

Late Cretaceous Elopomorpha (Actinopterygii: Teleostei) from the Mahajanga Basin of Madagascar and impacts on paleobiogeography

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ABSTRACT

The Upper Cretaceous deposits of Madagascar have produced a rich terrestrial vertebrate fauna. Studies of Madagascar's endemic fossils and recent fauna have led to multiple hypotheses surrounding the origin of these clades on the island following its complete isolation 88 m.y.a. This report is the first published description of several representatives of fossil Elopomorpha (Teleostei) from the Late Cretaceous of Madagascar. Elopomorphs are primarily marine fishes and one of the most morphologically diverse groups within teleosts. Fragmentary fossil elopomorph elements often consist of tooth plates and vertebrae. The tooth plates and dentary reported here are diagnostic and identifiable to the generic classification of *Albula*, *Egertonina*, and *Paralbula*. The vertebrae are numerous and morphologically variable, which indicates the abundance and importance of elopomorphs in the coastal environment of Madagascar during the Late Cretaceous. Most Cretaceous elopomorphs are from localities in the Northern Hemisphere. While several species of Cretaceous elopomorphs are also found in the Southern Hemisphere, there are not as many in number or kind. These Madagascar fossils represent the oldest *Albula* and *Paralbula* fossils recorded from Gondwana, increasing their known spatial range. The *Egertonina* material described here represents one of the earliest occurrences of the genus, adding to its record during the Cretaceous of Gondwana. The presence of these fishes supports a more global distribution of these genera during the Late Cretaceous and a higher diversity of Elopomorpha in the Southern Hemisphere during the Mesozoic than previously documented.

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INTRODUCTION

Elopomorpha is one of most morphologically diverse groups of teleosts and contains Elopiformes (tarpons), Albuliformes (bonefishes), Anguilliformes (true eels), and Notacanthiformes (halosaurs and spiny eels). This group of fishes has a deep-reaching fossil record back into the Upper Jurassic of Europe (Arratia, 2000; Rauhut et al., 2017). Elopomorpha are monophyletic, with leptocephalus larva as a notable synapomorphy (Greenwood et al., 1966; Arratia, 1997; Wiley and Johnson, 2010) along with other morphological and molecular traits (Faircloth et al., 2013; Chen et al., 2014; Dornburg et al., 2015; Betancur-R et al., 2017). Elopomorpha are mostly represented in Laurasian fossil localities throughout the Mesozoic and Cenozoic (Estes, 1969; Applegate, 1970; Nessov, 1981; Case and Schwimmer, 1988; Cicimurri, 2007). Fewer Mesozoic fossil elopomorphs have been described from Gondwanan deposits (Hector, 1874; da Silva Santos, 1971; Noubhani and Cappetta, 1994; Ostrowski, 2012; Cappetta et al., 2014; Halliday et al., 2016; Duque and Barreto, 2018).

The Upper Cretaceous strata of northwestern Madagascar, in the Mahajanga Basin (Figure 1), are known to contain very rich terrestrial vertebrate fossil assemblages (Krause et al., 2020). Over the past few decades, the Mahajanga Basin Project (MBP) has made many fossil discoveries and descriptions from this region. The MBP was initiated in 1993 by David W. Krause, then of Stony Brook University, and now of the Denver Museum of Nature & Science, in collaboration with the University of Antananarivo in Antananarivo, Madagascar. The fossil fishes described here are a product of that project. These Upper Cretaceous deposits of the Mahajanga Basin contain elopomorpha vertebrae in addition to teeth and jaw elements belonging to three genera of elopomorphs.

GEOLOGICAL SETTING

The geology and landscape of the Mahajanga Basin in northwestern Madagascar is dominated by four sedimentary formations overlying widespread Coniacian (89.8 - 86.3 m.y.a.) flood basalts deposited around the time Madagascar became geographically isolated (Boast and Nairn, 1982; Storey et al., 1995). The most fossiliferous formation is the

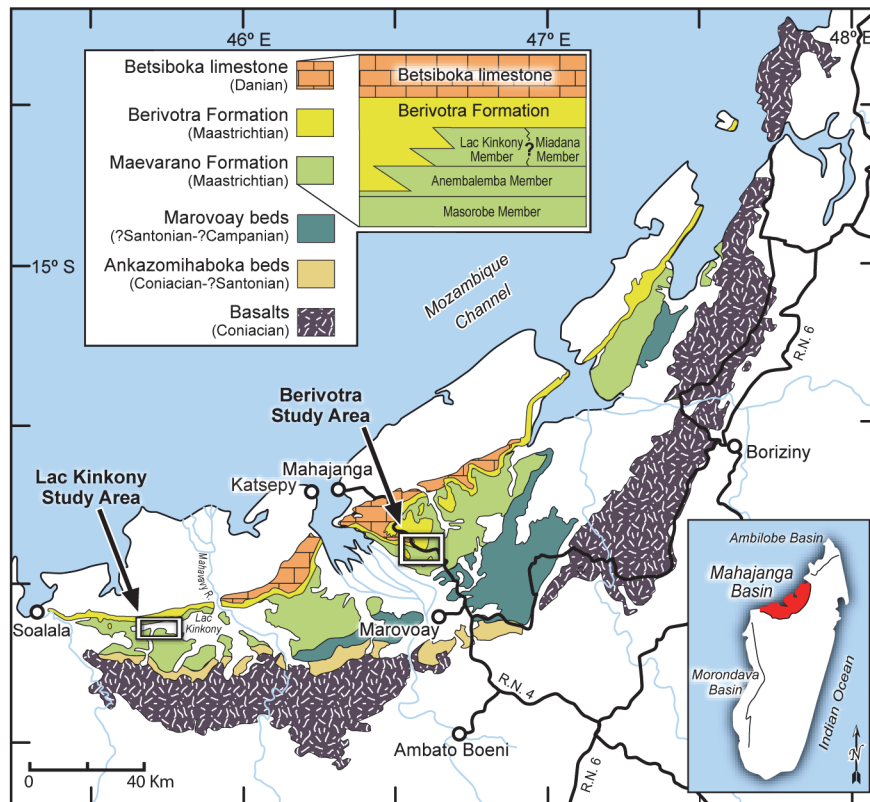


FIGURE 1. Geologic map of the Mahajanga Basin field area in northwestern Madagascar, including Berivotra and Lac Kinkony Study Areas. Modified with permission from Rogers et al. (2013).

Maastrichtian Maevarano Formation (72.1-66.0 m.y.a.), which is primarily terrestrial or coastal and interfingers with the strictly marine Berivotra Formation (Rogers et al., 2000). The palaeoenvironmental setting of the Maevarano Formation is deduced 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 fossil bearing members of the Maevarano Formation consist of four depositional units exhibiting continental to nearshore-marine environments (Figure 1). Fragmentary fish material has been found in all four members of this formation (Rogers et al., 2013). The elopomorphs described here occur within three of these members, the Anembalemba Member, Lac Kinkony Member, and the Miadana Member.

The Anembalemba Member sequence consists of two interbedded facies and contains the most abundant and well-preserved fossils within the Maevarano Formation. Some notable finds include the dinosaurs *Majungasaurus crenatissimus* (Depéret, 1886; Krause et al., 2007) and *Rapetosaurus krausei* (Curry Rogers and Forster, 2001), the crocodyliform *Simosuchus clarki* (Buckley et al., 2000; Krause and Klay, 2010), the mammal *Adalatherium hui* (Krause et al., 2020), and the bird *Falcatakely forsterae* (O'Connor et al., 2020). Rogers et al. (2000) described the palaeoenvironments as a product of downstream migration of fluvial bedforms (Facies 1) with rapid sediment dumping and debris flows (Facies 2). The Lac Kinkony Member exposures overlie the Anembalemba Member and contain abundant fish material along with crocodyliforms, turtles, the mammal *Vintana sertichi* (Krause et al., 2014), and non-avian dinosaurs (Rogers et al., 2013). Most vertebrate fossils in the Lac Kinkony Member are concentrated in microfossil bonebeds embedded within sandstones. This geology indicates a palaeoenvironment of siliciclastic and carbonate tidal flats dissected by tidally influenced rivers (Rogers et al., 2013). The Miadana Member is made of claystone, siltstone, and sandstone but exposures and fossils are rare and indicate a marine influenced environment (Rogers et al., 2000).

The localities of the fishes from this text are marked on Figure 1. The “Berivotra Study Area” is ~35 km southeast of the city of Mahajanga and is named after the village of Berivotra, near which many of the vertebrate fossils have been found by the MBP. Berivotra has localities from the Anembalemba Member and the Miadana Member. The “Lac Kinkony Study Area” is located ~65 km south-

west of the city of Katsepy and ~40 km east of Soalala and named for the nearby lake, Lac Kinkony.

MATERIAL AND METHODS

The fossil fish material from the Upper Cretaceous of Madagascar was collected by the MBP by standard surface collection and screen-washing methods at microsite localities during the field seasons ranging from 1993-2007. Based on collaboration agreements between the University of Antananarivo and first Stony Brook University and subsequently the Denver Museum of Nature & Science, the specimens were assigned catalog numbers based on the institution in which they will be permanently reposit. University of Antananarivo collections have a UA prefix while those housed at Denver Museum of Nature & Science have a DMNH prefix. All images were captured with a digital camera.

Institutional Abbreviations

UA – University of Antananarivo, Antananarivo, Madagascar. DMNH EVP – Denver Museum of Nature & Science, Denver, Colorado, United States of America. NHM – Natural History Museum, London, United Kingdom. FMNH – Field Museum of Natural History, Chicago, Illinois, United States of America. UMMZ – University of Michigan Museum of Zoology, Ann Arbor, Michigan, United States of America.

SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Cope, 1887

Superorder ELOPOMORPHA Greenwood et al., 1966

Order ALBULIFORMES Greenwood, 1977

Family ALBULIDAE Bleeker, 1849

Genus ALBULA Scopoli, 1777

Albula sp.

Figure 2

Material. Tooth plate (UA 11388) and dentary (DMNH EPV. 136301).

Occurrence. Berivotra Study Area (Anembalemba Member).

Description. The oral tooth plate UA 11388 (Figure 2A-B) measures 6 mm along the longest axis and 4 mm wide. The base is made of thin bone with broken edges. On the occlusal side, there are 37 pedestaled teeth ranging in size from 0.5-1.0 mm in diameter across the crown and 1 mm in height. There are 10 alveolar pits, most filled with broken tooth bases. The opposite side of the bony base has a smooth texture with a small ridge of

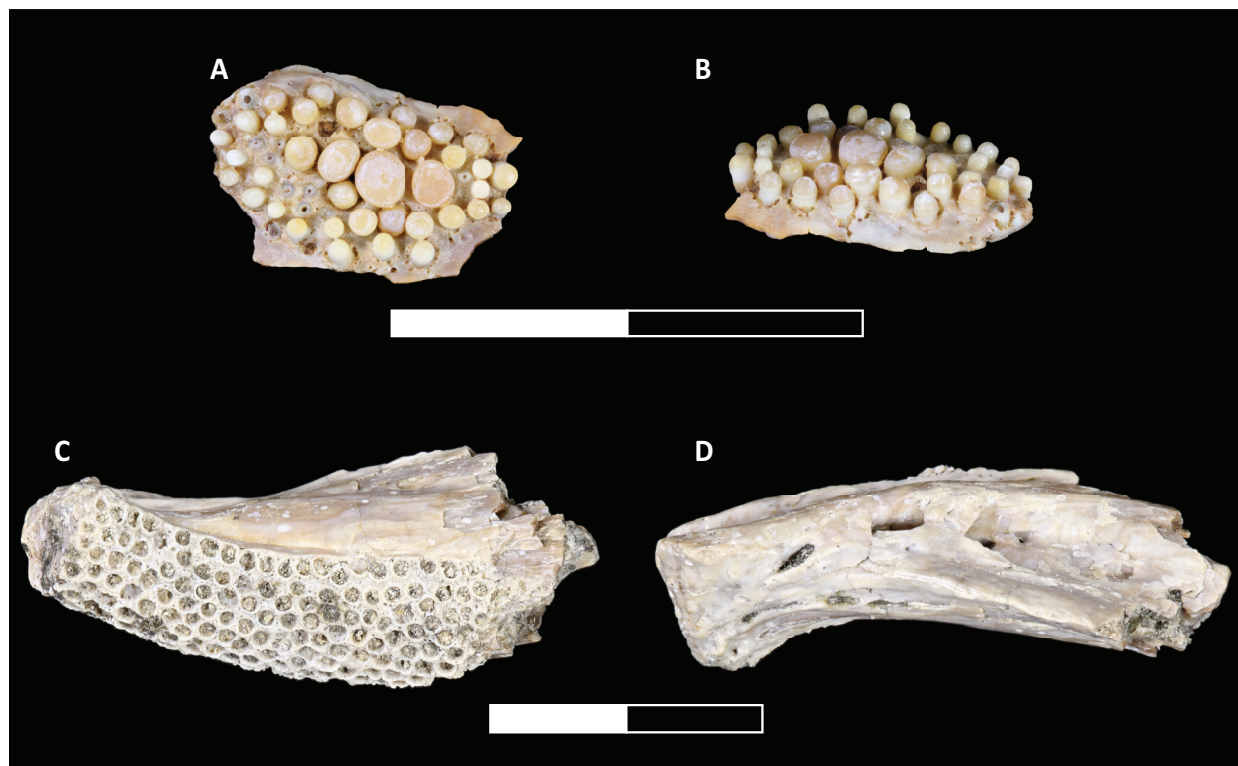


FIGURE 2. *Albula* sp. fossils from the Maevarano Formation. **A-B**, occlusal and lateral view of tooth plate (UA 11388). **C-D**, occlusal and ventral view of dentary (DMNH EPV. 136301). Scale bars equal 1 cm.

bone, likely a muscle scar, less than 2 mm in height. This incomplete specimen does not have enough anatomical information to determine the exact placement of the bone within the oral cavity.

DMNH EPV. 136301 (Figure 2C-D) is a left dentary with a complete symphyseal end, but incomplete, posterior articular end. The dentary measures 2.1 cm long, 0.5 cm wide, and 1.0 cm at its deepest point. Covering the dorsal surface, there is a rectangular tooth patch with 134 distinct, evenly spaced pits to accommodate villiform teeth. Each tooth pit measures 1 mm in diameter. The symphyseal end is 0.7 cm deep and vertically oriented. The lateral side of the dentary has several large foramina. The ventral margin has a prominent keel with a deep groove and a series of foramina for a sensory canal.

Remarks. Albulids have tooth plates with a crushing dentition that are used in benthic environments for preying upon small invertebrates (Forey, 1973). Within *Albula*, there are hundreds of small, pedestal-shaped teeth within the oral cavity as depicted by Applegate (1970). The dentary of DMNH EPV. 136301 (Figure 2C-D) is directly comparable with similarly aged fossils of *Albula dunklei* (FMNH P27494) from the Selma Formation in Alabama

(Applegate, 1970) and recent *Albula vulpes* (UMMZ 186965-S) skeletons. *Albula* maxillae and dentaries have a large “tooth patch” to accommodate hundreds of villiform teeth (Applegate, 1970). The modern *Albula* dentary was described as having a near vertical symphyseal margin, an extremely wide gutter on the ventral portion of the dentary (for the mandibular sensory canal) that opens laterally for most of its length (Nybelin, 1976) as seen in DMNH EPV. 136301.

Class ACTINOPTERYGII Cope, 1887

Superorder ELOPOMORPHA Greenwood et al., 1966

Order ELOPIFORMES Sauvage, 1875

Family PHYLLODONTIDAE Sauvage, 1875

Subfamily PHYLLODONTINAE Sauvage, 1875

Genus EGERTONIA Cocchi, 1864

Egertonia sp.

Figure 3

Material. Four tooth plates (UA 11389, DMNH EPV. 136302, DMNH EPV.136303, and UA 11390).

Occurrence. Berivotra Study Area (Anembalemba Member and Miadana Member).

Description. Tooth plate UA 11389 (Figure 3A-B) is incomplete on both ends and measures 0.9 cm

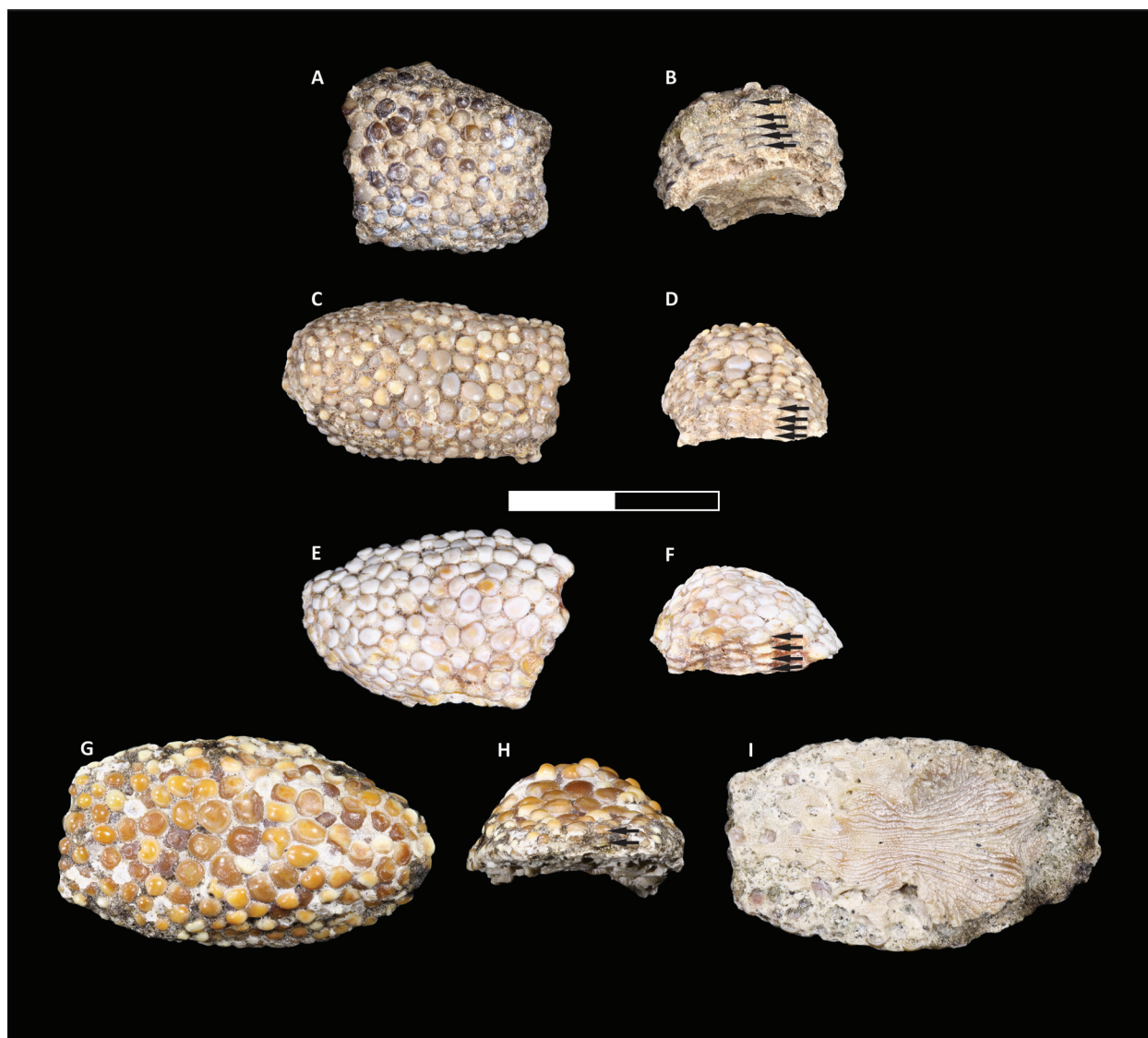


FIGURE 3. *Egertonia* sp. fossils from the Maevarano Formation. **A-B**, occlusal and cross-section views of tooth plate (UA 11389). **C-D**, occlusal and cross-section views of tooth plate (DMNH EPV. 136302). **E-F**, occlusal and cross-section views of tooth plate (DMNH EPV.136303). **G-I**, occlusal, cross-section, and basal views of tooth plate (UA 11390). Scale bar equals 1 cm; small arrows used in cross-section view to highlight vertically stacked teeth.

long, and 0.9 cm wide; the height is domed and ranges from 0.2-0.4 cm in thickness. On cross-sectional view through the thicker portion, there are five layers of vertically stacked teeth. The teeth are flattened hemispheres and range in width from 0.25-1 mm at the crown and have a smooth or slightly punctate surface texture. There is a remnant of a bony base that exhibits symmetry, but it is incomplete with little surface texture. Tooth plate DMNH EPV.136302 (Figure 3C-D) measures 1.4 cm long, 0.8 cm wide, and ranges in thickness from 0.2-0.5 cm. There is no clear bony base present, the surface is smooth, and the thin end is broken and incomplete. Upon view in cross-section

through the tooth plate, there are four layers of vertically stacked teeth. Individual teeth are mostly complete and flattened hemispheres range in size from 0.25-1 mm in width at the crown and have a smooth or slightly punctate texture. Tooth plate DMNH EPV.136303 (Figure 3E-F) measures 1.25 cm long and 0.8 cm wide, and ranges in thickness from 0.2-0.6 cm tall. The thicker end is relatively complete, but the thin end is broken. In cross-section there are four layers of vertically stacked teeth. Individual teeth are flattened hemispheres and have a uniform size distribution of 1 mm across the crown with a relatively smooth surface texture. No bony base is present. Tooth plate UA 11390 (Fig-

ure 3G-I) is oblong and 1.7 cm long, 0.9 cm wide, and ranges in thickness from 0.2-0.5 cm thick. The thicker end is complete, and the thin end is nearly complete, which shows vertically stacked teeth in cross-section. Individual teeth are flattened hemispheres and range from 0.25-1.0 mm in crown width and are mostly smooth in texture with relatively thick enamel. Opposite the occlusal surface, there is a poorly preserved, symmetrical, partial bony base with cortical bone texture.

Remarks. The first account of *Egertonia* from the Maevarano was mentioned by Gottfried and Krause (1999) and further described in the PhD thesis of Ostrowski (2012). *Egertonia* is an extinct genus within Phylloodontidae. *Egertonia* tooth plates are defined by having three characteristics: 1) vertically stacked replacement teeth; 2) regularly convex (nearly hemispherical or flattened) teeth; and 3) relatively thick enamel (Estes, 1969). These tooth plates alone cannot be identified finer than genus level. The holotype for *Egertonia isodonta* (NHM 38814) exhibits all three of these characteristics and is directly comparable to the four Madagascar specimens described above.

Class ACTINOPTERYGII Cope, 1887
Superorder ELOPOMORPHA Greenwood et al.,
1966

Order ELOPIFORMES Sauvage, 1875
Family PHYLLODONTIDAE Sauvage, 1875
Subfamily PHYLLODONTINAE Sauvage, 1875
Genus PARALBULA Blake, 1940

Paralbula sp.

Figure 4

Material. Three tooth plates (DMNH EPV.136304, UA 11391, and UA 11392).

Occurrence. Berivotra Study Area (Anembalemba Member) and Lac Kinkony Study Area (Lac Kinkony Member).

Description. Tooth plate DMNH EPV.136304 (Figure 4A-B) measures 1.4 cm long, 0.8 cm wide, and ranges in thickness from 0.1-0.3 cm. Lateral view of the tooth plate exhibits three to four layers of hemispherical teeth with irregular (offset, non-vertical) stacking. Individual teeth are 0.5-1.0 mm wide at the crown. No bony base is present. Tooth plate UA 11391 (Figure 4C-D) is incomplete with uneven margins and measures 1.1 cm long, 0.9 cm wide, and 0.25 cm thick. The thickness is relatively uniform with a slight undulating surface. The teeth are arranged in three or four layers with irregular stacking. Individual teeth are hemispherical with thick enamel exhibiting a punctate surface texture and are uniform at 1 mm in crown width. Tooth plate UA 11392 (Figure 4E-F) measures 1.2 cm long, 0.6 cm

wide, and ranges in thickness from 0.2-0.4 cm. The overall surface of the tooth plate is not smooth and shows undulations. From a lateral view of the tooth plate, the teeth are arranged in two to three layers with irregular stacking. Individual teeth range from 1-2 mm in width across the crown; many have broken enamel, and a punctate surface texture. Very little, poorly preserved bony base is present.

Remarks. *Paralbula* tooth plates 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 punctate (can occur radially); and 4) tooth plate with a curved occlusal surface (Estes, 1969). The tooth plates described here exhibit domed occlusal surfaces that are slightly flattened anatomically, 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 teeth are weathered on the occlusal surfaces. These tooth plates identified as *Paralbula* occur mostly within the Lac Kinkony Member but have been found in the Anembalemba Member. The holotype specimen of *Paralbula marylandica*, from the Eocene of Maryland (Blake, 1940), possesses the four features listed above and is directly comparable to the *Paralbula* tooth plates from Madagascar.

Class ACTINOPTERYGII Cope, 1887
Superorder ELOPOMORPHA Greenwood et al.,
1966

Genus indet.

Figure 5

Material. Six vertebrae (DMNH EPV.136305, DMNH EPV.136306, DMNH EPV.136307, DMNH EPV.136308, UA 11393, UA 11394,)

Occurrence. Berivotra Study Area (Anembalemba Member) and Lac Kinkony Study Area (Lac Kinkony Member).

Description. The elopomorph vertebrae from Madagascar encompass a wide range of morphotypes (Figure 5) and are found across several localities within the Maevarano Formation. These amphicoelous vertebrae range in size from small to large (less than 0.5 cm to over 2.5 cm at their widest point) and qualitative morphology from simple, slightly sub-circular, and thin (Figure 5A, 5C-F) to robust with a highly sigmoidal margin (Figure 5B). These vertebrae are also rostral-caudally flattened (plate-like), exhibit fine parallel fibers around the perimeter from edge to edge (oriented rostral-caudally), and deeper articular pits that accommodate the neural arch (dorsal) are widely spaced from the



FIGURE 4. *Paralbula* sp. fossils from the Maevarano Formation. **A-B** occlusal and lateral views of tooth plate (DMNH EPV.136304). **C-D** occlusal and lateral views of tooth plate (UA 11391). **E-F**, occlusal and lateral views of tooth plate (UA 11392). Scale bar equals 1 cm.

parapophyseal articular pits. Brinkman and Neuman (2002) noted that this combination of vertebral features are not found outside of Elopomorpha. The ventral side of the vertebrae may bear a shallow indentation to accommodate vasculature. Most of the elopomorph vertebrae from the Maevarano Formation are 1.0 – 1.5 cm at their widest point, and are subcircular. The vertebrae themselves are isolated, surface collected elements and not associated with any tooth plates. Because of the variability in teleost vertebrae within a single individual, we cannot assume a more specific taxonomic iden-

tification of these isolated vertebrae. The majority of the large, robust vertebrae occur within the Lac Kinkony Member, which is also more likely to have *Paralbula* tooth plates, but no official association can be made. No detailed descriptions have noted differences in isolated vertebrae between *Paralbula*, *Egertonina*, and *Albula*.

DISCUSSION

Vertebrate preservation within the Maevarano Formation is inconsistent. More robust taxa (dino-



FIGURE 5. Elopomorpha gen. indet centra from the Maevarano Formation. Each specimen is shown in cranial view (1s), lateral view (2s), dorsal view (3s), and ventral view (4s). **A**, vertebra (DMNH EPV. 136305). **B**, vertebra (DMNH EPV. 136306), note that B3 shows a broken dorsal margin view. **C**, vertebra (DMNH EPV.136307). **D**, vertebra (DMNH EPV. 136308). **E**, vertebra (UA 11393). **F**, vertebra (UA 11394). Scale bar equals 1 cm.

saur, crocodilians, etc.) are frequently found articulated and stunningly preserved (Rogers, 2005). Often, fossilized fish elements in the Maevarano Formation are disarticulated, disassociated, and broken. It is likely that these coastal marine fishes washed ashore during high-energy coastal events, which are part of Madagascar's natural history (Rogers et al., 1997). This preservation limits precise taxonomic identification for many of the fish fossils. However, some specimens are distinct enough to identify to the genus level. The *Albula*, *Egertonia*, and *Paralbula* fossil elements are diagnostic, especially the robust tooth plates and vertebrae, which have a greater likelihood of preservation. The description of three genera and their presence on Madagascar allows us to understand more about the distribution and diversity of these fishes during the Late Cretaceous. The presence of these genera in the Southern Hemisphere during the Late Cretaceous establish that these fishes had a broader (global) distribution than previously known based on their fossil records.

Paleobiogeography

Each of these elopomorph genera from Madagascar affects our understanding of their distributions during the Late Cretaceous (Figure 6).

***Albula*.** The family Albulidae reached its peak diversity and abundance 100 million years ago, during the mid-Cretaceous (Colborn et al., 2001). Recent *Albula* are found in equatorial and subtropical, coastal waters worldwide. This occurrence of *Albula* in Madagascar during the Late Cretaceous is the first record of *Albula* in the Southern Hemisphere at that time. The majority of *Albula* fossils from the Cretaceous are in North America (Hay, 1907; Wade, 1926; Russell and Landes, 1937; Stephenson, 1941; Bergquist, 1944; Zangerl, 1948; Reeside, 1955; Miller, 1967; Applegate, 1970; Sohl and Koch, 1983; Schwimmer, 1986; Case and Schwimmer, 1988; Grandstaff et al., 1992; Cicimurri, 2007), along with a few specimens from Uzbekistan (Nessov, 1981; Nessov, 1985). The occurrence of *Albula* in Madagascar greatly extends the geographical range of this genus into the Southern Hemisphere during the Late Cretaceous (Figure 6).

***Egertonia*.** The presence of *Egertonia* in the Late Cretaceous extends the known temporal range of this genus into the Maastrichtian (Ostrowski, 2012). The Madagascar specimens, along with a description of *Egertonia* from the Late Cretaceous of southern India (Halliday et al., 2016), places the two earliest (and only known Cretaceous) records

of *Egertonia* in the Southern Hemisphere (Figure 6).

***Paralbula*.** *Paralbula* is known from the Cretaceous in the Northern Hemisphere, mostly from North America (Hay, 1907; Estes, 1965; Langston, Jr., 1967; Miller, 1967; Estes, 1969; Sahni, 1972; Langston, Jr., 1975; Armstrong-Ziegler, 1978; Dodson, 1984; Lauginiger, 1984; Hutchinson and Kues, 1985; Brinkman, 1986; Danis, 1986; Schwimmer, 1986; Case, 1987; Case and Schwimmer, 1988; Fiorillo, 1989; Brinkman, 1990; Grandstaff et al., 1992; Storer, 1993; Eberth and Brinkman, 1997; Beavan and Russell, 1999; Lillegraven and Eberle, 1999; Gardner, 2000; Peng et al., 2001; Cicimurri, 2007; Brinkman, 2008; Montgomery and Clark, 2016; Hoganson et al., 2019), and localities in Europe (Vullo et al., 2009). 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. The presence of *Paralbula* in Madagascar extends the geographical distribution of this genus into the Southern Hemisphere during the Late Cretaceous (Figure 6).

As described above, the majority of these elopomorph genera have been found in the Northern Hemisphere, specifically North America and Europe. This is not surprising, as there is a sampling bias favoring Laurasian landmass exploration and taxonomic description (Benson et al., 2013) leading to an underrepresentation of Gondwanan taxa in the literature. As more expeditions and discoveries in Gondwanan landmasses are published, a more comprehensive picture is forming of spatial and temporal distributions of many taxa. The diversity of fossil elopomorphs and abundance of material in the Mahajanga Basin indicates that these taxa were a major component of the aquatic fauna in these coastal ecosystems during the Late Cretaceous. The taxa described here are most similar to what is present in the Northern Hemisphere and especially comparable to numerous North American localities biogeographically (Ostrowski, 2012). The presence of these elopomorphs in Madagascar, therefore, supports a more widespread distribution, spatially and temporally, of these genera than previously thought.

Evolution within Elopomorpha

These three elopomorph genera nest within two different families in Elopomorpha; *Albula* within Albulidae, and *Egertonia* and *Paralbula* within Phyllodontidae. Currently, there exists an inherent collection bias in the known vertebrate fossil mate-



FIGURE 6. Late Cretaceous Paleogeographic Map showing known fossil localities (clustered by state if applicable) of *Albula*, *Egertonia*, and *Paralbula* and the location of the Madagascar fauna. PaleoMap modified from global Molleweide projection at 66 Ma (Scotese, 2014). Localities are condensed by state or province in North America for clarity.

rial, namely a greater representation of “Laurasian taxa” over “Gondwanan taxa” (Benson et al., 2013). A compounding factor is that fishes can be difficult to identify to more specific taxonomic levels when they are disarticulated and disassociated. Some of the strongest hypotheses about the origin of certain elopomorph families and genera currently rest on Estes’s evaluations, which stated the origin of phyllodontids occurred in the Cretaceous of North America (Estes, 1969) and later elaborated to specify shallow epicontinental seas in the North Atlantic and around North America (Estes and Hiatt, 1978). This hypothesis is predicated by the “Laurasian pull” of described taxa. With the presence of a diverse assemblage of these genera in the Late Cretaceous of Madagascar, it is possible to hypothesize the origin and subsequent distribution of phyllodontids is more complex. The only known specimens of *Egertonia* in the Cretaceous are from Gondwanan landmasses of Madagascar (Gottfried and Krause, 1998; Ostrowski, 2012) and South India (Halliday et al., 2016). As in agreement with Halliday et al. (2016), these occurrences likely mean the origin of this genus is more complex than the purported Cretaceous North American (Estes, 1969) or North Atlantic (Estes and Hiatt, 1978) hypotheses.

CONCLUSIONS

The specimens described here represent three elopomorph genera: *Albula*, *Egertonia*, and *Paralbula*, present in Madagascar during the Late Cretaceous. The presence of these fishes within this coastal environment supports the deltaic and coastal marine-influenced paleoenvironment based on geologic data (Rogers et al., 2000; Rogers, 2005; Rogers et al., 2013). The presence of these fishes on a Gondwanan landmass also supports the idea of a broader distribution of these elopomorphs during the Late Cretaceous, which was previously limited to the Northern Hemisphere. The likeness of specimens further supports a faunal similarity between the Indian subcontinent and Madagascar even 20 million years after the separation of these landmasses. The *Albula* and *Paralbula* described here represent the only southern hemisphere occurrences in the Late Cretaceous and in the case of *Egertonia*, also the oldest. This improves our understanding of the distribution and biogeography in these elopomorphs during the Late Cretaceous, signifying a more global distribution than previously documented. Multiple early occurrences of *Egertonia* present in the Southern Hemisphere indicates a more complex origin of some elopomorph groups. These fossils also contribute to our understanding of diversity in coastal

marine ecosystems within Madagascar and Gondwana as a whole during the Late Cretaceous.

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