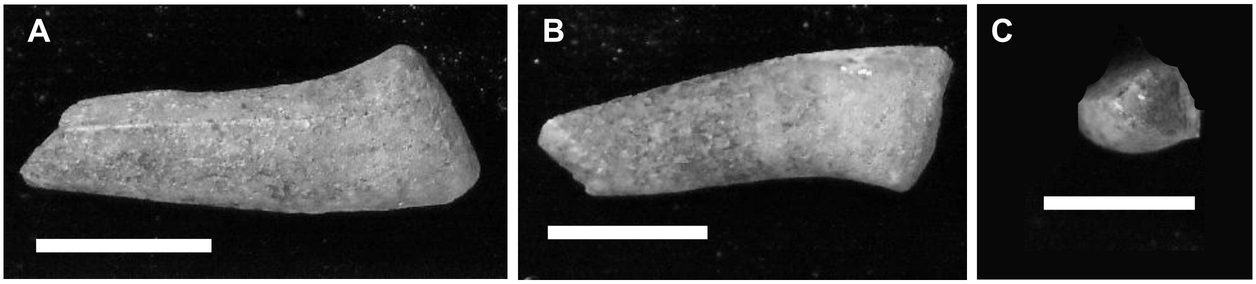


FIGURE 7: Specimen MAD 93014-17, an *Enchodus* tooth from the Late Cretaceous of Madagascar in lateral perspective (A and B) and cross-section of tip (C). Scale bar = 1 centimeter.

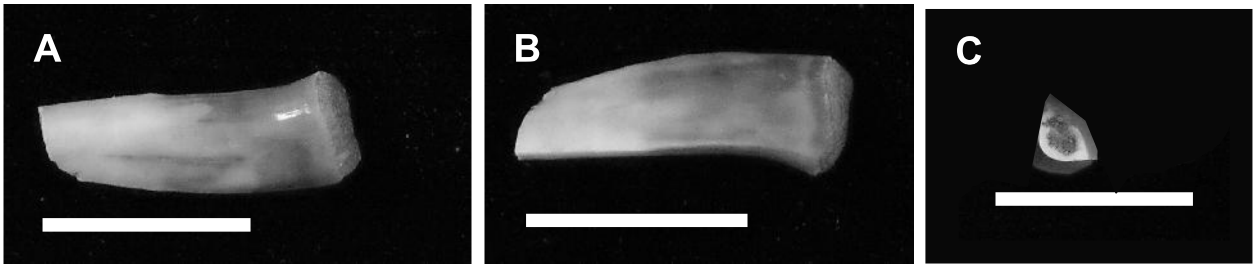


FIGURE 8: Specimen MAD 98470, *Enchodus* tooth with intact enamel in lateral perspective (A and B) and cross section of tip (C). Scale bar = 1 centimeter.

Enchodonts are also known as “saber-toothed herrings” and are common in fossil assemblages from the Late Cretaceous. Their general appearance is distinctive and easily recognizable. In articulated specimens of *Enchodus*, they have surprisingly large fangs for their body size (e.g., 6 centimeter long fangs in a specimen with a total body length only 1.5 meters) (Figure 9) (Goody, 1976).

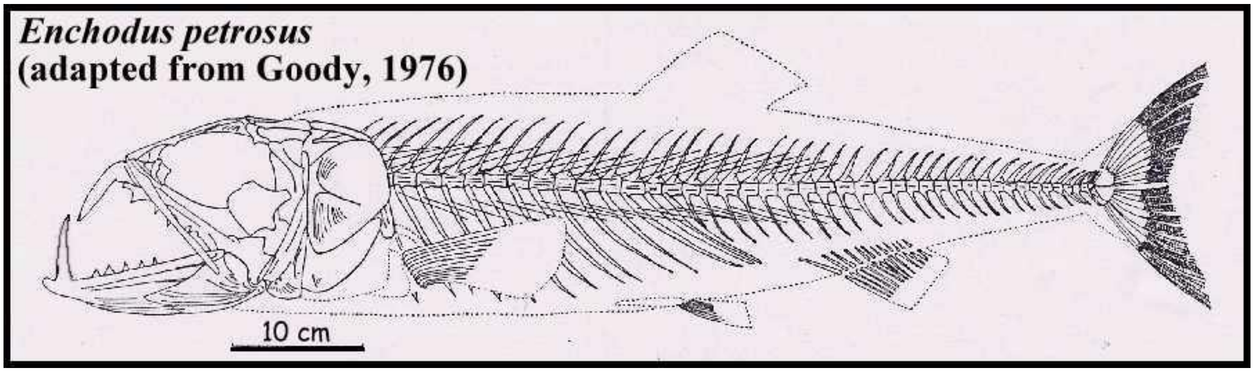


FIGURE 9: Drawing of a species of *Enchodus*, from the Late Cretaceous, Niobrara Chalk Formation in the central United States (Everhart, 2012).

The majority of named *Enchodus* species are from fragmentary material consisting of isolated teeth and jaw bones (Goody, 1969). Species are rarely known from articulated material. The teeth and jaw fragments of enchodonts are considered diagnostic based on large, pointed teeth that extend well beyond their closed gape. The type species of *Enchodus* was described from imperfect specimens (Goody, 1969), and that could be the reason for difficultly in assigning any *Enchodus* to a specific species. Much similarity exists between skulls and teeth within Enchodontoidei and is therefore difficult to specifically separate *Enchodus* from related genera (Chalifa, 1996). Most species were erected based on novel localities. However, based on the geological context of the Late Cretaceous of Madagascar, along with coexisting genera, and robustness of the teeth, the assignment of the studied material to *Enchodus* is reasonable. Assigning it to a species would be presumptuous.

***Enchodus* paleoecology and distributions:**

Enchodus was relatively widespread at the end of the Cretaceous, and the few teeth present in Madagascar are very similar to those found in other localities. According to a consensus tree, *Enchodus* is considered monophyletic, but one branch contains two species that are more closely related to *Parenchodus* which is nested within the *Enchodus* clade (Fielitz, 2004).

Enchodus is thought to have been a nektonic, mid-food-chain predator from the morphology of the skull and large upturned mouth (Fielitz, 2004). *Enchodus* was a popular prey item in large epicontinental sea based on the presence of their teeth in coprolites (Shimada and Everhart, 2003), and articulated specimens within other larger predatory fishes (Cavin, 1999; Everhart et al., 2010).

Enchodus ranges from the Albian to Paleogene and is speciose, widely distributed (Table 2), and predominantly within the Northern Hemisphere (Silva and Gallo, 2011)

TABLE 2: Geographic and stratigraphic distribution of *Enchodus* during the Cretaceous (modified from Silva and Gallo, 2011).

COUNTRY	FORMATION/LOCALITY	REFERENCE
Angola	Bentiaba locality	Jacobs et al., 2006
	Iembe locality	Jacobs et al., 2006
Bolivia	El Molino	Gayet, 1991; Gayet et al., 2001
Brazil	Atlantiada	Gallo et al., 2006
	Coqueiro	Coelho, 2004
	Gramame	Coelho, 2004; Gallo-da-Silva, 1993; Rebouças and Silva Santos, 1956
	Continguiba	Coelho, 2004; Silva Santos and Salgado, 1969
	Paraiba	Maury, 1930
Canada	Dinosaur Park (Alberta)	Beavan and Russell, 1999
	Kaskapau (Alberta)	Wilson and Chalifa, 1989
	Vermillion River (Manitoba)	Bardack, 1968
	Brown Bed (Northwest Territories)	Russell, 1967
	Lac du Bois (Northwest Territories)	Fielitz, 1996
	Ashville (Saskatchewan)	Cumbaa, 1993; Cumbaa et al., 1997
Egypt	Mut	Churcher, 1992
	Bahariya	Slaughter and Thurmond, 1974
	Niger Basin	Arambourg and Joleaud, 1943
France	Calcaire Nankin and Jadet	Breton et al., 1995
Germany	Niedersachsen	Kriwet and Gloy, 1995
	Sedenhorst	Siegfried, 1954
Holland		Goody, 1968
India	Lameta	Jain and Sahni, 1983
Israel	Mihash	Lewy et al., 1992
	Ber Meir/Amminadav	Chalifa, 1989; Haas, 1978
	Ghareb locality, West Desert locality, Sedenhorst, Lewes, Trieste-Komen, Sahel Alma, Hakel, Hajula, Jbel Tselfat	Chalifa, 1985
	Various localities without data	Chalifa, 1996
Italy	Gorizia	Dalla Vecchia and Cau, 2011; Poyato-Ariza et al., 2010
	Polazzo	Rigo, 1999

TABLE 2, continued

	Messina	Leonardi, 1966
	Cinto Euganeo	Sorbini, 1976
Japan	Ashizawa	Manabe et al., 2003
	Iwaki	Yabumoto and Uyeno, 1994
Jordan	Phosphorite unit	Arambourg, 1959; Avnimelich, 1949
	Reseifa	Bardet and Pereda Suberbiola, 2002
Lebanon	Sannine Limestone, Trieste-Komen, Sahel Alma, and Namoura	Forey et al., 2003
Mexico	Aguja	Cope, 2003
Morocco	Goulmima	Cavin, 1999
Slovenia	Trieste-Komen	Cavin et al., 2000
Spain	La Cabana	Vullo et al., 2009
Syria	Palmyrides	Bardet et al., 2000
	Unnamed phosphates	Bardet and Pereda Suberbiola, 2002
Tunisia	Amminadav	Arambourg, 1952
	Ouled Abdoun locality	Arambourg, 1952
United States	Selma (Alabama)	Applegate, 1970; Zangerl, 1948
	Eutaw	Whetstone and Collins, 1982
	Moreno (California)	Welles, 1943
	Greenhorn Limestone (Colorado)	Shimada et al., 2006
	Blufftown (Georgia)	Schwimmer, 1986
	Pierre Shale (Kansas)	Cicimurri and Everhart, 2001; Liggett et al., 2005
	Carlile Shale (Kansas)	Everhart, 2003; Martin and Stewart, 1977
	Severn (Maryland)	Harstein and Decina, 1986
	Navesink (New Jersey)	Chaffee, 1939
	Hornerstown (New Jersey)	Olson and Parris, 1987
	Marshalltown (New Jersey)	Lauginiger, 1984
	Matawan Group (New Jersey)	Gallagher, 1984
	Mount Laurel (New Jersey)	Baird, 1984
	Wenonah/Mount Laurel (New Jersey)	Gallagher, 1984
	Black Creek (North Dakota)	Miller, 1966
	Hell Creek (North Dakota)	Hoganson et al., 1994
	Donoho Creek	Cicimurri, 2007

TABLE 2, continued

	Pierre Shale (South Dakota)	Hargrave, 2007
	Greenhorn Limestone (South Dakota)	Schumacher, 2007
	Ripley (Tennessee)	Sohl, 1960
	Paluxy	Winkler et al., 1990
	Twin Mountains	Slaughter, 1969
	Cedar Mountain	Nelson and Crooks, 1987
	Localities in South Dakota and Wyoming	Goody, 1976

Though *Enchodus* is considered to be predominately a Mesozoic fish, there are some occurrences of this genus in Paleocene deposits of Tunisia (Arambourg, 1952); India (Rana et al., 2006); Saudi Arabia (Thomas et al., 1999); and New Jersey (USA) (Cook and Ramsdell, 1991). Localities of known *Enchodus* occurrences in the Cretaceous are plotted on the map below (Figure 10) including the occurrence in Madagascar reported here. This shows how the lack of fossil evidence from the Southern Hemisphere has affected our understanding of the genus' paleoecology. The addition of the Madagascar locality adds an additional Gondwanan record, even though *Enchodus* is normally recognized as staying close to the Tethys.

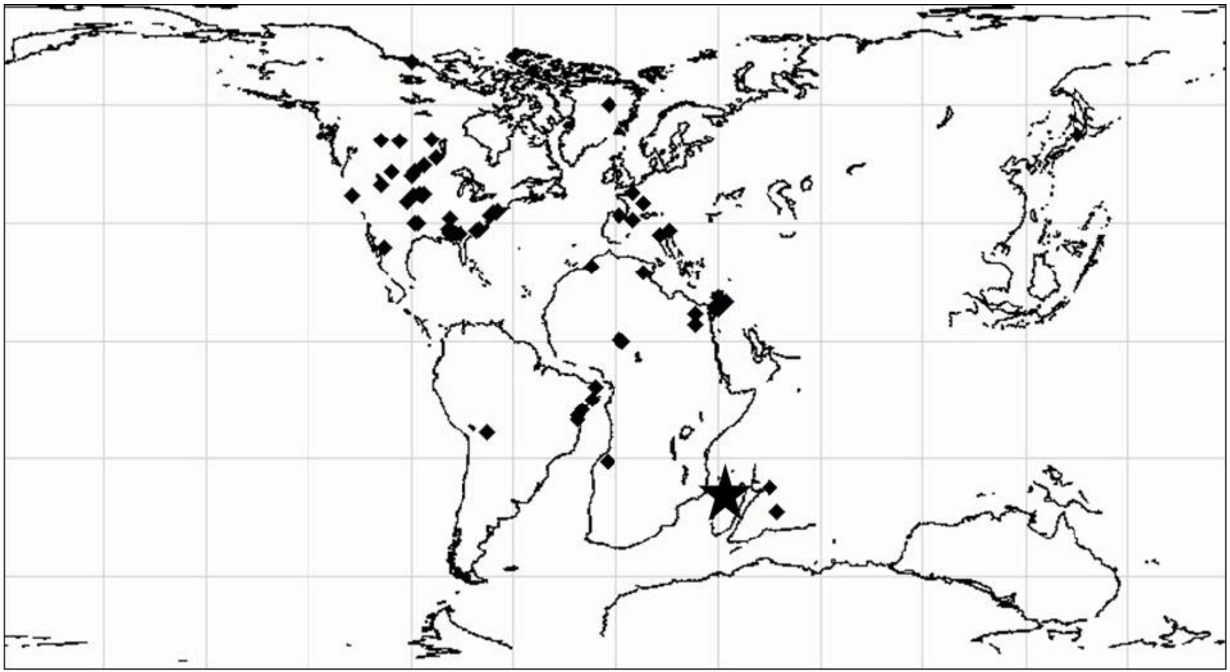


FIGURE 10: Location and distribution of *Enchodus* during the Cretaceous (diamonds), plus the addition of the Late Cretaceous of Madagascar (star) Map modified from Alroy, 2012.

TELEOSTEI Müller, 1846

OSTARIOPHYSI Jordan and Everman, 1896

SILURIFORMES Cuvier, 1816 indet.

Identification of material: MAD 96090, vertebra (Figure 11). The nearly complete vertebra is a typical catfish abdominal vertebra (Figure 11). The vertebral body is approximately 5 millimeters wide, 5 millimeters tall and 3 millimeters thick and subcircular in cross-section. The left articular process is complete and pronounced and extends dorsally 2.5 millimeters above the vertebral body, while the right articular process is broken. The preserved articular process extends slightly posteriorly to interlock with the next vertebra caudally.

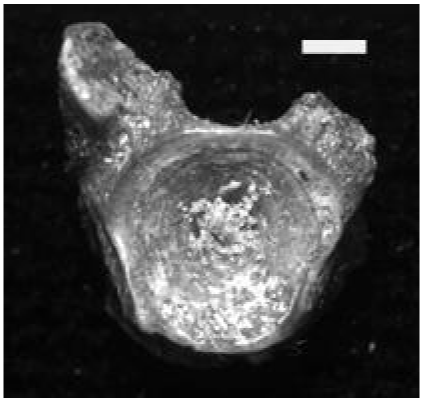


FIGURE 11: Specimen MAD 96090, caudal view of a siluriform vertebra from the Late Cretaceous of Madagascar. Scale bar = 1 millimeter.

Siluriform paleoecology and distributions: Siluriforms, otherwise known as catfish, are one of the most widely distributed and common fishes today in freshwater and marine environments. During the Cretaceous, siluriforms (Table 3) were more confined in distribution (Figure 12), and in many cases unlikely to be identifiable beyond “Siluriformes indet.” due to disarticulated and poorly preserved specimens. There are specimens from Argentina well enough preserved to be identified to Ariidae and Dyplomystidae (Bonaparte, 1984). During the Cretaceous, there was a relatively strong representation of siluriforms within Gondwana, less so in Laurasia.

TABLE 3: Geographic and stratigraphic distribution of siluriforms during the Cretaceous.

COUNTRY	FORMATION/LOCALITY	REFERENCE
Argentina	Allen	Martinelli and Forasiepi, 2004
	Los Alamitos	Bonaparte, 1984
Bolivia	El Molino	Gayet et al., 2001
Brazil	Adamantina	Candeiro et al., 2004
	Marilia	Kellner, 1994
India	Fatehgarh	Mathur et al., 2004
	Kisalpuri Locality	Khosla et al., 2004
Niger	In Beceten	Patterson, 1993
Spain	Lerida Province	de la Pena and Soler-Guijon, 1995
United States	Severn (Maryland)	Huddleston and Savoie, 1983
	Hell Creek (Montana; South Dakota)	Archibald, 1982

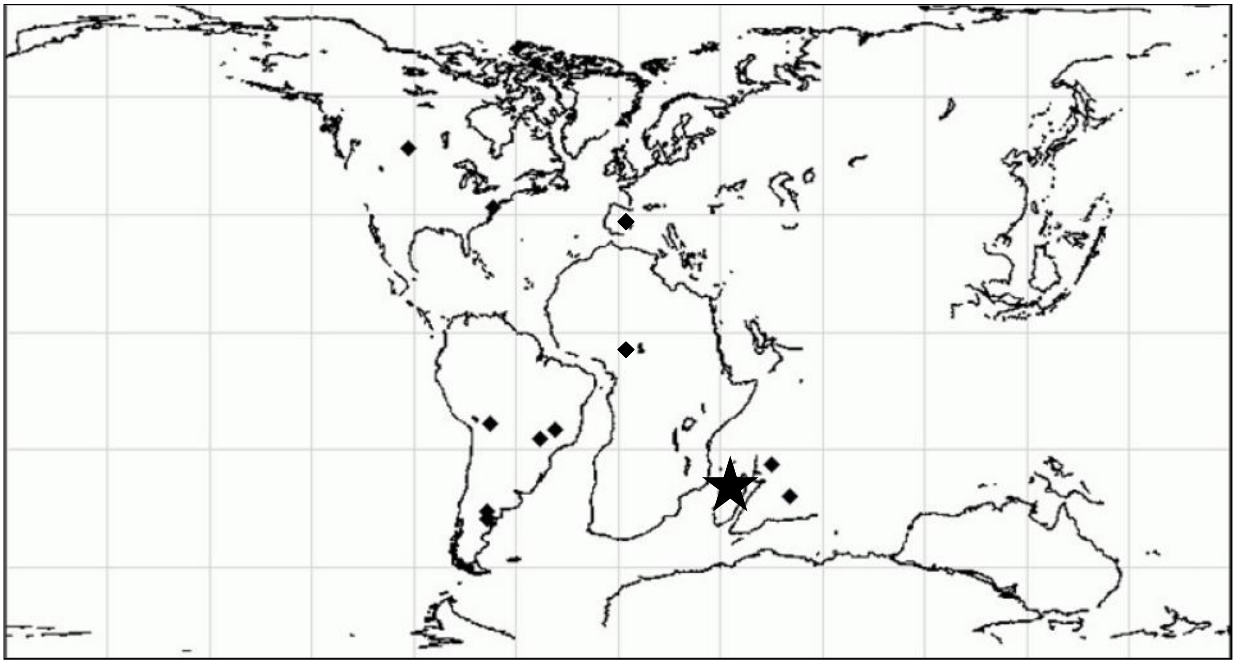


FIGURE 12: Location and distribution of siluriforms during the Cretaceous (diamonds), plus the addition of the Late Cretaceous of Madagascar (star). Map modified from Alroy, 2012.

The presence of siluriforms in the Late Cretaceous of Madagascar is not surprising based upon the proximity of other localities during that time in India and South America. The Family Ariidae, the marine catfishes, are also present within the Late Cretaceous of Madagascar (Gottfried and Ostrowski, 2008).

TELEOSTEI Müller, 1846

OSTARIOPHYSI Jordan and Everman, 1896

CHARACIFORMES Regan, 1911 indet.

Identification of material: Locality MAD 93-01 contains a large number of specimens from a variety of different taxa (beyond fishes). Within this locality, there are small jaw fragments (Figure 13). This is a small, incomplete characiform jaw element 7 millimeters long and slightly curved medially. It contains 11 teeth in various stages of eruption that all have tricuspid crowns, indicating the jaw is a characiform (Fink and Fink, 1981). The teeth range in size from 0.1 millimeters to 0.5 millimeters. Each tooth crown is a variation of the same morphotype with a large, pointed central cusp, which is approximately 75% of the crown area, surrounded by two symmetrical, laterally positioned cusps. This element is gracile, and does not appear to be the functional jaw of a fish as is, but is more likely a row of developing replacement teeth that would eventually develop into the functional jaw (Trapani and Schaefer, 2001).

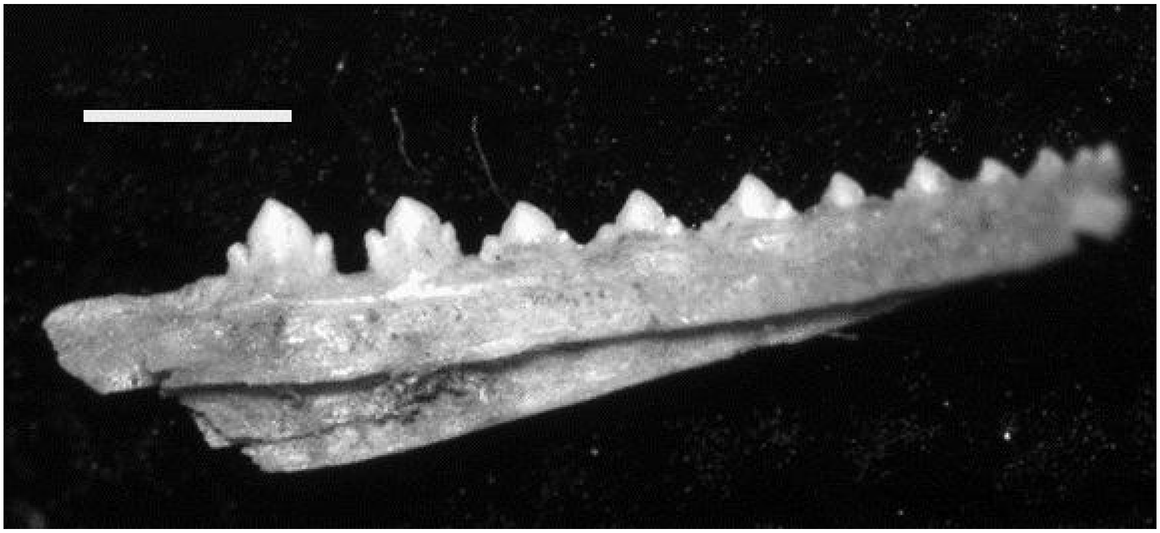


FIGURE 13: MAD 93-01, characiform jaw element from the Late Cretaceous of Madagascar. Scale bar = 1 millimeter.

Characiform osteology, paleoecology, and distributions: Today, characiforms are one of the most speciose groups of freshwater fishes with approximately 1,400 species (Otero et al., 2008) and they are nested within the Otophysi fishes which all possess a Weberian apparatus. Due to characiforms being mostly confined to freshwater, they are considered important in a biogeographic context but there are limitations due to the complicated nature of their phylogenetic relationships (Malabarba and Malabarba, 2010). Characiforms are monophyletic, but diversified quickly and the interrelationships within the clade are not well understood. There are seven synapomorphies that support characiform monophyly (Malabarba and Malabarba, 2010): 1) auditory foramen in prootic; 2) mediodorsal opening into posttemporal; 3) legenar capsule; 4) replacement teeth for outer row of dentary teeth and some premaxillary teeth formed in crypts; 5) multicuspid teeth; 6) transverse process of third neural arch; and 7) hypural 1 separated from compound centrum by hiatus in adults (Fink and Fink, 1981, 1996).

Freshwater characiforms from the Cretaceous have a very depauperate fossil record and consist mostly of isolated teeth or tooth-bearing bones. Table 4 shows that characiforms are found in the Cretaceous of the Iberian Peninsula (Otero et al., 2008), Northern Africa (Dutheil, 1999; Werner, 1993), and in South America (Bertini et al., 1993; Gayet et al., 2001; Gayet and Meunier, 1998). Recent discoveries of potentially marine-tolerant characiforms (Taverne, 2003) have had a distinct effect on the biogeography of this group, once thought to remain in freshwater only. However, few marine characiforms have been found that are widely accepted; therefore, only the undisputed taxa are in the locality information below. There have been reports of marine characiforms in Canada (Newbrey et al., 2009) and *Salimops* from Portugal (Fink and Fink, 1996) but both presences have created some controversy. The presence and increasing awareness of marine characiforms in the fossil record calls into question the biogeography of the group through geologic time. Mixture of freshwater characiforms and brackish or marine water taxa is relatively common, this is hypothesized to occur from transportation in coastal environments such as in Bolivia

(Gayet et al., 2001). The Late Cretaceous characiform of Madagascar is the southern-most record of the group (Figure 14). Their presence indicates a more complicated biogeographical history than previously suggested (e.g. Briggs (2005)). Because the Madagascar characiforms are found at a microsite locality, it is unclear whether it is a marine or freshwater fish, as there is a substantial amount of mixing of disarticulated taxa within these microsites.

TABLE 4: Geographic and stratigraphic distribution of characiforms (freshwater and marine) during the Cretaceous.

COUNTRY	FORMATION/LOCALITY	REFERENCE
Bolivia	El Molino	Gayet et al., 2001; Gayet and Meunier, 1998
Brazil	Marilia and Adamantina	Bertini et al., 1993
France	Verane and Les Pennes-Mirabeau	Otero et al., 2008
Morocco	Tafilalt	Dutheil, 1999
Sudan	Wadi Milk	Werner, 1993
Italy (marine)	Nardó locality	Taverne, 2003

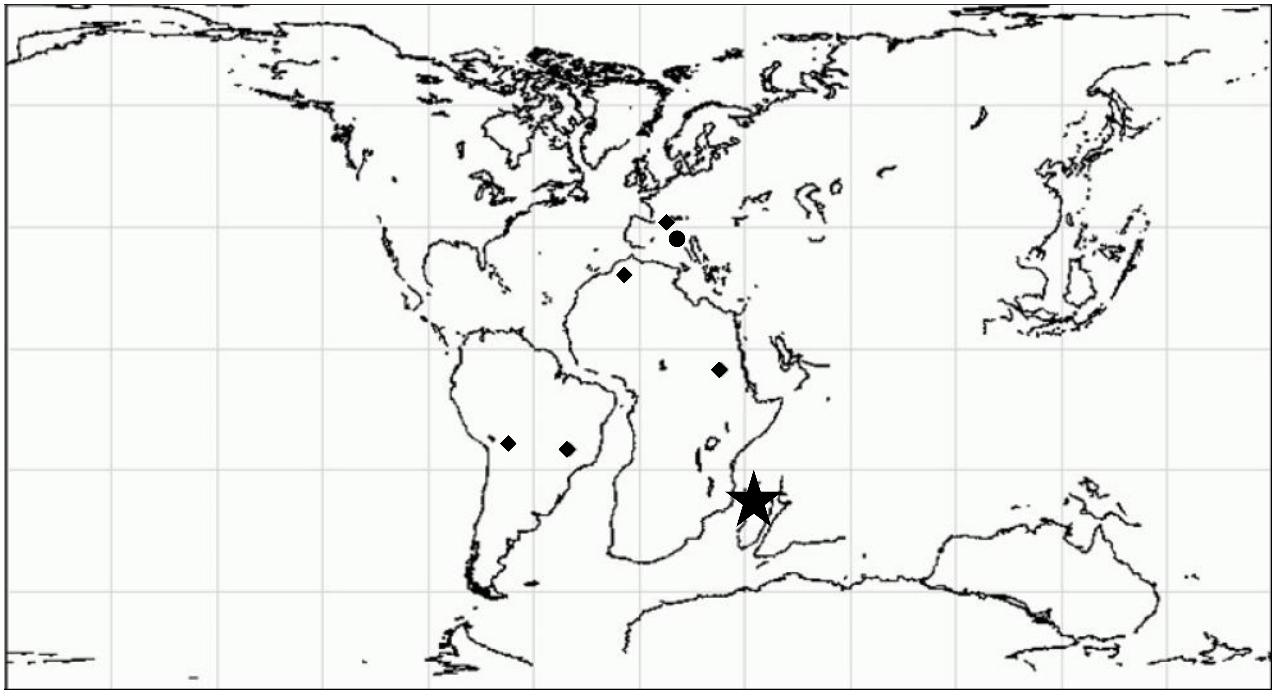


FIGURE 14: Location and distribution of characiforms during the Cretaceous (diamonds = freshwater, circle = marine), plus the addition of the Late Cretaceous of Madagascar (star). Map modified from Alroy, 2012.

Briggs (2005) proposed that characiforms originated in South America and migrated through Africa and into Eurasia, and never were a part of Madagascar's history. Their presence on Madagascar shows that they likely were not strictly freshwater, and thus did not have to rely on complete physical connections of landmasses to disperse. Their presence supports the hypothesis that by the Late Cretaceous, ostariophysans were already widely distributed, and that there is likely a bias in the fossil record influencing the apparent distribution of the group during this time.

TELEOSTEI Müller, 1846
OSTARIOPHYSI Jordan and Everman, 1896
?CYPRINIFORMES Bleeker, 1859 indet.

Identification of material: MAD 05008 (left operculum); MAD 05514 (right operculum); and MAD 05514 (left hyomandibula). The opercula are thin bones with a pronounced articular facet for the condyle on the hyomandibula. MAD 05088 (Figure 15) is a nearly complete operculum, 3.5 centimeters wide, 5.5 centimeters long and approximately 1 millimeter thick. The lateral surface is smooth with little texture and foramina that pierce the surface. The medial surface is smooth, with distinctive proximal features, and is thicker near the articulation point. There are two struts that diverge at approximately a 45^{o} angle, one along the anterior edge of the opercula, and one ventrocaudally. An opercular arm, with a slightly scalloped edge, extends dorsally to the articular facet. MAD 05514 (Figure 16A) is a less-complete right operculum with the same articular facet and medial features as in MAD05008. The hyomandibula

(Figure 16 B, C) is not complete, and measures 3.25 centimeters long and 1 centimeter wide at the greatest width. The hyomandibula has a pronounced, circular opercular process that would fit into the corresponding articular facet in the opercula. The dorsal edge of the hyomandibula bears a 0.75 centimeter fan-shaped ridge that has accommodating facets for the pterotic and sphenotic bones. Along the main strut there are two thin-boned flanges, one laterally that is curved near the opercular process, and one further ventrally on the strut that extends rostrally. There are foramina along the strut, particularly concentrated near the opercular process, and around the dorsal edge.

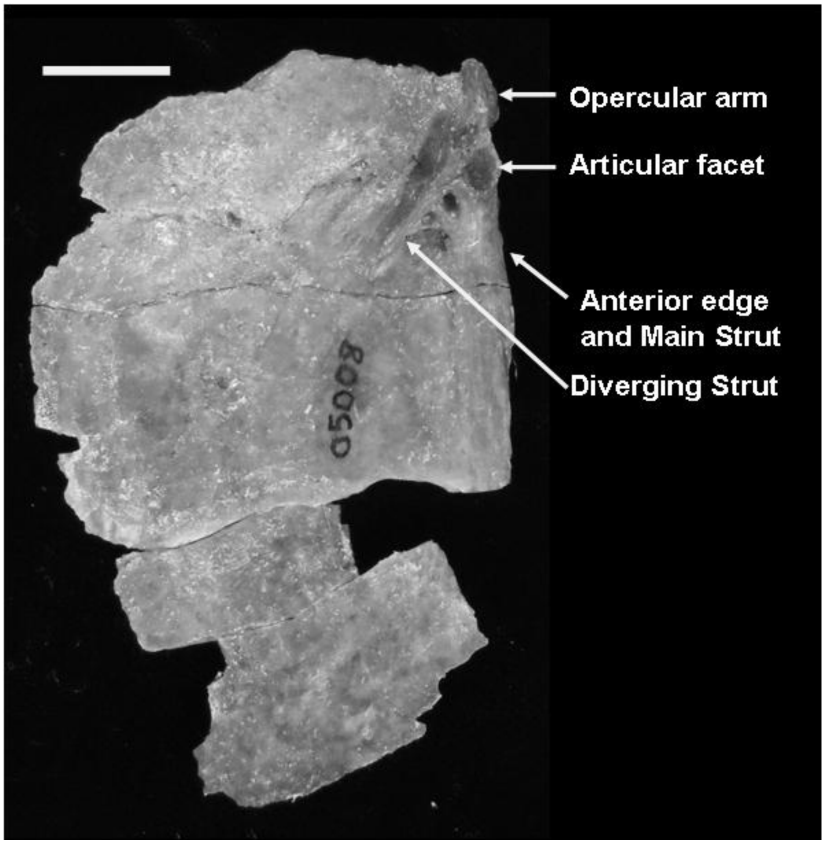


FIGURE 15: Specimen MAD 05008, Medial view of cypriniform left opercula labeled with important structures described in the text. Scale bar = 1 centimeter.

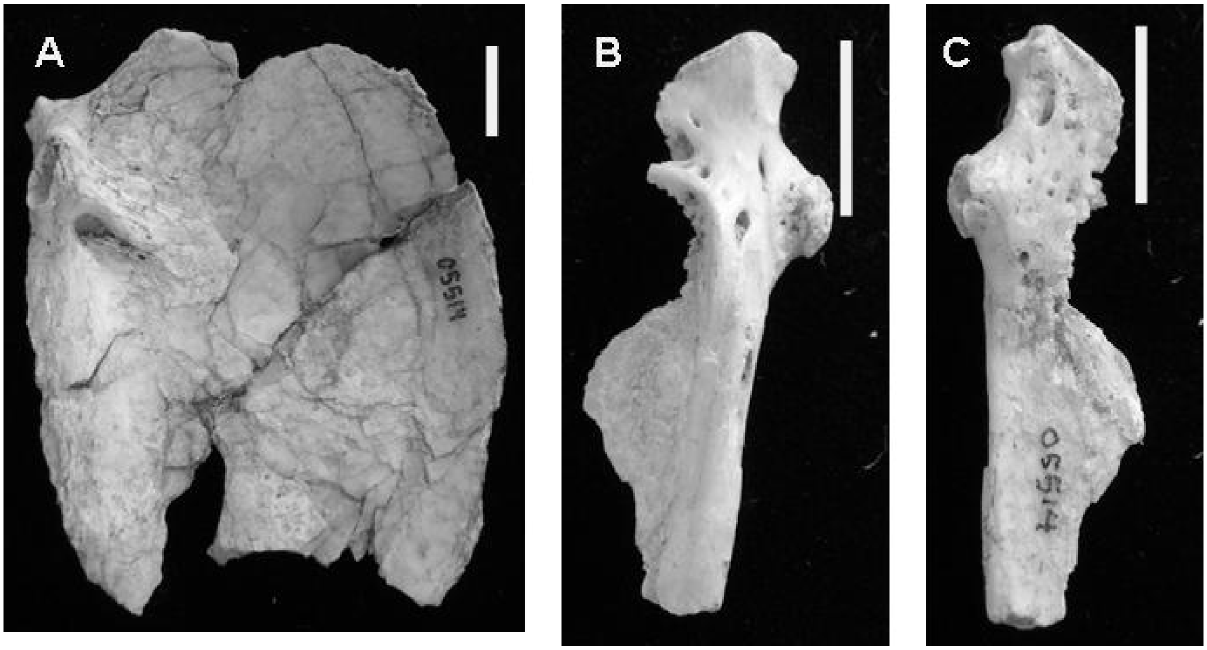


FIGURE 16: Specimens from MAD 05514, cypriniforms from the Late Cretaceous of Madagascar. Nearly complete right opercula (A), lateral and medial views of an almost complete left hyomandibula (B and C, respectively). Scale bars = 1 centimeter.

Cypriniform osteology: Many osteological descriptions for identifying cypriniforms follow Harrington (1955) which gives a detailed description of the osteocranium in a North American cyprinid, *Notropis bifrenatis*, and this convention is followed here to identify these probable cypriniforms within the Anembalemba Member. The distinct features of the operculum and hyomandibula likely related to this group’s unique feeding mechanism. The cypriniform hyomandibula has a thick strut of bone bounded by thin flanges on the rostral and caudal sides; strut has three branches, the anterior two articulate with the neurocranium, and the other is a rounded opercular condyle (to fit in the opercular facet) (Harrington Jr., 1955). A large foramen at the convergence of the struts runs within the main strut of the hyomandibula until exiting lower laterally via an oval foramen (Harrington Jr., 1955). The opercula is thin overall except for a thickening near the proximal attachment (around the articular facet) and has two mesial struts, one on the anterior edge of the bone and the other diverging ventrocaudally at the articular facet (Harrington Jr., 1955). The operculum has an opercular arm, which is presumably for muscle attachment (Nelson, 1949). Several foramina perforate the opercula on the anterior edge and ventral to the hyomandibular facet. These foramina facilitate passage of sensory innervation and are likely taxonomically significant (Harrington Jr., 1955).

Cypriniforms are freshwater fishes that today have a nearly worldwide distribution and over 3500 species (Nelson, 2006). The species richness has led to confusion both phylogenetically and taxonomically (Conway et al., 2010). Phylogenetically, ostariophysans make up a large portion of the teleost tree (Figure 3) and the internal relationships of this group is questioned. According to Diogo et al. (2008), Gymnotiformes and Siluriformes are sister taxa, with Characiformes being a sister group, and Cypriniformes being the most basal group in the monophyly. The lack of cypriniforms in Cretaceous sediments, have led to questioning relationships about the basal-most ostariophysan. Fink and Fink (1996) posited that Gymnotiformes are the basal ostariophysans because they are known from the Early Cretaceous, with Cypriniformes being the sister taxa of Characiformes + Siluriformes. The Tertiary fossil record and a poor to non-existent Cretaceous fossil record have made comprehensive phylogenetic studies difficult. The lack of preserved freshwater ecosystems from the Cretaceous is suggested as to why there are few reports of cypriniforms. Specimens tend to be disarticulated, poorly preserved, and therefore difficult to identify (Mayden, 2012). There are only three potential cypriniform fossil localities from the Mesozoic (Jurassic and Cretaceous) as listed in Table 5. Figure 17 shows the depauperate Mesozoic fossil record and the addition of the Late Cretaceous locality in Madagascar. The presence of Cretaceous cypriniforms in Madagascar contributes to our understanding of these fishes during the Mesozoic including how the break-up of Pangea affected the distribution and evolution of this order.

TABLE 5: Geographic and stratigraphic distribution of cypriniforms during the Mesozoic.

COUNTRY	FORMATION/LOCALITY	REFERENCE
Bolivia (Late Cretaceous)	El Molino	Gayet et al., 2001
Morocco (Early Cretaceous)	Kser Metlili	Sigogneau-Russell et al., 1988
Greenland (Late Jurassic)	Kap Leslie	Fursich 1999, (unprinted reference from Paleobiology Database, Alroy 2012)

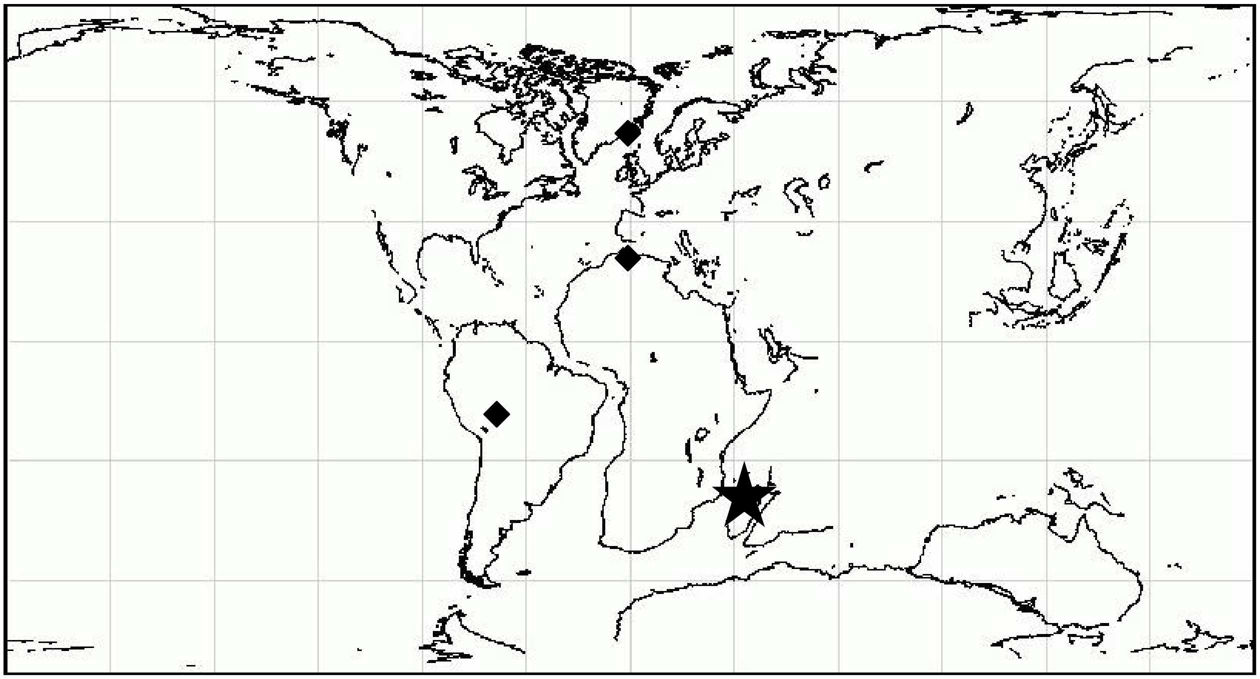


FIGURE 17: Mesozoic distribution of possible Cypriniformes localities (diamonds) with the added Late Cretaceous of Madagascar (star). Map modified from Alroy, 2012.

The presence of cypriniforms during the Late Cretaceous of Madagascar supports the longtime that cyprinids initially evolved and were widely distributed contrary to previous ideas on cypriniform biogeography and migration (Briggs, 2005). Cypriniforms have a more restrictive environmental tolerance of freshwater, or rarely brackish (Nelson, 1994). This reliance upon freshwater systems means that cypriniforms can be very informative on biogeographical analyses.

TELEOSTEI Müller, 1846

PERCIFORMES

PERCOIDEI Bleeker, 1859

SCIAENIDAE Cuvier and Valenciennes, 1828

Identification of material and sciaenid osteology: MAD 05028, a partial pharyngeal grinding mill of a drumfish (Figure 18). This incomplete pharyngeal arch of a drumfish is box-shaped and 1.75 centimeters long, 1.5 centimeters wide, and approximately 1.25 centimeters thick. The oral surface of the pharyngeal element is covered with 1 millimeter circular pits that would accommodate crushing teeth (characteristic of the pharyngeal elements of sciaenids). The toothpits have strongly beveled edges typical of sciaenids. The toothpits sit upon a complex mass of bone with large rounded knobs ornamented with crenulations, deep pits, and foramina.

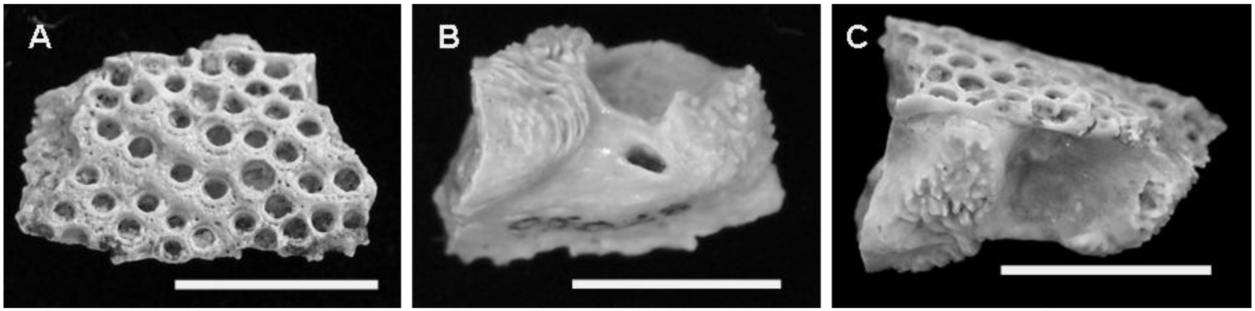


FIGURE 18: Specimen MAD 05028, Sciaenidae pharyngeal grinding mill from the Late Cretaceous of Madagascar in oral view (A), aboral view (B), and lateral view (C). Scale bars = 1 centimeter.

Sciaenidae paleoecology and distribution: Today, sciaenids occur along continental regions and in shallow waters, and are absent from islands within the Pacific and Indian oceans (Nelson, 1994). There are approximately 270 sciaenid species known (Nelson, 1994). Sciaenids are bottom-dwelling fishes and benthic feeders on invertebrates. Their pharyngeal elements are used to crush mollusk shells and their vomers and palatines lack teeth (Nelson, 1994). The sciaenid fossil record extends into the Cretaceous of Laurasia (Table 6 and Figure 19).

TABLE 6: Geographic and stratigraphic distribution of sciaenids during the Cretaceous.

COUNTRY	GEOLOGICAL FORMATION	REFERENCE
Canada (Alberta)	St. Mary River (Alberta)	Langston Jr, 1975
Canada (Saskatchewan)	Ravenscrag (Saskatchewan)	Sternberg, 1924
Italy	Scaglia Biana	O'Dogherty, 1994
United States	Hell Creek (Montana)	Archibald, 1982
	Lance (Wyoming)	Breithaupt, 1982; Clemens, 1964
	Fruitland (New Mexico)	Armstrong-Ziegler, 1978
	Marshalltown (New Jersey)	Grandstaff et al., 1992

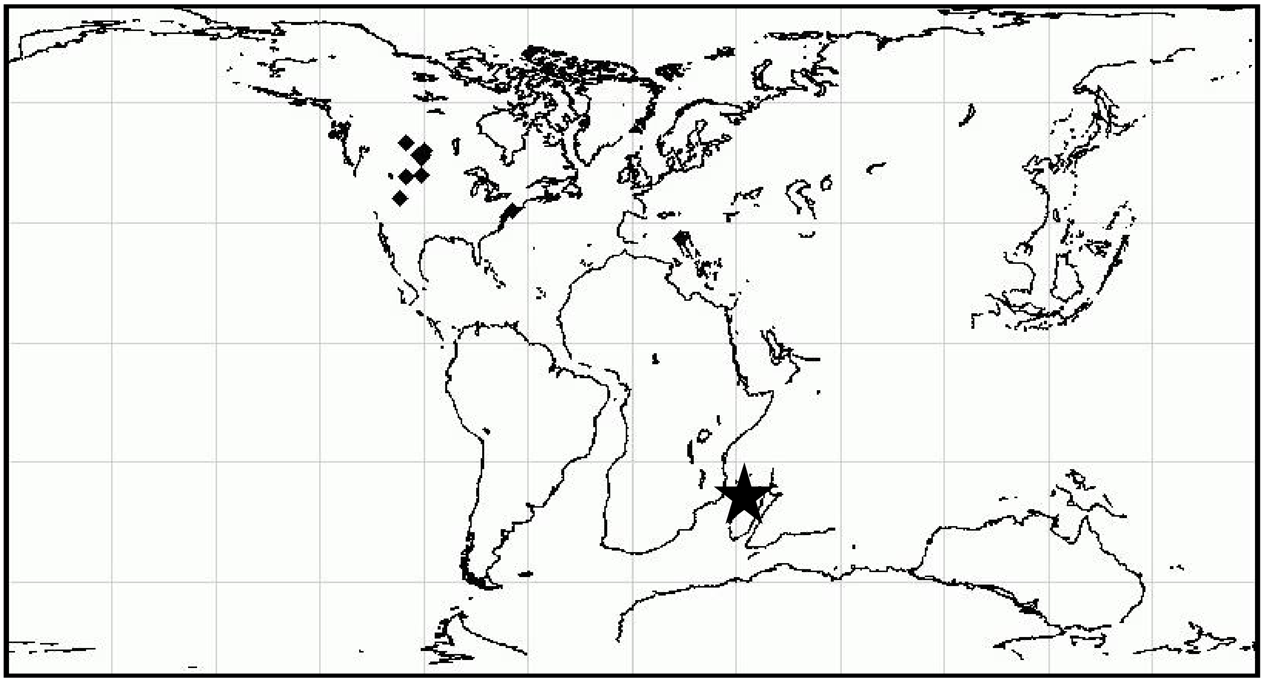


FIGURE 19: Location and distribution of sciaenids during the Cretaceous (diamonds), plus the addition of the Late Cretaceous of Madagascar (star). Map modified from Alroy, 2012.

The Madagascar sciaenid is the first occurrence of a Late Cretaceous sciaenid in Gondwana. Sciaenids' presence in Madagascar shows that the group had a broader distribution than has been previously reported. Nursall (1996a) suggested that many sciaenid pharyngeal elements have been misidentified as pycnodonts, which has contributed to the large diversity of pycnodonts during the Late Cretaceous. The misidentified specimens are likely due to their overall similarity teeth-bearing elements, especially if teeth are not present. The most common fossil sciaenids from the Late Cretaceous are *Platacodon* and *Pogonias*, the latter of which is an extant genus. Fossil genera are not well-described osteologically and it not possible to be more precise here than the assignment of Sciaenidae for the single, small Madagascar specimen.

"Lac Kinkony" Member:

Currently, the Lac Kinkony member is being evaluated and will be formally described and put into geological context in the Mahajanga Basin. Based upon the fossil fishes, there are differences between the Anembalemba and "Lac Kinkony" Members. There is a plethora of fish material within Kinkony deposits, and the elements are large and well-preserved, but are disarticulate and lack surface ornament, making them difficult to identify. A general overview of the Kinkony indicates that it is not as taxonomically rich as the Anembalemba. It contains an albuloid, *Paralbula*, which is discussed more thoroughly in Chapter 3. There are likely only two or three taxa represented within the collected material from the Kinkony, and there appears to be less mixing of the fish material with more terrestrial vertebrate fossils, likely leading to underestimating the taxa that were actually living in this area as this was a more autochthonous setting. Taxa that are present within the Kinkony include Cypriniformes, based on the same opercular characteristics as seen within the Anembalemba fauna (Figure 20). There also appear to be perciforms based on vertebrae, a parasphenoid (Figure 21), and urohyals (Figure 22), but these have not been identified to a finer taxonomic level.

FIGURE 20: Cypriniform operculum from the “Lac Kinkony” Member of the Late Cretaceous of Madagascar (MAD 07276). Scale bar = 1 centimeter.

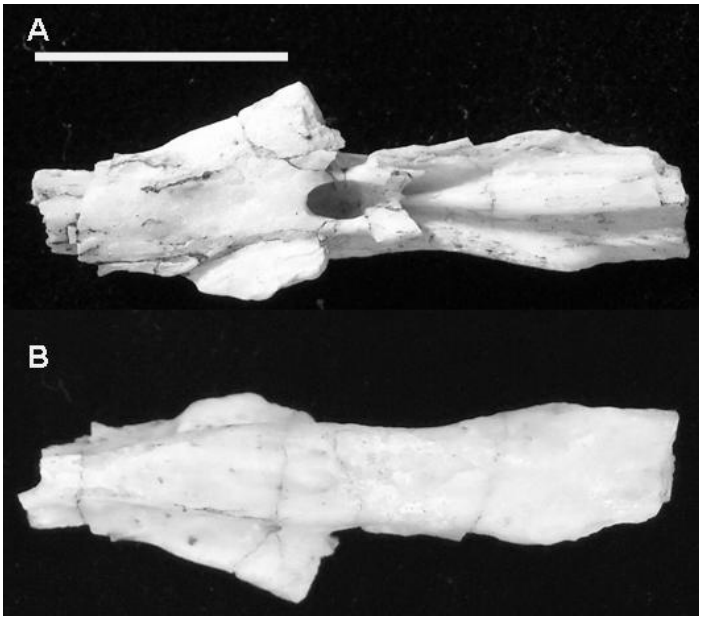


FIGURE 21: Unidentified ?perciform parasphenoid from “Lac Kinkony” (MAD 07276) in ventral (A) and dorsal (B) views. Scale bar = 1 centimeter.

FIGURE 22: Urohyal from a ?perciform from “Lac Kinkony” (MAD 07276) in dorsal view. Scale bar = 1 centimeter.

SUMMARY

Anembalemba Member: Many of the fossils collected from the Anembalemba Member occur in debris flow deposits containing mixtures of terrestrial and coastal marine fauna, indicating a seasonally wet terrestrial environment. The majority of the fishes from the Late Cretaceous of Madagascar are marine genera that would have lived in shallow epicontinental seas or along coastal margins, meaning they have a lower probability of being truly endemic to Madagascar. However, fishes that live along continental margins are thought to have limited dispersal capacity during larval stages even thought they have the tolerance to disperse further (Cowen et al., 2000). Isolated island also show the presence of endemic taxa that are affected by local ocean currents (Robertson and Allen, 1996). The taxa that are not considered exclusively marine (siluriforms, characiforms, and cypriniforms) are not able to be identified more precisely to the level of family. Consequently, these taxa are not incorporated into the analyses (which use genera) in subsequent chapters, but some general comments on their biogeographical implications are in order.

The current ideas for understanding fish diversity and distribution during the Mesozoic are based upon phylogenetic studies using living species and current distributions, which simplify the dimension of “time”. The poorly known fossil record is not able to add much information to ancient distributions. Some of the groups discussed here (e.g. Characiformes, Cypriniformes) do not occur on Madagascar today, and these groups would be excluded from any primary molecular clock based, DNA biogeographical analyses, even though they played an important role in Madagascar’s history. Their exclusion will bias past distributions if fossil record are not taken into account. The new taxa from the Late Cretaceous of Madagascar increase the biodiversity on the island, increase the geographical range of all groups of fishes discussed, and sometimes increase the temporal range of the group. It also highlights the complex nature of fish dispersal.

“Lac Kinkony” Member: The ichthyofauna of the Lac Kinkony of Madagascar exhibits differences from that of the Anembalemba Member. These variations do not lend to any definitive views on paleoecology of each member on the basis of fossil fishes alone. Based upon the samples collected from Kinkony during the 2007 and 2010 field seasons, there appears to fewer fish taxa preserved within the Kinkony. There are numerous (hundreds) of isolated, rarely complete elements, with a large variation in the quality of preservation of the surface ornament and other diagnostic features. Skull elements are abundant, rather than vertebral material as seen in the Anembalemba Member, and there seems to be some bias in the skull elements that are represented. There is a high number of urohyals (which usually do not preserve well) along with the opercular series of bones and hyomandibulae. The high

proportion of certain skull elements that remain intact beg the question of potential scavenging biases upon carcasses (G. Smith, personal communication). This could mean that once the fishes died and were scavenged, the scavengers had a signature bias in which some elements were left behind while others were destroyed or moved during the scavenging process. Within Kinkony, this scavenging left behind a higher number of large, flat skull elements over vertebrae. The fish diversity appears to be lower within Kinkony and there are only two or three taxa represented within the collected material, which is a mixture of surface collections and specimens prepared from blocks of matrix. Even though the material from collected blocks would seem to have a higher potential for being associated skeletal material, this is unlikely due to the number of elements present and mixing that appears to have occurred prior to deposition.

REFERENCES

REFERENCES

Agassiz, L., 1833-1844, Recherches su les poissons fossiles, v. 5 vols. 1420 pp. Neuchatel et Soleure (Petitpierre).

Alroy, J., 2012, Paleobiology Database, *in* Alroy, J., ed., Volume 2012. http://www.paleodb.org

Applegate, S., 1970, The vertebrate fauna of the Selma Formation of Alabama, Fieldiana, Geology Memoirs: Chicago, IL, Field Museum of Natural History, p. 383-433.

Arambourg, C., 1952, Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie): Notes Mem Serv geol Maroc, v. 92, p. 1-372.

—, 1959, *Titanopteryx philadelphinae* nov. gen., nov. sp., Pterosaurian giant [*Titanopteryx philadelphinae* nov. gen., nov. sp., Giant Pterosaurian], Contributions a la Stratigraphie et a la Paleontologie du Cretace et du Nummulitique de la Marge NW de la Pennsule Arabique. Notes et Memoires du Moyen Orient, Volume 7, p. 229-234.

Arambourg, C., and Joleaud, L., 1943, Vertébres fissiles du bassin du Niger [Fossil Vertebrates of the Niger basin]: Bulletin de la Service des Mines de l'Afrique Occidentale Française, v. 7, p. 28-85.

Archibald, J., 1982, A Study of Mammalia and Geology Across teh Cretaceous-Tertiary Boundary in Garfield County, Montana, University of California Publications Geological Sciences, 286 p.

Armstrong-Ziegler, J., 1978, An Aniliid Snake and Associated Vertebrates from the Campanian of New Mexico: Journal of Paleontology, v. 52, p. 480-483.

Avnimelich, M., 1949, On vertebrate remains in Senonian phosphate beds in Transjordan: Ecologae geologicae Heletiae, v. 42, p. 485-490.

Baird, D., 1984, Evidence of giant protostegid sea-turtles in the Creatceous of New Jersey: The Mosasaur, v. 2, p. 135-140.

Bardack, D., 1968, Fossil vertebrates from the marine Cretaceous of Manitoba: Canadian Journal of Earth Sciences, v. 5, p. 145-153.

Bardet, N., Cappetta, H., Pereda Suberbiola, X., Mouty, M., Al Maleh, A., Ahmad, A., Khrata, O., and Gannoum, N., 2000, The marine vertebrate faunas from the Late Cretaceous phosphates of Syria: Geological Magazine, v. 137, p. 269-290.

Bardet, N., and Pereda Suberbiola, X., 2002, Marine reptiles from the Lstae Cretaceous Phosphates of Jordan: palaeobiogeogrpahical implications: Geodiversitas, v. 24.

Beavan, N., and Russell, A., 1999, An Elasmobranch Assemblage from the Terrestrial-Marine Transitional Lethbridge Coal Zone (Dinosaur Park Formation: Upper Campanian), Alberta, Canada: Journal of Paleontology, v. 73, p. 494-503.

Berg, L., 1937, A classification of fish-like vertebrates: Bulletin de l'Académie des Sciences de l'URSS, Classe des Sciences mathématiques et naturelles, v. 4, p. 1277-1280.

Bertini, R., Marshall, L., Gayet, M., and Brito, P., 1993, Vertebrate faunas from the Adamantina and Marília Formations(Upper Baurú Group, Late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 188, p. 71-101.

Bleeker, P., 1859, Enumeratio specierum fiscium hucusque in Archipelago indico observatarum., Volume 6: Batavia, Act. Soc. Sci. Indo-Neerl., p. 1-276.

Blot, J., 1987, L'Orde des Pycnodontiformes. Studi e richerche sui giacimenti terziari di Bolca: Museo Civico di Storia naturale, Verona, v. 211.

Bonaparte, J., 1984, Nuevas pruebas de la conexion fisica entre Sudamerica y Norteamerica en el Cretácico Tardio (Campaniano) [New evidences for the physical connection between South and North America in the Late Cretaceous (Campanian)]: Actas del III Congreso Argentino de Paleontologia y Bioestratigrafia, v. 1, p. 141-149.

Breithaupt, B., 1982, Paleontology and paleoecology of the Lance Formation (Maastrichtian), east flank of Rock Springs Uplift, Sweetwater County, Wyoming: Rocky Mountain Geology, v. 21, p. 123-151.

Breton, G., Biolotte, M., and Sigro, G., 1995, *Dipsacaster jadeti* sp. nov., Astropectinidae (Asteroidea, Echinodermata) du Maastrichtien des Petites Pyrénées (France): Bull Soc Geol de Normandie et dea Amis du Muséum, v. 82, p. 35-42.

Briggs, J., 2005, The biogeography of otophysan fishes (Ostariophysi: Otophysi): a new appraisal: Journal of Biogeography, v. 32, p. 287-294.

Candeiro, C., Abranches, C., Abrantes, E., Avilla, L., Martins, V., Moreira, A., Torres, S., and Bergqvist, L., 2004, Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous): Journal of South American Earth Sciences, v. 18, p. 1-10.

Cavin, L., 1999, Occurrence of a juvenile teleost, *Enchodus* sp., in a fish gut content from teh Upper Cretaceous of Goulmima, Morocco: Paleontological Association, Special Paper Paleontology, v. 60, p. 57-72.

Cavin, L., Jurkovsek, B., and Kolar-Jukovsek, T., 2000, Stratigraphic succession of the Upper Createcous fish assemblages of Kras (Slovenia): Geologija, v. 43, p. 165-195.

Chaffee, R., 1939, A New Jersey Mosasaur of the subfamily Platecarpinae: Notulae Naturae [Philadelphia], v. 37, p. 1-5.

Chalifa, Y., 1985, Saurorhamphus judeaensis (Salmoniformes: Enchodontidae), a New Longirostrine Fish from the Cretaceous (Cenomanian) of Ein-Yabrud, near Jerusalem: Journal of Vertebrate Paleontology, v. 5, p. 181-193.

—, 1989, New species of *Enchodus* (Pisces, Enchodontoidei) from the Lower Cenomanian of Ein-Yabrud, Israel Journal of Paleontology, v. 63, p. 356-364.

—, 1996, New species of *Enchodus* (Aulopiformes: Enchodontidae) from the Northern Negev, Israel, with comments on evolutionary trends in Enchodontoidei, *in* Arratia, G., and Viohl, G., eds., Mesozoic Fishes -- Systematics and Paleoecology: München, Germany, Verlag Dr. Friedrich Pfeil, p. 349-367.

Chiplonker, G., and Ghare, M., 1977, Palaeontology of the Bagh Beds - Part VI - Pisces: Publication for the Centre of Advanced Study in Geology, v. 11, p. 130-138.

Churcher, C., 1992, Terrestrial vertebrates from Campanian strata in Wadi El-Gedid (Kharga and Dakhleh Oases), Western Desert of Egypt: Journal of Vertebrate Paleontology, v. 12, p. 23A.

Cicimurri, D., 2007, A late Campanian (Cretaceous) selachian assemblage from a classic locality in Florence County, South Carolina: Southeastern Geology, v. 45, p. 59-72.

Cicimurri, D., and Everhart, M., 2001, An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late Cretaceous) of Kansas: Transactions of the Kansas Academy of Science, v. 104, p. 129-143.

Clemens, W., 1964, Fossil mammals of the type Lance Formation, Wyoming Part I. Introduction and Marsupialia, University of California Publications in Geological Sciences, Volume 48, p. 1-105.

Coelho, P., 2004, Revisão sistemática dos Enchodontidae (Euteleostei: Aulopiformes) do Brasil [M.S. Thesis thesis]: Rio de Janeiro, Museu Nacional/Universidade Federal do Rio de Janeiro.

Conway, K., Hirt, M., Yang, L., Mayden, R., and Simons, A., 2010, Cypriniformes: systematics and paleontology, *in* Nelson, J., Schultze, H.-P., and Wilson, M., eds., Origin and Phylogenetic Interrelationships of Teleosts: München, Germany, Verlag Dr. Friedrich Pfeil, p. 395-316.

Cook, J., and Ramsdell, R., 1991, Macrofossils from the Vincentown Formation (Paleocene) of New Jersey: Bulletin of the New Jersey Academy of Sciences, v. 36, p. 11-15.

Cope, 2003, A Late Cretaceous (Campanian) marine vertebrate microfauna from the Aguja Formation of Chihuahua, Mexico: Journal of Vertebrate Paleontology, v. 23, p. 42A.

Cope, E., 1887, Zittel's Manual of Palaeontology: American Naturalist, v. 21, p. 1014-1019.

Cowen, R., Lwiza, K., Sponaugle, S., Paris, C., and Olson, D., 2000, Connectivity of Marine Populations: Open or Closed?: Science, v. 287, p. 857-859.

Cumbaa, S., 1993, Early Birds, Crocodile Tears, and Fish Tales: Cenomanian and Turonian Marine Vertebrates from Saskatchewan, Canada: Journal of Vertebrate Paleontology, v. 13, p. 31A-32A.

Cumbaa, S., Tokaryk, T., Collom, C., Steward, J., and Ercit, T., 1997, A Cenomanian age bone bed of marine origin, Saskatchewan, Canada: Journal of Vertebrate Paleontology, v. 17, p. 40A.

Cuvier, 1816.

Cuvier, G., and Valenciennes, A., 1828, Histoire naturelle des poissons. Tome second. Livre Troisième. Des poissons de la famille des perches, ou des percoïdes. , Volume 2.

Dalla Vecchia, F., and Cau, A., 2011, The first record of notosuchian crocodyliform from Italy: Rivista Italiana Di Paleontologia E Stratigrafia, v. 117, p. 309-321.

Dutheil, D., 1999, An overview of the freshwater fish fauna from the Kem Kem beds (Late Cretaceous: Cenomanian) of southeastern Morocco, *in* Arratia, G., and Schultze, H.-P., eds., Mesozoic Fishes 2 - Sytstematics and Fossil Record: München, Verlag Dr. Friedrich Pfeil, p. 223-563.

Everhart, M., 2003, A middle Turonian marine fish fauna from the Blue Hill Shale Member, Carlile Shale of north central Kansas: Journal of Vertebrate Paleontology, v. 23, p. 49A.

—, 2009, First Occurrence of Marine Vertebrates in the Early Cretaceous of Kansas: Champion Shell Bed, Basal Kiowa Formation: Transactions of the Kansas Academy of Science, v. 112, p. 201-210.

—, 2012, Oceans of Kansas Paleontology, http://www.oceansofkansas.com/.

Everhart, M., Hageman, S., and Hoffman, B., 2010, Another Sternberg "Fish-within-a-Fish" Discovery: First Report of Ichthyodectes ctenodon (Teleostei; Ichthyodectiformes) with Stomach Contents: Transactions of the Kansas Academy of Science, v. 113, p. 197-205.

Fielitz, C., 1996, A late cretaceous (Turonian) ichthyofauna from Lac des Bois, northwest territories, Canada, with paleobiogeographic comparisons with turonian ichthyofaunas of the Western Interior Seaway: Canadian Journal of Earth Sciences, v. 33, p. 1375-1389.

—, 2004, The phylogenetic relationships of th e tEnchodontidae (Teleostei: Aulopiformes), *in* Arratia, G., Wilson, M.V.H., and Cloutier, R., eds., Recent Advances in the Origin and the Early Radiation of Vertebrates: Munchen, Germany, Verlag Dr. Friedrich Pfeil, p. 619-634.

Fink, S., and Fink, W., 1981, Interrelationships of ostariophysan fishes (Teleostei): Zoological Journal of the Linnean Society, v. 72.

—, 1996, Interrelationships of ostariophysan fishes (Teleostei), *in* Stiassny, M., Parenti, L., and Johnson, D., eds., Interrelationships of Fishes: San Diego, Academic Press, p. 209-249.

Forey, P., Yi, L., Patterson, C., and Davies, C., 2003, Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon: Journal of Systematic Palaeontology, v. 1, p. 227-330.

Gallagher, W., 1984, Paleoecology of the Delaware Valley region, Part II: Cretaceous to Quaternary: The Mosasaur, v. 2, p. 9-43.

Gallo-da-Silva, V., 1993, A "Coleção Cope" do Museu Nacional/UFRJ: Vertebrados Fósseis da Bahia, Sergipe e Pernambuco (Brasil), e sua Correlação Estratigráfica. [M.S. thesis]: Rio de Janeiro, Instituto de Geociências/Universidade Federal do Rio de Janeiro.

Gallo, V., FJ, F., and Coelho, P., 2006, Paleoictiofauna da Formação Altântida, Cretáceo Superior da Bacia de Pelotas, sul do Brasil, *in* Gallo, V., Brito, P., Silva, H.M.A., and Figueiredo, F., eds., Paleontologia de Vertebrados: Grandes Temas e Contribuições Cientificas: Rio de Janeiro, Interciência, p. 113-131.

Gasparini, Z., and Buffetaut, E., 1980, *Dolichochampsa minima*, ngn sp., a representative of a new family of eusuchian crocodiles from the Late Cretaceous of northern Argentina: Neues Jahrbuch für Geologie und Paläontologie v. 5, p. 257-271.

Gayet, M., 1991, "Holostean" and teleostean fishes of Bolivia, *in* Suarez-Soruco, ed., Fosiles y Facies de Bolivia, Vol. 1: Vertebrados, Volume 12 (3-4), Rev. Tec. Yaci. Petrol. Fisc. Bol., p. 357-718.

Gayet, M., Marshall, L., Sempere, T., Meunier, F., Cappetta, H., and Rage, J., 2001, Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications: Palaeogeography Palaeoclimatology Palaeoecology, v. 169, p. 39-68.

Gayet, M., and Meunier, F., 1998, Maastrichtian to early late Paleocene freshwater Ostichthyes of Bolivia: additions and comments, *in* Malabarba, L., Reis, R., Var, R., Lucena, Z., and Lucena, C., eds., Phylogeny and Classificaiton of Neotropical Fishes: Porto Alegre, Edipucrs, p. 85-110.

Giers, R., 1964, Die Grossfauna der Mukronatenkreide (unteres Obercampan) im östlichen Münsterland: Fortsehr. Geol. Rheinld Westf., v. 7, p. 213-294.

Goody, P., 1968, Skull of *Enchodus faujasi* from Maastricht of Souther Holland .I. .2: Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series B-Physical Sciences, v. 71, p. 209-&.

—, 1969, The Relationships of Certain Upper Cretaceous Teleosts with Special Reference to the Myctophoids, Bulletin of The British Museum (Natural History): London, Geology, p. 256.

—, 1976, *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of the North American enchodontid species: Palaeontographica Abteilung A, v. A152, p. 91-112.

Gottfried, M., and Krause, D., 1998, First Record of Gars (Lepisosteidae, Actinopterygii) on Madagascar: Late Creatceous Remains form the Mahajanga Basin: Journal of Vertebrate Paleontology, v. 18, p. 275-279.

Gottfried, M., and Ostrowski, S., 2008, Fossil fishing one piece at a time, with a catfish example from the Late Creatceous of Madagascar: Journal of Vertebrate Paleontology, v. 28, p. 85A-86A.

—, 2009, A surprising Amiid fish from the Late Cretaceous of Madagascar: Journal of Vertebrate Paleontology, v. 29, p. 108A-108A.

Gottfried, M., and Rabarison, A., 1997, First Mesozoic Gondwanan record of a sawshark (Chondrichthyes, Pristiophoriformes) from the Late Cretaceous of Madagascar: Journal of Vertebrate Paleontology, v. 17, p. 750-751.

Gottfried, M., Rabarison, J., and Randriamiarimanana, L., 2001, Late Cretaceous elasmobranchs from the Mahajanga Basin of Madagascar: Cretaceous Research, v. 22, p. 491-496.

Gottfried, M., Rogers, R., and Curry Rogers, K., 2004, First record of Late Cretaceous coelacanths from Madagascar, *in* G. Arratia, M.V.H.W., and R. Cloutier, ed., Recent Advances in the Origin and Early Radiation of Vertebrates: München, Germany, Verlag Dr. Friedrich Pfeil.

Grandstaff, B., Parris, D., Denton Jr., R., and Gallagher, W., 1992, Alphadon (Marsupialia) and Multituberculata (Allotheria) in the Cretaceous of Eastern North America: Journal of Vertebrate Paleontology, v. 12, p. 217-222.

Haas, G., 1978, A new tutle of the genus *Podocnemis* from the lower Cenomanian of 'Ein Yabrud: Israel Journal of Zoology, v. 27, p. 169-175.

Hargrave, J., 2007, Pteranodon (Reptilia: Pterosauria): Stratigraphic distribution and taphonomy in the lower Pierre Shale Group (Campanian), western South Dakota and eastern Wyoming, *in* Martin, J.E.P.D.C., ed., Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas, Volume 427: Geological Society of America Special Papers, p. 215-225.

Harrington Jr., R., 1955, The Osteocranium of the American Cyprinid Fish, *Notropis bifrenatus*, with an Annotated Synonymy of Teleost Skull Bones: Copeia, v. 4, p. 267-290.

Harstein, E., and Decina, L., 1986, A new Severn Formation (Early Middle Maastrichtian, Late Cretaceous) locality in Prince Georges County, Maryland: The Mosasaur, v. 3, p. 87-95.

Heckel, J., 1854, Über den Bau und die Eintheilung der Pycnodonten, nebst kurzer Beschreibung einiger neuen Arten derselben: Sitzungsberichte der keiserlichen Akademie der Wissenchaften, Mathematisch-Naturwissenshchaftliche Klasse v. 12, p. 433-464.

Hoganson, J., Campbell, J., and Murphy, E., 1994, Stratigraphy and paleontology of the Cretaceous Hell Creek Formation, Stumpf Site, Morton County, North Dakota: North Dakota Academy of Science Proceedings, v. 48, p. 95.

Huddleston, R., and Savoie, K., 1983, Telostean otoliths from the Late Cretaceous (Maestrichtian age) Severn Formation of Maryland: Proceedings fo the Biological Socieyt of Washington, v. 96, p. 658-663.

Hussakof, L., 1916, A new pycnodont fish, *Coelodus syriacus,* from the Creatceous of Syria: Bulletin of the American Museum of Natural History, v. 35, p. 135-138.

Jacobs, L., Mateus, O., Polcyn, M., Schulp, A., Antunes, M., Moraos, M., and Tavares, T., 2006, The occurrence and geological setting of Cretaceous dinosaurs, mosasaurs, plesiosaurs, and turtles from Angola: Journal of the Paleontological Society of Korea, v. 91-110.

Jain, S., and Sahni, A., 1983, Some Upper Cretaceous vertebrates from Central India and their paleogeographic implications, *in* Maheshwari, ed., Proceedings of the Symposium on Cretaceous of India: Palaeoecology, Palaeogeography, and Time Boundary: Lucknow, Indian Association of Palynostratigraphers, p. 66-83.

Jordan, D., and Everman, B., 1896, Fishes of North and Middle America: Bulletin of the U.S. National Museum, p. 131-133. pt. 1.

Kellner, A., 1994, Preliminary report on the microvertebrate fauna from teh Late Cretaceous Bauru strata near Peirópolis, Minas Gerais, Brazil: Journal of Vertebrate Paleontology, v. 14, p. 31A.

Khosla, A., Prasad, G., Verma, O., Jain, A., and Sahni, A., 2004, Discovery of a micromammal-yielding Deccan intertrappean site near Kisalpuri, Dindori District, Madhya Pradesh: Current Science, v. 87, p. 380-383.

Kriwet, J., and Gloy, U., 1995, Zwei mesopelagische Raubfische (Actinopterygii: Euteleostei) aud sem Unterturon der Kronsberg-Mulde bei Hannover/Misburg (NW-Deutschland): Berliner Geowiss Abh E, v. 16, p. 335-355.

Kriwet, J., Poyato-Ariza, F., and Sylvie, W., 1999, A revision of the pycnodontid fish *Coelodus subdiscus* Wenz 1989, from the Early Cretaceou of Montsec (Lleida, Spain): Treballs del Museu de Geologia de Barcelona, v. 8, p. 33-65.

Langston Jr, W., 1975, The Ceratopsian Dinosaurs and Associated Lower Vertebrates from the St. Mary River Formation (Maestrichtian) at Scabby Butte, Southern Alberta: Canadian Journal of Earth Sciences, v. 12, p. 1576-1608.

Lauginiger, E., 1984, An upper Campanian vertebrate fauna from the Chesapeake and Delaware Canal The Mosasaur, v. 2, p. 141-149.

Leonardi, A., 1966, L'ittiofauna cenomaniana di Floresta-Messina: Paleontol Ital, v. 60, p. 33-67.

Lewy, Z., Milner, A., and Patterson, C., 1992, Remarkably preserved natural endocranial casts of pterosaur and fish from the Late Cretaceous of Israel: GeologicalSurvey of Israel Current Research, v. 7, p. 31-35.

Liggett, G., Shimada, K., Bennett, S., and Schumacher, B., 2005, Cenomanian (Late Cretaceous) reptiles from northwestern Russell County, Kansas: Paleobios, v. 25, p. 9-17.

Longbottom, A., 1984, New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali: Bulletin of the British Museum of Natural History (Geology, v. 38, p. 1-26.

Malabarba, M., and Malabarba, L., 2010, Biogeography of Characiformes: an evaluation of the available information of fossil and extant taxa, *in* Nelson, J., Schultze, H.-P., and Wilson, M., eds., Origin and Phylogenetic Interrelationships of Teleosts: München, Germany, Verlag Dr. Friedrich Pfeil.

Manabe, Y., Hasegawa, Y., and Takahashi, T., 2003, A hadrosaurid vertebra fro mthe Ashizawa Formation, Futaba Group, Fukushima, Japan, Bulletin of the Gunma Museum of Natural History, Volume 7, p. 7-10.

Martin, L., and Stewart, J., 1977, Oldest (Turonian) Mosasaurs from Kansas Journal of Paleontology, v. 51, p. 973-975.

Martinelli, A., and Forasiepi, A., 2004, Late Cretaceous Vertebrates from Bajo de Santa Rosa (Allen Formation), Rio Negro province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae): Revista del Museo Argentino de Ciencias Naturales, nuevo serie, v. 6, p. 257-305.

Mathur, S., Gaur, S., Loyal, R., Tripathi, A., Tripathi, R., and Gupta, A., 2004, Occurrence of magnetite spherules in the Maastrichtian bone bed sedimentary sequence of Fatehgarh Formation, Barmer basin, India: Current Science, v. 89, p. 1259-1268.

Maury, C., 1930, O cretáceo da *Parahyba* do norte, Seviço Geologico E Minerali gique do Brasil Monographia, Volume 8, p. 1-305.

Mayden, R., 2012, Tree of Life Cypriniformes, *in* Mayden, R., ed., Volume 2012.

Miller, H., 1966, Cretceous vertebrate fauna from Phoebus Landing, North Carolina: The Journal of the Elisha Mitchell Scientific Society, v. 82, p. 93.

Müller, J., 1846, Über den Bau und die Grenzen der Ganoiden und über das natürlichen System der Fische Abhandlungen Akademie der Wissenschaften, Berlin, v. 1844, p. 117-216.

Naish, D., and Sweetman, S., 2011, A tiny maniraptoran dinosaur in the Lower Cretaceous Hastings Group: Evidence from a new vertebrate-bearing locality in south-east England: Cretaceous Research, v. 32, p. 464-471.

Nelson, E., 1949, The opercular series of the Catostomidae: Journal of Morphology, v. 85, p. 559-568.

Nelson, J., 1994, Fishes of the World: New York, John Wiley & Sons, Inc., 600 p.

Nelson, L., 2006, Fishes of the World: New York, Wiley.

Nelson, M., and Crooks, 1987, Stratigraphy and paleontology of the Cedar Mountain Formation (Lower Cretaceous), eastern Emery County, Utah, *in* Averett, W., ed., Paleontology and Geology of the Dinosaur Triangle Guidebook for 1987 Field Trip: Grand Junction, Museum of Western Colorado, p. 55-63.

Newbrey, M., Murray, A., Wilson, M., Brinkman, D., and Neuman, A., 2009, Seventy-five-million-year-old tropical tetra-like fish from Canada tracks Cretaceous global warming: Proceedings of the Royal Society B: Biological Sciences, v. 276, p. 3829-3833.

Nursall, R., 1996a, Distribution and ecology of pycnodont fishes, *in* Arratia, G., and Viohl, G., eds., Mesozoic Fishes -- Systematics and Paleoecology: München, Germany, Verlag Dr. Ffriedrich Pfeil, p. 115-124.

—, 1996b, The phylogeny of pycnodont fishes, *in* Arratia, G., and Viohl, G., eds., Mesozoic Fishes -- Systematics and Paleoecology: München, Germany, Verlag Dr. Friedrich Pfeil, p. 125-152.

O'Dogherty, L., 1994, Biochronology and Paleontology of Mid-Cretaceous Radiolarians from Northern Apennines (Italy) and Betic Cordillera (Spain): Memoires de Geologie (Lausanne), v. 21, p. 1-415.

Olson, S., and Parris, D., 1987, The Cretaceous Birds of New Jersey.

Otero, O., Valentin, X., and Garcia, G., 2008, Cretaceous characiform fishes (Teleostei: Ostariophysi) from Northern Tethys: description of new material from the Maastrichtian of Provence (Southern France) and palaeobiogeographical implications, *in* Cavin, L., Longbottom, A., and Richter, M., eds., Geological Society, London, Special Publications, Volume 295, p. 155-164.

Patterson, C., 1993, Oseichthyes: Teleostei, *in* Benton, M., ed., The Fossil Record 2: London, Chapman and Hall, p. 622-656.

Poyato-Ariza, F., Grande, T., and Diogo, R., 2010, General overview of fossil and Recent Gonorynchiformes (Teleostei, Ostariophysi), *in* Nelson, J., Schultze, H.-P., and Wilson, M., eds., Origin and Phylogenetic Interrelationships of Teleosts: München, Germany, Verlag Dr. Friedrich Pfeil, p. 269-293.

Rana, R., Kumar, K., Loyal, R., Sahni, A., Rose, K., Mussell, J., Singh, H., and Kulshreshtha, S., 2006, Selachians from the early Eocene Kapurdi Formation (Fuller's Earth), Barmer district, Rajasthan: Journal of the Geological Society of India, v. 67, p. 509-522.

Rebouças, J., and Silva Santos, R., 1956, Fauna ictiológica do fosfato de Pernambuco: Bol DNPM/DGM, v. 162, p. 1-29.

Regan, C., 1911, II.—The classification of the teleostean fishes of the order Ostariophysi.—1. Cyprinoidea: Journal of Natural History Series 8, v. 8, p. 13-32.

Rigo, D., 1999, The fossils of the Cretaceous Laterstätte of Polazzo (Foglian-Rediplugia, Gorizia, NE Italy): Natura Nascota, v. 9, p. 10-19.

Robertson, D., and Allen, G., 1996, Zoogeography of the shorefish fauna of Clipperton Atoll: Coral Reefs, v. 15, p. 121-131.

Rosen, D., 1973, Interrelationships of higher euteleostean fishes, *in* Greenwood, P., Miles, R., and Patterson, C., eds., Interrelationships of Fishes, Volume 53 (1973): London, Zoological Journal of the Linnean Society, p. 397-513.

Russell, D., 1967, Cretaceous vertebrates from the Anderson River N.W.T. : Canadian Journal of Earth Sciences, v. 4, p. 21-38.

Schumacher, B., 2007, A new polycotylid plesiosaur (Reptilia; Sauropterygia) from the Greenhorn Limestone (Upper Cretaceous; lower upper Cenomanian), Black Hills, South Dakota, *in* Martin, J.E.P.D.C., ed., Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas, Volume 427: Geological Society of America Special Papers, p. 133-146.

Schwimmer, D., 1986, Late Cretaceous fossils from the Blufftown Formation (Campanian) in western Georgia The Mosasaur, v. 3.

Shimada, K., and Everhart, M., 2003, Ptychodus mammillaris (Elasmobranchii) and Enchodus cf. E. shumardi (Teleostei) from the Fort Hays Limestone Member of the Niobrara Chalk (Upper Cretaceous) in Ellis County, Kansas: Transactions of the Kansas Academy of Science, v. 106, p. 171-176.

Shimada, K., Schumacher, B., Parkin, J., and Palermo, J., 2006, Fossil marine vertebrates from the lowermost Greenhorn Limestone (Upper Cretaceous : Middle Cenomanian) in southeastern Colorado: Journal of Paleontology, v. 80, p. 1-45.

Siegfried, P., 1954, Die Fisch-Fauna des Westfälisches Ober-Senons: Palaeont Abh A, v. 106, p. 1-36.

Sigogneau-Russell, D., Monbaron, M., and Russell, D., 1988, Decouverte de mammiferes dan le Mosozoique moyen d'Afrique [Discovery of mammals in the middle Mesozoic of Africa]: Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Plantes, v. 307, p. 1045-1050.

Silva, H., and Gallo, V., 2011, Taxonomic review and phylogenetic analysis of Enchodontoidei (Teleostei: Aulopiformes): Anais Da Academia Brasileira De Ciencias, v. 83, p. 483-511.

Silva Santos, R., and Salgado, M., 1969, *Enchodus longipectoralis* SCHAEFFER, a Cretacean teleost fish from state of Sergipe, Brazil Anais Da Academia Brasileira De Ciencias, v. 41, p. 381-&.

Simionescu, J., 1913, Megalosaurus aus der Unterkreide der Dobrogea (Rumänien) [Megalosaurus from the Lower Cretaceous of Dobrogea (Romania)]: Centralblatt für Mineralogie, Geologie, and Paläontologie, v. 1913, p. 686-687.

Slaughter, B., 1969, Astraconodon Cretaceous Triconodonts: Journal of Mammalogy, v. 50, p. 102- 107.

Slaughter, B., and Thurmond, J., 1974, A lower Cenomanian (Cretaceous) ichthyofauna from the Bahariya Formation of Egypt: Annal of the Geological Survey of Egypt, v. 4, p. 25-40.

Sohl, N., 1960, Archeogastropoda, Mesogastropoda, and stratigraphy of the Ripley, Owl Creek, and Prairie Bluff Formations, United States Geological Survey Professional Paper, Volume 331, p. 1-151.

Sorbini, L., 1976, L'ittiofauna cretacea di Cinto Euganeo (Padoa-Nord Italia): Boll Mus Civ Stor Nat Verona, v. 3.

Sternberg, C., 1924, Report on a collection of vertebrates from Wood Mountain, Southern Saskatchewan, collected by C.M. Sternberg, 1921, *in* Bulletin, C.D.o.M.G.S., ed., Volume 38, p. 27-28.

Taverne, L., 2003, Les poissons crétacés de Nardò. 16° *Sorbinicharax verraesi* gen. et sp. nov. (Teleostei, Ostariophysi, Characiformes): Bollettino del Museo Civico di toria Naturale di Verona Geologia Paleontologia Preistoria, v. 27, p. 29-45.

Thomas, H., Roger, J., Halawani, M., Memesh, A., Lebret, P., Bourdillon, C., Buffetaut, E., Cappetta, H., Cavelier, C., Dutheil, D., Tonge, H., and Vaslet, D., 1999, Late Paleocene to Early Eocene marine vertebrates from the Uppermost Aruma Formation (northern Saudi Arabia): implications for the KT transition: Comptes Rendus de l'Academie des Sciences, Serie II. Sciences de la Terre et des Plantes, v. 329, p. 905-912.

Tintori, A., 1981, Two new pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy): Rivista Italiana di Paleontologia v. 86, p. 795-824.

Trapani, J., and Schaefer, S., 2001, Position of Developing Replacement Teeth in Teleosts: Copeia, v. 2001, p. 35-51.

Vullo, R., Bernárdez, E., and Buscalioni, A., 2009, Vertebrates from the middle?–late Cenomanian La Cabaña Formation (Asturias, northern Spain): Palaeoenvironmental and palaeobiogeographic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 276, p. 120-129.

Welles, S., 1943, Elasmosaurid plesiosaurs with description of new material from California and Colorado, Memoirs of the University of California, Volume 13, University of California Press, p. 125-254.

Wenz, S., 1989, A new *Coelodus* species (Pisces, Pycnodontiformes) from the Lower Cretaceous of Montsech (Lerida Province, Spain) - *Coelodus subdiscus* n. sp.: Geobios, v. 22, p. 515-522.

Werner, C., 1993, Eine neue Fundstelle terrestrischer Wirbeltiere aus der Kreide des Sudan [A new terrestrial vertebrate locality from the Cretaceous of Sudan], *in* Kohring, R., ed., Miscellanea Palaeontologica 2. Berliner Geowissenschaften Abhandlungen, Reihe, Volume E 9, p. 201-209.

Whetstone, K., and Collins, J., 1982, Fossil crabs (Crustacea, Decapoda) from the Upper Cretaceous Eutaw Formation of Alabama Journal of Paleontology, v. 56, p. 1218-1222.

Wilson, M., and Chalifa, Y., 1989, Fossil Marine Actinopterygian fishes from the Kaskapau Formation (Upper Cretaceous, Turonian) near Watino, Alberta Canadian Journal of Earth Sciences, v. 26, p. 2604-2620.

Winkler, D., Murry, P., and Jacops, L., 1990, Early Cretaceous (Comanchean) Vertebrates of Central Texas: Journal of Vertebrate Paleontology, v. 10, p. 95-116.

Yabumoto, Y., and Uyeno, T., 1994, Late Mesozoic and Cenozoic fish faunas of Japan: Island Arc, v. 3, p. 255-269.

Zangerl, R., 1948, The vertebrate fauna of the Selma formation of Alabama I. Introduction. II. The Pleurodiran turtles: Fieldiana Geol, v. 3, p. 1-56.

CHAPTER 3: THE ALBULOID FISHES (TELEOSTEI: ELOPOMORPHA) OF THE LATE CRETACEOUS OF MADAGASCAR

INTRODUCTION

Elopomorpha history: The Elopomorpha is a superorder of teleosts with a relatively poor fossil record. These fishes are grouped together based upon the shared presence of a leptocephalus larval stage (pre-metamorphic stage) (Greenwood et al., 1966) which can last from two to 24 months (Castle, 1984; Mojica Jr. et al., 1995; Pfeiler et al., 1988). The majority of researchers agree that leptocephalus larva is a specialized trait and a synapomorphy of Elopomorpha (Inoue et al., 2004). The Elopomorpha is placed near the base of teleost phylogeny (Figure 3), and is thought to be the sister taxon to all other extant groups of teleosts. Additional characters used to categorize elopomorphs (Forey, 1973a, b) include: 1) presence of prenasal and rostral ossicles; 2) presence of pectoral splint; 3) fusion between angular and retroarticular bones with the lower jaw (Nelson, 1973), and 4) sperm morphology (Jamieson, 1991). Within the Elopomorpha, there are four orders: Elopiformes, Albuliformes, Notacanthiformes, and Anguilliformes (Forey et al., 1996). The fossils discussed here are placed in the Elopiformes and Albuliformes. Fish within “elopomorpha” tend to be referred to colloquially as elopomorph, elopiform, albuloid, or albulid. The fossil record of these fishes is mainly comprised of distinctive toothplates and vertebrae, with diagnostic elements other than teeth and vertebrae rare. This study analyses the presence of elopomorphs from the Late Cretaceous of the Mahajanga Basin in northwestern Madagascar and assesses the utility of using geometric morphometrics in placing isolated elopomorpha vertebrae into a taxonomically restricted group.

MATERIALS AND METHODS

Institutional abbreviations

BMNH – Museum of Natural History, London, England; **R.G.** - Royal Museum for Central Africa, Tervuren, Belgium; **UMMZ** – University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; **P** - Field Museum of Natural History Paleontological Collections (also known as FMNH), Chicago, Illinois, USA; **CNHM** – Chicago Natural History Museum Ichthyology collections (synonymous with Field Museum); **MAD** – Mahajanga Basin Project field number. Madagascar specimens were compared to identified museum specimens and literature descriptions with photographs.

Field Collection and Image Capture

The fish material from the Late Cretaceous of Madagascar was collected by the Mahajanga Basin Project by standard surface collection methods at microsite localities during field seasons ranging from 1993 – 2010. The specimens herein from Madagascar have a prefix of "MAD" followed by a field number. When the specimens are accessioned upon publication, they will be housed in the University of Antananarivo in Antananarivo, Madagascar (UA prefix), or in the Field Museum of Natural History in Chicago, Illinois (FMNH prefix). All images were captured using a Nikon Coolpix L18.

Systematic Paleontology

ACTINOPTERYGII Cope, 1887

TELEOSTEI Müller, 1846

ELOPOMORPHA Greenwood et al., 1966

ELOPIFORMES Sauvage, 1875

ALBULOIDEI Greenwood et al., 1966

Family Phyllodontidae Dartevelle and Casier, 1943

Egertonia Cocchi, 1864

Comparative material: BMNH 38814, *Egertonia isodonta,* holotype (Figure 23); R.G. 4599, *Egertonia sp.* (Figure 24).

Referred material: Madagascar specimens MAD 93194A, partial toothplate (Figure 25); MAD 93194B, partial toothplate (Figure 26).

***Egertonia* osteology:** *Egertonia* toothplates which are described by Estes (1969) as having the following characteristics*:* 1) vertically stacked replacement teeth; 2) regularly convex (nearly hemispherical or flattened) teeth; and 3) relatively thick enamel (Estes, 1969). Toothplates of *Egertonia isodonta* (Figure 23) and *Egertonia* sp. (Figure 24) both exhibit the key characteristics of *Egertonia.*

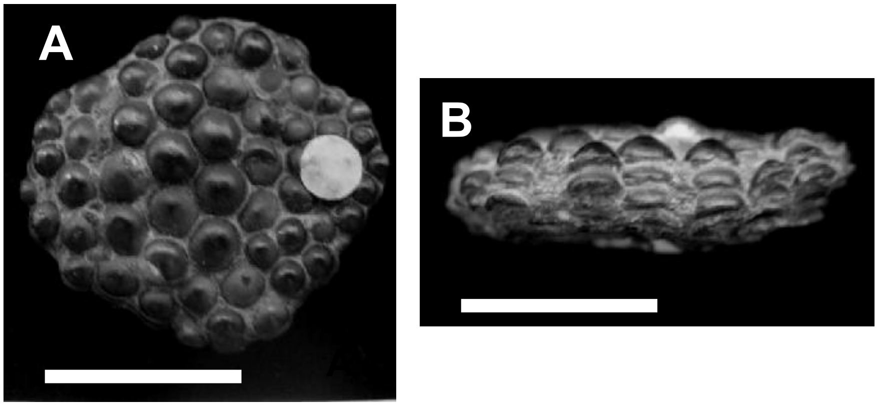


FIGURE 23: BMNH 38814, Holotype of *Egertonia isodonta.* Toothplate shows the occlusal (A) and lateral (B) views. Scale bar = 1 centimeter. Photo courtesy of M. Gottfried.

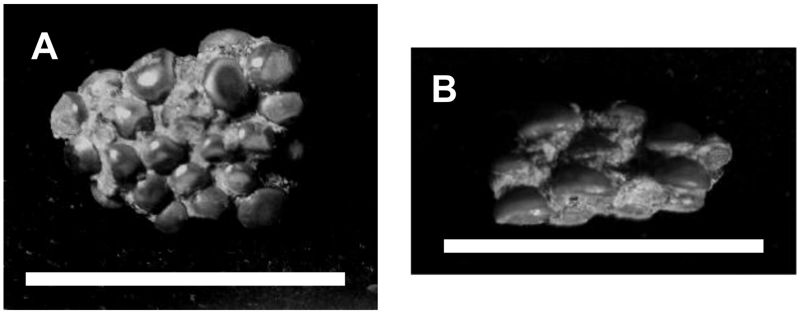


FIGURE 24: R.G.4599, *Egertonia sp.* toothplate in occlusal (A) and lateral (B) views. Scale bar = 1 centimeter. Photo courtesy of M. Gottfried.

Identification of material: The toothplates from the Mahajanga Basin of Madagascar are incomplete and do not preserve a complete bony base and, and therefore cannot be identified as basibranchial versus parasphenoid toothplates. There are complete series of replacement teeth and several are directly comparable to the known *Egertonia* specimens. The Madagascar toothplates (Figures 25 and 26) can be assigned to *Egertonia* based on the above three characteristics. Based on the cross-sections of each of these specimens, their tooth placement is similar, and they exhibit vertically stacked, hemispherical replacement teeth with relatively thick enamel.

Figure 25 (MAD 93194) is an incomplete toothplate lengthwise at 1 centimeter long and 0.8 centimeters wide with varying thickness across the toothplate. Many albuloid toothplates have varying degrees of thickness within one toothplate, in order to provide a fitted crushing surface area and fit against the antagonistic toothplate. Figure 26 (MAD 93194) is an incomplete toothplate approximately 1.25 centimeters long and 0.8 centimeters wide. In Figure 26, the toothplate is oblate on the left hand side and thins towards the right of the toothplate. The individual teeth of both toothplates are very small (less than or equal to 0.5 millimeters). These two specimens have the same field number "MAD 93194" but they are not assumed to be associated, they were collected no the same day.

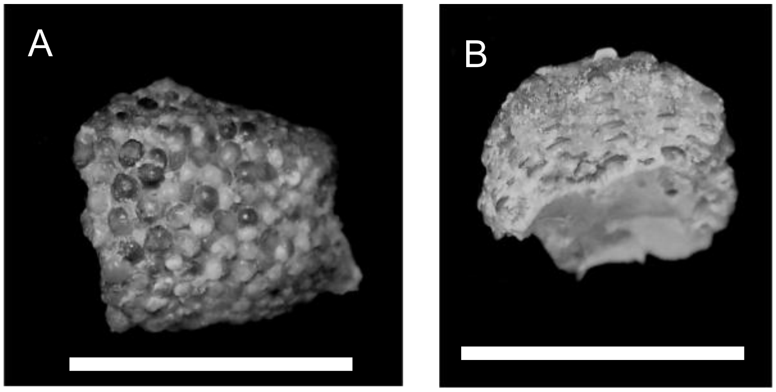


FIGURE 25: MAD 93194, *Egertonia* from Madagascar shown in occlusal (A) and lateral (B) view. Scale bar = 1 centimeter.

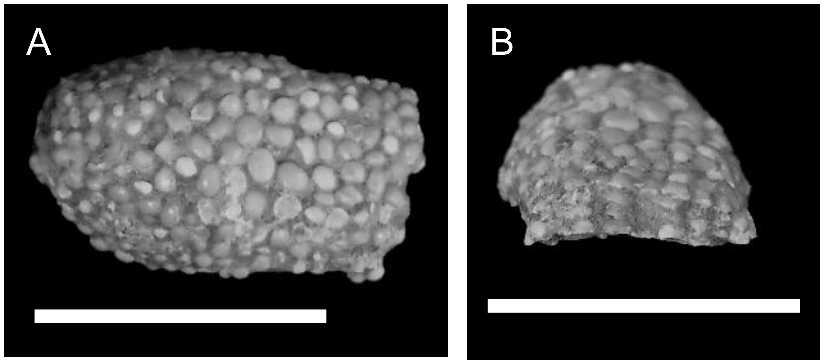


FIGURE 26: MAD 93194, *Egertonia* from Madagascar shown in occlusal (A) and lateral (B) view. Scale bar = 1 centimeter.

ACTINOPTERYGII Cope, 1887

TELEOSTEI Müller, 1846

ELOPOMORPHA Greenwood et al., 1966

ELOPIFORMES Sauvage, 1875

ALBULOIDEI Greenwood et al., 1966

Family Phyllodontidae Dartevelle and Casier, 1943

Paralbula Blake, 1940

Comparative material: No numbers were given for referred material within Estes 1969 paper (Figure 27).

Referred material*:* MAD 07235, *Paralbula* partial toothplate (Figure 28) and MAD 07274, *Paralbula* partial toothplate (Figure 29). Both toothplates are from the "Lac Kinkony" Member of the Maevarano formation.

Paralbula osteology: *Paralbula* toothplates are identified on the basis of the following criteria: 1) alternate tooth placement; 2) hemispherical teeth with a basilar foramen; 3) tooth surface is smooth or sparsely punctuate (can occur radially); and 4) toothplate with a curved occlusal surface (Estes, 1969). The holotype specimen of *Paralbula marylandica,* from the Eocene of Maryland, possesses the four features listed above (Figure 27).

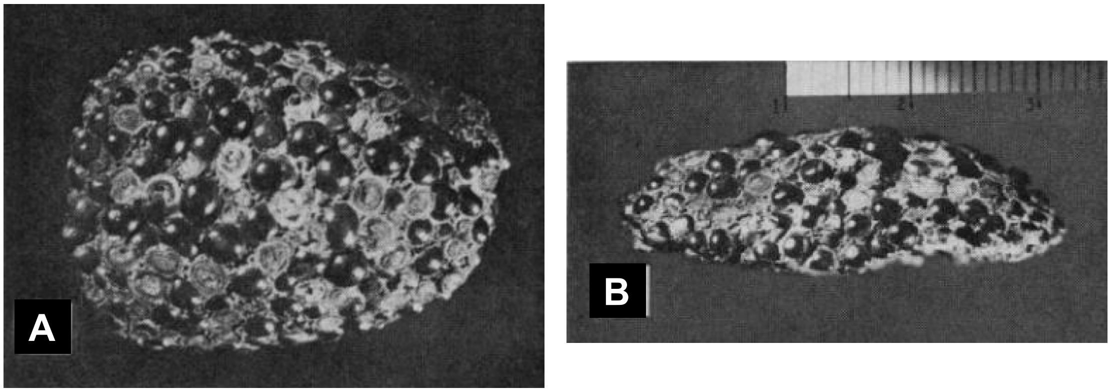


FIGURE 27: Holotype of *Paralbula marylandica* shown in occlusal (A) and lateral (B) views from the Eocene of Maryland (scale bar is indeterminate) (Estes, 1969).

Identification of material: The Madagascar specimens of *Paralbula* (Figures 28 and 29) are incomplete with weathered edges, but are oval in shape when complete. There are no bony bases associated with these toothplates. MAD 07235 (Figure 28) is 1.10 centimeters long, 1 centimeter wide, and 0.30 centimeters thick. MAD 07274 (Figure 29) is 1 centimeter long by 1centimeter wide and 0.25 centimeters thick. The toothplates exhibit curved occlusal surfaces that are slightly flattened, not from deformation. Individual teeth have relatively smooth surface textures, and are hemispherical or slightly flattened, irregular to slightly elongate, with thick enamel. The individual teeth are strongly cemented together, and several of the individual teeth are weathered on the occlusal surfaces. These toothplates identified as *Paralbula* occur only within the Lac Kinkony member of the Maevarano Formation, which also contains very large, albuloid vertebrae that will be addressed below. Taxonomic association of these toothplates and vertebrae is unknown.

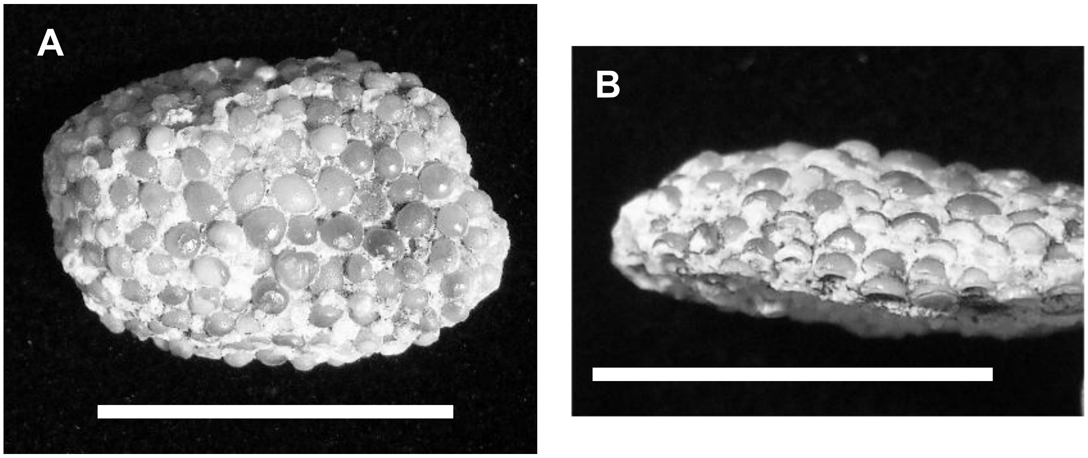


FIGURE 28: MAD 07235, *Paralbula* from Madagascar shown in occlusal (A) and lateral (B) view. Scale bar = 1 centimeter.

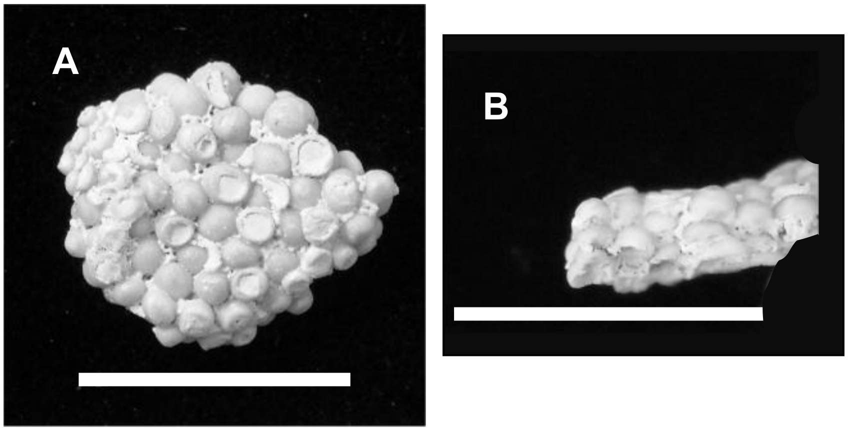


FIGURE 29: MAD 07274, *Paralbula* from Madagascar shown in occlusal (A) and lateral (B) view. Scale bare = 1 centimeter.

ACTINOPTERYGII Cope, 1887

TELEOSTEI Müller, 1846

ELOPOMORPHA Greenwood et al., 1966

ALBULIFORMES Greenwood et al., 1966

Family Albulidae Bleeker, 1859

Albula Scopoli, 1777

Comparative material: *Albula plumieri,* no catalogue number given (Figure 30) (Estes, 1969); UMMZ 186965-S, skull of recent *Albula vulpes* (Figure 31). P27494, *Albula dunklei* (Figure 33).

Referred material : MAD 03302, Partial toothplate of *Albula sp*. from Madagascar (Figure 32); MAD 01020, incomplete right dentary with symphysial end (Figure 34); MAD 03020, incomplete dentary with tooth patch (Figure 35).

***Albula* osteology and identification of material:** *Albula* is a moderately diverse fish genus, ranging from Cretaceous to Recent. Albulines have toothplates with a crushing dentition that are used in coastal benthic environments for preying upon small invertebrates (Forey, 1973b). Figure 30 shows a recent specimen of *Albula plumieri* from Estes (1969), which is now accepted as synonymous with *Albula vulpes* (Linnaeus, 1758), (Whitehead, 1986). Recent *Albula vulpes* (Figure 31) shows an articulated palate with both occlusal and lateral views of toothplates still within the skull. The Madagascar *Albula* MAD 03302 (Figure 32) is a single, incomplete toothplate approximately 0.5 centimeters long, of uncertain orientation. The toothplate base is thin and shows muscles scars, but there is not enough anatomical information to determine the precise location of the toothplate within the oral cavity, and it is too small to fully determine its shape, as most alubloid toothplates have at least slight curvature (Estes, 1969). The teeth themselves are on pedestals (averaging 1 millimeter in height) sitting on the bony plate, and range between wide (1 millimeter) and narrow (less than 0.25 millimeter) across the crown, over the surface of the specimen. As in typical *Albula* toothplates, the teeth in the center are larger and decrease in size as you most towards the perimeter (Estes, 1969).

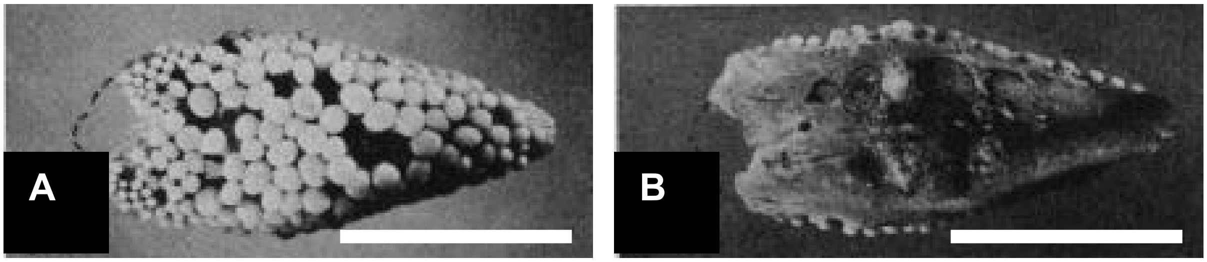


FIGURE 30: From Estes (1969) showing the occlusal (A) and basal attachment area (B) (with lateral view of individual teeth) aspects of a toothplate of Recent *Albula plumieri* (= *Albula vulpes*). No catalogue number provided.

FIGURE 31: Recent *Albula vulpes* (UMMZ 186965-S). This is a medial view of the left side of the skull from the midline. The rostrum is to the right. The toothplates show the pedestal teeth. Scale bar = 1 centimeter.

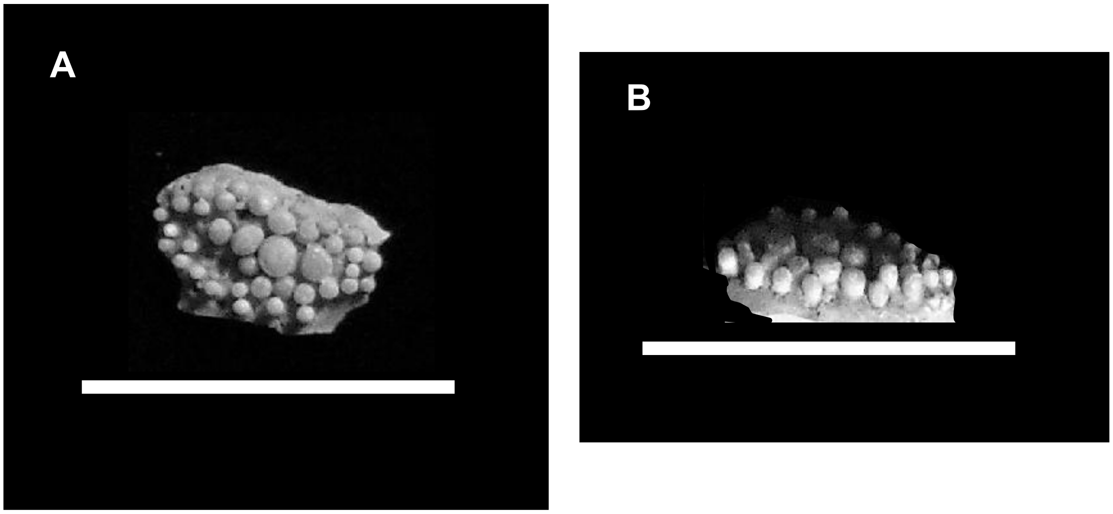


FIGURE 32: MAD 03302, *Albula* toothplate from Madagascar in occlusal (A) and oblique (B) views. Scale bar = 1 centimeter.

In addition to the *Albula* toothplate found in this work, there are also remains of partial dentaries that have been attributed to *Albula*. There are two separate, incomplete dentaries from the Late Cretaceous of Madagascar that are comparable to Recent *Albula* and the Late Cretaceous *Albula dunklei* from the Selma Formation in Alabama (Applegate, 1970). The *Albula dunklei* dentary has a " tooth patch" which is also evident in Recent *Albula*. The fossil *Albula dunklei* dentary (Figure 33) has a tooth patch dorsally for villiform teeth. Ventrally, there is a large flange and deep groove for a mandibular sensory canal. The Madagascar *Albula* dentary MAD 01020 (Figure 34), is the distal portion (2 centimeters long, 0.5 centimeters wide, and 1 centimeter at its deepest point) of the left dentary, with the symphysial end intact. Dorsally, there is a tooth patch, with over 100 millimeter-sized pits that would have accommodated individual teeth. Ventrally, there is the same large flange and a deep groove with a sensory canal. These features are indicative of Recent *Albula vulpes* dentaries (Forey, 1973b). (Nybelin, 1976) detailed the *Albula* dentary, stating it as having a nearly vertical symphysial margin, an extremely wide gutter on the ventral portion of the dentary (for mandibular sensory canal) that is open laterally for most of its length. Madagascar *Albula* MAD 03020 (Figure 35) is a partial dentary midportion. The specimen shows a deep groove ventrally and tooth patch dorsally and is akin to the other *Albula* partial dentary, but slightly less complete.

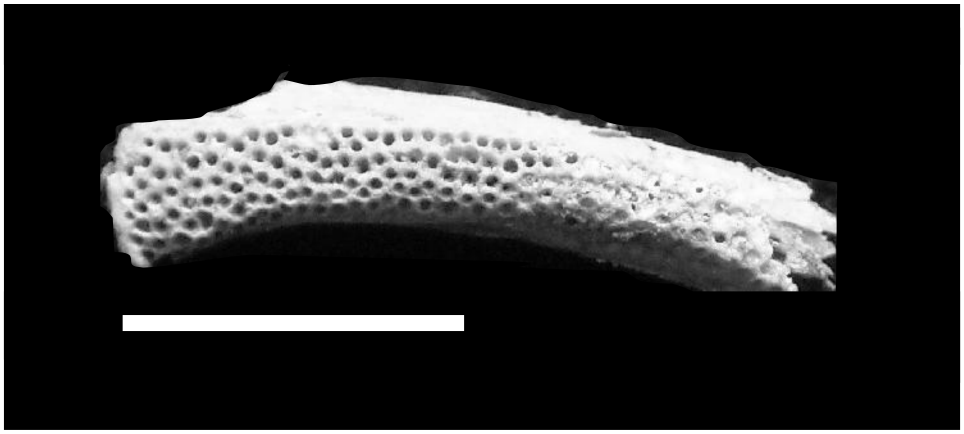


FIGURE 33: P27494, *Albula dunklei,* distal right dentary (dorsal view) of tooth patch, from the Selma Formation of Alabama. Scale bar = 1 centimeter.

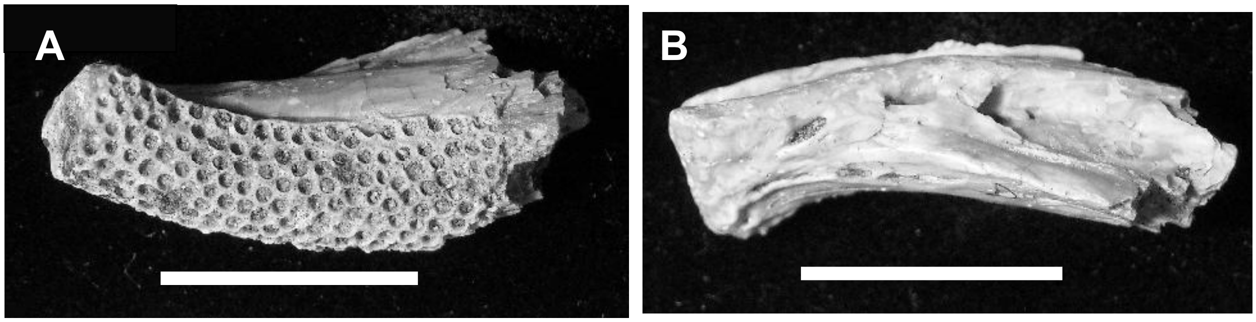


FIGURE 34: MAD 01020, *Albula,* left dentary from Madagascar. The dorsal side (A), with the tooth patch; ventral side (B) with the deep groove and sensory canal. Scale bar = 1 centimeter.

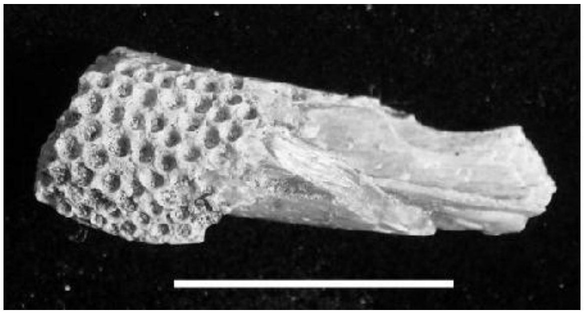


FIGURE 35: MAD 03020, *Albula,* dentary from Madagascar showing the dorsally situated tooth patch. Scale bar = 1 centimeter.

DISTRIBUTIONS OF TAXA

Egertonia:

Egertonia is known from the Paleocene and Eocene in the Northern Hemisphere (Table 7). This relatively rare phyllodontid has never been recorded in, or proximate to, Africa, nor earlier than the Late Paleocene. *Egertonia* is inferred to have originated in the Cretaceous (Estes 1969), because it appeared to be a specialized phyllodontid by the time of the first appearance datum.

TABLE 7: Geographic and stratigraphic distribution of *Egertonia* during the Paleocene and Eocene.

COUNTRY	FORMATION/LOCALITY	REFERENCE
Belgium	Dormaal	Estes, 1969
England	Bracklesham	Bone et al., 1991
	London Clay	Casier, 1966
India	Sri Kolayat-Ji	Jolly and Loyal, 1985
	Khuiala	Kumar et al., 2007
United States	Tuscahoma and Bashi (Mississippi)	Case, 1986
	Cannonball (North Dakota)	Cvancara and Hoganson, 1993
	Berkeley County (South Carolina)	Weems, 1998
	Fisher/Sullivan Site (Viginia)	Rose, 1999

The presence of *Egertonia* in the Late Cretaceous extends the temporal range of this genus by 12 million years, from 58.2 to now at least 70 Ma to the Maastrichtian of Madagascar. All previous accounts of *Egertonia* were within the Northern Hemisphere, and its occurrence in Madagascar extends the geographic range into the Southern Hemisphere, and to Gondwanan Landmasses (Figure 36). There is an occurrence of this genus in Rajasthan, India from the Eocene (Jolly and Loyal, 1985; Kumar et al., 2007). These Indian occurrences are known from singular teeth that are potentially comparable to *Egertonia*, but identification based on single teeth is difficult to verify. The Indian fossils are Early Eocene (Kumar et al., 2007) and Middle Eocene

(Jolly and Loyal, 1985) which is much younger than the Mahajanga Basin material, and corresponds to the time when the Indian subcontinent was converging with Asia.

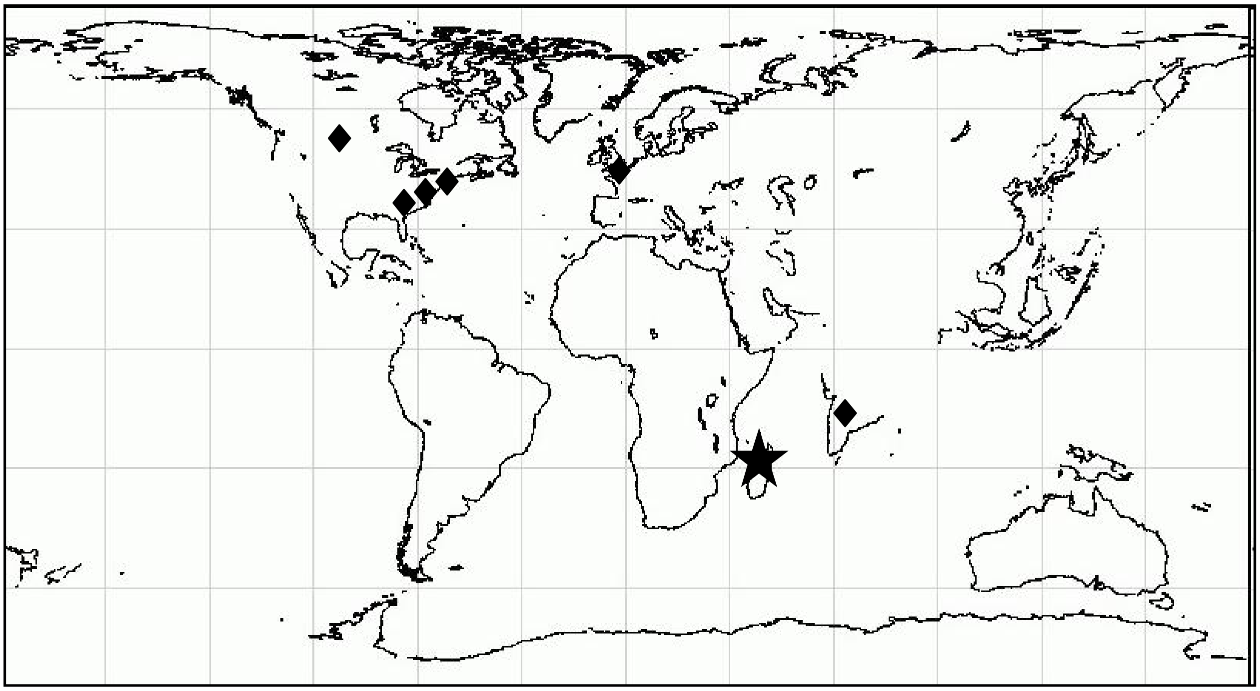


FIGURE 36: *Egertonia* localities (black diamonds) and distribution during the Paleocene and Eocene, with the addition of the Late Cretaceous of Madagascar occurrence (star). Map modified from Alroy, 2012.

Paralbula:

Paralbula is known from the Cretaceous in the Northern Hemisphere (Table 8). The presence of *Paralbula* in the Maastrichtian of Madagascar extends the geographical distribution of this genus into the Southern Hemisphere (Figure 37). Given the regular occurrences of *Paralbula* from the Early Campanian to the Middle-Eocene, it is not surprising to have additional geographic occurrences of *Paralbula* within this timeframe.

TABLE 8: Geographic and stratigraphic distribution of *Paralbula* during the Cretaceous.

COUNTRY	**GEOLOGY/LOCALITY**	**REFERENCE**
Canada	Judith River (Alberta, Saskatchewan)	Beavan and Russell, 1999; Brinkman, 1990, 2008; Eberth and Brinkman, 1997
	Foremost and Oldman Formations (Alberta)	Peng et al., 2001
	St. Mary River (Alberta)	Langston Jr, 1967
Spain	La Cabaña	Vullo et al., 2009
United States	Blufftown (Georgia)	Case, 1987; Schwimmer, 1986
	Hell Creek (Montana)	Estes, 1965, 1969
	Judith River (Montana)	Dodson, 1984; Fiorillo, 1989; Sahni, 1972
	Fruitland (New Mexico)	Armstrong-Ziegler, 1978
	Lewis Shale (New Mexico)	Hutchinson and Kues, 1985
	Mount Laurel (New Jersey)	Lauginiger, 1984
	Hornerstown (New Jersey)	Olson and Parris, 1987
	Marshalltown (New Jersey)	Grandstaff et al., 1992
	New Jersey Coastal Plain (New Jersey)	Gallagher et al., 1986
	Black Creek (North Carolina)	Miller, 1967
	Donoho Creek (South Carolina)	Cicimurri, 2007
	Ferris (Wyoming)	Lillegraven and Eberle, 1999

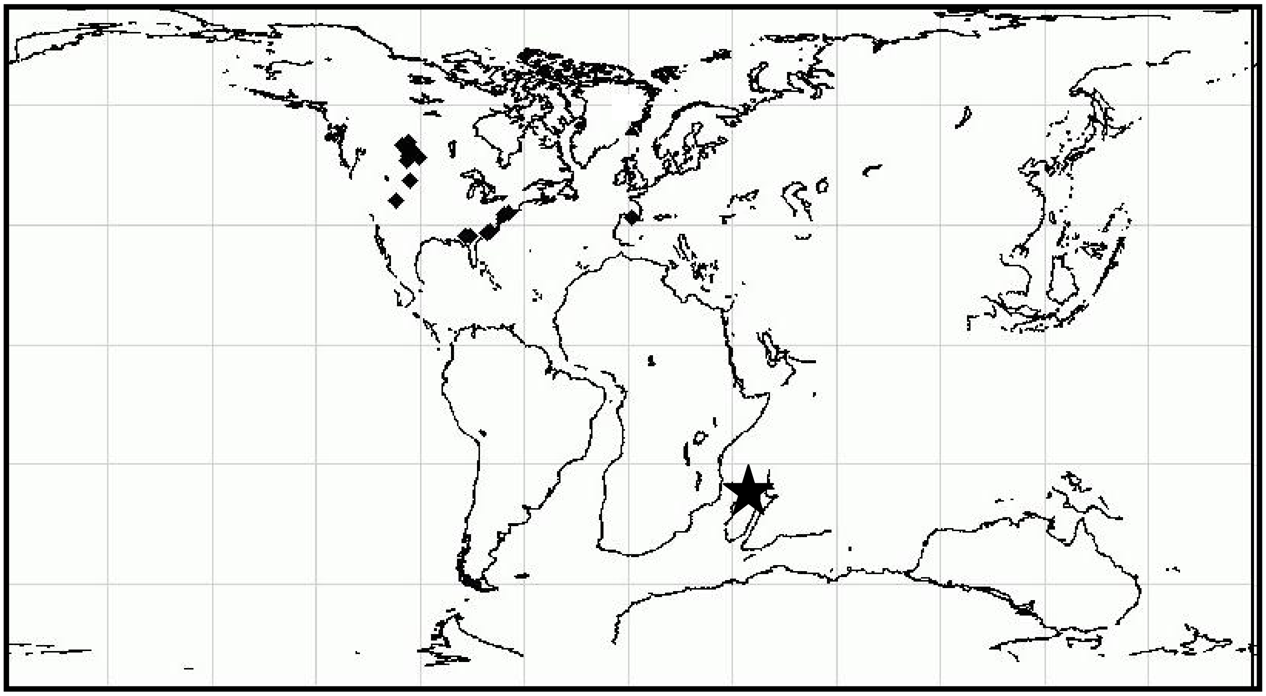


Figure 37: *Paralbula* localities and distribution during the Cretaceous (diamonds) and added Madagascar occurrence (star). Map modified from Alroy, 2012.

Albula:

The family Albulidae reached its peak diversity and abundance approximately during the Mid-Cretaceous (100 million years ago) (Colborn et al., 2001). During the Cretaceous, *Albula* fossils have been recorded within the Northern Hemisphere (Table 9).

TABLE 9: Geographic and stratigraphic distribution of *Albula* during the Cretaceous.

COUNTRY	**GEOLOGY/LOCALITY**	**REFERENCE**
Canada	Bearpaw (Alberta)	Russell and Landes, 1937
	Blood River Sandstone (Alberta)	Russell and Landes, 1937
	Eastend (Alberta)	Russell and Landes, 1937
	Judith River (Alberta)	Russell and Landes, 1937
	Powkowki (Alberta)	Russell and Landes, 1937
United States	Selma (Alabama)	Applegate, 1970; Sohl and Koch, 1983; Zangerl, 1948
	Moreno (California)	Anderson, 1958
	Blufftown (Georgia)	Case, 1987; Schwimmer, 1986

TABLE 9, continued

United States	Maryland	Sohl and Koch, 1984
	Coleraine (Minnesota)	Bergquist, 1944
	Chiwapa (Mississippi)	Sohl and Koch, 1983
	Marshalltown (New Jersey)	Grandstaff et al., 1992
	Black Creek (North Carolina)	Miller, 1967
	Donoho (South Carolina)	Cicimurri, 2007
	Coon Creek (Tennessee)	Wade, 1926
	Owl Creek (Mississippi; Tennessee)	Sohl and Koch, 1983
	Navarro (Texas)	Stephenson, 1941
	Escondido (Texas)	Sohl and Koch, 1984
	Vermilion Creek (Wyoming)	Reeside, 1955
Uzbekistan	Kyzyl-Kum	Nessov, 1981; Nessov, 1985

The vast majority of *Albula* fossils from the Cretaceous and Paleogene are from North America, along with a few specimens from Uzbekistan (Nessov, 1981). The occurrence of *Albula* in the Late Cretaceous of Madagascar extends the geographical range of this genus during this time frame. A map of the Cretaceous *Albula* deposits is shown below, to indicate the impact of the addition of the Madagascar material (Figure 38).

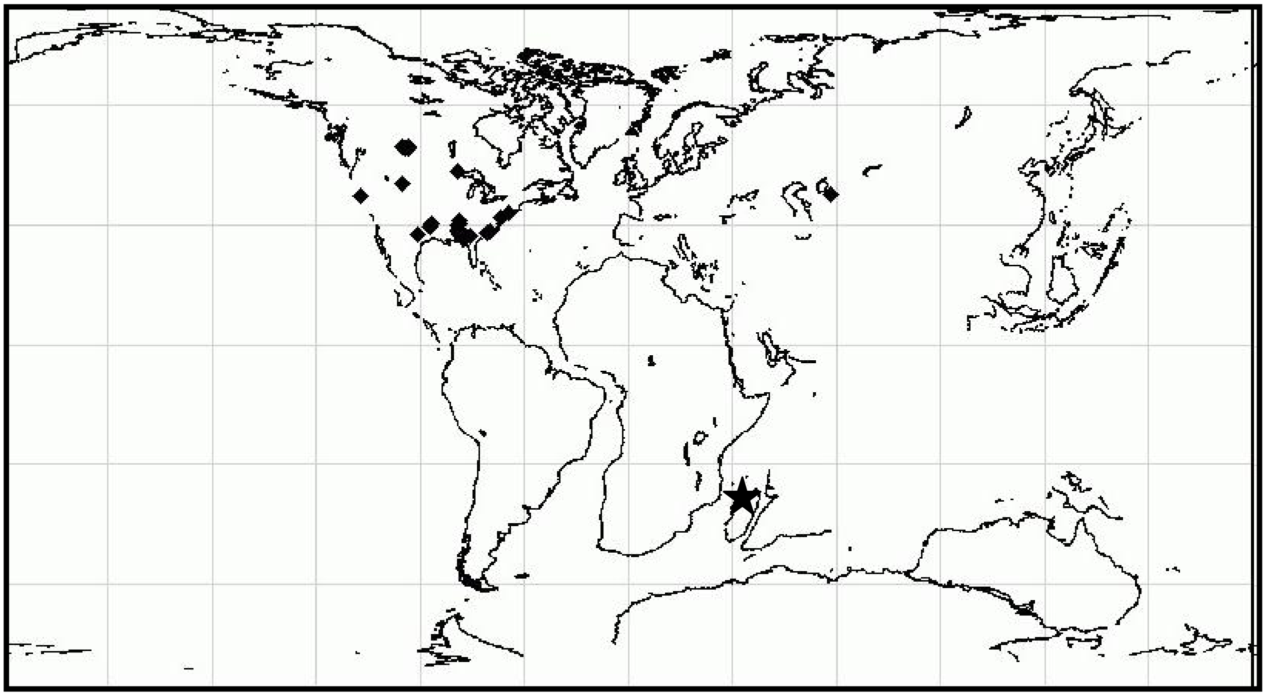


Figure 38: *Albula* localities and distribution during the Cretaceous (diamonds) with the added Madagascar occurrence (star). Map modified from Alroy, 2012.

SUMMARY OF NEWLY IDENTIFIED TAXA

The Mahajanga Basin in Madagascar has a diverse presence of elopomorph fossils from the Late Cretaceous. The identification of elopomorphs in the fossil record is reliant upon identifications of toothplates and vertebrae, which is challenging. The taxa discussed in this work, *Egertonia, Paralbula,* and *Albula* all increase our understanding of their true distribution during the Cretaceous. The presence of *Egertonia* increases their temporal range back into the Cretaceous as well. The presence of these taxa within the Southern Hemisphere shows how the elopomorphs were likely widely distributed and diverse during the Cretaceous, especially in shallow seas. As more of these taxa are discovered in Cretaceous sediments, the more light will be shed on their paleoecology and evolution.

ANALYSIS OF VERTEBRAL VARIATION WITHIN AND AMONG ELOPOMORPHS

In an attempt to enhance known taxonomic diversity of elopomorphs, an analysis was conducted on the outline of vertebral bodies using geometric morphometrics.

Description of elopomorph vertebrae: Albuloid vertebrae are distinct from those of other teleosts. Superficially, the vertebrae are similar to shark centra in shape and thickness. Elopomorph vertebrae are circular to oval and have amphicoelous centra (Figure 39). The vertebrae are flattened compared to other teleosts and have a relatively simple structure around the perimeter. The vertebrate have areas of striated bone around the edge, with spaces that accommodate the neural arch (dorsally), hemal arch (ventrally), or ribs (ventrolaterally) as you move down the vertebral column. The ventral side of the vertebrae may bear shallow indentation, presumably to aid in accommodating vasculature. There are two main types of fish vertebrae, “trunk” vertebrae (also known as abdominal vertebrae) do not have a hemal arch, but with basopohyses) and “caudal” vertebrae which are located more caudally and have a hemal arch, but no basopophyses (Homberger and Walker Jr., 2004). The shape of the vertebrae can be symmetrical (caudal or some abdominal) or slightly asymmetrical. The vertebral width can be greater on the ventral portion of the vertebra (abdominal vertebrae with ribs) or greater on the dorsal side of the vertebra (in more rostral vertebrae).

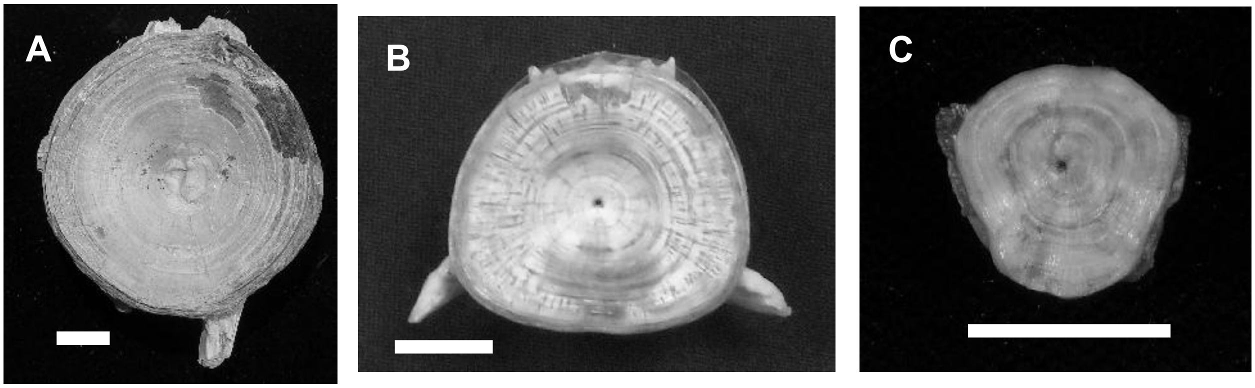


FIGURE 39: Comparative elopomorph vertebrae to show the variation in shape along the vertebral column. Dorsal is at the top of each picture. Symmetrical caudal vertebra (A; P27416), wider ventrally abdominal vertebra (B; CNHM 51336), and wider dorsally rostral vertebra (C; UMMZ 186965-S). Scale bar = 1 centimeter.

The elopomorph vertebrae from Madagascar encompass a wide range of morphotypes (Figure 40) that are distributed across the localities of the Maevarano Formation. Vertebrae range in size from small to large (less than 0.5 centimeters to over 2.5 centimeters at their widest point). The vertebrae range qualitatively from simple, slightly sub-circular and thin to heavily reinforced with a highly sigmoidal margin. Most of the vertebrae are around 1.0 – 1.5 centimeters at their widest point, and are subcircular.

FIGURE 40: Examples of morphological variation in elopomorph vertebrae from the Late Cretaceous of Madagascar. Scale bar = 1 centimeter.

Vertebral Analysis Materials and Methods

Geometric morphometrics were used to determine whether the noticeable and distinctive shape difference in vertebral centrum outlines could be distinguished quantitatively. The vertebral centra from known Recent and fossil elopomorphs were compared to unknown fossil elopomorph vertebrae from the Late Cretaceous of Madagascar. Vertebral shape was examined within and between individuals of the same taxa, and between individuals of different taxa. The goal of this analysis is to determine the possibility of using isolated elopomorph vertebrae for taxonomic identifications.

Image preparation: Seventy-five vertebrae were photographed from three museum collections and from Madagascar including: From the Field Museum of Natural History (Geology division FMNH) there were 18 fossil vertebrae from *Albula, Paratarpon?, and Pachyrhizodus;* From the Field Museum of Natural History

Ichthyology division (CNHM) there were 12 dried skeletal vertebrae from *Meglops* and Tarpon; University of Michigan Museum of Zoology (UMMZ) there were 20 dried skeletal vertebrae from *Albula*; and 25 unidentified fossil vertebrae from the Late Cretaceous of Madagascar. All images were photographed using the same a Nikon Coolpix L18 camera.

Each image was digitized with tpsDig2 (Rohlf, 2010) with sliding semi-landmarks, chosen at the author's discretion as there are no universal landmark points used to analyze fish vertebral body shape. The use of sliding semi-landmarks decreases the amount of deformation energy required to analyze the shape of each set of semi-landmarks (Zelditch et al., 2004). TpsDig2 was used to digitize 40 approximately equidistant points, around the perimeter of each vertebra to create an outline of the vertebral body (Figure 41).

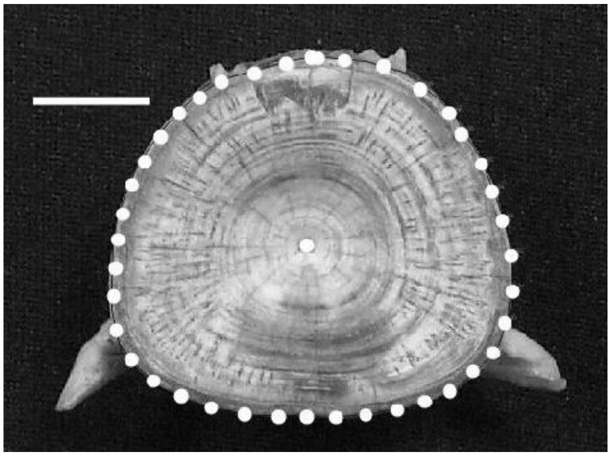


FIGURE 41: Vertebra showing the placement of the sliding semi-landmarks as dots around the perimeter of the vertebral body. (CNHM 51336).
Scale bar = 1 centimeter.

These digitized points were then analyzed using tpsRelw (Rohlf, 2011). This program automatically uses the digitized points to assign each specimen to a point within a shape space. Within this shape space, the program superimposes, scales, and rotates each image based on an average consensus image which reduces the variation between all data points to provide the most conservative estimate of shape differences. Within tpsRelw, a partial warps analysis was run to determine shape change and variation of landmarks. These partial warp scores (as eigenvalues) were used in a relative warps analysis plot to determine if there were any markedly similar vertebral body shapes that grouped together (Zelditch et al., 2004). The relative warps analyses were keyed by individual to determine the spread of variation among taxa and among vertebral region.

Vertebral Analysis Results

General Relative Warps Ordination Plot: This general relative warps ordination plot contains the raw vertebral morphometrics data (Figure 42). Figure 42 displays the overall vertebral body shape variation among the 75 specimens. This plot can be read as a principal components analysis with each axis showing certain amount of variation. The x-axis explains the highest amount of variation between the vertebrae, and the y-axis shows the second-highest amount of variation between the vertebrae. At the end point of each axis is the vertebral body shape on a grid that displays the bending energy (deformation) required to make the vertebra look different from the consensus image (which would be at the intersection of the axes). The greater the amount of deformation in the grid, the greater the amount of deformation needed to conform to the consensus image to the shapes captured from the digitized images of elopomorphs. The following analyses will use this general plot and code each point for taxonomic identification and vertebral type to determine if quantifiable differences exist.

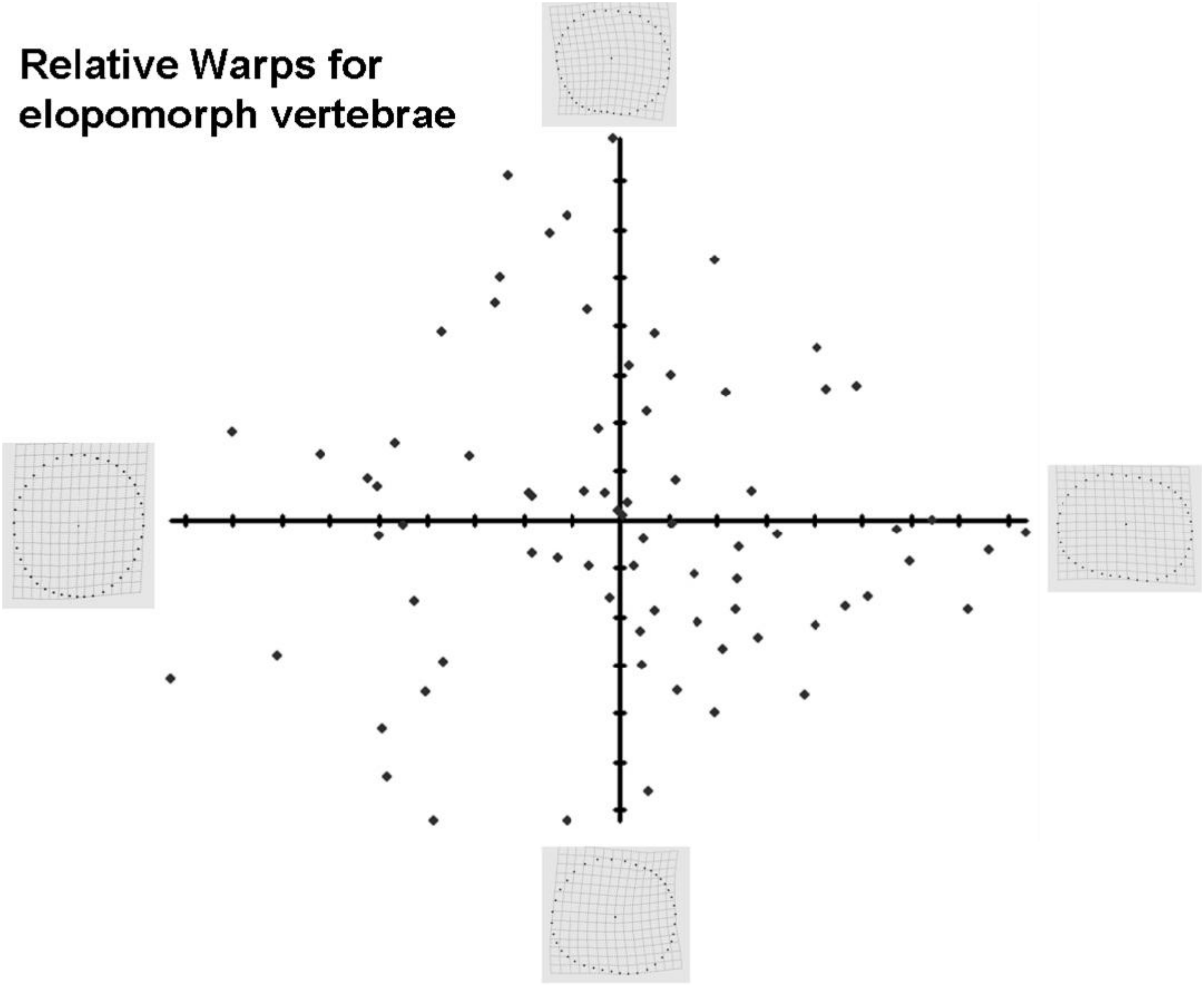


FIGURE 42: A relative warps ordination plot showing all variation in vertebral body shape from the 75 measured specimens.

Relative Warps with Taxonomic Identification: When the general ordination plot is coded by taxonomic identification (Figure 43), the relative warps analysis shows that the vertebral centra of the sampled elopomorphs do not fall into distinct groups. Some basic patterns appear, such as *Elops* are all confined to the left of the y-axis, which means their vertebral centra are more laterally compressed. *Albula* makes up the most numerous vertebrae used, and they tend to lay to the right of the y-axis, indicating that they generally have a more dorso-ventrally compressed vertebra centra shape. However, there are few *Albula* that lie far to the left of the y-axis, so this method cannot be a reliable indicator of definitely identifying a vertebra as belonging to *Albula*. The unidentified fossil vertebrae from Madagascar have the widest breadth of shape differentiation. This leads to the conclusion that several different genera of elopomorpha may be present, but it would be difficult to taxonomically assign each vertebra based on centrum shape alone. Based on this analysis, the greater the sample size the more morphological diversity. Therefore, a more equally sampled dataset would be desirable for future analyses.

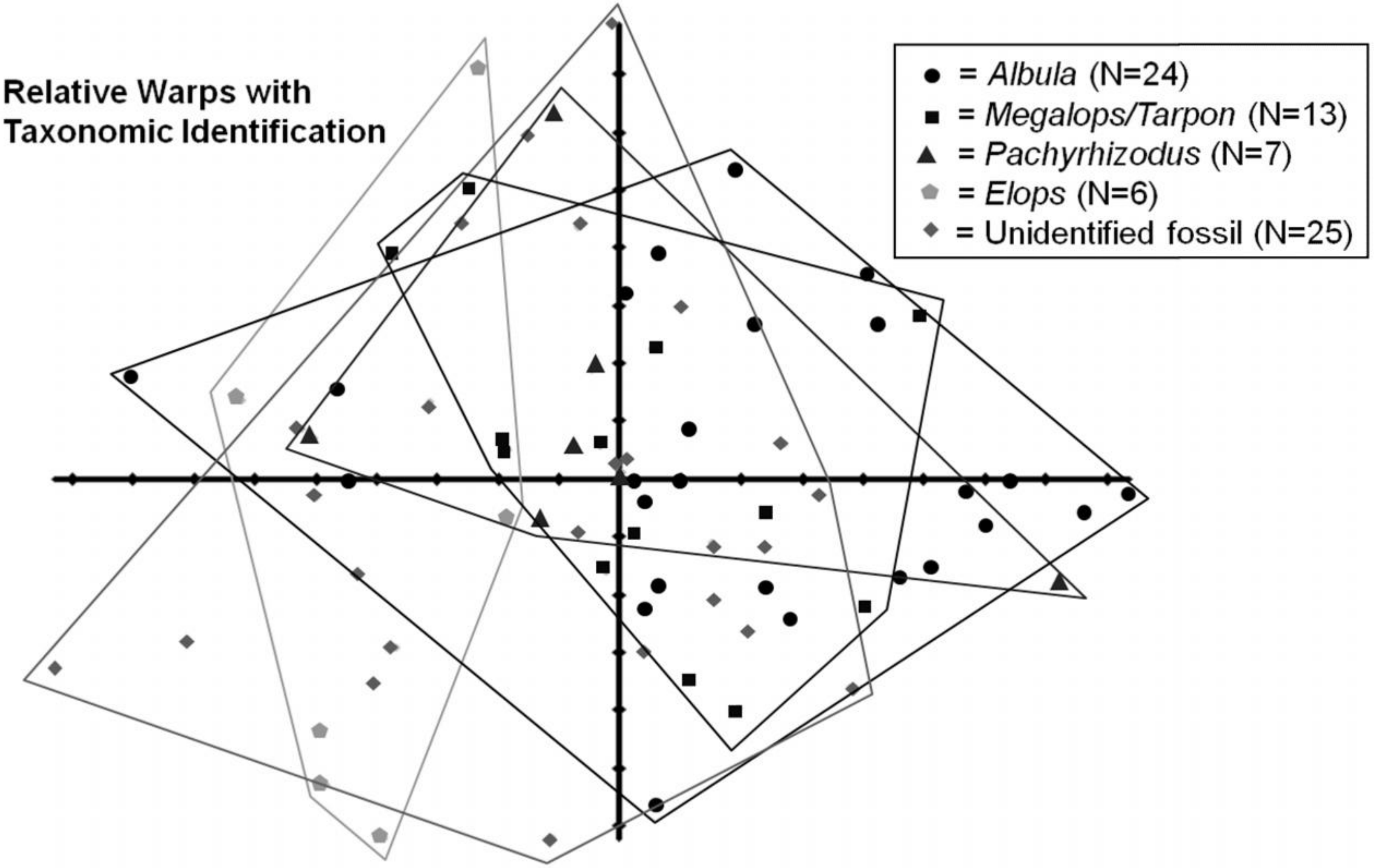


FIGURE 43: A relative warps plot showing the variation in shape based on taxonomic identification with convex hulls. Unidentified fossils are specimens from Madagascar.

Relative Warps with Vertebral Type: Figure 44 shows the Relative Warps plot differentiated by vertebral type, trunk, trunk (first five vertebrae, called "first five" herein), caudal, and unidentified large fossils. The first five vertebrae of Recent *Albula* specimens show a very distinctive, sigmoidal outline that gradually becomes less sigmoidal as you move caudally. The first five vertebrae were analyzed separately to determine whether this sigmoidal outline affected their position in shape space on the plot. The first five vertebrae were taken from two different *Albula* individuals to test if there were any correlations of centrum shape within an individual fish. Identification of multiple vertebrae within an individual was not possible for the fossil specimens because all vertebrae were disarticulated and some were not associated. The plot (Figure 44) indicates that there are no distinct groupings based on vertebral type, but there are some patterns are present. Thirteen of the fourteen caudal vertebrae fall to the left of the y-axis, indicating that they are laterally compressed in shape. This is not surprising given that most caudal vertebrae have a circular to laterally compressed shape in most teleosts. Trunk vertebrae are the most abundant and are scattered across the diagram, indicating their shape has the most variability. The first five from the skull, tend to lie near the x-axis, but have a wide range over the length of the x-axis. These plotted points indicate that the first five vertebrae have a markedly different shape from the other trunk vertebrae. Two large vertebrate (approximately 2.5 centimeters in diameter) show strongly sigmoidal outlines. This morphology is not a preservational artifact. Multiple specimens (at least 5) from different localities have this sigmoidal outline. These large vertebrae were plotted on the relative warps by vertebral type plot as "unidentified large fossils" and they did not occur near each other on the plot, or necessarily near any other vertebrae. Therefore, it appears these large vertebrae are trunk vertebrae from an elopomorph with an unusual vertebral shape.

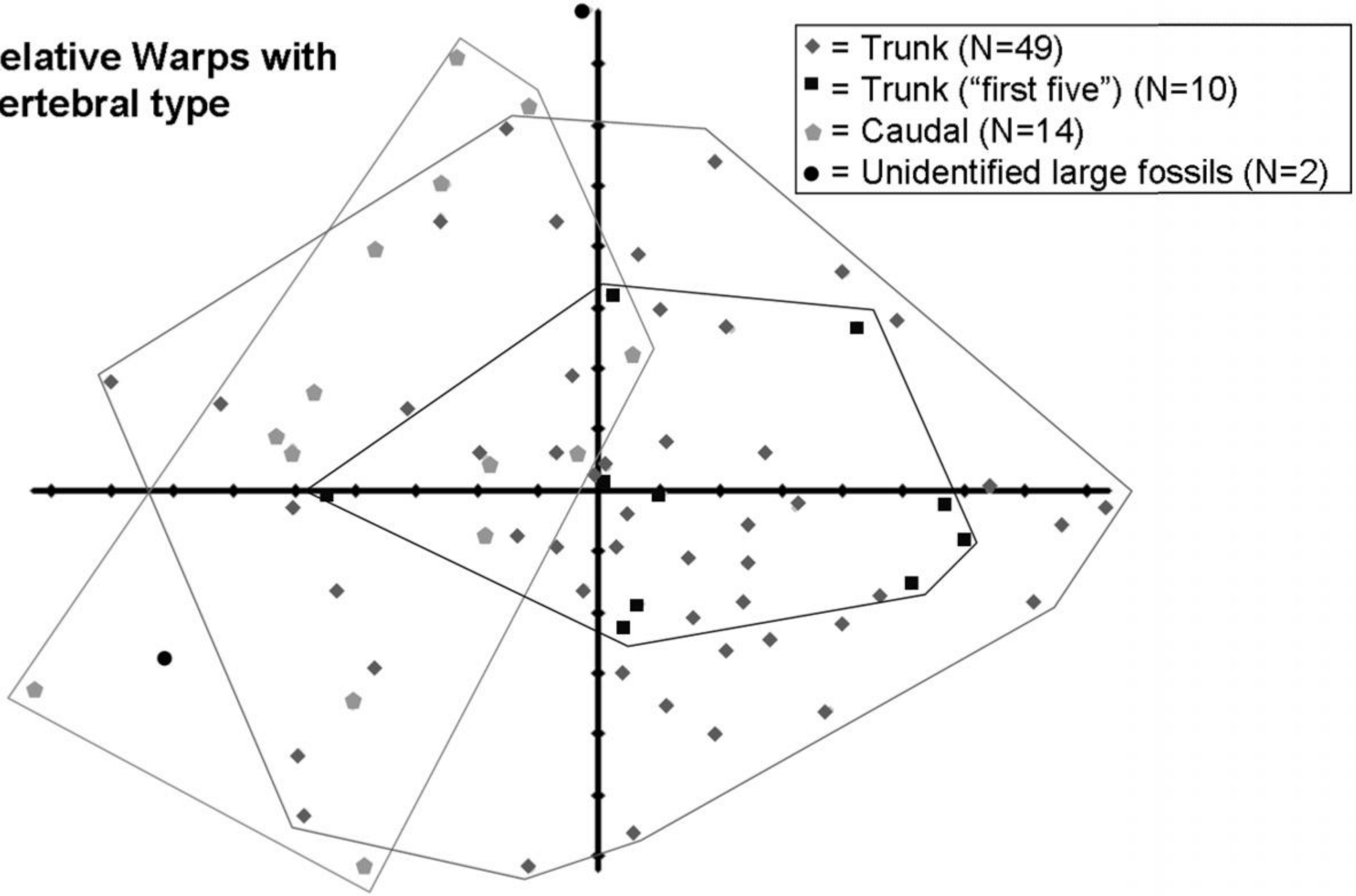


FIGURE 44: A relative warps plot showing the variation in shape based on vertebral location within the body with convex hulls. Trunk vertebrae within the first 5 from the skull are noted. Unidentified large fossils are from Madagascar.

Summary of Vertebral Analysis

The geometric morphometric vertebral analysis is in many respects inconclusive. In identifying vertebrae taxonomically based on centra shape, there is some separation along the X-axis between *Albula* and *Elops*, mainly demarcated by the Y-axis, but lacking clear boundaries. *Elops* tends to cluster within one quadrant, but the occurrence of other taxa appear randomly in that quadrant and therefore it would not be the only reliable indicator in identification.

The analysis did not differentiate vertebrae by vertebral type or by taxa. When looking at the differences when identified by vertebral type, there are not any groups that stand out as being markedly quantitatively different from others. Caudal vertebrae tend to cluster on one side of the Y-axis, probably due to their symmetrical centra shape. The first five vertebrae also cluster, as they share a sigmoidal shape, and they are wider along the dorsal margin as compared to the ventral margin. Vertebrae from the same individuals did not cluster together anymore than by vertebral type or taxonomic identification. Vertebral centra shape differs greatly enough within single individuals as to not be useful for the only taxonomic identification or location along the vertebral column.

DISCUSSION AND SUMMARY

The presence of *Egertonia, Paralbula, and Albula* in the Late Cretaceous of Madagascar extends each genus geographically, and *Egertonia* temporally as well. All of these genera are today coastal species that do not traverse large ocean distances. As elopomorphs, they would have had a leptocephalus larval stage that could potentially facilitate great distances during the larval stage; however, that does not guarantee that they would take advantage of this possible dispersal opportunity. Based on a recent genetic study, leptocephalus larvae have likely evolved this life history which causes them to stay in nearshore waters (Colborn et al., 2001). This is likely why bonefish ecology and morphology has remained relatively conserved over time (Colborn et al., 2001). Therefore, it can be stated that during the Late Cretaceous, genera were more cosmopolitan along coastal margins than previously thought.

For elopomorph vertebrae, there is not a clear relationship between vertebral centra shape and taxonomic identification, or location along the vertebral column. This lack of relationship could be a result of inadequate taxon sampling and sample size. Differences in preservation could also affect how vertebral type or taxa are identified. Also, there could be questionable identifications of fossil vertebrae due to the differences in preservation (especially for identifying location along the vertebral column). This specific analysis would likely not be useful for other vertebrae. However, there could be a geometric morphometric method that could be developed to quantify differences in vertebrae between taxa. If successful, this analysis would be very helpful in identifying the large amounts disarticulated fish vertebrae that remain in collections, unstudied.

REFERENCES

REFERENCES

Alroy, J., 2012, Paleobiology Database, *in* Alroy, J., ed., Volume 2012. http://www.paleodb.org

Anderson, F., 1958, Upper Cretaceous of the Pacific Coast, Geological Society of America Memoir, Volume 71.

Applegate, S., 1970, The vertebrate fauna of the Selma Formation of Alabama, Fieldiana, Geology Memoirs: Chicago, IL, Field Museum of Natural History, p. 383-433.

Armstrong-Ziegler, J., 1978, An Aniliid Snake and Associated Vertebrates from the Campanian of New Mexico: Journal of Paleontology, v. 52, p. 480-483.

Beavan, N., and Russell, A., 1999, An Elasmobranch Assemblage from the Terrestrial-Marine Transitional Lethbridge Coal Zone (Dinosaur Park Formation: Upper Campanian), Alberta, Canada: Journal of Paleontology, v. 73, p. 494-503.

Bergquist, H., 1944, Cretaceous of the Mesabi Iron Range, Minnesota: Journal of Paleontology, v. 18, p. 1-30.

Blake, S., 1940, *Paralbula*, a new fossil fish based on dental plates from the Eocene and Miocene of Maryland.: Journal of the Washington Academy of Sciences, v. 30, p. 205-209.

Bleeker, P., 1859, Enumeratio specierum fiscium hucusque in Archipelago indico observatarum., Volume 6: Batavia, Act. Soc. Sci. Indo-Neerl., p. 1-276.

Bone, D., Todd, J., and Tracey, S., 1991, Fossils from the Bracklesham Group exposed in the M27 Motorway excavations, Southhampton, Hamshire: Tertiary Research, v. 12, p. 131-137.

Brinkman, D., 1990, Paleooecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: Evidence from vertebrate microfossil localities: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 78, p. 37-54.

—, 2008, The structure of the Late Cretaceous (late Campanian) non-marine aquatic communities: a guild analysis of two vertebrate microfossil localities in Dinosaur Provincial Park, Alberta, Canada, *in* Sankey, J.T., and Baszio, S., eds., Vertebrate microfossil assemblages: their rol in paleoecology and paleobiogeography: Bloomington, Indiana University Press.

Case, G., 1986, The bony fishes (teleosts) of the Tuscahoma and Bashi Formations, Early Eocene, Meridian, Lauderdale County, Mississippi: Mississippi Geology, v. 6, p. 6-8.

—, 1987, *Borodinopristis schwimmeri*, a new ganopristine sawfish from the Upper Blufftown Formation (Campanian) of the Upper Cretaceous of Georgia: Bulletin of the New Jersey Academy of Science, v. 32, p. 25-32.

Casier, E., 1966, Faune Ichthyologique du London Clay, Trustees of the British Museum (Natural History): London.

Castle, P., 1984, Notacanthiformes and Anguilliformes: development, Ontogeny and systematics of fishes. Special Publication no. 1 American Society Ichthyologists and Herpetologists: Lawrence, KS, Allen Press, p. 62-93.

Cicimurri, D., 2007, A late Campanian (Cretaceous) selachian assemblage from a classic locality in Florence County, South Carolina: Southeastern Geology, v. 45, p. 59-72.

Cocchi, I., 1864, Monografia dei Pharyngodopilae, nuova famiglia di pesci labroidei: Ann. Mus. Fis. Stor. Nat. Firenze (N.S.), v. 1, p. 65-152.

Colborn, J., Crabtree, R., Shaklee, J., Pheiler, E., and Bowen, B., 2001, The evolutionary enigma of bonefishes (*Albula* spp.): Cryptic species and ancient separations in a globally distributed shorefish: Evolution, v. 55, p. 807-820.

Cope, E., 1887, Zittel's Manual of Palaeontology: American Naturalist, v. 21, p. 1014-1019.

Cvancara, A., and Hoganson, J., 1993, Vertebrates of the Cannonball Formation (Paleocene) in North and South Dakotas: Journal of Vertebrate Paleontology, v. 13, p. 1-23.

Dartevelle, E., and Casier, E., 1943, Les poissons fossiles du Bas-Congo et de régions voisines (Premiére Partie) Ann. Mus. Congo Belge, v. Ser. A, 2, p. 1-200.

Dodson, P., 1984, Small Judithian ceratopsids, Montana and Alberta, *in* Reif, W.-E., and Westphal, F., eds., Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers: Tubingen, Verlag.

Eberth, D., and Brinkman, D., 1997, Paleoecology of an Estuarine, Incised-Valley Fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of Southern Alberta, Canada: PALAIOS, v. 12, p. 43-58.

Estes, R., 1965, A New Fossil Salamander from Montana and Wyoming: Copeia, v. 1965, p. 90-95.

—, 1969, Studies on Fossil Phyllodont Fishes: Interrelationships and Evolution in the Phyllodontidae (Albuloidei): Copeia, v. 1969, p. 317-331.

Fiorillo, A., 1989, The Vertebrate Fauna from the Judith River Formation (Late Cretaceous) of Wheatland and Golden Valley counties, Montana: The Mosasaur, v. 4, p. 127-142.

Forey, P., 1973a, Relationships of elopomorphs, *in* Greenwood, P., Miles, R., and Patterson, C., eds., Interrelationships of Fishes: London, Academic Press, p. 351-368.

—, 1973b, A Revision of the Elopiform Fishes, Fossil and Recent, Bulletin of the British Museum (Natural History) Geology - Supplement 10: London, England.

Forey, P., Littlewood, D., Ritchie, P., and Meyer, A., 1996, Interrelationships of Elopomorph Fishes, *in* Stiassny, L., Parenti, L., and Johnson, G., eds., Interrelationships of Fishes: San Diego, CA, Academic Press, p. 175-190.

Gallagher, W., Parris, D., and Spamer, E., 1986, Paleontology, biostratigraphy, and depositional environments of the Cretaceous-Tertiary transition in the New Jersey Coastal Plain The Mosasaur, v. 3, p. 109-123.

Grandstaff, B., Parris, D., Denton Jr., R., and Gallagher, W., 1992, Alphadon (Marsupialia) and Multituberculata (Allotheria) in the Cretaceous of Eastern North America: Journal of Vertebrate Paleontology, v. 12, p. 217-222.

Greenwood, P., Rosen, D., Weitzman, S., and Meyers, G., 1966, Phyletic studies of telesotean fishes, with a provisional classificaiton of living forms: Bulletin of the American Museum of Natural History, v. 131, p. 339-456.

Homberger, D., and Walker Jr., W., 2004, Vertebrate Dissection: Belmont, CA, Brooks/Cole - Thompson Learning, 379 p.

Hutchinson, P., and Kues, B., 1985, Depositional environments and paleontology of Lewis Shale to lower Kirtland shale sequence (Upper Cretaceous), Bisti area, northwestern New Mexico, New Mexico Bureau of Mines and Minearl Resources Circular, Volume 195, p. 25-54.

Inoue, J., Miya, M., Tsukamoto, K., and Nishida, M., 2004, Mitogenomic evidence for the monophyly of elopomorph fishes (Teleostei) and the evolutionary origin of the leptocaphus larva: Molecular Phylogenetics and Evolution, v. 32, p. 274-286.

Jamieson, B., 1991, Fish Evolution and Systematics: Evidence from Spermatozoa: Cambridge, UK, Cambridge University Press.

Jolly, A., and Loyal, R., 1985, Record of Microvertebrates from the Middle Eocene Marh Stage of Sri Kolayat-Ji, Rajasthan: Bull. Geol., Min. Metall. Soc. India, v. 52.

Kumar, K., Singh-Rana, R., and Singh, H., 2007, Fishes of the Khuiala Formation (Early Eocene) of the Jaisalmer Basin, Western Rajasthan, India: Current Science, v. 93, p. 553-559.

Langston Jr, W., 1967, The Thick-headed ceratopsian dinosaur Pachyrhinosaurus (Reptilia: Ornithischia), from the Edmonton Formation near Drumheller, Canada Canadian Journal of Earth Sciences, v. 4, p. 171-186.

Lauginiger, E., 1984, An upper Campanian vertebrate fauna from the Chesapeake and Delaware Canal The Mosasaur, v. 2, p. 141-149.

Lillegraven, J., and Eberle, J., 1999, Vertebrate Faunal Changes through Lancian and Puercan Time in Southern Wyoming: Journal of Paleontology, v. 73, p. 691-710.

Linnaeus, C., 1758, *Systema Naturae*, 10th Ed.: Stockholm, p. 824 pp.

Miller, H., 1967, Cretaceous Vertebrates from Phoebus Landing, North Carolina: Proceedings of the National Academy of Sciences of Philadelphia, v. 119, p. 219-239.

Mojica Jr., R., Shenker, J., Harnden, C., and Wagner, D., 1995, Recruitment of bonefish *Albula vulpes*, around Lee Stocking Island, Bahamas: Fish Bulletin, v. 93, p. 666-674.

Müller, J., 1846, Über den Bau und die Grenzen der Ganoiden und über das natürlichen System der Fische Abhandlungen Akademie der Wissenschaften, Berlin, v. 1844, p. 117-216.

Nelson, G., 1973, Relationships of clupeomorphs, with remarks on the structore of the lower jaw in fishes, *in* Greenwood, P., Miles, R., and Patterson, C., eds., Interrelationships of Fishes: London, Academic Press, p. 333-349.

Nessov, 1981, Nakhodka cheliusti naezemnoi Iashcheritsy v verkhnem melu Uzbekistana (The discovery of a terrestrial lizard jaw in the Upper Cretaceous of Uzbekistan): Vestnik Leningradskogo Universiteta, v. 2, p. 105-107.

Nessov, L., 1985, Rare bony fishes, terrestrial lizards and mammals in the estuarine and coastal lowland zone of the Kyzyl-Kum Cretaceous: Yearbook of the All-Union Paleontological Association, v. 28, p. 199-219.

Nybelin, O., 1976, Note on the Osteology of the Lower Jaw of *Albula vulpes* (L.) (Pisces, Teleostei): Zoologica Scripta, v. 5, p. 235-237.

Olson, S., and Parris, D., 1987, The Cretaceous Birds of New Jersey.

Peng, J., Russell, A., and Brinkman, D., 2001, Vertebrate microsite assemblage (exclusive of mammals) from the Foremost and Oldman Formation of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide, Provincial Museum of Alberta Natural History Occasional Paper: Edmonton, Provincial Museum of Alberta, p. 1-25.

Pfeiler, E., Mendoza, M., and Manrique, F., 1988, Premetamorphic bonefish (*Albula* sp.) leptocephali from the Gulf of California with comments on life history: Environmental Biology of Fishes, v. 21, p. 241-249.

Reeside, J., 1955, Revised Interpretation of the Creatceous section of the Vermilion Creek, Moffat County, Colorado, Wyoming Geological Association Guidebook, Volume 1955, p. 85-88.

Rohlf, F., 2010, tpsDig2 Version 2.16, *in* Department of Ecology and Evolution, S.U.o.N.Y., Stony Brook, NY, ed.

—, 2011, tpsUtil Version 1.47, *in* Department of Ecology and Evolution, S.U.o.N.Y., Stony Brook, NY, ed.

Rose, K., 1999, Fossil Mammals from the Early Eocene Fisher/Sullivan Site: Virginia Division of Mineral Resources Publication, v. 152, p. 133-138.

Russell, L., and Landes, R., 1937, Geology of the Southern Alberta Plains. Part II. Paleontology of the marine formations of the Montana Group, Geological Survey of Canada Memoir, Volume 221.

Sahni, A., 1972, The Vertebrate Fauna of the Judith River Formation, Montana, Bulletin of the American Museum of Natural History, Volume 147: New York City, American Museum of Natural History, p. 321-412.

Sauvage, H., 1875.

Schwimmer, D., 1986, Late Cretaceous fossils from the Blufftown Formation (Campanian) in western Georgia The Mosasaur, v. 3.

Scopoli, 1777, Introductio ad historiam naturalem sistema genera lapidum, plantarum et animulium: Prague.

Sohl, N., and Koch, C., 1983, Upper Cretaceous (Maestrichtian) Mollusca from the *Haustator bilira* zone in the East Gulf Coastal Plain, United States Geological Survey Open-File Report, United States Geological Survey, p. 239.

—, 1984, Upper Creatceous (Maestrichtian) Mollusca from teh Haustator bilira zone in the Atlantic Coastal Plain with further data for the East Gulf, United States Geological Survey Open-File Report, United State Geological Survey, p. 172.

Stephenson, L., 1941, The larger invertebrate fossils of the Navarro group of Texas: The University of Texas Publication, v. 4101, p. 625.

Vullo, R., Bernárdez, E., and Buscalioni, A., 2009, Vertebrates from the middle?–late Cenomanian La Cabaña Formation (Asturias, northern Spain): Palaeoenvironmental and palaeobiogeographic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 276, p. 120-129.

Wade, B., 1926, The fauna of the Ripley Formation on Coon Creek, Tennessee: United States Geological Survey Professional Paper, v. 137.

Weems, R., 1998, Acitnopterygian Fish Remains from the Paleocene of South Carolina: Transactions of the American Philosophical Society, v. 88, p. 147-164.

Whitehead, P., 1986, The synonymy of *Albula vulpes* (Linnaeus, 1758) (Teleostei, Albulidae): Historie natualle des poissons, v. 10, p. 211-230.

Zangerl, R., 1948, The vertebrate fauna of the Selma formation of Alabama I. Introduction. II. The Pleurodiran turtles: Fieldiana Geol, v. 3, p. 1-56.

Zelditch, M., Swiderski, D., Sheets, H., and Fink, W., 2004, Geometric Morphometrics for Biologists: A Primer: Oxford, UK, Elsevier Academic Press, 444 p.

CHAPTER 4: CHANGES IN ICTHYOFAUNA ON MADAGASCAR OVER TIME AND IMPLICATIONS FOR GONDWANAN BIOGEOGRAPHY

INTRODUCTION

Madagascar's extant biota is known for its endemicity, meaning many species are unique to the island. The majority of Madagascar's fauna exhibits over 80% endemicity (Goodman and Benstead, 2005). Among vertebrates, endemism is high at 84%, and reaching 92-100% among non-volant taxa (Goodman and Benstead, 2005).

The tectonic and geologic history of Madagascar is relatively well known (Figure 51). The initial separation of eastern and western Gondwana began in the Early Jurassic (~180 Ma) (deWit, 2003). East Gondwana shifted southward along a plate boundary in the Davie Ridge (Bassias, 1992; Reeves and de Wit, 2000). The western coast of Madagascar was separated completely from Africa by the Early Cretaceous (~140 Ma) (Seward et al., 2004). Madagascar and the east coast of Africa have remained in their current relative positions ~400 kilometers apart since the Middle Cretaceous (~118 Ma) (Harland et al., 1990; Rabinowitz et al., 1983; Seward et al., 2004). Madagascar remained associated with the Indian/Seychelles subcontinent until the Late Cretaceous (~88 Ma) when the landmasses separated and the Indian subcontinent began moving rapidly (in tectonic terms) northeastward (Storey, 1995). Madagascar has been an island for the past 88 million years without any apparent connections to other large landmasses; however, the fauna on the island has changed dramatically over that time.

The high level of endemicity on Madagascar has made it a prime target area for studying biogeographic patterns of terrestrial organisms (de Queiroz, 2005; Krause et al., 2006; Vences, 2004). There is controversy regarding changes in faunal composition on Madagascar since its isolation, and concerning the mechanisms driving the changes in faunal distributions that have occurred there over geologic time. Two primary mechanisms for explaining biogeographic patterns, within fishes in particular (and other groups), are vicariance versus marine dispersal.

Vicariance can be characterized as allopatric speciation that has occurred due to a tectonic or other major physical event that geographically separates congeneric species and thus isolates them, allowing their descendants to diversify independently (Humphries and Parenti, 1986; Nelson and Platnick, 1981). Those who posit vicariance as the main factor in the distribution of extinct taxa accept that plate tectonics is the major physical driver determining these distributions. Vicariance is treated as a null hypothesis because an area cladogram can be used to determine relationships between landmasses and how well these correlate with hypothesized speciation events and phylogenetic relationships. Some vicariance proponents support the vicariance-based hypothesis that the extant fishes now on Madagascar can be attributed to Gondwanan fragmentation; see Sparks and Smith (2004), for example, regarding the origin and diversification of cichlids (Stiassny, 1991). Based on molecular evidence, derived morphology of fossil cichlids, and the idea that cichlids are primary freshwater fishes, Stiassny (1991) suggested cichlids originated in the Early Cretaceous and rapidly diversified prior to the initial break-up of Gondwana ~125 Ma. This interpretation is controversial because the earliest known fossil cichlids are from the Eocene of Tanzania (Murray, 2000) and some argue that due to the absence of fossils older than the Eocene, it is unlikely that cichlids had evolved and widely diversified prior to the initial break-up of Gondwana (Briggs, 2003). If Cretaceous cichlids were discovered, the hypothesis that some of the freshwater fishes on Madagascar today are the result of vicariant speciation events would be supported.

Proponents of marine dispersal do not oppose the idea of vicariance, but they regard it as inadequate in explaining the geographic distribution of all terrestrial taxa. Dispersal posits that certain taxa can cross barriers and immigrate to other geographic areas in which they were not previously represented. This principle applies to Madagascar, an island separated by a marine barrier from Africa, India, the western Pacific, Antarctica, and South America. Fishes could hypothetically disperse across these barriers, including groups that originated after the initial fragmentation of Gondwana. This Pan-Gondwanan scenario hypothesizes that constituents of the fauna were able to disperse across shallow seaways between landmasses while Gondwanan landmasses were still proximal to one another, but no longer connected. A Pan-Gondwanan scenario can be supported by a more cosmopolitan fauna, in addition to the usual increased provincialism associated with vicariance. For example, Madagascar contains Late Cretaceous gondwanatherian mammals which were earlier thought to have a uniquely South American distribution; however, the discovery of gondwanatheres on Madagascar greatly broadened the known distribution (Krause et al., 1997). Dispersal hypotheses are based on the absence of evidence (i.e. fossils have not been found, leading to a lack of correlation between phylogenies and tectonic activity). The biogeographic patterns of some land vertebrates suggests that intermittent land bridges were present between Gondwanan landmasses during the Mid- and Late- Cretaceous (Sereno et al., 2004) allowing for faunal interchange. For Madagascar in particular, high endemicity and sparse existence of some groups in the

Cretaceous suggests Paleogene dispersal events may have been the primary mechanism for the distribution of extant taxa (Briggs and Clarkson, 1990). Still others suggest that strict marine dispersal and vicariance are too restrictive to explain distribution patterns and have suggested the idea of geodispersal. Geodispersal requires the disappearance of a preexisting barrier subsequently followed by large faunal dispersal (Upchurch, 2008). Samonds et al. (2012) explored the complexity of multiple dispersal factors using models of ocean surface currents and the likelihood of establishing viable animal populations after Madagascar's initial rifting from Africa.

Much of the work examining the distribution of the extant terrestrial fauna of Madagascar has revolved around the mammals that exist there today (lemurs, carnivorans, rodents, and lipotyphlan insectivores) because of their known limited ability for dispersal between landmasses (Yoder et al., 2003). Yoder et al. (2003) suggested, based on molecular evidence, that there were four separate colonization events (one for each group of mammals currently present), and that all subsequent species evolved from those individual colonizations. Simpson's "sweepstakes" model of over-water dispersal (Simpson, 1952) has been posited for chameleon distribution on Madagascar (Raxworthy et al., 2002). A recent review of 17 Malagasy clades (including amphibians, reptiles, and non-flying vertebrates) concluded that though much of the Malagasy fauna is more similar (genetically) to African clades, it is likely that these clades were not present until the Cenozoic, well after Madagascar was isolated (Vences, 2004). Hence, some works hypothesized that clades first arrived in Madagascar by marine dispersal events from mainland Africa, rather than as a results of vicariance, and subsequently underwent species-rich radiations, all within the Cenozoic (Vences, 2004).

Ali and Huber (2010) modeled ocean currents in the Mozambique Channel during the Paleogene (~60 Ma to 20 Ma). These models asserted that currents were strong enough and moving in the correct direction to plausibly transport rafts, mats of vegetation, or logs from northeast Mozambique to the western Madagascar coast (Ali and Huber, 2010). When the ocean currents changed in the Miocene, new mammalian species could not longer be transported to the island. This rafting hypothesis would explain the unbalanced assortment of mammals on Madagascar, more so than land bridges. Landbridges would have experienced subaerial exposure, allowing mammals to walk across, in which case one would expect a greater variety of mammals to be present (Ali and Huber, 2010), especially at the higher taxonomic levels.

The potential for animals rafting upon floating debris has been demonstrated, observed and analyzed for many years. There is distribution and genetic evidence that rafting plays an important role in population dynamics and biodiversity of coastal, marine environments (Thiel and Gutow, 2005). Fish are often associated with rafting debris and have greater diversity and concentrations around the mats than in open waters, mainly as consumers, but they rarely take up residence within the mats (Thiel and Gutow, 2005). There are some species of fishes that spawn on vegetation rafts, and a higher percentage of juveniles feed on these vegetation mats (Thévenin, 1907), but it is not clear how long they rely upon these mats of vegetation and if they could realistically colonize novel marine and coastal environments in this manner. However, this is a mechanism that has been shown to successfully move around species today into novel environments (e.g. rafting iguanas in the Caribbean (Censky et al., 1998)).

Doubts have been raised about the ocean current argument based on the low likelihood of animals being able to maintain an establishing population across large marine barriers (Krause, 2010). One approach to determining how animals arrived on Madagascar was assessing the probability of arrival based on distance needed to travel, ocean currents, and ancestor type (Samonds et al., 2012). Samonds et al. (2012) show that in the Early Cenozoic, there was a greater probability of being able to traverse the Mozambique Channel either via rafting or swimming. This probability greatly diminished by 15-20 million years ago, meaning that the current species on Madagascar were most likely to have emigrated during before that time in geologic history (Samonds et al., 2012). Species that lived on the island previous to the Early Cenozoic colonization either went extinct before the new arrivals or were driven to extinction by new populations of arriving fauna. Crottini et al. (2012) recently used a molecularly derived vertebrate time-tree that indicates pulses of colonizations from different landmasses that lasted for different stretches of time, based upon the similarity of the existing clades. This analysis shows that colonization from Asia ceased after the Eocene, likely due to the now vast ocean separating it from Madagascar from the Indian subcontinent (Crottini et al., 2012). Shared taxa between South America and Madagascar could have diverged earlier than expected in the Early Cretaceous, which would bring into doubt of the importance of the Kerguelen/Gunnerus ridges (Hay et al., 1999) that have been invoked as facilitating the movement of animals between Gondwanan continents (Crottini et al., 2012) after the landmasses became isolated.

HYPOTHESES TO BE TESTED

Hypotheses to be addressed here regarding the fishes from the Late Cretaceous of Madagascar include:

1. Vicariance:
    a. Prediction: *Vicariance is the main mechanism driving diversity and distribution of fishes seen on Madagascar during the Maastrichtian.* Test: Parsimony Analysis of Endemism (PAE) diagram would cluster together those landmasses (based on faunal composition) that have more recently been geologically associated on a PAE diagram.
    b. Prediction: *Vicariance is the main mechanism driving diversity and distribution of Recent fishes on Madagascar.* Test: Compare the orders of known fishes on Madagascar through time. The majority of taxonomic orders or families in the fossil record after the geographical isolation of Madagascar (in the Late Cretaceous) would be similar to those found on Madagascar today.
2. Marine Dispersal:
    a. Prediction: *Dispersal is the main mechanism driving diversity and distribution of fishes seen on Madagascar during the Maastrichtian.* Test: Parsimony Analysis of Endemism would not cluster landmasses (based on faunal composition) that have more recently been

geologically associated (i.e. faunal mixing between landmasses that does not correspond tectonic events).

   b. Prediction: *Dispersal is the main mechanism driving diversity and distribution of Recent fishes on Madagascar.* Test: Compare the orders of known fishes on Madagascar through time. The majority of taxonomic orders or families in the fossil record after the geographical isolation of Madagascar (in the Late Cretaceous) would be different from those found on Madagascar today.

3. Prediction: *Some fish clades have a more cosmopolitan distribution that previously thought.* Test: Cluster analyses of faunal similarity, would cluster landmasses they have had greater faunal exchange more recently, than those that have not, but would not be recently geologically associated.
4. *Highly endemic faunas are depauperate at higher taxonomic levels, and more speciose (due to the isolation and subsequent evolution).* Test: More endemic fauna would have fewer higher taxonomic levels but be species rich; whereas, less endemic faunas would be relatively rich at higher taxonomic levels (orders and families).

MATERIALS AND METHODS

Parsimony Analysis of Endemism (PAE): This study represents the first determined biogeographical analysis of the Late Cretaceous of Madagascar ichthyofauna. Parsimony Analysis of Endemism (PAE) is used as a first approximation to look at biogeographical relationships during the Late Cretaceous, especially among

Gondwanan landmasses. Parsimony Analysis of Endemism (Rosen and Smith, 1988) is employed using presence and absence data for localities and organisms (within parameters described below). These presence/absence data are used to determine the relationships among landmasses based upon shared taxa (Fortey and Cocks, 1992; Rosen and Smith, 1988) analogous to a cladogram using taxa and presence/absence of morphological characters to determine evolutionary relationships. Shared presences of organisms between geographical areas are considered a "synapomorphies" among the geographical areas (Hallam, 1994). PAE has been used by, e.g. Fortey and Cocks (1992) to determine paleobiogeographic patterns, and in biogeographical analyses of extant terrestrial vertebrates (Raxworthy and Nussbaum, 1996) and Lepidoptera (Emerson et al., 1997). Although this analysis is widely used, it is limited in its reach because it does not take into account the evolutionary relationships of the taxa involved in the analysis (Lieberman, 1999).

In the PAE analysis of the Late Cretaceous fishes of Madagascar, certain criteria had to be met to determine whether a locality would be included in the analysis. These criteria define the Operational Biogeographic Unit (OBU). The locality age used was the "Maastrichtian" to match the Late Cretaceous of Madagascar, and was defined as any formation that has any portion deposited during the Maastrichtian. There were many changes occurring tectonically and evolutionarily during the Cretaceous (Thomson, 1977), so narrowing the time period of the analysis diminished the noise introduced by those changes and allowed for a more focused time period of interest. There were many formations meeting the "Maastrichtian" criteria. To be included in the analysis, a formation must also have at least four different, identified actinopterygian genera of fishes and a geologic setting indicating a coastal environment comparable to the paleoenvironment of the Late Cretaceous of Madagascar. The parameter of four genera was chosen because based on the collected information of genera in Maastrichtian formations, there was a natural break in the data between having 1 or 2 genera described to more than 4.

PAST (Paleontological Analysis Statistical Software) (Hammer et al., 2001) was used to conduct the analysis. Formations were placed in the "row" of the spreadsheet, and the genera were placed as "columns" on the spreadsheet; the first row is treated as a "hypothetical ancestor outgroup," and contains all zeros to represent an ancestral geographic area void of the taxa used in the analysis. A cladistical analysis was run using the Fitch optimization method. With Fitch optimization, each "step" is reversible and unordered; this is usually the preferable method for cladistics (Hammer and Harper, 2006). A heuristic algorithm was used, which searches a subset of potential trees. The tree bisection and reconnection (TBR) option is a branch swapping scheme employed to reconnect as many branches as possible to find the fewest steps for the most parsimonious trees (Hammer and Harper, 2006) was employed. The compiled presence/absence dataset used in this analysis contained 19 geological formations (Figure 45) and 54 actinopterygian genera (Appendix A, Table 16). A strict majority consensus tree was used to average the number of most parsimonious trees (MPTs). This analysis was run multiple times to determine the highest and lowest number of MPTs to compare differences between their consensus area cladograms.

Similarity Indices: The same criteria (for OBU and taxa) and presence/absence matrix used in the PAE was used for the similarity indices. The presence/absence matrix was analyzed using PAST. Each of the similarities will be depicted as a dendrogram to be able to place the similarity between the faunas into an interpretable context for all of the Maastrichtian actinopterygians. This dendrogram is then read as a cladogram, grouping together groups of greater similarity with each other.

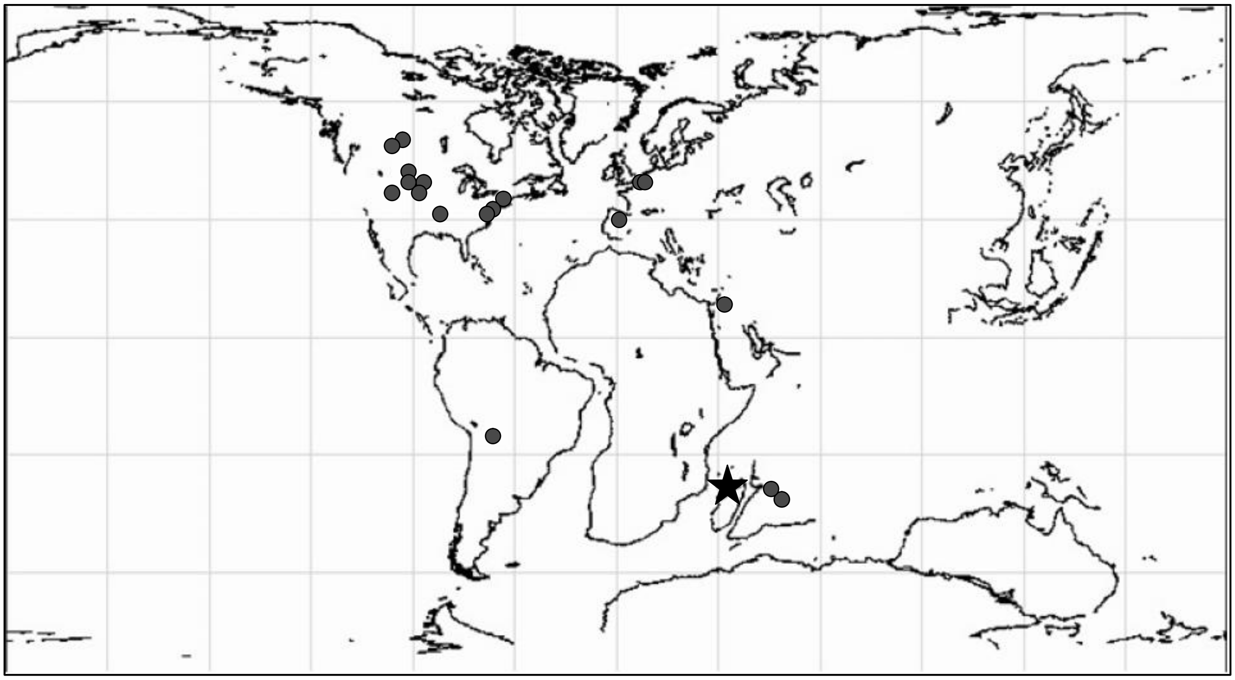


Figure 45: Map of formation locations used in these biogeographical analyses (star = Madagascar, circles = all other formation localities). Map modified from Alroy, 2012.

Simpson's Coefficient: Simpson's coefficient (S) (Simpson, 1943) is used to determine the percentage of similarity between two faunal assemblages (Raup and Crick, 1979). It varies from zero to 100 and is calculated as $S = 100k/B$; where k = the number common taxa between the two assemblages, and B = the total taxa found in the smaller assemblage ($B \leq A$). Based on these algorithms, *S* is insensitive to the sample size of the localities, and therefore can be more suitable where sampling is incomplete (Hammer and Harper, 2006).

Jaccard similarity: Jaccard similarity is calculated simply as the number of shared taxa between localities divided by the number of total taxa. If M = number of shared taxa, and N = total number of all remaining taxa; then, Jaccard = M/(M+N). Mutual absences are not taken into account with this analysis (Hammer and Harper, 2006). Jaccard's is helpful to use because it emphasizes the presence of the taxa, therefore, determining relationships based on taxa that is more likely to be endemic.

RESULTS

Parsimony Analysis of Endemism

The analysis was run over twenty times and produced the same repetition between 3 and 50 most parsimonious trees. The analyses of 4 MPTs are used for an example. In each analysis, the overall results were the same. The tree length was 80, meaning there were 80 transitions among the presence of fossil taxa throughout the area cladogram. The ensemble consistency index was 0.675. The consistency index equals the smallest number of generic changes possible divided by the actual number of changes (this determines the degree of homoplasy) and values ranges between 0 and 1, closer to 1 exhibiting less homoplasy (Hammer and Harper, 2006). The ensemble retention index (RI) describes the amount of generic similarity (synapomorphies in a cladistic analysis). The RI ranges from 0 to 1, with values closer to 1 meaning more common similarities. For this analysis the RI was 0.6438. Figure 46 depicts the strict consensus tree of the 4 MPTs.

The strict consensus tree shows a relatively clean area relationship that does make sense in many ways. There are three main clusters formed from the analysis, with a polytomy at the base of these three clusters (discussed using Figure 46 from top to bottom). Cluster One contains eastern North America, Spain, Bolivia, India, and Jordan. Cluster Two contains most of western North America and Madagascar. Cluster Three contains the Netherlands a sister group to the Sharon Springs formation. Within Cluster One, two northeastern North American faunas (Navesink and Mount Laurel) cluster with the Spanish fauna of Albaina. The India localities (Intertrappen beds and Lameta) cluster with the Bolivia locality (El Molino), and are a sister group to Jordan (Phosphorite Unite), indicating large scale connections through the Tethys seaway that would have allowed fauna to migrate. The southeastern North American faunas (Severn, Fox Hills, and Arkadelphia) formations cluster together. The Western North American fauna of Canada (Horseshoe Canyon and St. Mary River) and the USA (Hell Creek, Lance, and Fruitland) cluster. The North American fauna group with the Maevarano of Madagascar in a polytomy. The Netherlands fauna (Ciply-Mologne and Maastricht) cluster with the central North American fauna of Sharon Spring. There is also a large polytomy of unknown relationship between Western North America (with Madagascar), Eastern North America (with India, Bolivia, and Jordan), and Europe (and central North American).

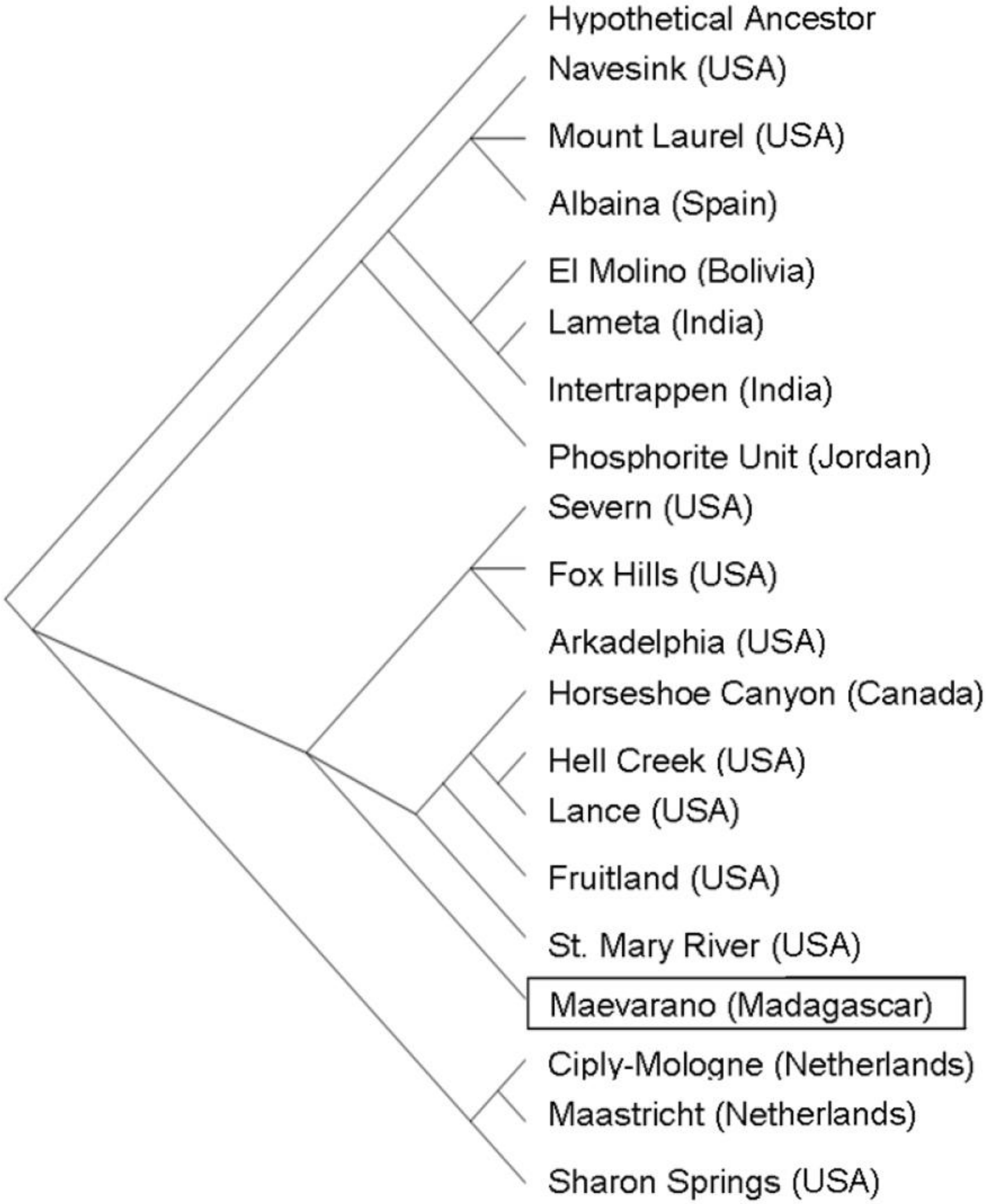


FIGURE 46: Strict consensus area cladogram from a Parsimonious Analysis of Endemicity. This analysis produced 4 most parsimonious trees. Tree length is 80. The taxa and locality matrix is listed in Appendix A, Table 16

Similarity Indices:

The similarity dendrograms are pictured in Figure 47 and Figure 48 for Simpson’s and Jaccard's respectively.

Simpson’s similarity dendrogram (Figure 47) with a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) shows 4 main clusters (described from top to bottom from Figure 46). Cluster One is eastern North America, Spain, India and Jordan. The North American faunas have the greatest similarity and cluster with Spain. The fauna of India and Jordan cluster. Cluster Two is central North America, Bolivia, and Madagascar. The Fox Hills, Arkadelphia, and Severn faunas from North America cluster while Bolivia and Madagascar cluster as their sister group. Cluster Three contains the two Netherlands formations with Sharon Springs from North America. Cluster Four groups the western North American faunas (Fruitland, Lance, Hell Creek, Horseshoe Canyon, and St. Mary River). The Lance and Hell Creek fauna have an identical faunal similarity. This Cluster 4 of western North American faunas is the least similar to the other three clusters.

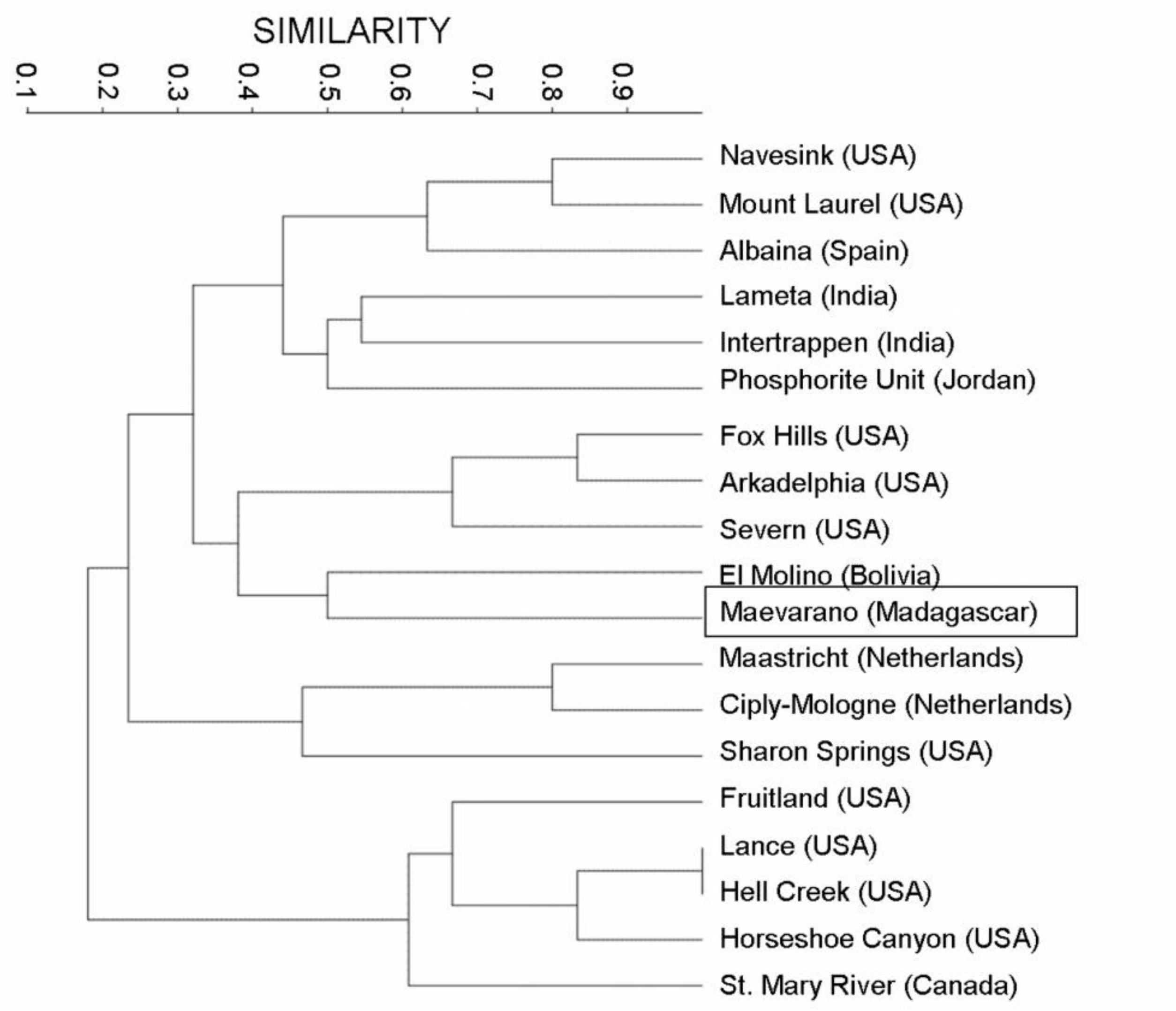


FIGURE 47: Simpson's Similarity Dendrogram for Maastrichtian actinopterygian faunas. Faunas with greater similarity show a similarity value closer to 1.0.

Jaccard’s Similarity dendrogram (Figure 48), emphasizes the shared presence (not absence of taxa), therefore, it provides a more conservative estimate of the faunal similarity and also uses UPGMA. Overall, the clusters have lower similarity between faunas than shown with Simpson’s similarity. There are two large clusters within the dendrogram (described from the top of the dendrogram as pictured in Figure 48). Cluster One contains fauna from India, North America, Spain Jordan Bolivia, and the Netherlands. The faunas from India cluster and are most similar to fauna from eastern North America, Spain, Jordan, and Bolivia. These taxa have minimal similarity with the clustering Netherlands and Sharon Spring (North American fauna). Cluster Two has two distinct groupings. One group exhibits a strong clustering of the Western North American faunas. The second grouping shows the Madagascar fauna being more similar to Fox Hills, Arkadelphia, and Severn faunas from North America. This is similar to the result from the PAE.

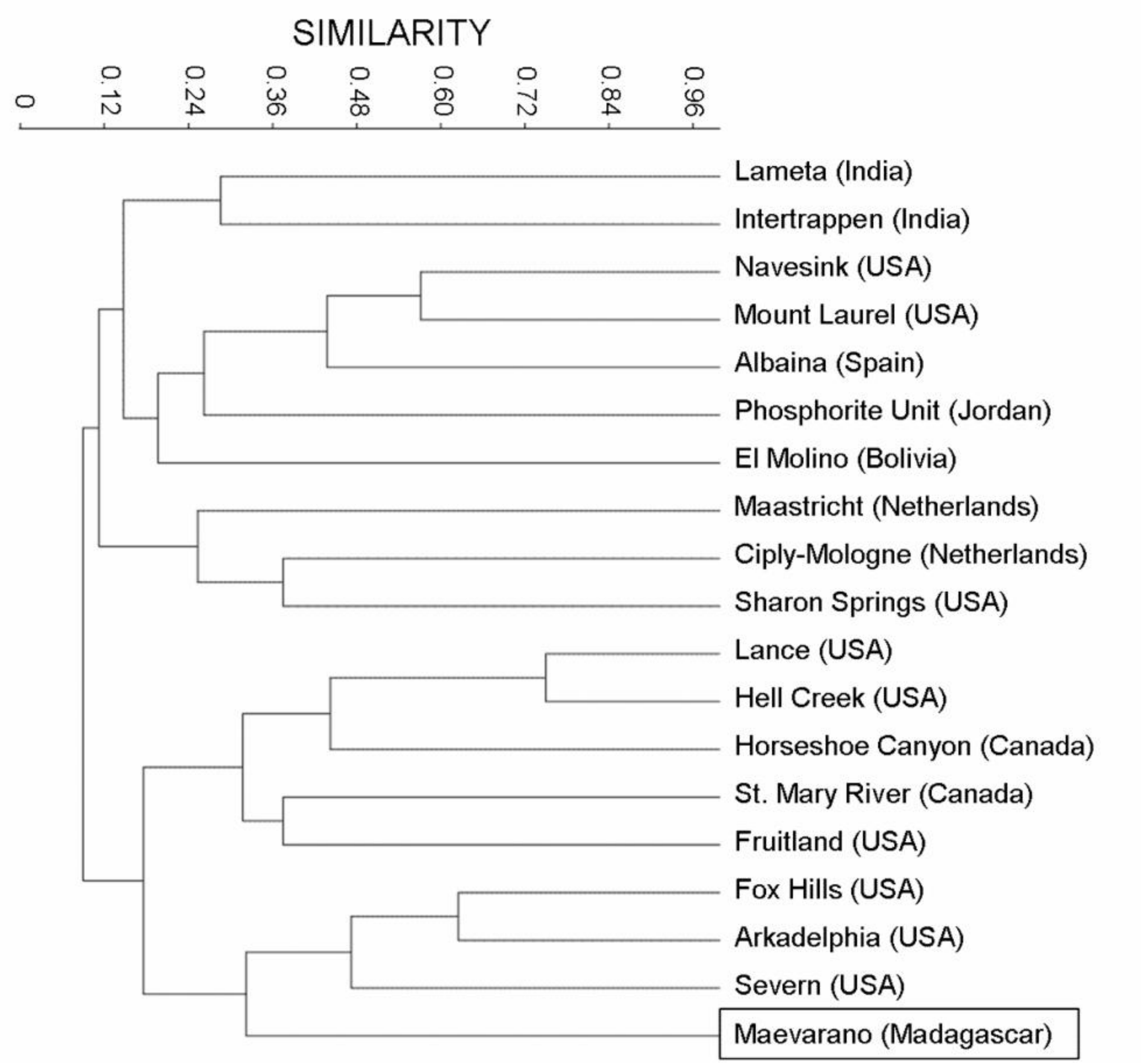


Figure 48: Jaccard's similarity dendrogram for Maastrichtian actinopterygian faunas. Those with great similarity have a value closer to 1.0

DISCUSSION OF PAE AND SIMILARITY ANALYSES

As seen in Figure 45, most of the formation localities that met the criteria for this analysis are Laurasian. Therefore, Madagascar has a much higher probability of clustering with a Northern Hemisphere formation. A lack of comprehensively described fossil fishes within the Southern Hemisphere will bias the results and emphasize associations based on only a few similar taxa. If there is a low number of OBUs, cosmopolitanism will be favored over true endemics, as seen here involving Madagascar. The pattern in this analysis where Madagascar clusters with North American landmasses is driven by there being elopomorphs that are only known from North America and Madagascar during the Maastrichtian. It is likely that these elopomorphs are more pandemic than endemic to any of these landmasses. Simpson's similarity emphasizes the entire assemblage and treats absences as true absences (not an artifact of the fossil record). This will not emphasize endemics, and in that analysis, Madagascar has a greater similarity with Bolivia, which would be expected since they are both Gondwanan landmasses. Jaccard's similarity emphasizes the shared presence, which is why that result is similar to the cluster from the PAE.

If vicariance was driving the distribution of these taxa, it would have been expected that India and/or Bolivia would have clustered with Madagascar, due to their more recent physical association in geological history. However, these results points to a more cosmopolitan nature of the coastal margin genera that would have been predicted for the strictly freshwater inhabitants.

CHANGES IN MADAGASCAR'S FISH FAUNA OVER TIME

Recent fishes on Madagascar

Coastal fauna: Madagascar's size and current isolated geographical position has resulted in the island having over 5000 kilometers of coastlines, spanning 14 degrees of latitude with a variety of marine niche environments including brackish, hypersaline, intertidal, shallow marine and pelagic (Cooke et al., 2003). Due to this large amount of habitat diversity, it is estimated that Madagascar possesses the greatest diversity in marine biota of any country in the western Indian Ocean (Cooke et al., 2003). The fishes in these coastal waters include the coelacanth, an estimated 100 elasmobranchs, at least 300 pelagic and benthic teleosts, and more than 700 coral reef fishes (Cooke et al., 2003). Many of the pelagic coastal fishes are euryhaline and migratory and inhabit the water around Madagascar on a seasonal basis, such as varieties of tuna, marlin, and swordfish. Madagascar's coral reefs are similar to those of eastern Africa and other western Indian Ocean islands. Table 10 shows superorders, orders, and families that are the most speciose within Madagascar's coral reef environment.

TABLE 10: A subset of superorders, orders, and families of most speciose coastal reef fishes currently considered Madagascar (Cooke et al., 2003)

SUPERORDER	ORDER	FAMILY
Acanthopterygii	Beryciformes	Holocentridae
	Tetraodontiformes	Tetraodontidae
	Perciformes	Acanthuridae Chaetodontidae Labridae Lethrinidae Lutjanidae Mullidae Pomacentridae Scaridae Serranidae

Unlike the freshwater ecosystems in Madagascar, it is not surprising that the coastal fishes do not exhibit the same degree of specific endemism, but it is likely that the fishes of the coastal waters exhibit regional endemicity (being found in the western Indian Ocean only) (Cooke et al., 2003). Based on the families that were represented during the Late Cretaceous of Madagascar, this concept of "regional endemicity" also appears to have changed through geologic time, as discussed below.

Freshwater fauna: Madagascar's extant freshwater fauna is typical for an oceanic island (Sparks and Stiassny, 2003). There is not as much richness at the broader taxonomic levels than geographically larger areas. Table 11 shows the families (with taxonomic orders and superorders) currently found on Madagascar and those with species endemic to the island (based on Sparks and Stiassny (2003)). Table 12 shows the percentage of endemicity currently within the freshwater ichthyofauna of Madagascar as a whole, calculated from the information from Sparks and Stiassny (2003). This table shows that various regions within Madagascar, even today, exhibit extremely different endemic percentages and patterns.

TABLE 11: Extant freshwater fishes families, orders, and superorders on Madagascar (Sparks and Stiassny, 2003). Bold families contain at least one endemic species endemic to Madagascar. A detailed list of species and locations is in Appendix B (Table 17).

SUPERORDER	**ORDER**	**FAMILY**
Elopomorpha	Anguilliformes Elopiformes	Anguillidae Megalopidae
Clupeomorpha	Clupeiformes	**Clupeidae**
Ostariophysi	Siluriformes	**Ariidae** **Ancharidae**
	Gonorhynchiformes	Chanidae
Acanthopterygii	Atheriniformes	**Atherinidae** **Bedotidae**
	Cyprinidontiformes	**Aplocheilidae** **Poeciliidae**
	Sygnathiformes	Sygnathidae

TABLE 11, continued

	Perciformes	**Ambassidae** **Terapontidae** Kuhlidae Monodactylidae Scatophagidae Carangidae **Cichlidae** Mugilidae **Gobidae** **Eleotridae**

TABLE 12: Percent endemicity within the extant Madagascar freshwater fish fauna. Based off the information in Appendix B (Table 17).

Number of:	**Total**	**Endemic to Madagascar**	**Percent Endemism**
Families	21	2	9.52
Genera	54	14	25.93
Species	143	93	65.03

Endemicity by Basin:	**Total**	**Endemic to Madagascar**	**Percent Endemism**
Southern Basins	10	6	60.00
Western Basins	49	12	24.49
Northwestern Basins	71	33	46.48
Eastern Highlands	51	33	64.71
Eastern Lowlands	69	31	44.93

Fossil fish record of Madagascar

Triassic: Triassic rocks occur in northwestern Madagascar in the Diego Basin (Figure 49), approximately 400 km northeast of the Late Cretaceous sediments of the Mahajanga Basin. These Triassic beds (which occur in a Carboniferous to Middle Jurassic sequence) correspond to the African Karoo Supergroup (interpreted as mainly continental with minor marine influence). The Karoo has three groups in Madagascar (Isalo Group, Sakamena Group, and Sakao Group) (Beltan, 1996). The Triassic fishes found in Diego Basin of the Karoo are marine, and the basin is surrounded by plutonic, metamorphic, and volcanic rocks dated as Lower Triassic (251 – 245.9 Ma). Negative imprints of the fossils are preserved in ellipsoidal, siliceous-clayed nodules. The fossils are usually articulated and laterally flattened (Beltan, 1996). Diego Basin localities that have produced Triassic-aged fishes include Betsiaka, Anjabimilay, Bobasatrana, Andigoza, Mahatsara, Ankikotazo, Kinganio, Ambarakaraka, Bobatomendry, Anaborano, Bobantsetry, and Antasaba (North and South) (Beltan, 1996).

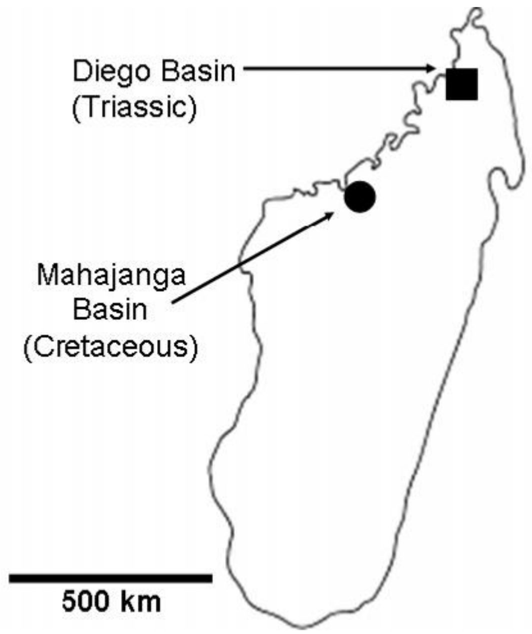


FIGURE 49: Location of Diego Basin in Northwestern Madagascar containing the Triassic fossiliferous sediments in comparison to the location of the Mahajanga Basin, Late Cretaceous study area.

The fossil actinopterygian orders present during the Triassic of Madagascar differ greatly from those in the Late Cretaceous and today. This is from, in part, the Triassic open-marine paleoenvironment and tectonic relationships between the continents in each respective time period. A detailed list of the species is presented in Appendix C (Table 18) including 21 identified genera and 28 species. Table 13 shows the larger taxonomic groups of these Triassic fishes on Madagascar in the Diego Basin. The fauna overall is phylogenetically basal within the actinopterygians. The majority of the actinopterygian genera are monospecific and endemic to Madagascar (Beltan, 1996). None of these orders (except the Palaeonisciformes) are known to persist into the Cretaceous. Since these fishes no longer exist, there were large changes that occurred in the fish fauna after the isolation of Madagascar was completed.

There is also a terrestrial assemblage of Middle to Late Triassic (~225 – 251 Ma) age that contains a rich diversity of vertebrates of Dinosauria, Rhynchosauria, Phytosauridae, Stagonolepidae, and Kannemeyeriidae (Flynn et al., 1999).

TABLE 13: Triassic actinopterygian orders and families from Northwestern Madagascar (modified from Beltan (1996)). Extinct orders are denoted with a †.

ORDER	**FAMILY**
Palaeonisciformes †	Birgeriidae Palaeoniscidae
Elonichthyiformes†	Acrolepidae EiliIiidae
Saurichthyiformes†	Saurichthyidae
Platysomidiformes	Bobasatraniidae
Errolichthyiformes†	Errolichthyidae
Parleidiformes†	Perleididae
Pholidopleuriformes†	Pholidopleuridae
Parasemionotiformes†	Parasemionotidae

Late Cretaceous: Based on the identified fish taxa in the previous chapters, the Late Cretaceous fauna is summarized in Table 14. Detailed information about each of these taxa is included in Chapter 2 and 3.

Table 14: Actinopterygian fauna from the Late Cretaceous of Madagascar. Previously known taxa from(Gottfried and Krause, 1998; Gottfried and Ostrowski, 2008).

Taxa identified herein		
ORDER	**FAMILY**	**GENUS**
Albuliformes	Albulidae	*Albula*
Aulopiformes	Enchodontidae	*Enchodus*
Elopiformes	Phyllodontidae	*Egertonia*
		Paralbula
Characiformes	indet.	
Cypriniformes	indet.	
Perciformes	Sciaenidae	indet.
	indet.	
Pycnodontiformes†	Pycnodontidae	*Coelodus*
Silurifomes	indet.	
Previously known taxa		
ORDER	**FAMILY**	**GENUS**
Lepisosteiformes	Lepisosteidae	*Lepisosteus*
Siluriformes	Ariidae	indet.

Geographical changes from the Triassic to the recent, and their effect on paleoecology:

Geographically, Madagascar went through many changes during from the Triassic until the Recent. During the Mesozoic, Pangea was fracturing, forming Gondwana in the southern hemisphere and Laurasia in the northern hemisphere. During the Triassic, Madagascar was sandwiched between East Africa and India in the Pangea Supercontinent. There were large epicontinental, warm shallow seas (200-300 meters in average depth) surrounded by semi-arid terrestrial environments (Grindley et al., 1981) (Figure 50). During the Cretaceous, the Mozambique channel grew, separating Madagascar further from mainland Africa, while still keeping its connection to India, and with suspect landbridges with other landmasses. By the end of the Cretaceous (K/T or K/Pg boundary) Madagascar was completely isolated as the Indian subcontinent migrated rapidly towards Asia. Figure 51 shows the growing isolation of Madagascar through geologic history after the break-up of Pangea. Since the Late Cretaceous, Madagascar has remained fairly stable in its position relative to other landmasses. However, ocean currents in the Mozambique Channel have been greatly affected due to changes in orientation and position of other landmasses, which in turn affected the global ocean current system (Ali and Huber, 2010).

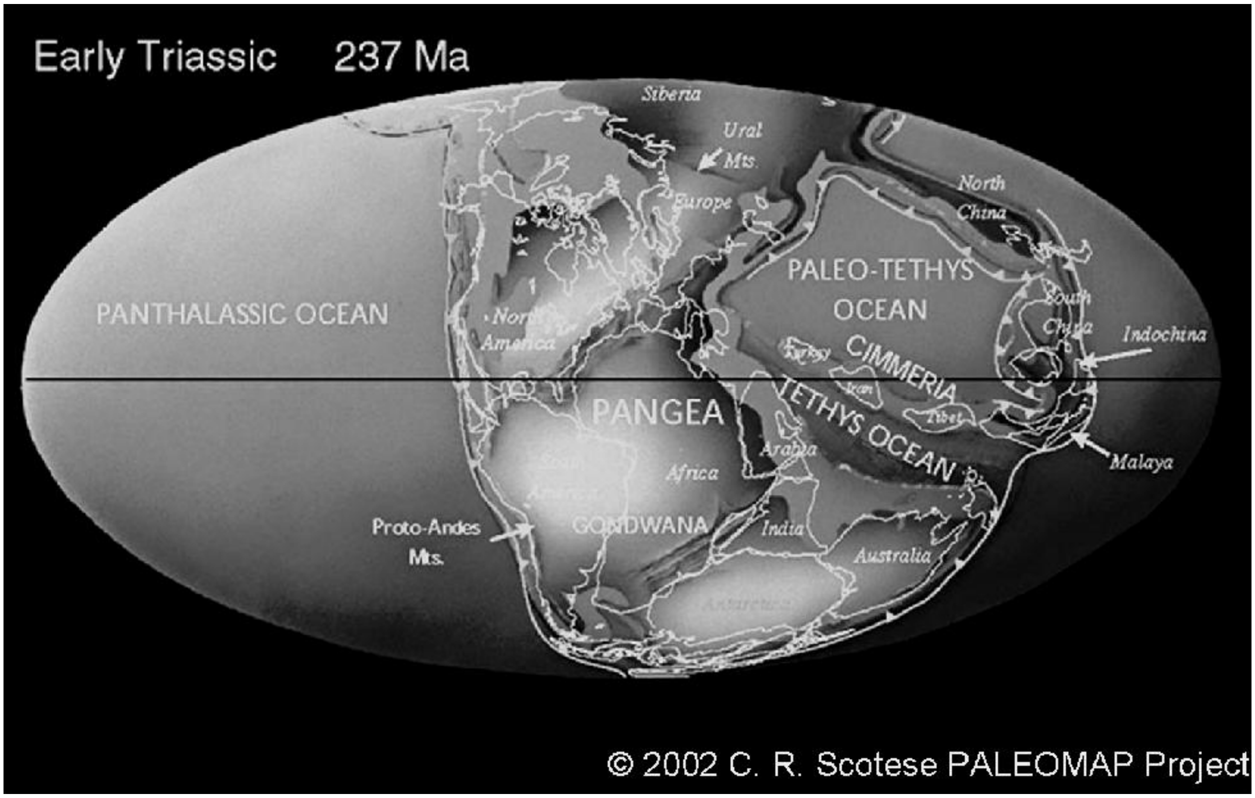


FIGURE 50: Continental positions during the Early Triassic (Scotese, 2012).

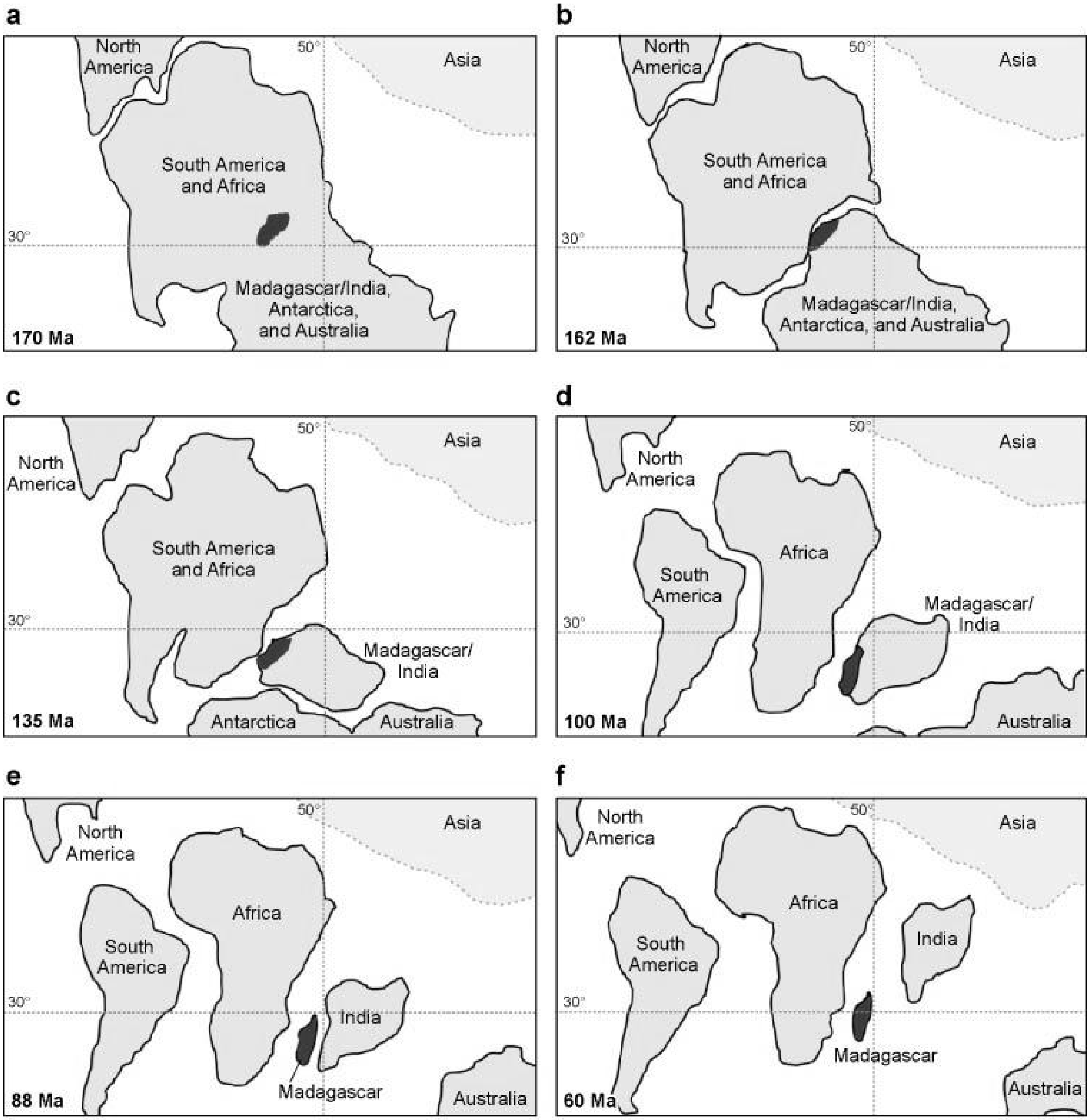


FIGURE 51: Landmass relationships through the fractionation of Gondwana and highlighting the growing isolation of Madagascar (highlighted landmass) through the past 200 million years. (Yoder and Nowak, 2006)

CONCLUSIONS

There have been dramatic changes in the ichthyofauna of Madagascar from the Triassic to the Recent. Table 15 displays the orders present in the time periods discussed in this chapter, Triassic, Late Cretaceous and Recent (marine and freshwater). It is readily apparent that the amount of turnover is large. All of the orders (except for Palaeonisciformes) from the Triassic were extinct by the Cretaceous. There is similarity at the ordinal level of Siluriformes, Elopiformes, and Perciformes between the Late Cretaceous and Recent fishes. But within these 3 orders, there is no overlap in the families, genera, or species present through these two time periods. The majority of orders from the Late Cretaceous, even though still living today, no longer are found on Madagascar. There is minimal amount of overlap at higher taxonomic levels through Madagascar's history, meaning large changes have occurred in fish fauna after Madagascar's complete isolation 88 million years ago.

TABLE 15: Comparison of ichthyofauna orders present during the Triassic, Late Cretaceous, and Recent of Madagascar and the environmental conditions. Extinct clades denoted by †. Previously described taxa indicated by *.

TRIASSIC (MARINE)	LATE CRETACEOUS (MIXTURE)	RECENT (MARINE)	RECENT (FRESHWATER)
Elonichthyiformes†	Albuliformes	Beryciformes	Anguilliformes
Errolichthyiformes†	Aulopiformes	Perciformes	Atheriniformes
Palaeonisciformes†	Elopiformes	Tetraodontiformes	Clupeiformes
Parasemionotiformes†	Characiformes		Cyprinidontiformes
Perleidiformes†	Cypriniformes		Elopiformes
Pholidopleuriformes†	Perciformes		Gonorhynchiformes
Platysomidiformes†	Pycnodontiformes†		Perciformes
Saurichthyiformes†	Silurifomes		Siluriformes
	*Lepisosteiformes		Sygnathiformes

Based on the information presented above, in conjunction with the PAE and Similarity indices reported earlier, the following conclusions can be made with respect to earlier posited hypotheses.

1. Vicariance:
    a. Prediction: *Vicariance is the main mechanism driving diversity and distribution of fishes seen on Madagascar during the Maastrichtian.* Madagascar did not cluster with more recently associated landmasses in the PAE, such as India, based on the presence and absence of genera. It does not appear that vicariance is driving the biogeographical patterns during the Late Cretaceous.
    b. Prediction: *Vicariance is the main mechanism driving diversity and distribution of Recent fishes on Madagascar.* Throughout the growing isolation of Madagascar during the Mesozoic and Cenozoic, there have been several major faunal turnovers, not only in fishes (coastal and freshwater), but also in land vertebrates (dinosaurs and crocodiles to lemur, fossa, and chameleons). This shows that though vicariance likely played an important role in the initial establishment of populations when Madagascar first became isolated, this vicariant pattern was overwritten by dispersed fauna colonizing the island.
2. Marine Dispersal:
    a. Prediction: *Dispersal is the main mechanism driving diversity and distribution of fishes seen on Madagascar during the Maastrichtian.* Madagascar is most closely clustering with formations from North

America, therefore suggesting that it is most parsimonious to say that they were more recently geologically associated, which is false. Since it is known that they were not geologically associated, this leads to the conclusion that dispersal has had an impact on the Late Cretaceous fauna of Madagascar and on general coastal marine taxa globally were cosmopolitan.

   b. Prediction: *Dispersal is the main mechanism driving diversity and distribution of Recent fishes on Madagascar.* Based on the answers to prediction 1b and the large faunal turnovers that have taken place on Madagascar over 200 million years, it is likely that dispersal has had an effect on the endemic populations that exist there today.

3. *Some fish clades have a more cosmopolitan distribution that previously thought.* Based on the two similarity indices, there are two different scenarios for Madagascar. Simpson's index indicates a greater similarity with fauna from South America. Jaccard's index indicates a greater similarity with North America. Therefore, the taxa that are influencing these results are more cosmopolitan in nature (e.g., *Egertonia, Paralbula, and Albula*). This shows that the parameters of these indices produce different results, making a clear pattern difficult to assess.
4. *Highly endemic faunas are depauperate at higher taxonomic levels, and more speciose (due to the isolation and subsequent evolution).* It is known that the recent fishes of Madagascar are depauperate at the higher taxonomic levels, but very speciose within them. It is not clear if this high level of specific

endemicity is also present in the fossil faunas, owing to the nature of the fossil record. The longer something has been a fossil, the less likely it is that it will be discovered and described, and it is often easier to assign species to living rather than fossil taxa. The newly identified Late Cretaceous taxa have a broader distribution at the order level which could indicate more of a "regional endemicity" or even cosmopolitanism.

A recent review of the Malagasy fauna concluded that Recent fauna mainly derive from Cenozoic dispersalists from mainland Africa (Yoder and Nowak, 2006). Yoder and Nowak (2006) admitted that fishes were a tricky problem in these analyses and predicted that the faunal turnover seen in other terrestrial vertebrates from the Late Cretaceous to the Recent would also be seen within the fossil fishes. Yoder and Nowak (2006) suggested that ancient vicariance would be supported if there were area cladograms of certain fishes that exist there today (Bedotiidae, Pachypanchax, and Cichlidae) that match tectonic events. However, since some of these fish taxa have not been found within the Late Cretaceous (on Madagascar, or anywhere globally), there is no evidence that these groups were present during the fractionation of Gondwana.

APPENDIX A

APPENDIX A, TABLE 16: Presence/absence matrix of Maastrichtian formations and genera used in the biogeographical analyses

	GENUS					
FORMATION/LOCALITY	*Acipenser*	*Albula*	*Amia*	*Anomoeodus*	*Apateodus*	*Apogonidarum*
Albaina (Spain)	0	0	0	1	0	0
Arkadelphia (Arkansas, USA)	0	0	0	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0	0	0
El Molino (Bolivia)	0	0	0	0	0	0
Fox Hills (South Dakota, USA)	0	0	0	0	0	0
Fruitland (New Mexico, USA)	1	0	1	0	0	0
Hell Creek Formation (Western, USA)	1	0	1	0	0	0
Horseshoe Canyon (Alberta, Canada)	1	0	1	0	0	0
Intertrappen beds (India)	0	0	0	0	1	1
Lameta Formation (India)	0	0	0	0	0	0
Lance Formation (Western USA)	1	0	1	0	0	0
Maastricht (Netherlands)	0	0	0	1	1	0
Maevarano (Madagascar)	0	1	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	1	0	0
Navesink (New Jersey, USA)	0	0	0	1	0	0
Phosphorite Unit (Jordan)	0	0	0	0	0	0
Severn (Maryland, USA)	0	0	0	1	0	0
Sharon Springs (South Dakota, USA)	0	0	0	0	0	0
St. Mary River (Alberta, Canada)	0	0	1	0	0	0

TABLE 16, continued

	GENUS					
FORMATION/LOCALITY	*Apsopelix*	*Arius*	*Atractosteus*	*Belonostomus*	*Ceratodus*	*Cimolichthys*
Albaina (Spain)	0	0	0	0	0	0
Arkadelphia (Arkansas, USA)	0	0	1	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0	0	1
El Molino (Bolivia)	0	0	0	0	1	0
Fox Hills (South Dakota, USA)	0	0	0	0	0	1
Fruitland (New Mexico, USA)	0	0	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	0	1	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0	0	0	0
Intertrappen beds (India)	0	0	0	1	0	0
Lameta Formation (India)	0	1	0	0	0	0
Lance Formation (Western USA)	0	0	0	1	0	0
Maastricht (Netherlands)	0	0	0	1	0	1
Maevarano (Madagascar)	0	0	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0	0	0
Navesink (New Jersey, USA)	0	0	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	0	0	0
Severn (Maryland, USA)	0	0	0	0	0	0
Sharon Springs (South Dakota, USA)	1	0	0	0	0	0
St. Mary River (Alberta, Canada)	0	0	0	1	0	0

TABLE 16, continued

	GENUS					
FORMATION/LOCALITY	*Clupeidarum*	*Coelodus*	*Coriops*	*Cyclurus*	*Cylindracanthus*	*Dastilbe*
Albaina (Spain)	0	0	0	0	0	0
Arkadelphia (Arkansas, USA)	0	0	0	0	1	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0	0	0
El Molino (Bolivia)	0	1	0	0	0	0
Fox Hills (South Dakota, USA)	0	0	0	0	1	0
Fruitland (New Mexico, USA)	0	0	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	1	1	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	1	1	0	0
Intertrappen beds (India)	1	0	0	0	0	0
Lameta Formation (India)	0	0	0	0	0	1
Lance Formation (Western USA)	0	0	1	1	0	0
Maastricht (Netherlands)	0	0	0	0	0	0
Maevarano (Madagascar)	0	1	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0	1	0
Navesink (New Jersey, USA)	0	0	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	0	0	0
Severn (Maryland, USA)	0	0	0	0	1	0
Sharon Springs (South Dakota, USA)	0	0	0	0	1	0
St. Mary River (Alberta, Canada)	0	0	0	0	0	0

TABLE 16, continued

	GENUS					
FORMATION/LOCALITY	*Dercetis*	*Egertonia*	*Enchodus*	*Eoserranus*	*Eotrigonodon*	*Gasteroclupea*
Albaina (Spain)	0	0	1	0	0	0
Arkadelphia (Arkansas, USA)	0	0	1	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	1	0	0	0
El Molino (Bolivia)	0	0	1	0	0	1
Fox Hills (South Dakota, USA)	0	0	1	0	0	0
Fruitland (New Mexico, USA)	0	0	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	1	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0	0	0	0
Intertrappen beds (India)	0	0	1	0	0	0
Lameta Formation (India)	0	0	1	1	1	0
Lance Formation (Western USA)	0	0	0	0	0	0
Maastricht (Netherlands)	1	0	1	0	0	0
Maevarano (Madagascar)	0	1	1	0	0	0
Mount Laurel (New Jersey, USA)	0	0	1	0	0	0
Navesink (New Jersey, USA)	0	0	1	0	0	0
Phosphorite Unit (Jordan)	0	0	1	0	0	0
Severn (Maryland, USA)	0	1	0	0	0	0
Sharon Springs (South Dakota, USA)	0	0	1	0	0	0
St. Mary River (Alberta, Canada)	0	0	0	0	0	0

TABLE 16, continued

	GENUS				
FORMATION/LOCALITY	*Hadrodus*	*Holopteryx*	*Horseshoeichthys*	*Indotrigonodon*	*Lepidotes*
Albaina (Spain)	0	0	0	0	0
Arkadelphia (Arkansas, USA)	1	0	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	1	0	0	0
El Molino (Bolivia)	0	0	0	0	0
Fox Hills (South Dakota, USA)	1	0	0	0	0
Fruitland (New Mexico, USA)	0	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	1	0	0
Intertrappen beds (India)	0	0	0	1	1
Lameta Formation (India)	0	0	0	1	1
Lance Formation (Western USA)	0	0	0	0	0
Maastricht (Netherlands)	0	1	0	0	0
Maevarano (Madagascar)	0	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0	0
Navesink (New Jersey, USA)	0	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	0	0
Severn (Maryland, USA)	1	0	0	0	0
Sharon Springs (South Dakota, USA)	0	0	0	0	0
St. Mary River (Alberta, Canada)	1	0	0	0	0

TABLE 16, continued

	GENUS			
FORMATION/LOCALITY	*Lepisosteus*	*Megalocoelacanthus*	*Melvius*	*Notopteridarum*
Albaina (Spain)	0	0	0	0
Arkadelphia (Arkansas, USA)	1	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0
El Molino (Bolivia)	1	0	0	0
Fox Hills (South Dakota, USA)	1	0	0	0
Fruitland (New Mexico, USA)	1	0	0	0
Hell Creek Formation (Western, USA)	1	0	1	0
Horseshoe Canyon (Alberta, Canada)	1	0	0	0
Intertrappen beds (India)	1	0	0	1
Lameta Formation (India)	1	0	0	0
Lance Formation (Western USA)	1	0	1	0
Maastricht (Netherlands)	0	0	0	0
Maevarano (Madagascar)	1	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0
Navesink (New Jersey, USA)	0	1	0	0
Phosphorite Unit (Jordan)	0	0	0	0
Severn (Maryland, USA)	1	0	0	0
Sharon Springs (South Dakota, USA)	0	0	0	0
St. Mary River (Alberta, Canada)	1	0	0	0

TABLE 16, continued

	GENUS			
FORMATION/LOCALITY	*Ophidercetis*	*Osteoglossidarum*	*Pachyrhizodus*	*Palaeolabrus*
Albaina (Spain)	0	0	0	0
Arkadelphia (Arkansas, USA)	0	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	1	0
El Molino (Bolivia)	0	0	0	0
Fox Hills (South Dakota, USA)	0	0	0	0
Fruitland (New Mexico, USA)	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	0	1
Horseshoe Canyon (Alberta, Canada)	0	0	0	0
Intertrappen beds (India)	0	1	0	0
Lameta Formation (India)	0	0	0	0
Lance Formation (Western USA)	0	0	0	0
Maastricht (Netherlands)	1	0	1	0
Maevarano (Madagascar)	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0
Navesink (New Jersey, USA)	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	0
Severn (Maryland, USA)	0	0	0	0
Sharon Springs (South Dakota, USA)	0	0	1	0
St. Mary River (Alberta, Canada)	0	0	0	0

TABLE 16, continued

	GENUS				
FORMATION/LOCALITY	*Paleopsephurus*	*Paralbula*	*Paramicrodon*	*Percoideorum*	*Phareodus*
Albaina (Spain)	0	1	1	0	1
Arkadelphia (Arkansas, USA)	0	1	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0	0
El Molino (Bolivia)	0	0	0	0	0
Fox Hills (South Dakota, USA)	0	1	0	0	0
Fruitland (New Mexico, USA)	0	1	0	0	0
Hell Creek Formation (Western, USA)	1	1	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0	0	0
Intertrappen beds (India)	0	0	0	1	1
Lameta Formation (India)	0	0	0	0	1
Lance Formation (Western USA)	1	0	0	0	0
Maastricht (Netherlands)	0	0	0	0	0
Maevarano (Madagascar)	0	1	0	0	0
Mount Laurel (New Jersey, USA)	0	1	0	0	0
Navesink (New Jersey, USA)	0	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	0	0
Severn (Maryland, USA)	0	1	0	0	0
Sharon Springs (South Dakota, USA)	0	0	0	0	0
St. Mary River (Alberta, Canada)	0	1	0	0	0

TABLE 16, continued

	GENUS				
FORMATION/LOCALITY	*Pisdurodon*	*Platacodon*	*Protosphyraena*	*Pseudoegertonia*	*Pycnodus*
Albaina (Spain)	0	0	0	0	0
Arkadelphia (Arkansas, USA)	0	0	0	1	0
Ciply-Mologne Chalk (Netherlands)	0	0	1	0	0
El Molino (Bolivia)	0	0	0	0	0
Fox Hills (South Dakota, USA)	0	0	0	0	0
Fruitland (New Mexico, USA)	0	0	0	1	0
Hell Creek Formation (Western, USA)	0	1	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0	0	0
Intertrappen beds (India)	0	0	0	0	1
Lameta Formation (India)	1	0	0	0	0
Lance Formation (Western USA)	0	1	0	0	0
Maastricht (Netherlands)	0	0	0	0	0
Maevarano (Madagascar)	0	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0	0
Navesink (New Jersey, USA)	0	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	1	0
Severn (Maryland, USA)	0	0	0	0	0
Sharon Springs (South Dakota, USA)	0	0	1	0	0
St. Mary River (Alberta, Canada)	0	1	0	0	0

TABLE 16, continued

	GENUS			
FORMATION/LOCALITY	*Salmoniformorum*	*Sauroceaphalus*	*Serranidarum*	*Stratodus*
Albaina (Spain)	0	0	0	0
Arkadelphia (Arkansas, USA)	0	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0	0
El Molino (Bolivia)	0	0	0	0
Fox Hills (South Dakota, USA)	0	0	0	0
Fruitland (New Mexico, USA)	0	0	0	0
Hell Creek Formation (Western, USA)	0	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0	0
Intertrappen beds (India)	1	0	1	0
Lameta Formation (India)	0	0	0	0
Lance Formation (Western USA)	0	0	0	0
Maastricht (Netherlands)	0	1	0	0
Maevarano (Madagascar)	0	0	0	0
Mount Laurel (New Jersey, USA)	0	0	0	0
Navesink (New Jersey, USA)	0	0	0	0
Phosphorite Unit (Jordan)	0	0	0	1
Severn (Maryland, USA)	0	0	0	0
Sharon Springs (South Dakota, USA)	0	0	0	0
St. Mary River (Alberta, Canada)	0	0	0	0

TABLE 16, continued

	GENUS		
FORMATION/LOCALITY	*Stephanodus*	*Tiupampichthys*	*Xiphactinus*
Albaina (Spain)	1	0	0
Arkadelphia (Arkansas, USA)	0	0	0
Ciply-Mologne Chalk (Netherlands)	0	0	0
El Molino (Bolivia)	1	1	0
Fox Hills (South Dakota, USA)	0	0	0
Fruitland (New Mexico, USA)	0	0	0
Hell Creek Formation (Western, USA)	0	0	0
Horseshoe Canyon (Alberta, Canada)	0	0	0
Intertrappen beds (India)	1	0	0
Lameta Formation (India)	1	0	0
Lance Formation (Western USA)	0	0	0
Maastricht (Netherlands)	0	0	0
Maevarano (Madagascar)	0	0	0
Mount Laurel (New Jersey, USA)	1	0	1
Navesink (New Jersey, USA)	1	0	1
Phosphorite Unit (Jordan)	1	0	0
Severn (Maryland, USA)	0	0	0
Sharon Springs (South Dakota, USA)	0	0	1
St. Mary River (Alberta, Canada)	0	0	0

APPENDIX B

APPENDIX B, TABLE 17: Extant freshwater fishes on Madagascar (Sparks and Stiassny, 2003). Families denoted with *, endemics are bolded. Species without “X” = unknown location. Abbreviations: S.B = Southern Basins; W.B = Western Basins; NW.B = Northwestern Basins; E.H = Eastern Highlands; E.L = Eastern Lowlands.

*FAMILY Genus	Species	S.B	W.B	NW.B	E.H	E.L
*ANGUILLIDAE						
Anguilla	*bicolor*	X	X	X	X	X
	marmorata	X	X	X	X	X
	mossambica	X	X	X	X	X
*CLUPEIDAE						
Pellona	*dichela*		X	X		X
Sauvagella	***madagascariensis***	X			X	X
	nov. sp. "robusta"			X		
Spratellomorpha	*bianalis*		X	X		
*ARRIDAE						
Arius	*africanus*		X	X		X
	dussumieri		X	X		
	madagascariensis			X		X
	nov. sp. "ankofia"			X		
	nov. sp. "sofia"			X		
***ANCHARIIDAE**						
Ancharius	***brevibarbus***				X	X
	fuscus				X	X
	nov. sp. "southwest"		X			
	nov. sp. "southeast"				X	
*ATHERINIDAE						
Atherinomoros	*cf. duodecimalis*	X			X	X
Teramulus	***kieneri***				X	
	waterloti			X		
***BEDOTIIDAE**						
Bedotia	***geayi***					X
	madagascariensis					X
	longianalis					X
	marojejy				X	
	masoala				X	
	tricolor					X
	vondrozo				X	
	nov. sp."bemarivo"					X
	nov. sp."betampona"				X	X
	nov. sp."garassa"					

TABLE 17, continued

***FAMILY Genus**	**Species**	**S.B**	**W.B**	**NW.B**	**E.H**	**E.L**
***BEDOTIIDAE**						
Bedotia	***nov. sp. "lazana"***				X	
	nov. sp."mahanara"					X
	nov. sp. "manombo"					X
	nov. sp. "marosivy"				X	X
	nov. sp. "nosivolo"				X	
	nov. sp."ranomafana"				X	
	nov. sp. "sambava"					
Rheocles	***alaotrensis***				X	
	derhami			X		
	lateralis				X	
	pellegrini				X	
	sikorae				X	
	wrightae				X	
	nov. sp. "ambatovy"				X	
	nov. sp. "andapa"				X	
	nov. sp. "ranila"				X	
*APLOCHDILIDAE						
Pachpanchax	***sakaramyi***			X		
	omalonotus			X		
	nov. sp. "anjingo"			X		
	nov. sp. "betsiboka"		X			
	nov. sp. "manambery"					
	nov. sp. "sofia"			X		
*POECILIIDAE						
Pantanodon	***madagscariensis***					X
	nov. sp. "manombo"					X
*SYNGNATHIDAE						
Coelonotus	*leiaspis*			X	X	X
Hippichthys	*cyanospilus*		X	X		X
Microphis	*brachyurus*				X	
	fluviatilis		X	X		X
*AMBASSIDAE						
Ambassis	***fontoynonti***					
	natalensis		X	X	X	X
	productus		X	X	X	X

TABLE 17, continued

*FAMILY Genus	Species	S.B	W.B	NW.B	E.H	E.L
*TERAPONTIDAE						
Terapon	*jarbua*		X	X		X
Mesopristes	***elongatus***				X	X
*KUHLIDAE						
Kuhlia	*rupestris*		X	X	X	X
*MONODACTYLIDAE						
Monodactylus	*argenteus*		X	X		X
*SCATOPHAGIDAE						
Scatophagus	*tetracanthus*		X	X		X
*CARANGIDAE						
Caranx	*sexfasciatus*		X	X		X
*CHANIDAE						
Chanos	*chanos*		X	X		X
*CICHLIDAE						
Paratilapia	***polleni***	X	X	X	X	
	bleekeri		X	X		X
	nov. sp. "all black"				X	
	nov. sp. "fony"				X	
	nov. sp. "ihotry"		X			
Ptychochromis	***grandidieri***				X	
	oligacanthus	X	X	X		X
	nov. sp. "black saroy"					
	nov. sp. "green garaka"				X	X
	nov. sp. "inornatus"			X		X
	nov. sp. "kotro/onilahy"		X			
	nov. sp. "mipentina"					X
	nov. sp. "nossibeensis"			X		X
Ptychochromoides	***betsileanus***		X			
	katria				X	
	vondrozo				X	
	nov. sp. "itasy"		X			
Oxylapia	***polli***				X	
Paretroplus	***damii***			X		
	kieneri		X	X		
	maculatus			X		
	maromandia			X		
	menarambo			X		
	nourissati			X		

TABLE 17, continued

***FAMILY Genus**	**Species**	**S.B**	**W.B**	**NW.B**	**E.H**	**E.L**
*CICHLIDAE						
Paretroplus	***petiti***			X		
	polyactis	X			X	
	nov. sp. "ankarafantsika"			X		X
	nov. sp. "dambabe"			X		
	nov. sp. "dridrimena"			X		
	nov. sp. "lac parinadrina"			X		
	nov. sp. "sofia"			X		
	nov. sp. "tsimoly"			X		
	nov. sp. "ventitry"					
*MUGILIDAE						
Agonostromus	*telfairii*				X	
Liza	*macrolepis*		X	X		X
	alata		X	X		X
Mugil	*caphalus*		X	X		
Valamugil	*buchanani*		X	X		X
	robustus		X	X		X
*GOBIDAE						
Acentrogobis	*audax*		X	X		X
	therezieni		X			
Awaous	*aeneofuscus*		X	X	X	
Chonophorus	***macrorhynchus***			X		X
Glossogobius	*biocellatus*		X	X		
	giuris		X	X	X	X
	ankaranensis			X		X
	callidus		X	X		
Gobius	*hypselosoma*			X		X
Bathygobius	***sambiranoensis***			X		
	fuscus				X	
Istigobius	*ornatus*		X	X		X
Oliolepis	*acutipennis*					
Oxyrichthys	*tentacularis*		X	X		X
Papillogobius	*reichei*		X	X		X
Redigobius	*baltaetops*					X
	bikolanus					X
Sicyopterus	*laticeps*				X	X
	franouxi				X	X
	nov. sp. "masoala"				X	X

TABLE 17, continued

***FAMILY Genus**	**Species**	**S.B**	**W.B**	**NW.B**	**E.H**	**E.L**
*Gobidae						
Stenogobius	*genivittatus*		X	X		X
Taeniodes	*gracilis*					X
Yonogichthys	*nebulosus*		X	X		X
*Eleotridae						
Butis	*butis*		X	X	X	
Eleotris	*acanthopoma*					X
	fusca		X	X	X	X
	melanosoma		X			X
	pellegrini			X		X
	vomerodentata					X
Hypseleotris	***tohizonae***			X		X
Ophiocara	*porocephala*		X	X		X
	macrolepidota				X	X
Ratsirakia	***legendrei***				X	X
Typhleotris	***madagascariensis***	X				
	pauliani		X			
	nov. sp. "anomaly"	X				
*Megalopidae						
Megalops	*cyprinoides*		X	X		

APPENDIX C

APPENDIX C, TABLE 18: Listing of the Triassic actinopterygian fauna from Northwestern Madagascar (modified from Beltan (1996).

ORDER	FAMILY	GENUS	SPECIES
Palaeonisciformes	Birgeriidae Aldinger, 1937	*Birgeria* Stensiö, 1919	*B. nielseni* Lehman, 1948
	Palaeoniscidae Vogt, 1852	*Ambodipia* Beltan, 1968	*A. madagascariensis* Beltan, 1968
Elonichthyiformes	Acrolepidae Aldinger, 1937	*Boreosomus* Stensiö, 1921	*B. gillioti* Priem, 1924
	Eililiidae Kazanstseva-Selezneva, 1981	*Pteronisculus* White, 1933	*P. cicatrosus* White, 1933 *P. macropterus* White, 1933 *P. broughi* Lehman, 1952 *P. arambourgi* Lehman, 1952
Saurichthyiformes	Saurichthyidae Goodrich, 1909	*Saurichthys* Agassiz, 1833-1844	*S. stensioei* Lehman, 1952 *S. madagascariensis* Piveteau, 1944-1945 *S. piveteaui* Beltan, 1968
Platysomidiformes	Bobasatraniidae Stensiö, 1932	*Bobasatrania* White, 1932	*B. mahavavica* White, 1932
		Ecrinesomus Woodward, 1910	*E. dixoni* Woodward, 1910
Errolichthyiformes	Errolichthyidae Lehman, 1952	*Errolichthys* Lehman, 1952	*E. mirabilis* Lehman, 1952
Perleidiformes	Perleididae Brough, 1931	*Perleidus* de Alessandri, 1910	*P. madagascariensis* Piveteau, 1934 *P. piveteaui* Lehman, 1952
Pholidopleuriformes	Pholidopleuridae Wade, 1932	*Australosomus* Piveteau, 1934	*A. merlei* Piveteau, 1934 *A. longirostris* Beltan, 1968 *A. altisquamosus* Beltan, 1980
Parasemionotiformes	Parasemionotidae Stensiö, 1932	*Ospia* Stensiö, 1932	*O. whitei* Stensiö, 1932
		Broughia Stensiö, 1932	*B. perleidoides* Stensiö, 1932
		Watsonulous Brough, 1939	*W. eugnathoides* Piveteau, 1934

TABLE 18, continued

ORDER	FAMILY	GENUS	SPECIES
Parasemionotiformes	Parasemionotidae Stensiö, 1932	*Parasemionotus* Piveteau, 1934	*P. labroidei* Piveteau, 1934
		Stensioenotus Lehman, 1952	*S. intercessus* Lehman, 1952
		Jacobulus Lehman, 1952	*J. novus* Lehman, 1952
		Thomasinotus Lehman, 1952	T. divisus Lehman, 1952
		Lehmanotus Beltan, 1968	*L. markubai* Beltan, 1968
		Devillersia Beltan, 1968	*D. madagascariensis* Beltan, 1968
		Piveteaunotus Beltan, 1968	*P. ifasiensis* Beltan, 1968
		Icarealcyon Beltan, 1980)	*I. malagasium* Beltan, 1980

REFERENCES

REFERENCES

Agassiz, L., 1833-1844, Recherches su les poissons fossiles, v. 5 vols. 1420 pp. Neuchatel et Soleure (Petitpierre).

Aldinger, H., 1937, Permishe Ganoidfische aus Ost Grønland: Medd. Grønland, v. 102, p. 1-392; Copenhagen.

Ali, J., and Huber, M., 2010, Mammalian biodiversity on Madagascar controlled by ocean currents: Nature, v. 463, p. 653-656.

Alroy, J., 2012, Paleobiology Database, *in* Alroy, J., ed., Volume 2012. http://www.paleodb.org.

Bassias, Y., 1992, Petrological and geochemical investigation of rocks from the Davie Fracture Zone (Mozambique Channel) and some tectonic implications: Journal of African Earth Sciences, v. 15, p. 321-39.

Beltan, L., 1968, La faune ichthyologique de l'Eotria du NW de Madagascar: le neurocrâne, Cahiers Paléontol.: Paris, p. 125.

—, 1980, Sur la presénce d'un poisson volant, *Icarealcyon malgasium* n.g. n.sp. dans l'Eotrias malagache: International Geology Congress, v. 26, p. résumés; 155; Paris.

—, 1996, Overview of systematics, paleobiology, and paleoecology of Triassic fishes of northwestern Madagascar, *in* Arratia, G., and Viohl, G., eds., Mesozoic Fishes - Systematics and Paleoecology: München, Germany, Verlag Dr. Friedrich Pfeil, p. 479-500.

Briggs, D., and Clarkson, E., 1990, The late Paleozoic radiation of malacostracan crustaceans, p. Syst. Assoc. Spec. Vol 42: 165-186.

Briggs, J., 2003, Fishes and Birds: Gondwana Life Rafts Reconsidered: Systematic Biology, v. 52, p. 548-553.

Brough, J., 1931, On fossil fishes from the Karroo system and general considerations on the bony fishes of the Triassic period: Proceedings of the Zoological Society of London, v. 1931, p. 235-296.

—, 1939, The Triassic Fishes of Besano, Lombardy, London (British Museum of Natural History): London, p. 112.

Censky, E., Hodge, K., and Dudley, J., 1998, Over-water dispersal of lizards due to hurricanes: Nature, v. 395, p. 556.

Cooke, A., Lutjeharms, J., and Vaaeur, P., 2003, Marine and Coastal Ecosystems, *in* Goodman, S.M., and Benstead, J.P., eds., The Natural History of Madagscar: Chicago, University of Chicago Press, p. 179-228.

Crottini, A., Madsen, O., Poux, C., Strauß, A., Vieites, D., and Vences, M., 2012, Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar: Proceedings of the National Academy of Sciences.

de Alessandri, G., 1910, Studii sui pesci triasici della Lombardia: Mem. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat., v. 7, p. 1-145; Pavia, Italy.

de Queiroz, A., 2005, The resurrection of oceanic dispersal in historical biogeography: Trends in Ecology and Evolution, v. 20, p. 68-73.

deWit, M., 2003, Madagascar: Heads It's a Continent, Tails It's an Island: Annual Review of Earth and Planetary Sciences, v. 31, p. 213-48.

Emerson, B., Wallis, G., and Patrick, B., 1997, Biogeographic area relationships in southern New Zealand: a cladistic analysi of Lepidoptera distributions: Journal of Biogeography, v. 24, p. 89-99.

Flynn, J., Parrish, J., Rakotosamimanana, B., Simpson, W., Whatley, R., and Wyss, A., 1999, A Triassic Fauna from Madagascar, Including Early Dinosaurs: Science, v. 286, p. 763-765.

Fortey, R., and Cocks, L., 1992, The early Palaeozoic of the North Atlantic region as a test case for the use of fossils in continental reconstruction: Tectonophysics, v. 206, p. 427-444.

Goodman, S., and Benstead, J., 2005, Updated estimates of biotic diversity and endemism for Madagascar: Oryx, v. 39, p. 73-77.

Goodrich, E., 1909, Vertebrata Craniata (First fascicle: Cyclostomes and Fishes): London, xvi + 509 p.

Gottfried, M., and Krause, D., 1998, First Record of Gars (Lepisosteidae, Actinopterygii) on Madagascar: Late Createceous Remains form the Mahajanga Basin: Journal of Vertebrate Paleontology, v. 18, p. 275-279.

Gottfried, M., and Ostrowski, S., 2008, Fossil fishing one piece at a time, with a catfish example from the Late Createceous of Madagascar: Journal of Vertebrate Paleontology, v. 28, p. 85A-86A.

Grindley, G., Olivier, P., and Sukroo, J., 1981, Lower Mesozoic position of Southern New Zealand determiend from paleomagnetism of the Glenham Porphyry--Mirihiku Terrane, Eastern Southland *in* Cresswell, M., and Vella, P., eds., Gondwana V, Wellington, New Zealand: Rotterdamm, A.A. Balkema Publisher, p. 319-326.

Hallam, A., 1994, An Outline of Phanerozoic Biogeography: Oxford, Oxford University Press, 246 p.

Hammer, Ø., and Harper, D., 2006, Paleontological Data Analysis: Malden, MA, Wiley-Blackwell, 351 p.

Hammer, Ø., Harper, D., and Ryan, P., 2001, PAST: Paleontological Statistics Software Package for Education and Data Analysis: Palaeontological Electronica, v. 4, p. 9.

Harland, W., Armstrong, R., Cox, A., Craig, L., Smith, A., and Smith, D., 1990, A Geological Time Scale: Cambridge, Cambridge University Press, 263 p.

Hay, W., DeConto, R., Wold, C., Wilson, K., Voigt, S., Schulz, M., Wold-Rossby, A., Dullo, W.-C., Ronov, A., Bulukhovsky, A., and Söding, E., 1999, Alternative global Cretaceous paleogeography, *in* Barrera, E., and Johnson, C., eds., Evolution of the Cretaceous Ocean-Climate System, Volume Special Paper 332: Boulder, CO, The Geological Society of America, p. 1-48.

Humphries, C., and Parenti, L., 1986, Cadistic Biogeography: Clarendon, Oxford.

Kazanstseva-Selezneva, A., 1981, Les paléoniscidés du Paléozoïque supérieur du Kazakhstan oriental, Trudy Paleontol. Inst. Acad. Sci. U.R.S.S., Volume 180: Moscow, p. 5-139.

Krause, D., 2010, Washed up in Madagsacar: Nature, v. 463, p. 613-614.

Krause, D., O'Connor, P., Curry Rogers, K., Sampson, S., Buckley, G., and Rogers, R., 2006, Late Cretaceous Terrestrial Vertebrates from Madagascar: Implications for Latin American Biogeography: Annals of the Missouri Botanical Garden, v. 93, p. 178-208.

Krause, D., Prasad, G., von Koenigswald, W., Sahni, A., and Grine, F., 1997, Cosmopolitanism among Late Cretaceous Gondwanan mammals: Nature, v. 390, p. 504-507.

Lehman, J., 1948, Sur la présence du genre *Birgeria* (Paléoniscoidé) dan l'Eotrias de Madagascar. : C R Academy of Sciences, v. 226, p. 426-428; Paris.

—, 1952, Etude complémentaire des Poissons de l'Eotrias de Madagascar: Kgl. Sv. VetAkad. Handl., v. 4, p. 1-192; Stockholm.

Lieberman, B., 1999, Paleobiogeography: Using fossils to study Glogal Change, Plate Tectonics, and Evolution: New York, Kluwer Academic/Plenum Publishers, 208 p.

Murray, A., 2000, The oldest fossil cichlids (Teleostei: Perciformes): indication of a 45 million-year-old species flock: Proceedings of the National Academy of Sciences of London, v. 268, p. 279-684.

Nelson, G., and Platnick, N., 1981, Systematics and Biogeography: Cladistics and Vicariance: New York, Columbia University Press.

Piveteau, J., 1934, Les Poissons du Trias inférieur: contribution a l'étude des Actinoptérygians: Ann. Paléontol., v. 23, p. 83-178; Paris.

—, 1944-1945, Les poissons du Trias inférieur. La familie des Saurichthyidés. Paléontologie de Madagascar: Ann. Paléontol., v. 25, p. 79-88; Paris.

Priem, F., 1924, Paléontologie de Madagascar. XII. Les poissons fossiles: Annals de Paléontologie v. 13, p. 107-132.

Rabinowitz, P., Coffin, M., and Falvey, D., 1983, The separation of Madagascar and Africa: Science, v. 220, p. 67-69.

Raup, D., and Crick, R., 1979, Measurement of Faunal Similarity in Paleontology: Journal of Paleontology, v. 53, p. 1213-1227.

Raxworthy, C., Forstner, M., and Nussbaum, R., 2002, Chameleon radiation by oceanic dispersal: Nature, v. 415, p. 784-787.

Raxworthy, C., and Nussbaum, R., 1996, Patterns of endemism for terrestial vertebrates in eastern Madagascar: Biogeography of Madagascar, v. 1996, p. 369-383.

Reeves, C., and de Wit, M., 2000, Making ends meet in Gondwana: Retracing the tranforms of the Indian Ocean and reconnecting shear zones: Terra Nova, v. 12, p. 272-280.

Rosen, B., and Smith, A., 1988, Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from Late Cretaceous to Recent, using a new method, *in* Hallam, M.G.A.-C.a.A., ed., Analytical biogeography: London, Chapman and Hall, p. 275-306.

Samonds, K., Godfrey, L., Ali, J., Goodman, S., Vences, M., Sutherland, M., Irwin, M., and Krause, D., 2012, Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type: Proceedings of the National Academy of Sciences.

Scotese, C., 2012, Early Triassic 237 Ma, *in* Scotese, C., ed., PaleoMap Project.

Sereno, P., Wilson, J., and Conrad, J., 2004, New dinosaurs link southern landmasses in the Mid-Cretaceous: Proceedings of the Royal Society B.

Seward, D., Grujic, D., and Schreurs, G., 2004, An insight into the breakup of Gondwana: identifying events through low-temperature thermochronology from the basement rocks of Madagascar: Tectonics, v. 23.

Simpson, G., 1943, Mammals and the nature of continents: American Journal of Science, v. 241, p. 1-31.

—, 1952, Probabilities of dispersal in geologic time: Bulletin of the American Museum of Natural History, v. 99, p. 163-176.

Sparks, J., and Smith, W., 2004, Phylogeny and Biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae): Cladistics, v. 20, p. 501-517.

Sparks, J., and Stiassny, M., 2003, Introduction to Freshwater Fishes, *in* Goodman, S., and Benstead, J., eds., A Natural History of Madagascar: Chicago, IL, University of Chicago Press.

Stensiö, E., 1919, Einege Bemerkungen über die systematische Stellung von *Saurichhys mougetoi*, Agassiz: Senckenbergiana, v. 1, p. 177-191; Frankfurt.

—, 1921, Triassic Fishes from Spitzbergen. I.: Vienna (Adolf Holzhausen), p. xxviii + 307.

—, 1932, Triassic fishes from the East Greenland collected by Danish expeditions 1929-1931: Medd. Grønland, v. 83, p. 1-305; Copenhagen.

Stiassny, M., 1991, Phylogenetic intrarelationships of the family Cichlidae: An overview, *in* Keenleyside, M., ed., Cichlid fishes: Behaviour, ecology, and evolution: London, Chapman and Hall.

Storey, B., 1995, The role of mantle plumes in continental breakup: case histories from Gondwanaland: Nature, v. 377, p. 301-308.

Thévenin, A., 1907, Dinosauriens (Paléontologie de Madagascar IV): Anneles de Paléontologie, v. 2, p. 121-136.

Thiel, M., and Gutow, L., 2005, The ecology of rafting in the marine environment. II. The rafting organisms and community, *in* Gibson, R., Atkinson, R., and Gordon, J., eds., Oceanography and Marine Biology: An Annual Review, Volume 43, Taylor & Francis, p. 279-418.

Thomson, K., 1977, The Pattern of Diversification Among Fishes, *in* Hallam, A., ed., Patterns of Evolution as Illustrated by the Fossil Record, Volume 5: Amsterdam, Elsevier.

Upchurch, P., 2008, Gondwanan break-up: legacies of a lost world?: Trends in Ecology & Evolution, v. 23, p. 229-236.

Vences, M., 2004, Origin of Madagascar's extant fauna: A perspective from amphibians, reptiles and other non- flying vertebrates: Italian Journal of Zoology, v. 71, p. 217-228.

Vogt, C., 1852, Classification des poissons ganöides: Ann. Sci. Natur., v. 4, p. Paris.

Wade, R., 1932, Preliminary note on *Marcoathes brookvalei*, representing a new family of chondrostean fishes the Pholidopleuridae: Annual Magazine of Natural History, v. 10, p. 473-475.

White, E., 1932, On a new Triassic fish from North-East Madagascar: Annual Magazine of Natural History, v. 10, p. 80-83.

—, 1933, New Triassic Palaeoniscides from Madagascar: Annual Magazine of Natural History, v. 10, p. 118-128.

Woodward, A., 1910, On some Permo-Carboniferous fishes from Madagascar: Annual Magazine of Natural History, v. 8, p. 1-6; London.

Yoder, A., Burns, M., Zehr, S., Delefosse, T., Veron, G., Goodman, S., and Flynn, J., 2003, Single Origin of Malagasy Carnivora from an African ancestor: Nature, v. 421, p. 734-737.

Yoder, A., and Nowak, M., 2006, Has Vicariance or Dispersal been the Predominant Biogeographic Force in Madagascar? Only time will tell: Annual Review of Ecology and Evolutionary Systematics, v. 37, p. 405-431.

CONCLUSIONS AND FUTURE DIRECTIONS

This study shows that the fish from Late Cretaceous deposits of Madagascar provide insight into the biogeography of Madagascar, including the level of endemicity in Recent fauna. This study also affects the understanding of biogeography of particular groups of teleosts. Conclusions from the previous chapters are summarized and synthesized below.

Importance of new faunal identifications

The fossil fishes of the Late Cretaceous of Madagascar are one of the last remaining groups to be described and analyzed from the Maevarano Formation. The terrestrial vertebrate fauna from this time has lead to important analyses and hypotheses of the biogeography of Madagascar and how fauna have changed over time. The fish fauna adds another piece to this puzzle.

Our understanding of fossil fishes during the Mesozoic is continuously growing, but is still far from being complete. The adaptive radiation of teleostean fishes makes it difficult to ascertain phylogenetic relationships. Diversification is more rapid and more complex than the lithologic record can preserve. The identification of fish taxa new to the Late Cretaceous of Madagascar supports two major themes:

1. Our idea of “Laurasian” vs. “Gondwanan” fauna after the break-up of Pangea is not applicable to all faunal groups. Some of the fishes identified here were before only known from Laurasian deposits, but it appears that there is a more cosmopolitan nature to the epicontinental seaway fish fauna during the fractionation of Pangea, and subsequently Laurasia and Gondwana. A broader scale regional endemicity or cosmopolitanism plays a role.

2. Our understanding of teleost groups, especially Ostariophysans, and their diversification during the Mesozoic is still limited. Even with such a poor fossil record of ostariophysans, the group is the subject of continual hypotheses. Too much emphasis is placed upon the current distribution of species to construct distribution diagrams for 70 million years ago, which is unrealistic for migratory fauna. As more of these depauperate faunas are found and identified within fossil assemblages, we will be able to better assess the true distributions, paleoecology and evolutionary history of these groups.

Biogeography of Madagascar

From the Triassic to the Late Cretaceous and then to the Recent, there have been major faunal turnovers of the fishes on Madagascar. Throughout this geologic window, Madagascar became progressively more isolated from other landmasses. Dispersal is clearly a significant part of the history of the fauna on Madagascar, and is likely to have overwritten older vicariance events after Madagascar became isolated. The endemicity of species on Madagascar during the Late Cretaceous is difficult to quantify (as is with most fossil assemblages), but based on the newly identified taxa, there appears to have been less endemicity during the Late Cretaceous than there is today. Most of the taxa represented in the Late Cretaceous of Madagascar identified to genus level, are now extinct genera (*Enchodus, Coelodus, Paralbula, and Egertonia*), or even extinct at the family level (Enchodontidae and Phyllodontidae), but were widespread during the Late Cretaceous.

If marine dispersal has had a large impact on the fauna of Madagascar and its endemicity, then it is natural to ask where these fauna came from and how. Currently, researchers are trying to determine how terrestrial fauna can move between islands, or from the mainland to an island. Extant taxa have been observed rafting on material between landmasses (e.g. iguanas (Censky et al., 1998) and invertebrates (Thiel and Gutow, 2005)). Thiel and Gutow (2005), also noted occurrences of fish populations following rafting material. Samonds et al. (2012) recently evaluated the probability of rafting animals based on ocean currents through the Mesozoic and Tertiary, and argued for the probability that fauna successfully traversed the Mozambique Channel (including rafting and swimming) to reach Madagascar from Africa. Paleoceanography and paleontology were synthesized to explain how and when populations could be established in novel environments. This synthesis concluded that African groups were able to traverse the Mozambique Channel by rafting during opportune times of oceanic currents (Samonds et al., 2012), which could be referred to as “opportunistic endemicity” as seen on Madagascar.

Future Directions

This project is a step towards reevaluating and better understanding the highly complex nature of the teleost fossil record. Teleost fishes are often considered a nightmare among paleoichthyologists, however, their fossil history can answer many questions, if properly analyzed and understood. The rapidity of teleost adaptation and diversification allows for analyses on the scale of faunal responses to global change (climatic and tectonic), but it is difficult to view in the fossil record. Often fossil fishes within faunal assemblages are the last to be described, and it is often very difficult material to identify and work with. Our understanding of the fish fossil record could start becoming more complete by looking through museum collections and identifying fishes that have remained unidentified. Even when identification is at a cruder taxonomic level, it is still significant, especially within Mesozoic assemblages when teleosts noticeably started diversifying. Large Gondwanan landmasses with Cretaceous fossil records such as Africa, South America, Antarctica, and Australia, still have relatively poor fish records, so filling in these gaps will lead to a greater representation of global diversity instead of the reliance upon Laurasian assemblages, for reconstructing ancient global distributions.

I plan on remaining involved in the Mahajanga Basin Project due to the plethora of material, though it is difficult to work with. As of right now, there is a lack of understanding of Cretaceous teleosts. The poor Cretaceous fossil fish record and frustrating teleost osteology, does not leave many described and comparative collections that can be used for precise taxonomy of disarticulated material. Being able to compare the Maevarano fauna more directly with other Gondwanan fauna will be imperative to unraveling the evolutionary history of teleosts.

REFERENCES

REFERENCES

Censky, E., Hodge, K., and Dudley, J., 1998, Over-water dispersal of lizards due to hurricanes: Nature, v. 395, p. 556.

Samonds, K., Godfrey, L., Ali, J., Goodman, S., Vences, M., Sutherland, M., Irwin, M., and Krause, D., 2012, Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type: Proceedings of the National Academy of Sciences.

Thiel, M., and Gutow, L., 2005, The ecology of rafting in the marine environment. II. The rafting organisms and community, *in* Gibson, R., Atkinson, R., and Gordon, J., eds., Oceanography and Marine Biology: An Annual Review, Volume 43, Taylor & Francis, p. 279-418.