

EOCENE SELACHIAN FAUNA FROM NEARSHORE MARINE DEPOSITS, AMPAZONY,  
NORTHWESTERN MADAGASCAR

by

Lane A. Wallett

A Paper Presented to the  
Faculty of Mount Holyoke College in  
Partial Fulfillment of the Requirements for  
the Degree of Bachelors of Arts with  
Honor

Department of Biological Sciences

South Hadley, MA 01075

May, 2006

This paper was prepared  
under the direction of  
Professor Karen Samonds  
for eight credits.

## **DEDICATION**

For my mother the miracle worker and my father the fixer, who said I could be anything and meant it. Whatever that anything may be, I've had the privilege to be your daughter first. Thank you.

For my sister, who keeps my words and sometimes thinks I'm interesting. You were always worth the wait.

For Jeanne, who switched artfully between ponies and dinosaurs and still listens to it all. Thank you for being inexplicable.

For Frank, who knows everything. Thank you for sharing it.

And for Grandma, who read the books over and over until I had the words.

## **ACKNOWLEDGEMENTS**

Dr. Karen Samonds

Dr. Stan Rachootin

Dr. Margery Coombs

The Harvard Museum of Comparative Zoology

The Mount Holyoke College Biology Department

Ms. Sarah Oelker

Ms. Amy Gracey

Ms. Stephanie Hsieh

## TABLE OF CONTENTS

	Page
List of Figures.....	v
Abstract.....	vi
Introduction.....	1
Materials and Methods.....	9
Species Identification.....	11
Discussion.....	28
Literature Cited.....	34

## LIST OF FIGURES

	Page
Figure 1. Distribution of Eocene selachian fossil localities.....	6a
Figure 2-1. Specimens of <i>Galeocerdo latidens</i> from Ampazony, Madagascar.....	15a
Figure 2-2. Comparison of Ampazony <i>G. latidens</i> with type specimen.....	15b
Figure 2-3. Comparison of Ampazony <i>G. latidens</i> with type specimen.....	15b
Figure 3-1. Specimens of <i>Carcharhinus</i> sp. from Ampazony.....	18a
Figure 3-2. Comparison of Amazony <i>Carcharhinus</i> with <i>C. priscus</i> type specimen.....	18b
Figure 4-1. Specimens of <i>Rhizoprionodon terraenovae</i> from Ampazony.....	21a
Figure 4-2. Full dentition of recent <i>R. terraenovae</i> .....	21b
Figure 5-1. Specimen of <i>Nebrius blankenhorni</i> from Ampazony.....	23a
Figure 5-2. Comparison of Ampazony <i>N. blankenhorni</i> to type specimen.....	23b
Figure 5-3. . Comparison of Ampazony <i>N. blankenhorni</i> to type specimen.....	23b
Figure 6-1. Specimens of Rhinopteridae from Ampazony.....	27a
Figure 6-2. Specimens of Rhinopteridae from Ampazony.....	27a
Figure 6-3. Specimens of Rhinopteridae from Ampazony.....	27a
Figure 6-4. Specimens of Rhinopteridae from Ampazony.....	27b
Figure 6-5. Specimens of Rhinopteridae from Ampazony.....	27b
Figure 6-6. Rhinopterid tooth in profile.....	27c
Figure 6-7. Myliobatid tooth in profile.....	27c

## ABSTRACT

A new fossil-bearing locality near the northwestern Malagasy town of Ampazony yielded fossils of several selachian genera during the summer field seasons of 2001 and 2003. The sedimentology of the site and the temporal range of selachians recovered suggest that this site is Eocene in age. This designation places the locality within a large gap in Madagascar's Cenozoic fossil record. Extremely few studies have previously been done in this area of Malagasy paleontology, making each new contribution particularly significant.

Identification of the Ampazony collection indicates the presence of rays of the family Rhinopteridae and a variety of sharks. These include a species of *Carcharhinus*, *Galeocerdo latidens*, and *Rhizoprionodon terraenovae*. This study explored the identification and distribution of Madagascar's Eocene sharks and rays, with particular emphasis on their tooth size, shape, and abundance. The resulting fauna was then compared to selachian distributions throughout the Indian Ocean basin and in other biogeographically significant zones during the Paleocene and Eocene. This research contributes the first significant glimpse into the 80 million year period of Madagascar's marine paleontological record, and helps place into context the selachian faunas collected from the Ampazony region.

## INTRODUCTION

### I. Madagascar's Geologic History

The present-day island of Madagascar is located just over 400 km off the southeastern coast of Mozambique, separated from Africa by the Mozambique Channel. In the Early Jurassic, however, both Madagascar and Africa were part of the supercontinent of Gondwana. Madagascar resided between the landmasses that would eventually become Africa and the Indian subcontinent, remaining in direct contact with Africa until 150-160 Ma (Krause et al. 1997). At this time - between the late-early Jurassic (Geiger et al. 2004) and the Middle Jurassic (Rabinowitz et al. 1983) - Madagascar moved southeast along the Davie Fracture Fault (Norton and Sclater 1979; Scrutton et al. 1981). Approximately 130 Ma, in the mid-Early Cretaceous, further continental drift began to separate Gondwana into smaller components, and India and Madagascar pulled away from the larger body and moved north through open ocean (Reeves et al 1987). In the Late Cretaceous, Madagascar separated from India to remain very nearly in its present position relative to Africa (Cochran 1988). Opinion differs as to the exact timing of the break, but consensus places the date at either 88 Ma (Storey et al. 1995) or 94.5 Ma (Storetvedt et al. 1992), dependent on interpretations of data from the Marion hot spot.

### II. Madagascar's species history and the fossil gap

Madagascar's modern terrestrial species have drawn much interest and investigation. A high rate of species endemism sets much of the recent fauna apart from the

rest of the world. Not only are many of the island's denizens remarkably unique, the very fact that Madagascar *is* an island adds an intriguing element to their history. Many Malagasy species, while found only on the island, are closely related to those which developed on larger landmasses well after the island's separation from them. The low overall number of species may also be an indication of the difficulty of colonization. In concert, these factors have led to a great deal of exploration of Madagascar as it illustrates colonization events and evolution in isolation.

Despite many biogeographic studies on Malagasy terrestrial species (Douady et al. 2002; Jansa and Carleton 2003; Yoder and Flynn 2003; Poux et al. 2005), a corresponding body of research does not yet exist for air- and marine-based life forms sharing the island. Broadly, the assumption appears to be that animals that fly or swim are less constrained in their colonization habits, and thereby less interesting in terms of biogeographic history. The result has been a relative dearth of knowledge about Madagascar's modern volant and marine species' origins.

What literature does exist on the context of Madagascar's species – terrestrial, volant, and aquatic alike - consists of studies focused heavily on two time periods: the Cretaceous and the recent (Krause et al. 1997; Buckley et al. 2000; Curry Rogers and Forster 2001; Sampson et al. 2001; Gaffney and Forster 2003). Cretaceous fossils include species of fish, frogs, turtles, lizards, snakes, crocodyliforms, non-avian dinosaurs (both theropod and sauropod), birds, and mammals (Krause et al. 1994, 1997, 1999; Forster et al. 1996; Gottfried et al. 1998; Buckley and Brochu 1999; Buckley et al. 2000; Krause 2001, 2003; Curry Rogers and Forster 2001; Sampson et al. 2001; Carrano et al. 2002; Gaffney and Forster 2003). Studies of recent sediments describe subfossil taxa which include

crocodiles, turtles, lemurs, bats, carnivorans, pigs, rodents, pygmy hippos, and elephant birds (e.g., Goodman 1994; Burney et al. 1997; Burney 1999; Godfrey et al. 1999).

By contrast, the span in between – including nearly all of the Cenozoic – is extremely unexplored. This unexamined span is referred to as Madagascar's fossil gap. The gap presents an extensive enough problem for researchers focused on terrestrial and volant species; for those interested in marine animals, the complication is even greater. There is no subfossil documentation for these species, leaving an even wider chasm between the island's ancient inhabitants and their recent relatives. The important contributions that subfossil history holds for animals which spend much of their lives on land are unavailable to selachians.

The gap itself is bounded by well-preserved fossil selachian assemblages on its ancient aspect and well-catalogued modern faunal observations on the other. Madagascar's extinct selachian fauna includes rays of the rhinobatoid genus *Parapalaeobates* and the myliobatoid genus *Brachyrhizodus*, both from the Maastrichtian of the Upper Cretaceous (74-65 Ma; Gottfried et al. 2001). Of shark genera, *Carcharias* is most commonly represented, although two species each of *Squalicorax* and *Cretolamna*, and a single species of *Serratolamna* are also present in the Cretaceous assemblage of the Berivotra Formation in the Mahajanga Basin.

### III. Modern Malagasy Selachians

The island's extant shark fauna, first described in 1930 by Petit, is thought to include at least 56 species (Goodman and Benstead 2003). Notable genera include *Galeocerdo*, *Carcharhinus*, and *Rhizoprionodon* (Petit 1930; Smale 1998). The modern

tiger shark (*Galeocerdo cuvier*) and the great white shark (*Carcharodon carcharias*) have both been sighted in the island's waters (Smale 1998; Cliff et al. 2000). The type species of *Carcharhinus*, *C. melanopterus*, is among a host of reef sharks noted by divers. The tawny nurse shark (*Nebrius ferrugineus*) – the only extant example of its genus – is also known from the Toliara region in the south and the Nosy Be region to the north.

In the same locations, representatives of the island's extant ray species are commonly sighted (Goodman and Benstead 2003). These include giant guitarfish (*Rhynchobatus djiddensis*; WWF 1993, Smale 1998), manta rays (*Manta birostris*), and devil rays (*Mobula tarapacana*). Species of *Taenuria*, *Torpedo*, *Rhinobatus*, *Dasyatis*, and *Raja* also occur in specific locations surrounding the island. Both *Rhinobatus* and *Dasyatis* have been spotted in rivers and estuaries (Kiener 1964). At least two species of *Aeobatus* are also common (Smale 1998).

#### IV. The Fossil Gap and The Eocene

Beginning approximately 56 Ma and ending 34 Ma, the Eocene epoch falls firmly within the massive unknown sector of Madagascar's past. Although the island itself had already reached its present position, the world at large continued to be in flux as continents shifted and collided. To the east, North and South America reached their modern locations. To the south, Australia separated from Antarctica and shifted northeast. India, leaving Madagascar behind, progressed through the open ocean on its collision course with Eurasia.

The shifting of the landmasses resulted in corresponding changes within the oceans. The large, continuous body of the Tethys Ocean became sectioned into smaller waterways, the largest of which would be the Indian Ocean. Africa and Europe compacted into more

solid bodies, leaving a water corridor between them which became the Tethys Seaway. The Tethys Current flowed westward through this corridor throughout the Eocene, with the Tethys Seaway narrowing and finally closing in the Early Miocene (26-5 Ma; Ricou 1987, Omta and Henk 2002). At approximately the same time, the westward current through the Panama Straits reversed direction (Nesbit and Young 1997).

The changing face of the globe had even farther-reaching consequences. The paleoclimatology of most of the epoch was primarily warm and relatively uniform (Huber and Nof 2006). By the late Eocene, however, the widening gap between Australia and Antarctica produced new patterns in ocean movement as the Drake Passage developed (Omta and Henk 2002). The formation of the eastward Circum-Antarctic Current has been linked to this shift (Leclaire 1974). The sudden circulation of cooler waters brought about an overall reduction in global temperatures. Additionally, global sea levels throughout the Eocene are proposed to have been approximately 100-400 m above present levels (Hallam 1984, 1992; Haq et al 1987, 1988).

#### V. Eocene Fossils From Other Landmasses

Eocene geologic formations occur on all seven continents. In North America, the Green River formation of Wyoming is particularly well known for its preservation of specimens, primarily insects, bony fishes and plants, but Eocene strata have been catalogued throughout the United States and Canada (de Carvalho et al. 2004). The Barton Clay and Selsey formations of England have also produced Eocene fossils as eroding beaches reveal and in turn destroy more of these sediments.

Eocene shark faunal localities are just as widespread (Figure 1). In Africa, Morocco has been particularly rich in fossils, exhibiting Ypresian (56-49 Ma) and Lutetian (49-40 Ma) samples of *Galeocerdo*, *Rhizoprionodon*, and *Nebrius* (Noubhani and Cappetta 1997, Cappetta 2004). Egypt, too, has produced *Nebrius* and *Galeocerdo*, with additional representations of *Carcharhinus*. In Europe, *Galeocerdo* occurs in the Middle Eocene of both England (Dixon 1850) and Belgium (Leriche 1905). *Carcharhinus* and *Rhizoprionodon* are also known from France in this period (Agassiz 1843; Cappetta and Nolf 1981). Across the Atlantic, the Jackson Formation of Alabama also produces *Galeocerdo* (Leriche 1942). *Carcharhinus* has even been found in Antarctic Eocene deposits (Kriwet 2005).

Eocene rays are similarly globally distributed. Species of *Myliobatis* occur in England (*M. dixonii*; Agassiz 1843), Morocco (*M. dixonii*; Arambourg 1952), and New Jersey (*M. jugosus*; Leidy and Gabb 1877). The single known Eocene species of *Rhinoptera*, *R. sherboni*, has been found in the Lutetian of both Nigeria (White 1926) and Morocco (Arambourg 1952).

## VI. Importance of This Study

The relatively small number of species native to the island and their distinctiveness lends great importance to Madagascar's fauna, both past and present. The origins of these modern species, however, remain largely a mystery. This informational dearth is doubly evident in marine species. The Ampazony locality represents the first fossil-bearing site from within this gap. As such, the Ampazony fossils present a unique opportunity to

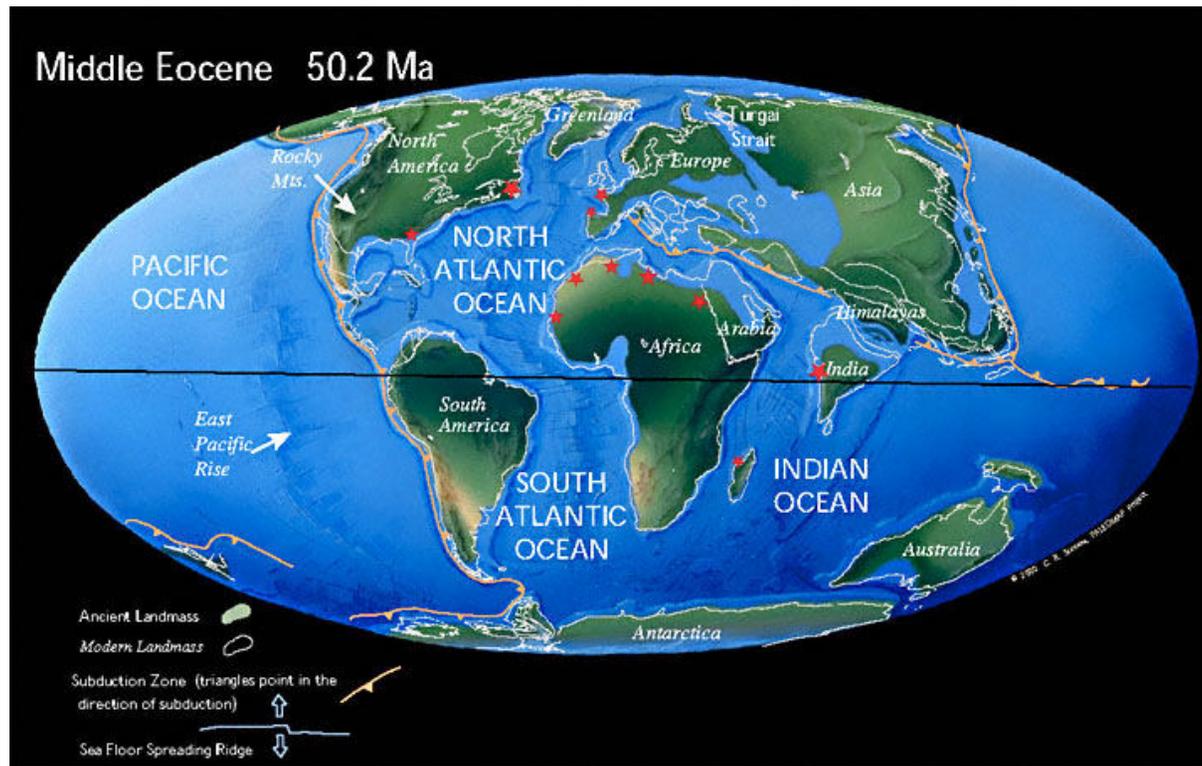


Figure 1. Distribution of Eocene selachian fossil-bearing localities plotted against the continental arrangement of the Middle Eocene. Illustration modified from Scotese 2001.

glimpse the selachian fauna of Madagascar's nearshore marine Eocene, and to elucidate the island's paleoenvironment.

Because selachians – particularly sharks – have well defined temporal representations, looking at the overlapping temporal ranges of the entire selachian community can help to constrain the age of the sediments. This in turn provides a geologic context for other fossils collected there, including gastropods, turtles, crocodylians, bony fish, and a species of sea cow which represents the first mammal known from Madagascar's fossil gap (Samonds et al 2001, 2005; Samonds and Zalmout 2002).

In addition, establishing the selachian community at Ampazony and its age allows this fossil assemblage to be placed within the context of elasmobranch assemblages from other landmasses of the same age. From such data, a more complete picture of the biogeographic and evolutionary history of these species and of all Eocene marine fauna can be better revealed.

## MATERIALS AND METHODS

### I. Collection

The fossil materials utilized in this study were collected in the field seasons of 2001 and 2003 by the team of Dr. Karen Samonds. Funding for the expedition was provided by the National Geographic Society's Research and Exploration Fund, the Geological Society of America and the Paleontological Society. The fossil-bearing locality itself is near the village of Ampazony, northwestern Madagascar (latitude -15.648 degrees and longitude 46.504 degrees). The area in question was originally mapped as containing Pliocene terrestrial sediments, including sandstones, alluvium, and sandy carapace, based on mapping done in the 1950's and 1960's by French explorers. Instead, the research team discovered an isolated outcrop of nearshore marine deposits, including both limestone and limey sandstone.

Site composition and the presence of marine species suggest that the locality is paralic (or estuarine) in nature. In fact, the site is presently only four kilometers inland from the island's modern northwest coast. Terrestrial sediments surrounding the marine layer – both above and below - bear mud cracks and evidence of fossilized plant life, indicating that the locality was periodically dried. This intermingling of terrestrial and marine fossil environments implies that Madagascar's coastline has undergone intermittent change as the ocean intruded and receded.

## II. Fossil Accession

The Ampazonny fossils were surface collected by Dr. Samonds and her team, and catalogued according to locality and collection date. Some fossils received preliminary species identifications and individual specimen numbers, and the collection was then shipped to the United States from Madagascar. During the period of this research, this collection of selachians was housed at Mount Holyoke College under the auspices of the Department of Biological Sciences.

For the purposes of this work, further labeling became necessary. Fossils previously grouped under a single identification number were given individual specimen number designations. Labeling consisted of preparation of a small section with hardening resin, and application of a light basecoat (in cases where the specimen itself was very dark). The specimen number was then written with a fine-tipped archival marker and a second layer of hardening resin was sometimes introduced to protect the number.

## SPECIES IDENTIFICATION

### I. Terminology and Measurements Used

Crown – portion of the tooth covered in enamel/enameloid; in shark species, synonymous with blade

Crown Height – (ray species) the maximum distance from the edge of the lingual shelf adjacent to the crown to the grinding surface of the crown itself

Crown Width – (ray species) the maximum distance from the crown's labial edge to its lingual projection

Dignathic heterodonty – teeth of the upper and lower jaws of the same specimen have different morphologies

Distal – pertaining to the region closest to the posterior of the mouth

Homodonty – all teeth of a specimen exhibit the same morphology

Labial – pertaining to the region closest to the exterior of the mouth

Lingual – pertaining to the region closest to the interior of the mouth

Mesial – pertaining to the region closest to the anterior of the mouth

MCZ – the Harvard Museum of Comparative Zoology

Root Width – (ray species) the maximum distance from the root's labial projection to its lingual surface

Tooth Height – (shark species) the distance from the basal face of the root to the apex of the blade

Tooth Width – (shark species) the distance from the most mesial point of each tooth to the most distal point

## II. Quantitative Methods

Specimens were prepared with identification numbers and measured for various values of height and width determined by their family. Measurements were obtained using a set of Mitutoyo digital calipers, accurate to 0.01 mm. Average measures were compiled for groups containing large numbers of specimens. Specimens were recorded through digital photography and a large body of comparative photographs was compiled for identification purposes.

## III. Systematic Paleontology

**Class CHONDRICHTHYES Huxley 1880**

**Subclass ELASMOBRANCHII Bonaparte 1838**

**Cohort EUSELACHII Hay 1902**

**Subcohort NEOSELACHII Compagno 1977**

**Superorder GALEOMORPHII Compagno 1973**

**Order CARCHARHINIFORMES Compagno 1973**

**Family CARCHARHINIDAE Jordan and Evermann 1896**

**Genus *Galeocerdo* Müller and Henle 1837**

### Included Species and Distribution:

The type species, *Galeocerdo cuvier* (Peron and Le Sueur 1822), is extant and can be found in all tropical and temperate seas, including those of Madagascar (Smale 1998; Cappetta 2004). *G. cuvier* is also known from the Pliocene of Italy (Lawley 1876), South

Africa (Davies 1964), and North Carolina (Cappetta 2004), as well as from the Pleistocene of Celebes (Hooijer 1954).

Other species include *G. aduncus* (Agassiz 1843), known from the Lower Oligocene of Europe (Wittich 1898; Priem 1908; Leriche 1910), the Miocene of Europe (Leriche 1927; Leriche and Signeux 1957; Antunes and Jonet 1970; Cappetta 1970; Schultz 1977; Menesini 1974), the United States (Gibbes and Hubbs 1849; Leriche 1942), Zaire (Darteville and Casier 1943), Ecuador (Longbottom 1979), Japan (Itoigawa et al 1985), and India (Mehrotra et al. 1973) and the Pliocene of Japan (Uyeno et al 1974).

The Miocene species *G. contortus* is known only in Virginia, U.S.A. (Gibbes and Hubbs 1849). *G. mayumbensis* occurs in the Miocene of Cabinda (Darteville and Casier 1943) and from the Eocene to the Pliocene of Angola (Antunes 1972, 1978). The Middle Eocene *G. eaglesomi* is known from the Lutetian of Nigeria (White 1955), Qatar (Casier 1971), and Tunisia and Togo (Cappetta 2004).

The Eocene species *G. latidens* (Agassiz 1843) is known from the Upper Ypresian and Lutetian of Morocco (Arambourg 1952; Cappetta 1981). Other Lutetian fossils occur in Belgium (Winkler 1874; Leriche 1905) and Egypt (Dames 1883; Priem 1897). The species also appears in the Eocene-dated Jackson Formation of Alabama (Leriche 1942).

***Galeocerdo latidens* (Agassiz 1843)**

(For synonyms see Case and Cappetta, 1990: 13)

Referred Specimens:

Two intact lateral teeth (01148b2, 01148b5; Figure 2-1, *A-D*), one lateral tooth with damage to distal heel (01148b1; Figure 2-1, *E-F*), two lateral partial teeth (01148b3, 01148b4; Figure 2-1, *G-H*).

Description:

Both intact teeth (01148b2, Figure 2-1, *A-B*; 01148b5, Figure 2-1, *C-D*) and the primarily intact tooth (01148b1, Figure 2-1, *E-F*) exhibit broad, triangular crowns and serrations on both the mesial and distal cutting edges. The average height of these teeth is 9.73 mm; their average width is 15.45 mm. The mesial heel is concave, while the distal heel is convex. The distal heel is longer than the mesial, with much finer serrations and a shorter cutting edge. The root has a higher lingual face than labial, and the labial surface is concave. The basal surface is likewise concave. Particularly in 01148b5 and 01148b1, a strong lingual groove bisects the root.

Of the partial teeth, 01148b4 (Figure 2-1, *H*) comprises the mesial heel of a lateral tooth, intact from mesial root through lingual groove. Strong serrations appear, and the labial surface shows evidence of concavity. The second partial tooth (01148b3; Figure 2-1, *G*) is further degraded and displays only a brief mesial cutting edge and section of root, again broken at the lingual groove.

#### Comparison and Discussion:

The dentition of members of *Galeocerdo* is characterized by cutting-type teeth, with relatively similar morphology on both jaws. The upper laterals and anteriors both mirror their lower counterparts. Therefore, it is difficult to ascribe a specific placement within the jaw to independent teeth, but relatively easy to assign teeth to the genus. The angle of the cusp indicates a posterior placement for both 01148b2 and 01148b5. Neither partial tooth is intact enough to reconstruct position within the jaw.

The Ampazony teeth resemble most clearly *G. latidens* specimens collected in Morocco by Arambourg (1952; Figure 2-2, 2-3), and to a lesser extent those collected in east Jordan (Mustafa and Zalmout 2000). They display the high, broad, triangular crown and rear-bent cusp described by Cappetta as typical of the species (2004). The long, serrated distal heel and shorter, also serrated mesial heel are characteristic of the species, as is the relatively high root. Serration continues much higher toward the apex of the cusp of the Ampazony teeth than on either Moroccan or Jordanian specimens. The Ampazony teeth are also, on average, larger than their Jordanian counterparts.

### **Genus *Carcharhinus* Blainville 1816**

#### Included Species and Distribution:

The genus' type species, *Carcharhinus melanopterus* (Quoy and Gaimard 1826), is Recent and occurs in all temperate and tropical seas, including those of Madagascar (Cappetta 2004). The genus as a whole is known from the Middle Eocene on, beginning with *C. egertoni* in Egypt (Agassiz 1843; Stromer 1905) and *C. gibbesi* in Alabama, South

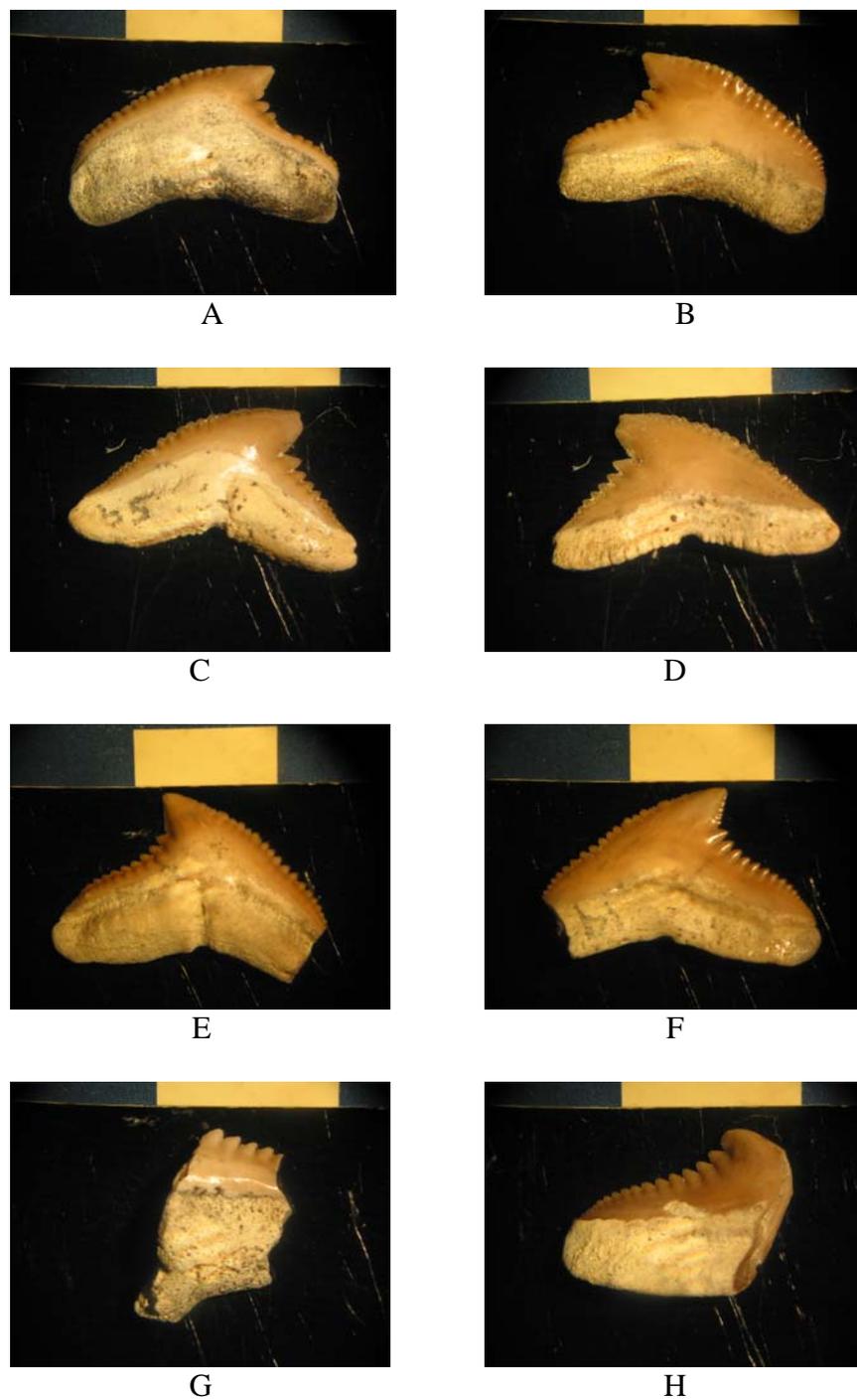
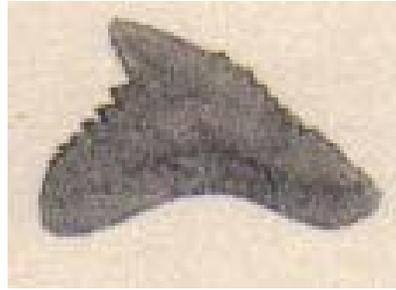


Figure 2-1. Specimens of *Galeocerdo latidens* from Ampazony, Madagascar. *A-B* 01148b2, lateral tooth; *A*, lingual view; *B*, labial view. *C-D* 01148b5, lateral tooth; *C*, lingual view; *D*, labial view. *E-F* 01148b1, lateral tooth; *E*, lingual view; *F*, labial view. *G* 01148b3, partial lateral tooth, lingual view. *H* 01148b4, partial lateral tooth, labial view.



A

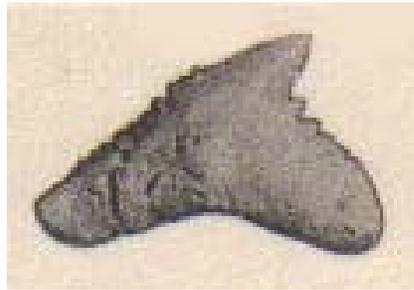


B

Figure 2-2. Comparison of Ampazony *G. latidens* to type specimen. A 01148b2, lateral tooth, lingual view. B type specimen from Arambourg 1952, lateral tooth, lingual view.



A



B

Figure 2-3. Comparison of Ampazony *G. latidens* to type specimen. A 01148b2, lateral tooth, labial view. B type specimen from Arambourg 1952, lateral tooth, labial view.

Carolina (Woodward 1889), and North Carolina (Case 1980). *C. frequens* occurs in the Late Eocene of Egypt (Case and Cappetta 1990), and recent studies speculate it is also present in the Late Eocene of Jordan (Mustafa and Zalmout 2000). *C. elongatus* (Leriche 1910) appears in the Miocene of Europe (Leriche 1926; Leriche and Signeux 1957; Menesini 1974; Antunes and Jonet 1970; Cappetta 1970), North Africa (Arambourg 1927), North America (Leriche 1942), Australia (Chapman and Cudmore 1924), South America (Longbottom 1979), and India (Mehrotra et al 1973; Sahni and Mehrotra 1981). It further surfaces in the Pliocene of Europe (Lawley 1876; Herman 1974; Landini 1977), Japan (Uyeno and Matsushima 1975), and Angola (Antunes 1978). Its latest known occurrence is the Pleistocene of Celebes (Hooijer 1954). *C. priscus* (Agassiz 1843) is one of the most commonly occurring members of the genus (Cappetta 2004). Its distribution is believed to have been worldwide during the Miocene, with the type specimen known from the Langhian, Miocene of Southern France (Cappetta 2004).

### ***Carcharhinus* sp.**

#### Referred Specimens:

Two upper lateral teeth (01148a1 and 01148a2; Figure 3-1, A-D), both intact.

#### Description:

The first upper lateral tooth (01148a1; Figure 3-1, A-B) exhibits a high cusp, angled posteriorly and faintly serrated. The tooth is 9.72 mm in height and 9.04 mm in width. The mesial and distal heels are low and short. Both are serrated more strongly than the cusp. The distal cutting edge is concave. The blade itself is concave lingually and overhangs the

root slightly on the labial face as it curves convexly. The lingual root is higher than the labial and bisected by a strong lingual groove. The basal face is concave.

The second upper lateral tooth (01148a2; Figure 3-1, *C-D*) is very broad with no differentiated heels on the blade. The tooth is 14.30 mm in height and 15.34 mm in width. Both mesial and distal cutting edges show serrations which become stronger approaching the apex of the blade. The blade displays lingual convexity and slight labial convexity, overhanging the labial root. The root itself is much higher lingually, with a very pronounced bisecting lingual groove. The root exhibits labial concavity, and its basal face is concave as well.

#### Comparison and Discussion:

Members of *Carcharhinus* exhibit cutting-clutching morphology and dignathic heterodonty of the jaws. Differentiation of upper and lower jaw is fairly easy, the upper jaw being characterized by much broader crowns than the lower, and tooth position within the jaw is indicated by the angle of bend to the posterior evident in the crown and breadth of crown.

The first upper lateral tooth (01148a1) closely resembles *C. priscus* from Southern France (Cappetta 2004; Figure 3-2). Serration appears to be slightly finer approaching the apex of the Ampazon tooth, but this difference may be due to greater wear in the French specimen. The slender crown of 01148a1 argues for a posterior location within the jaw.

The second tooth exhibits a much broader crown, indicating a more anterior placement. It does possess a faint curvature to the posterior, however, and as such remains

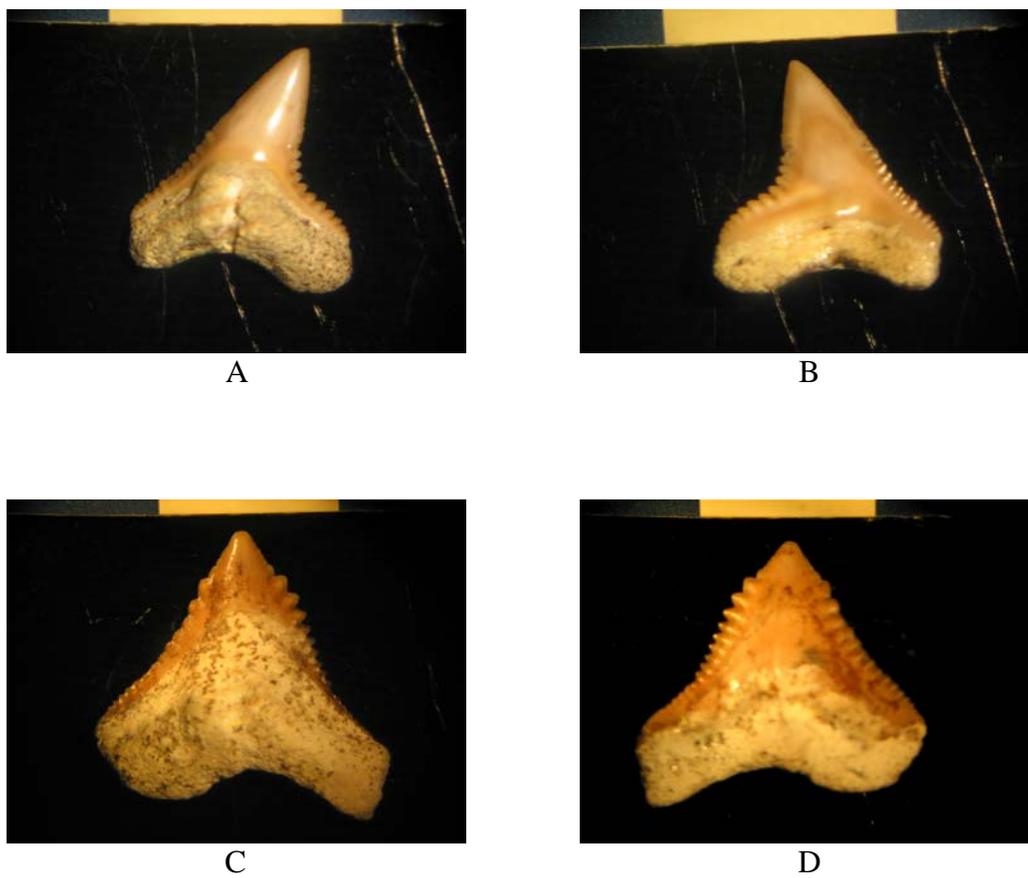


Figure 3-1. Specimens of *Carcharhinus* sp. from Ampazony, Madagascar. *A-B* 01148a1, upper lateral tooth; *A*, lingual view; *B*, labial view. *C-D* 01148a2, upper lateral tooth; *C*, lingual view; *D*, labial view.

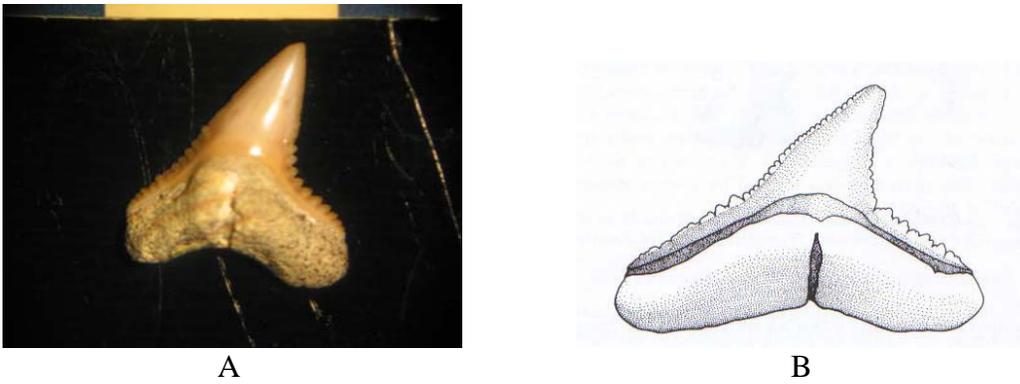


Figure 3-2. Comparison of Ampazonia *Carcarhinus* sp. to type specimen of *C. priscus* (Cappetta 2004). *A* 01148a2, upper lateral tooth, lingual view; *B* type specimen upper lateral tooth, lingual view.

a lateral tooth. Based on comparison to the jaws of the recent *C. melanopterus*, 01148a2 is likely a second lateral tooth.

The Ampazony specimens do not resemble the widely occurring Eocene species *C. egertoni*, which displays serration only in the uppermost portions of the blade. At the same time, the Malagasy teeth possess enough distinction from known examples of *C. priscus* to prevent their easy classification as such. It is unclear, however, whether this dissimilarity is due to true morphology or wear in the available *C. priscus* specimen. The Ampazony teeth are subsequently herein classified as of unknown species until clearer examples of *C. priscus* may be used for comparison.

### **Genus *Rhizoprionodon* Whitley 1929**

#### Included Species and Distribution:

The type species of this genus, *Carcharias (Scoliodon) crenidens* is today native to the tropical Atlantic and Indo-Pacific oceans (Klunzinger 1880). Three species are known from the Cenozoic, including *R. ganntourensis* (Arambourg 1952), *R. fischeuri* (Joleaud 1912), and *R. terraenovae* (Richardson 1848). *R. ganntourensis* occurs in the Lutetian and Upper Ypresian of Morocco, and the Upper Eocene of the Paris Basin of France (Cappetta and Nolf 1981). *R. fischeuri* appears in the Miocene of Southern France (Cappetta 1970), Belgium (Leriche 1927), and Portugal (Antunes and Jonet 1970).

The third species known from the Cenozoic, *R. terraenovae* (sometimes listed as *Scoliodon terraenovae*), is recognized from the Late Eocene through to Recent times (Mustafa and Zalmout 2000). Fossil localities include North Carolina and Georgia of the

U.S. (Case 1980, 1981) and east Jordan (Mustafa and Zalmout 2000). Modern members of the species inhabit the western Atlantic, having been sighted along coastlines from Canada to Brazil (Bigelow and Schroeder 1948). There is additional evidence that this species may tolerate environments with low salinity.

***Rhizoprionodon (Scoliodon) terraenovae* (Richardson 1848)**

Referred Specimens:

One intact upper anterior tooth (01148d1; Figure 4-1, *A-B*), one nearly intact upper anterior tooth (01148c3; Figure 4-1, *C-D*), one intact lower anterolateral (01148c1; Figure 4-1, *E-F*), and one intact lower lateral (01148c2; Figure 4-1, *G-H*).

Description:

Both upper anterior teeth (01148d1 and 01148c3; Figure 4-1, *A-D*) display a tall blade with separation of the distal heel and lesser distinction of the mesial heel. 01148d1 is 5.76 mm in height and 6.37 mm in width. 01148c3 is 4.40 mm in height, and is lacking the distal-most portion of both blade and root. All cutting edges are smooth and the blade exhibits posterior curvature, more pronounced in the damaged tooth. The labial face is flat, while the lingual shows slight concavity. The root possesses evidence of a central lingual groove. Its basal face is only mildly concave.

The lower anterolateral tooth (01148c1; Figure 4-1, *E-F*) possesses the same tall blade and distinct distal heel, with additional clearer distinction of the mesial heel. The tooth is 5.28 mm in height and 8.21 mm in width. Again, the cutting surfaces lack serration.

The blade displays lingual concavity and curvature to the posterior. The root exhibits a well-defined lingual groove and concavity of its labial surface. The basal face displays more pronounced concavity than those of the upper teeth.

The lower lateral tooth (01148c2; Figure 4-1, *G-H*) exhibits a much lower, longer blade, still with distinction of the distal heel. Height is 4.19 mm and width is 6.05 mm. Serrations are again absent. The blade itself angles to the posterior, but shows evidence of recurve toward the anterior. Its lingual face is concave. The labial root is also slightly concave; the lingual root face is worn, limiting clarification of the lingual groove. The basal face is flat, but this may be due to wear.

#### Comparison and Discussion:

The teeth of *Rhizoprionodon* resemble those of several other genera, including *Sphyrna* and the recent *Loxodon* and *Scoliodon* (Richardson 1848). The species *R. terraenovae* has been associated with a variety of genera, prior to its designation as a member of *Rhizoprionodon*. Several factors contribute to the difficulty of classification and identification of the species. The lack of serrations removes one of the more distinctive characteristics which often contribute to identification. Sexual dimorphism also plays a role. Additionally, the slight but noticeably recurved blades in the lower jaw – extremely faint in the upper – creates an illusion of two morphologically similar species rather than one.

The survival of this species to the present time allows for improved accuracy of positional identification among teeth as complete specimens are available (Figure 4-2). Comparison with illustrations of modern *R. terraenovae* specimens and preserved samples at the MCZ suggests that 01148d1 is a second right upper anterior, and 01148c3 a third



A



B



C



D



E



F



G



H

Figure 4-1. Specimens of *Rhizoprionodon terraenovae* from Ampazony, Madagascar. *A-B* 01148d1, upper anterior tooth; *A*, lingual view; *B*, labial view. *C-D* 01148c3, upper anterior tooth; *C*, lingual view; *D*, labial view. *E-F* 01148c1, lower anterolateral tooth; *E*, lingual view; *F*, labial view. *G-H* 01148c2, lower lateral tooth; *G*, lingual view; *H*, labial view.

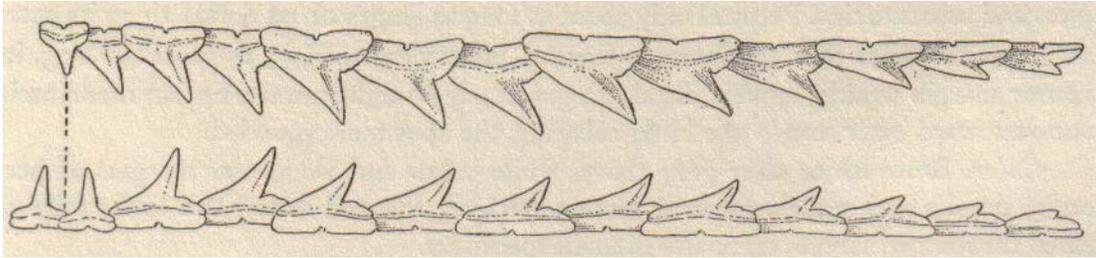


Figure 4-2. Full dentition of recent *R. terraenovae*, adapted from Bigelow and Schroder 1948.

right upper anterior (Bigelow and Shroeder 1948). 01148c1 most closely resembles the fifth and sixth lower right lateral, while 01148c2 appears very similar to the seventh lower right lateral.

**Order ORECTOLOBIFORMES Applegate 1972**

**Family GINGLYMOSTOMATIDAE Gill 1862**

**Genus *Nebrius* Rüppell 1837**

Included Species and Distribution:

Members of *Nebrius* are known from the Lower Paleocene in Europe, North America, North and West Africa (Cappetta 2004). Recent species are located within the Indian Ocean, including the type species *N. ferrugineus*, also sighted in the waters of Madagascar (Smale 1998).

Cenozoic species include *N. bequaerti* (Leriche 1920), *N. thielensis* (Winkler 1874), and *N. blankenhorni* (Stromer 1905). *N. bequaerti* is known from the Paleocene of Western Africa (Casier 1960) and Morocco (Cappetta 2004). *N. thielensis* occurs in the Middle Eocene of Belgium and the Late Eocene of Georgia, U.S.A. [Case 1981, as *Ginglymostoma obliquum* (Leidy and Gabb 1877)].

*N. blankenhorni* appears in the Middle Eocene of Cairo, Egypt and Togo (Stromer 1910). The Eocene of Senegal, Guinea Bissau, and Tunisia has produced fossils of this species (Cappetta 2004). It is also common in Lower Ypresian (Lower Eocene) Moroccan deposits (Cappetta 1981).

### *Nebrius blankenhorni* (Stromer 1905)

#### Referred Specimens:

One anterolateral tooth (01153; Figure 5-1).

#### Description:

The tooth exhibits a high, broad, and asymmetrical crown (Figure 5-1). Its height is 5.58 mm and width is 7.85 mm. Both cutting edges are serrated, with serrations growing coarser approaching the apex. The distal cutting edge is concave, the mesial slightly convex. The crown displays a large labial apron, tapering to overhang the base of the root (Figure 5-1, A). The lingual face of the crown possesses a less extraordinary apron, ending at the base of the root (Figure 5-1, C). The root itself is broad laterally but thin vertically. Its basal face is broad and flat.

#### Comparison and Discussion:

The teeth of *Nebrius* are extremely distinct, possessing a fan-like morphology and ostentatious apron. They do exhibit homodonty, however, making differentiation between upper and lower jaw virtually impossible in disassociated teeth. The apex of the blade angles toward the posterior of the mouth, which places 01153 as either a lower right or upper left anterolateral.

The Ampazony specimen most closely resembles the Moroccan sample from Cappetta (2004; Figure 5-2, 5-3). The Ampazony tooth possesses a slightly more angular appearance, however; its mesial heel is lacking the convexity of the Moroccan specimen, while its apex overhangs the distal heel to a greater extent.

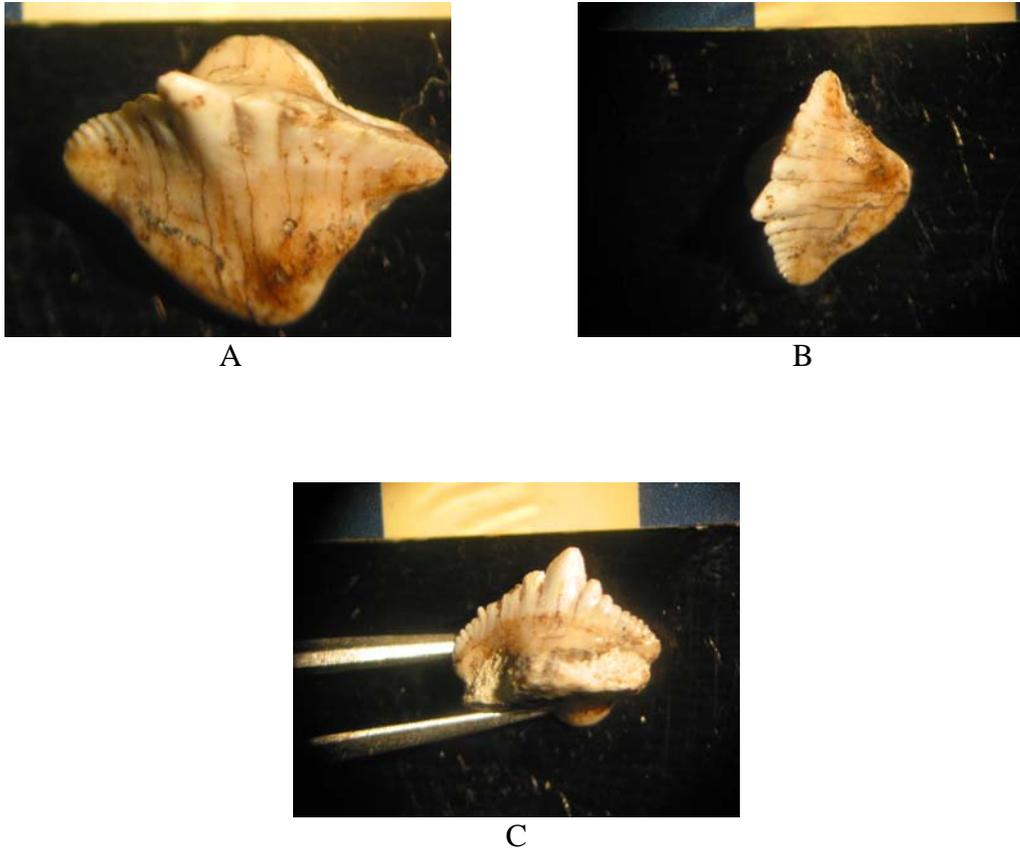
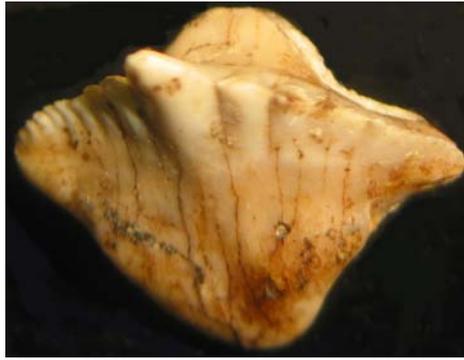
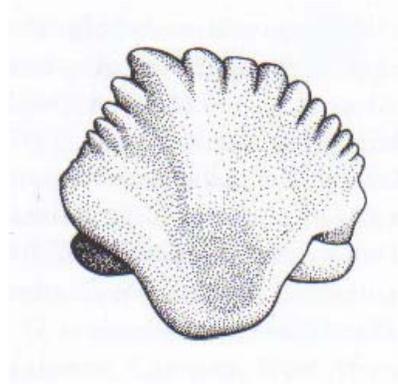


Figure 5-1. Specimen of *Nebrius blankenhorni* for Ampazony, Madagascar. A-C 01153, anterolateral tooth; A, superolabial view; B, occlusal view; C, lingual view.



A

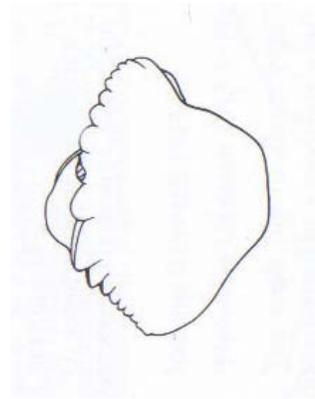


B

Figure 5-2. Comparison of Ampazonia *N. blankenhorni* to type specimen. A 01153, anterolateral tooth, superolabial view. B, type specimen anterolateral tooth from Cappetta 2004, labial view.



A



B

Figure 5-3. Comparison of Ampazonia *N. blankenhorni* to type specimen. A 01153, anterolateral tooth, occlusal view. B, type specimen anterolateral tooth from Cappetta 2004, occlusal view.

**Superorder BATOMORPHII Cappetta 1980**

**Order MYLIOBATIFORMES Compagno 1973**

**Superfamily MYLIOBATOIDEA Compagno 1973**

**Family RHINOPTERIDAE (?) Jordan and Evermann 1896**

Included Species and Distribution:

The Rhinopteridae are comprised of a single genus, *Rhinoptera*. The genus is known from the Paleocene in North and West Africa, and Europe (Cappetta 2004). Its recent incarnations can be found in all tropical seas.

The type species is the recent *Myliobatis marginata* (Saint-Hilaire 1817). Other species include *R. prisca* from the Paleocene of Brasil (Woodward 1907), *R. raeburni* from the Paleocene of Nigeria (White 1934) and Zaire (Darteville and Casier 1943), *R. studeri* from the Lower Miocene of Switzerland and France (Agassiz 1843) and most other marine Neogene deposits (Leriche 1927; Cappetta 1970). *R. sherboni* is the lone member of the genus recognized from the Eocene, specifically from the Lutetian of Nigeria (White 1926) and Morocco (Arambourg 1952)

Referred Specimens:

Two hundred ninety-six individual teeth (01146a1-81, 01151a1-78, 01151b1-63, 03648a1-17, 03716a1-4, 03731a1-48, 03768a1-a3, and 03772a1-a7) and one partial palate (01150d).

#### Description:

Nearly all individual teeth display some form of wear. A very few appear to have intact crowns, but the root structures of all evidence some damage. In particular, the labial projection of each tooth seems to have suffered the greatest wear. In most cases, the tooth is fractured on one or both of its ends, preventing accurate measurement of length (Figure 6-1). The average root width is 6.08 mm; the average crown width is 5.32 mm; and the average crown height is 2.34 mm. The observable qualitative relationship of width to length indicates that the vast majority of specimens are median teeth, although the rare primarily intact examples more closely resemble lateral teeth in shape (Figure 6-2).

The Ampazony teeth possess prominent but thin lingual shelves (Figure 6-3). Extension of the lingual projection of the root in relation to that of the crown varies between specimens. In some, the lingual root overhangs the crown by a distinct margin (Figure 6-4, A); in others, the lingual crown extends far beyond the limits of the root (Figure 6-4, B).

The partial palate appears to be that of an adolescent, based on the size of its embedded teeth (Figure 6-5). These teeth include three intact medial and two intact lateral representatives, with a third partial lateral visible. The lateral teeth are hexagonal in shape.

#### Comparison and Discussion:

Of the Eocene rays, both rhinopterids and myliobatids (*Myliobatis*, Cuvier 1817) utilize grinding dentition consistent with the structure of the Ampazony collection (Cappetta 2004). At first glance, the overall character of the Ampazony ray fossils seems to place them among the rhinopterids. Many of the specimens possess the extensive labial

transverse projection diagnostic of this family (Cappetta 2004). This is an especially important consideration in ray classification; the teeth form an upper and lower palate employed to grind food in digestion. The construction of the palate – namely the mechanism of tooth articulation – is specific to separate ray families. In rhinopterids, this is accomplished largely via root shape. The labial projection interlocks with a corresponding depression and lingual shelf projection.

The Ampazon teeth, however, do not exhibit the level of lingual root shelf extension typical of rhinopterids (Figure 6-6). Instead, the lingual shelf resembles those of the myliobatids, thinner and more closely associated with the crown (Figure 6-7). Additionally, the general myliobatid labial root shape, which tends to vertical planes rather than the rhinopterid curves, appears in several of the Ampazon teeth.

Further complicating the matter, classification between these families is also based on the relationship of crown extension to root projection on the lingual face. Eocene rhinopterids generally possess roots that extend lingually beyond the crown, while myliobatid crowns typically outreach their roots. In the Ampazon teeth, both structural forms appear, but are often associated with the opposite system of articulation than might be expected; i.e., the same tooth exhibits a rhinopterid labial projection and myliobatid crown extension (Figure 6-4, *B*), or the reverse (Figure 6-4, *A*).

The partial palate (O1150d; Figure 6-5) from the locality does not definitively resolve the matter. While both shape and size of the lateral teeth it contains are typically myliobatid, both indicators may be subject to the age of the organism. A full palate from a mature specimen may be required to assure certainty.

Based on the complexity of the labial/lingual interlocking apparatus, the Ampazonys are tentatively classified here as rhinopterids. If the teeth are indeed those of rhinopterids, they are likely members of *R. sherboni*, given that it is the dominant representative of the genus throughout the Eocene. In particular, its presence in the Middle Eocene of Egypt suggests access to the Indian Ocean of the epoch (Arambourg 1952). However, this diagnosis should be viewed as tentative until more complete material can be recovered.

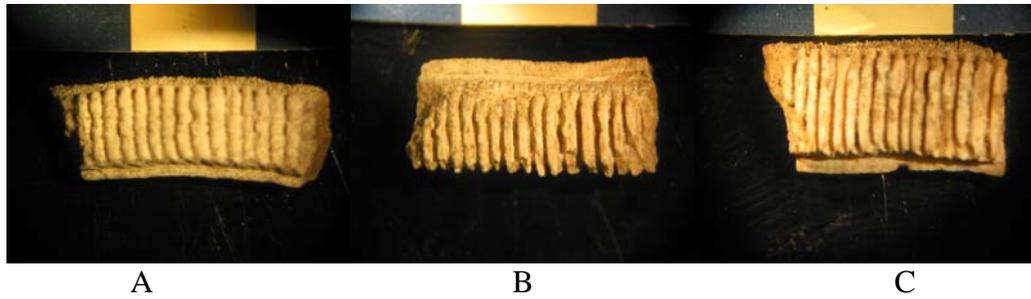


Figure 6-1. Specimens of Rhinopteridae from Ampazony, Madagascar. *A* 01146a66, occlusal view; *B* 01151b58, occlusal view; *C* 01151b52, occlusal view.



Figure 6-2. Specimen 01151b44 of Rhinopteridae from Ampazony, Madagascar.

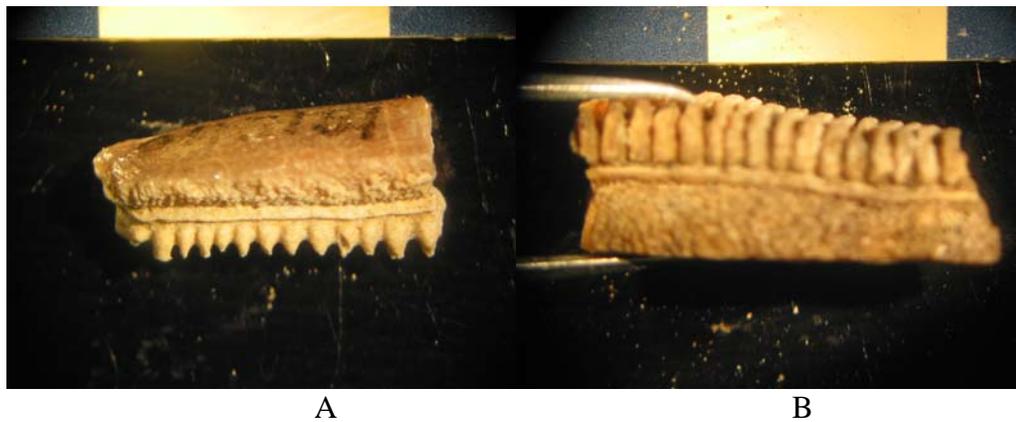


Figure 6-3. Specimen of Rhinopteridae from Ampazony, Madagascar. *A* 01151b1, lingual view; *B* 01151b58, lingual view.

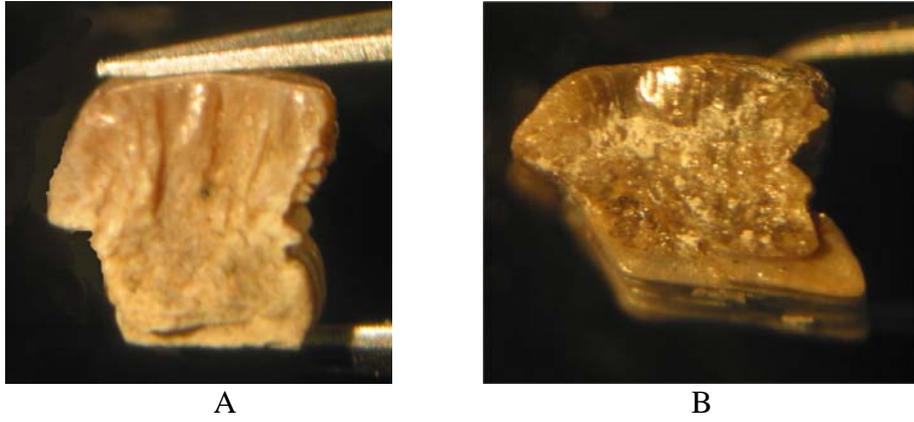


Figure 6-4. Specimens of Rhinopteridae from Ampazony, Madagascar. *A* 01151b34, profile; *B* 03648a14, profile.



Figure 6-5. Specimen 00150d of Rhinopteridae from Ampazony, Madagascar; partial palate, occlusal view.

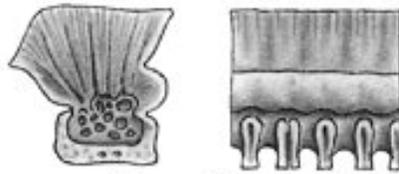


Figure 6-6. Rhinopterid tooth, profile and lingual view (Bourbon 2002).

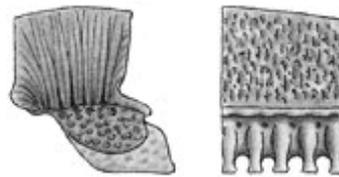


Figure 6-7. Myliobatid tooth, profile and lingual view (Bourbon 2002).

## DISCUSSION

### I. Fossil Abundance and Preservation

Where abundance is concerned, the Ampazony collection is inarguably heavily weighted toward ray fossils. Even the sharks most abundant in the collection - *G. latidens* and *R. terraenovae*, with four teeth each - are dwarfed next to the nearly three hundred rhinopterid fossils. One explanation for this relationship is that it is representative of the corresponding abundance of these species in the Eocene. This approach, however, both oversimplifies the preservation process and overlooks several important differences in the morphology of these species.

To begin with, caution must be used in any attempt to link fossil abundance to the same quality in the living animals. Only a very small fraction of the species that once lived on Earth have been preserved in the rock record and subsequently discovered and described by science. The fossil record is therefore selective, and much is lost without any evidence remaining. This very phenomenon yields the pattern seen in selachian preservation; because their bodies are cartilaginous, in many cases the only evidence of an extinct selachian's presence lies in its teeth. Whether the conditions are favorable or disadvantageous to fossilization is extremely variable, and the critical factors yielding preservation remain to be well documented.

Assuming a given tooth does fossilize, there remains the challenge faced by all antiquities: that of surviving the ravages of time. It is at this point that the basic differences in species morphology come into play. Ray dentition is based on interlocking teeth forming two large palates within the mouth, one upper and one lower. The teeth of the

sharks studied here, by contrast, are arrayed in independent rows along the jaw. As such, shark teeth are more likely to be separate and scattered from one another than their ray counterparts, decreasing the chances of collecting associated shark fossils from the same individual. Additionally, the overall physically lighter structure of the shark teeth in the collection – with the exception of the largest *Carcharhinus* specimen (01148a2) - may also be partially responsible for their rarity.

## II. Faunal Overview and Age Convergence

The Ampazony collection encompasses four species of shark and a probable single species of ray. Of these, each represents a separate genus. Given the likelihood that those specimens collected may represent only a fraction of the species actually present, this period in Madagascar's marine history possesses a wide range of diversity.

The identification of the species in question allows comparison of their respective ages. Both rhinopterids and myliobatids are known from the Paleocene to the recent, while *Rhizoprionodon terraenovae* and *Carcharhinus* both span from the Middle Eocene to the Recent (Capetta 2004). *Galeocerdo latidens* and *Nebrius blankenhorni*, however, are limited to the Eocene, narrowing the range of possible ages for the Ampazony site. The only age common to all identified species is therefore the Eocene, with some indication for preference of the middle to later portions of the epoch.

### III. Biogeographic Context

Madagascar's Ampazony selachian fauna appears to bear a striking resemblance to that of several other locations, foremost among them Morocco and Egypt. Moroccan Eocene deposits have produced two of the shark species identified from Ampazony (*G. latidens* and *N. blankenhorni*), members of both remaining shark genera (*Carcharhinus* and *Rhizoprionodon*), and representatives of both *Myliobatis* and *Rhinoptera* (including *R. sherboni*). Egypt's Eocene sediments are likewise populated with *G. latidens*, *N. blankenhorni*, and species of *Carcharhinus*, *Myliobatis* and *Rhinoptera*.

When mapped in the context of Eocene continental arrangement, the distribution of the Ampazony species reveals a distinct pattern (Figure 1). Fossil localities for these species lie along a corridor formed by Africa to the south and Asia and Europe to the north. Their positions describe the Eocene location of the Tethys Seaway, a remnant body of water which connected the Atlantic and Indian Oceans after partitioning of the Tethys Ocean. This may be an indication that selachian migration utilized the Tethys Seaway, at least in the case of these species, as a means of transport between larger waterways.

### IV. Madagascar's Selachians: Past and Present

Of the four Ampazony Eocene shark genera identified here, all are represented in Madagascar today. The type species of both *Galeocerdo* and *Carcharhinus* are common to the island, as is the lone extant species of *Nebrius*. Conversely, while the genus *Rhizoprionodon* is represented there by two extant species, the *R. terraenovae* does not inhabit the island. Instead, *R. terraenovae* is today found only in the western Atlantic

Ocean. Similarly, no species of the ray family Rhinopteridae are known from Madagascar's recent oceans.

It may be significant that the larger-bodied genera continue to appear, while those of lighter build are no longer found near the island. With the close of the Tethys Seaway in the Early Miocene, it is possible that transport to the Indian Ocean became unfeasible for these smaller species. At the very least, the energetic cost may have begun to outweigh the benefits. The simultaneous development of the Antarctic Circumpolar Current (ACC) may also have been an important factor. Cooler waters circulated via the Drake Passage might have hindered passage through lower latitudes. Additionally, reversal of the current through the Panama Seaway in the Miocene, from its formerly western direction to an eastern tack, could have further inhibited species movement. Even if the selachians themselves had remained capable of the journey, their food sources may well not have done the same.

At present, selachian migratory patterns are extremely uncharted; while several studies are currently underway to map shark movement – primarily as it pertains to attacks on humans – published data are rare. Of what information does exist, species such as *Galeocerdo cuvier* have been noted to travel as much as 1,850 nautical miles in the course of study (Randall 1992), while members of *Carcharhinus* are known to migrate based on water temperature (Lucifora et al 2005). Further investigation of the habits of recent species may shed more light on the disappearance of Eocene genera from Madagascar's waters.

## V. Conclusions and Contributions

The Ampazony collection provides the first glimpse into the previously poorly represented 80 million year span of Malagasy history. The fossils included in this study are important for a variety of reasons. To begin with, they mark the first attempt to identify and systematically describe any marine species from Madagascar's fossil gap. None of the five species discussed herein were known from Madagascar previously. Their presence, and in some cases the absence of their recent descendants, reveals a great deal about Madagascar's oceans through the ages. Although the island itself has been relatively stationary since the Cretaceous, the fluctuations of its marine fauna point to continuing transitions in its waters far into the Cenozoic.

Beyond the implications for Madagascar, this research also leads to a clearer picture of the Eocene selachian fossil record in general. In the cases of *R. terraenovae* and the Rhinopteridae, the Ampazony collection stands as the first record of their presence in the southern Indian ocean. With so little information available on the habits of even recent species, every new addition to this body of knowledge is especially valuable.

As more fossils are recovered from the gap, understanding of Madagascar's natural history can only increase. At the same time, this knowledge will give further depth and interpretation to the Ampazony collection. More complete specimens would greatly assist in clarifying species identification and context (e.g., rays).

Finally, the assemblage of species identified from the Ampazony locality allows the site itself to be dated to the Eocene with relative confidence. This information in turn provides a basis for study of all other species collected there. Among these is the sea cow

first discovered in 2003 which represents the first mammal recovered from the fossil gap, marine or terrestrial (Samonds et al 2005). Such an application marks only the start of the importance of the Ampazonny selachian fauna and the information it discloses. Ultimately, research extending from this work may eventually erase Madagascar's fossil gap entirely, and give the island a complete and understood biogeographic history.

## LITERATURE CITED

- Agassiz, L. 1843. Recherches sur les Poissons fossiles. Neuchâtel and Soleure, Petitpierre.
- Antunes, T. M. 1972. Faunules ichthyologiques oligo – miocenes de Guinee portugaise. Rev. Fac. Cienc., Univ. Lisboa, 17(1):1-18.
- Antunes, T. M. 1978. Faunes ichthyologiques du Niogene superieur d'Angola, leur age, remarques sur le Pliocene marin en Afrique australe. Cienc. Terra, Univ. Lisboa, 4:59-90.
- Antunes, T. M. and Jonet, S. 1970. Requins de l'Helvetien superieur et du Tortonien de Lisbonne. Revist. Fac. Cienc., Univ. Lisboa, 16(1), 119-280.
- Applegate, S. P. 1972. A revision of the higher taxa of Orectolobids. Marine Biol. Assoc. India, 14(2):743-751.
- Arambourg, C. 1927. Les poissons fossiles d'oran. J. Carbonel, Alger.
- Arambourg, C. 1952. Les vertebres fossiles des gisements de phosphates (Maroc, Algerie, Tunisie). Typographie Firmin-Didot, Paris.
- Blainville, H. M. D. 1816-1830. Vers et zoophytes. F.G. Levrault, Paris.
- Bigelow, H. B. & Schroeder, W. C. 1948. Fishes of the Western North Atlantic. Sears Foundation for Marine Research, Yale University, New Haven.
- Bonaparte, C. L. 1838. Selachorum tabula analytica.
- Bourbon, J. 2000. The Life and Times of Long Dead Sharks: Myliobatid Teeth. Available online at <http://www.elasmo.com>.
- Buckley, G. A., and C. A. Brochu. 1999. An enigmatic new crocodile from the Upper Cretaceous of Madagascar. In D. Unwin (ed.) Cretaceous Fossil Vertebrates. Paleontological Association Special Papers in Paleontology 60:149-175.
- Buckley, G. A., C. Brochu, D. W. Krause, and D. Pol. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405:941-944.
- Burney, D. A., H. F. James, F. V. Grady, J. G. Rafamantanantsoa, Ramilisonina, H. T. Wright, and J. B. Cowart. 1997. Environmental change, extinction and human activity: evidence from caves in NW Madagascar. Journal of Biogeography 24:755-767.

- Burney, D. A. 1999. Rates, patterns and processes of landscape transformation and extinction in Madagascar, pp. 145-164 in R. D. MacPhee (ed.), *Extinctions in Near Time*. Kluwer Academic Press/Plenum Publishers, New York.
- Cappetta, H. 1970. Les selaciens du Miocene de la region de Montpellier. Labor. de Paleontologie, Montpellier.
- Cappetta, H. 1980. Modification du statut generique de quelques especes de selaciens cretaces et tertiaires. *Palaeovertebrata*, 10(1):29-42.
- Cappetta, H. 1981. Additions a la faune de selaciens fossils du Maroc. *Geobios*, 14(5):563-575.
- Cappetta, H. 2004. *Chondrichthyes II : Mesozoic and Cenozoic elasmobranchii*. G. Fischer Verlag, New York.
- Cappetta, H. and Nolf, D. 1981. Les selaciens de l'Auverisien de Ronquerolles (Eocene superieur de Bassin de Paris). *Meded. Werkgr. Tert. Kwart. Geol.*, 18(3):87-107.
- Carrano, M. T., S. D. Sampson, and C. A. Forster. 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *J. Vert. Paleo.*, 22(3):510-534.
- Case, G. R. 1980. A selachian fauna from the Trent Formation, Lower Miocene (Aquitanian) of Eastern North Carolina. *Palaeontographica Abt. A*, 171:75-103.
- Case, G. R. 1981. Late Eocene selachians from South Central Georgia. *Palaeontographica Abt. A*, 176:52-79.
- Case, G. R., & Cappetta, H. 1990. The Eocene selachian fauna from the Fayum depression in Egypt. *Palaeontographica. Abteilung A: Palaeozoologie-Stratigraphie*, 212(1-6):1-30.
- Casier, E. 1960. Note sur la collection des poissons paleocenes et eocenes de L'Enclave de Cabinda (Congo). *Annales du Musee Royal du Congo Belge, Bruxelles*, 3(1):1-48.
- Casier, E. 1971. Sur un Material Ichthologique des "Midra (and Saila) Shales" du Qatar, Golfe Persique. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 47(2):1-9.
- Chapman, F. and Cudmore, F. A. 1924. New or little-known fossils in the National Museum. Part XXVII: Some Cenozoic fish remains, with a revision of the group. *Proceedings of the Royal Society of Victoria*, 36:107-162.
- Cliff, G., L. J. V. Compagno, M. J. Smale, R. P. van der Elst, and S. P. Wintner. 2000. First records of white sharks, *Carcharodon carcharias*, from Mauritius, Zanzibar, Madagascar, and Kenya. *South African J. of Science*, 96(7):365-367.

- Cochran, J. R. 1988. Somali basin, chain ridge, and the origin of the northern somali gravity and geoid low. *Journal of Geophysical Research*, 93(B10), B11985-B12008.
- Compagno, L. J. V. 1973. Interrelationships of living Elasmobranchs (In Greenwood, H., Miles, R., and Patterson, C. eds. *Interrelationships of fishes*), Academic Press, London. p. 15-60.
- Compagno, L. J. V. 1977. Phyletic relationships of living sharks and rays. *Amer. Zool.*, 17:303-322.
- Curry Rogers, K. A., and C. A. Forster. 2001. The last of the dinosaur titans: A new sauropod from Madagascar. *Nature* 412:530-534.
- Dames, W. B. 1883. *Über eine tertiäre Wirbelthier Fauna von der westlichen Insel des Birket el Quruen im Fayum (Aegypten)*. *Sitzungsberichte der Königlich-preussischen Akademie der Wissenschaften*, Berlin, 1883:129-153.
- Darteville, E. and Casier, E. 1943-1959. *Les poissons fossiles du bas-congo et des régions voisines*. Tervuren (Belgique): Musée du Congo belge.
- Davies, D. H. 1964. The Miocene shark fauna of the southern St. Lucia area. *Ocean. Res. Inst., Invest. Rep.* 10, p. 1-16.
- De Carvalho, M. R., Maisey, J.G., and Grande, L. 2004. Freshwater stingrays of the Green River Formation of Wyoming (early Eocene), with the description of a new genus and species and an analysis of its phylogenetic relationships (Chondrichthyes : Myliobatiformes). *Bulletin of the American Museum of Natural History*, v. 284, p. 1-136.
- Dixon, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. Longman, Brown, Green and Longmans, London.
- Douady, C. J., F. Catzeflis, D. J. Kao, M. S. Springer, and M. J. Stanhope. 2002. Molecular evidence for the monophyly of Tenrecidae (Mammalia) and the timing of the colonization of Madagascar by Malagasy tenrecs. *Molecular Phylogenetics and Evolution* 22:357-363.
- Forster, C. A., L. M. Chiappe, D. W. Krause, and S. D. Sampson. 1996. The first Cretaceous bird from Madagascar. *Nature* 382:532-534.
- Gaffney, E. S. and C. A. Forster. 2003. Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. *American Museum Novitates*. 3397, 13 pp.
- Geiger, M., C. D. Normal, and W. Mette. 2004. Reappraisal of the timing of the breakup of Gondwana based on sedimentological and seismic evidence from the Morondava Basin, Madagascar. *Journal of Africa Earth Sciences* 38:363-381.
- Gibbes, R. W. and Hubbs, C. L. 1849. *Monograph of the fossil squalidae of the United States*. Dulau, London.

- Gill, T. 1862. Catalogue of the fishes of the eastern coast of North America from Greenland to Georgia. Proceedings of the Academy of Natural Sciences of Philadelphia, 13(addendum).
- Godfrey, L. R., W. L. Jungers, E. L. Simons, P. S. Chatrath, and B. Rakotosamimanana. 1999. Past and present distributions of lemurs in Madagascar; pp. 19-53 in B. Rakotosamimanana, H. Rasamimanana, J. U. Ganzhorn and S. M. Goodman (eds.), New Directions in Lemur Studies. Plenum Publishers, New York.
- Goodman, S. M. 1994. The enigma of antipredator behavior in lemurs: evidence of a large extinct eagle in Madagascar. International Journal of Primatology 15:129-134.
- Goodman, S. M., & Benstead, J. P. 2003. The natural history of Madagascar. University of Chicago Press, Chicago.
- Gottfried, M. D., L. L. Randriamiarimanana, J. A. Rabarison, and D. W. Krause. 1998. Late Cretaceous fish from Madagascar: implications for Gondwanan biogeography. Journal of African Earth Sciences 27:91-92.
- Gottfried, M. D., J. A. Rabarison, and L. L. Randriamiarimanana. 2001. Late Cretaceous elasmobranchs from the Mahajanga Basin of Madagascar. Cretaceous Research, v. 22, no. 4, p. 491-496.
- Hallam, A. 1984. Pre-Quaternary changes of sea level. Annual Reviews of Earth and Planetary Science 12:205-243.
- Hallam, A. 1992. Phanerozoic sea-level changes. Columbia University Press, New York.
- Haq, B., J. Hardenbol, and P.R. Vail. 1987. Chronology of fluctuating sea levels since the Triassic. Science 235:1156-1167.
- Haq, B., J. Hardenbol, and P.R. Vail. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. Pages 71-108 in C.K. Wilgus et al, eds. Sea-level changes – and integrated approach. Society of Economic Paleontologists and Mineralogists Special Publication 42.
- Hay, O. P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. G.P.O., Washington D.C.
- Herman, J. 1974. Compléments paléoichthyologiques à la faune Eocène de la Belgique. Bull. Soc. Belg. Geol., 83(1):33-34.
- Hooijer, D. A. 1954. Pleistocene vertebrates from Celebes: dentition and skeleton of *Celebochoerus heekereni hooijer*. E.J. Brill, Leiden.
- Huber, M., and Nof, D. 2006. The ocean circulation in the Southern Hemisphere and its climatic impacts in the Eocene. Palaeogeography, Palaeoclimatology, Palaeoecology, 231(1-2), 9-28.
- Huxley, T. H. 1880. A manual of the anatomy of vertebrated animals. D. Appleton, New York.

- Itoigawa, J., H. Nishimoto, H. Karasawa, and Y. Okumura. 1985. Miocene fossils of the Mizunami group, central Japan. *Monogr. Mizunami Fossil Mus.*, 5:1-99.
- Jansa, S. A., and M. D. Carleton. 2003. Systematics and phylogenetics of Madagascar's native rodents; pp. 1257-1265 in S. M. Goodman and J. P. Benstead (eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago, Illinois.
- Joleaud, L. 1912. *Geologie et paleontologie de la Plaine du Comtat et de ses abords*. Mem. Acad. Vaucluse, p. 1-143.
- Jordan, D. S. and Evermann, B. W. 1896-1900. *The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama*. G.P.O., Washington.
- Kennett, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic ocean, and their impact on global paleoceanography. *Journal of Geophysical Research*, 82(27), 3843-3860.
- Kiener, A. N. 1964. *Contribution a l'etude ecologique et biologique des eaux saumâtres malgaches. Les poisons euryhalins et leur role dans le developpement des peches*. These de Doctorat, Universite de Marseille.
- Klunzinger, K. B. 1880. *Synopsis der fische des Rothen Meeres*. J. Kramer, Weinheim.
- Krause, D. W. 2001. Fossil molar from a Madagascan marsupial. *Nature* 412:497-498.
- Krause, D. W. 2003. Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of the dinosaurs, pp. 40-47 in S. M. Goodman and J. P. Benstead (eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago, Illinois.
- Krause, D. W., J. H. Hartman, N. A. Wells, G. A. Buckley, C. A. Lockwood, C. E. Wall, R. E. Wunderlich, J. A. Rabarison, and L. Randriamiamanana. 1994. Late Cretaceous mammals. *Nature* 368:298.
- Krause, D. W., J. H. Hartman, and N. A. Wells. 1997. Late Cretaceous vertebrates from Madagascar: implications for biotic change in deep time; pp. 3-43 in S. M. Goodman and B. D. Patterson (eds.), *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington D. C.
- Krause, D. W., Rogers, R. R., Forster, C. A., Hartman, J. H., Buckley, G. A. and Sampson, S. D., 1999. The Late Cretaceous vertebrate fauna of Madagascar: Implications for Gondwanan Paleogeography. *GSA Today*, v. 9, p. 1-7.
- Kriwet, J. 2005. Additions to the Eocene selachian fauna of Antarctica with comments on Antarctic selchian diversity. *Journal of Vertebrate Paleontology*, 25(1), 1-7.
- Landini, W. 1977. Revisione degli <<Ittiodontoliti pliocenici>> della collezione Lawley. *Palaeontographia Italica*, 70:92-134.

- Lawley, R. 1876. Nuovi studi sopra ai pesci ed altri vertebrati fossili delle colline toscane. Tip. dell'Arte della Stampa, Firenze.
- Leclaire, L. 1974. Late Cretaceous and Cenozoic pelagic deposits: paleoenvironment and paleoceanography of the central western Indian Ocean. Pages 481-513 in E.S.W. Simpson et al, eds. Initial reports of the Deep Sea Drilling Project. Vol. 25. U.S. Government Printing Office, Washington, D.C.
- Leidy, J. and Gabb, W. M. 1877. Description of vertebrate remains, chiefly from the phosphate beds of South Carolina. Proceedings of the Academy of the Natural Sciences of Philadelphia, Philadelphia.
- Leriche, M. 1905. Les poissons eocenes de la Belgique. Polleunis & Ceuterick, Bruxelles.
- Leriche, M. 1910. Les poissons oligocenes de la Belgique. Polleunis & Ceuterick, Bruxelles.
- Leriche, M. 1920. Les poissons tertiaires de la Belgique. 1. Les poissons paleocenes. Mem. Mus. Roy. Hist. Natur. Belg., 5:1-48.
- Leriche, M. 1927. Les poissons de la molasse suisse. premier fascicule. Comité de rédaction, Muséum d'histoire naturelle, Genève.
- Leriche, M. 1942. Contribution a l'étude des faunes ichthyologiques marines des terrains tertiaires de la plaine cotiere atlantique et du centre des Etats-unis; le synchronisme des formations tertiaires des deux cotes de l'atlantique. Paris.
- Leriche, M., and Signeux, J. 1957. Les poissons neogenes de la Bretagne, de L'anjou et de la Touraine. Paris.
- Longbottom, A. 1979. Miocene shark's teeth from Ecuador. Bull. Brit. Mus. Natur. Hist. (Geol.), 32(1), 57-70.
- Lucifora, L. O., Menni, R. C., and Escalante, A. H. 2005. Reproduction and seasonal occurrence of the copper shark, *Carcharhinus brachyurus*, from north Patagonia, Argentina. ICES Journal of Marine Science, 62(1), 107-115.
- Mehrotra, D. K., Mishra, V. P., & Srivastava, S. 1973. Miocene sharks from India. In: Verma, V.K. (Ed.), Recent Researches in Geology, 1, 180-200.
- Menesini, E. 1974. Ittiodontoliti delle formazioni terziarie dell' arcipelago Maltese. Palaeontographia Italica, 67, 122-162.
- Muller, J. and Henle, J. 1837. Ueber die gattungen der aifische und rochen, nach ihrer arbeit: Uber die naturgeschichte der knorpelfische. Ber. Preuss. Akad. Wiss., 1, 111-118.

- Mustafa, H. and Zalmout, I. 2000. Elasmobranchs from the late Eocene Wadi Esh-Shallala formation of Qa'Faydat ad Dahikiya, east Jordan. *Tertiary Research*, 21(1-4), 77-94.
- Nesbitt, H. W. and Young, G. M. 1997. Sedimentation in the Venezuelan Basin, circulation in the Caribbean Sea, and onset of Northern Hemisphere glaciation. *Journal of Geology*, 105(5), 531-544.
- Norton, I.O. and J.G. Sclater. 1979. A model for the evolution of the Indian Ocean and the break-up of Gondwanaland. *Journal of Geophysical Research*, 84(B12), 6803-6830.
- Noubhani, A., and Cappetta, H. 1997. Les orectolobiformes, carcharhiniformes et myliobatiformes (elasmobranchii, neoselachii) des bassins a phosphate du Maroc (maastrichtien-Lutetien basal) : Systematique, biostratigraphie, evolution et dynamique des faunes. Verlag Friedrich Pfeil, München.
- Omta, A. W., and Dijkstra, H. A. 2003. A physical mechanism for the Atlantic-Pacific flow reversal in the early Miocene. *Global and Planetary Change*, 36(4), 265-276.
- Peron, F. and C. A. Lesueur. 1822. Description of *Galeocerdo cuvier* in Descriptions of the five new species of the genus Cichla of Cuvier. Philadelphia.
- Petit, G. 1930. L'industrie des peI'ches a Madagascar. Société d'édicions géographiques, maritimes et colonials, Paris.
- Poux, C., O. Madsen, E. Marquard, D. R. Vieites, W. W. de Jong, and M. Vences. 2005. Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Systematic Biology* 54:719-730.
- Priem, M. F. 1897. Note sur Propristis Dames du Tertiair inferieur d'Egypte. Bulletin de la Societe Geologique de la France. Serie 3, vol. 25: 228-232.
- Priem, F. 1908. Etude des poissons fossiles du bassin Parisien. Masson et cie, Paris.
- Quoy, J. R. C., Gaimard, P., L. de Freycinet. 1826. Zoologie [poissons]. Pilet Aîné, Paris.
- Rabinowitz, P.D., M.C. Coffin, and D. Falvey. 1983. The separation of Madagascar and Africa. *Science*, 220, 67-69.
- Randall. J. E. 1992. Review of the biology of the tiger shark (*Galeocerdo cuvier*). *Australian J. of Marine and Freshwater Research*, 43(1):21-31.
- Reeves, C.V., F.M. Karanja, and I.N. Macleod. 1987. Geophysical evidence for a failed Jurassic rift and triple junction in Kenya. *Earth and Planetary Science Letters*, 81, 299-311.
- Richardson, J., Sir, and Adams, A. 1848. Fishes. Reeve, London.

- Ricou, L. E. 1987. The Tethyan oceanic gates: a tectonic approach to major sedimentary changes within Tethys. *Geodynamica Acta*, 1, 225--232.
- Ruppell, E. 1835-1840. *Neue Wirbelthiere zu der Fauna von Abyssinen* gehorig. 2 vols. Frankfurt, a-M.
- Sahni, A. and Mehrotra, D. K. 1981. The elasmobranch fauna of Coastal Miocene sediments of peninsular India. *Biol. Mem. Lucknow*, 5(2):83-121.
- Saint-Hilaire, E. 1817. *La menagerie du Museum d'histoire naturelle, ou les animaux vivans, avec des observations curieuses faites sur les individus de chaque espece*. T. Denesle, Paris.
- Samonds, K. E., M. A. Loewen, G. A. Buckley, and R. L. Whatley. 2001. Vertebrate fossils from the Cenozoic of Madagascar. *Geological Society of America* 33(6): A-389.
- Samonds, K. E. and Zalmout, I., 2002. New selachian assemblage from the marine Paleogene of Madagascar. *Journal of Vertebrate Paleontology* 22 (Supplement 3): 102A.
- Samonds, K. E., I. Zalmout, and D. W. Krause. 2005. New sirenian fossils from the late Eocene of Madagascar. *Journal of Vertebrate Paleontology* 25:108A.
- Sampson, S. D., M. T. Carrano, and C. A. Forster. 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature* 409:504-506.
- Schultz, O. 1977. Neue und fehlinterpretierte fischformen aus dem miozan des wiener beckens. *Ann. Naturhist. Mus. Wien*, 81, 203-219.
- Scotese, C. R. 2001. *Atlas of Earth history, volume 1: Paleogeography, PALEOMAP project.1*, 52.
- Scrutton, R.A., W.B. Heptonstall, and J.H. Peacock. 1981. Constraints on the motion of Madagascar with respect to Africa. *Marine Geology*, 43, 1-20.
- Smale, M. J. 1998. Evaluation of shark populations around the Masoala Peninsula, north east Madagascar. Final report. Antananarivo: Report prepared for the Wildlife Conservation Society, Madagascar Country Program. Available from A. Cooke.
- Storetvedt, K.M., J.G. Mitchell, M.C. Abranches, D. Maaloe, and G. Robin. 1992. The coast parallel dolerite dykes of east Madagascar; age of intrusion, remagnetization and tectonic aspects, *J. Afr. Earth Sci*, 15, 237-249.
- Storey, M., J. J. Mahoney, A. D. Saunders, R. A. Duncan, S. P. Kelly, and M. F. Coffin. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science* 267:852-855.

- Stromer, E. 1905. Sie Fischreste des mittlern und oberen Eocene Von Agypten. Beitrage zur Palaeontologie und Geologie Osterreich-Ungarns und Orients. Universitats-Buchhandler in Wein. XVIII:163-190.
- Stromer, E. 1910. Ueber das gebiss der lepidosireniden u. die verbreitung tertiärer lungenfische. Jena.
- Uyeno, T., T. Nohara, and Y. Hasegawa. 1974. Fossil fishes from the Okinawa Islands. Mem. Nat. Sci. Mus., Tokyo, 7, 53-60.
- Uyeno, T. and Matsushima, Y. 1975. Pliocene shark remains of *Carcharodon*, *Carcharias*, and *Dalatias*, from Kanagawa Prefecture, Japan. Bull. Kanagawa Prefect. Mus. (Natur. Sci.), 8:41-55.
- White, E. I. 1926. Eocene fishes from Nigeria. Bull. Geol. Surv. Nigeria, 10, 1-82.
- White, E. I. 1934. Fossil fishes of Sokoto Province. Geol. Surv. Nigeria, Bull., 14:1-78.
- White, E. I. 1955. The Eocene fishes of Alabama. Bulletins of American Paleontology, 36(156):123-152.
- Whitley, G. P. 1929. Additions to the checklist of the fishes of the New South Wales. Australian Zoology, 5:353-537.
- Winkler, T. C. 1874. Memoire Sur dents de poissons du systeme heersien, Archives du Musee Teyler, Haarlem, 3(4):295-304.
- Wittich, E. 1989. Beitrage zur Kenntnis der Messeler Braunkohle und ihre fauna. Giessen Univ., Darmstadt.
- Woodward, A. S. 1889-1901. Catalogue of the fossil fishes in the British Museum of Natural History. Printed by order of the Trustees, London.
- Woodward, A. S. 1907. On the Cretaceous formation of Bahia (Brazil), and on vertebrate fossils collected therein. II. The vertebrate fossils. Quarterly J. of the Geological Society of London, 63:131-139.
- WWF. 1993. Coral reefs and coastal zone of Toliara – conservation and development through ecotourism: Pre-project, ed. A. J. Cooke. Antananarivo: WWF. Available from A. Cooke.
- Yoder, A. D. and J. J. Flynn. 2003. Origin of Malagasy Carnivora; pp. 1253-1256 in S. M. Goodman and J. P. Benstead (eds.), The Natural History of Madagascar. The University of Chicago Press, Chicago.