

SYSTEMATICS, PALEOBIOLOGY, AND PALEOECOLOGY OF LATE MIOCENE
SHARKS (ELASMOBRANCHII, SELACHII) FROM PANAMA:
INTEGRATION OF RESEARCH AND EDUCATION

By

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To my husband

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LIST OF ABBREVIATIONS

CTPA	Center of Tropical Paleobiology and Archaeology
CH	Crown Height
FLMNH	Florida Museum of Natural History
NMNH	National Museum of Natural History
UF	University of Florida, Gainesville, Florida
SMU	Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas.
STRI	Smithsonian Tropical Research Institute, Panama, Republic of Panama
TL	Total Length
W	Crown Width

Abstract of Thesis Presented to the Graduate School
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SYSTEMATICS, PALEOBIOLOGY, AND PALEOECOLOGY OF LATE MIOCENE
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INTEGRATION OF RESEARCH AND EDUCATION

By

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Chair: Bruce MacFadden

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Major: Zoology

The late Miocene Gatun Formation of northern Panama contains a highly diverse and well sampled neritic fossil assemblage that was located in the Central American Seaway that connected the Pacific and Atlantic (Caribbean) oceans ~10 million years ago. The Gatun Formation likewise contains a relatively diverse selachian assemblage. Based on field discoveries and analysis of existing collections, the sharks from this unit consist of at least 16 taxa, including four species that are extinct today. The remaining portion indicates relatively long-lived species. Based on the known habitat preferences for modern selachian, the Gatun sharks were primarily adapted to shallow waters within the neritic zone. Also, in comparison with modern species, the Gatun shark fauna has mixed Pacific-Atlantic biogeographic affinities. Comparisons of Gatun dental measurements with other formations suggest that many of the species have an abundance of small individuals. One of this small-size species is the extinct *Carcharocles megalodon*, paradoxically the biggest shark that ever lived. Here, the tooth sizes from the Gatun Formation were compared with isolated specimens and tooth sets from different aged, but analogous localities. In addition, the total lengths of the individuals were calculated. This comparisons and estimates suggest that the small size of Gatun's *C. megalodon* is not

related to timing (chronoclines), or to the tooth position within a variant jaw, and that the individuals from Gatun were mostly juveniles and neonates. I therefore propose the Miocene Gatun Formation as the first documented paleo-nursery area for *C. megalodon* from the Neotropics. It hence shows that sharks have used nursery areas for millions of years as an adaptive strategy during their life histories.

For this research, approximately 400 fossil shark teeth were collected. This large collection has the great potential to be used not only for scientific research, but also as a teaching tool for young learners. One important goal of this non-traditional thesis is to convey scientific knowledge to the general public, and therefore a broader impact deliverable was produced: A kid-friendly and bilingual website about fossil sharks from Panama (<http://stri.org/english/kids/sharks/>), to engage young learners to science. The site was designed to create a quality online experience based on evaluations to different-aged young learners and following the best practices.

CHAPTER 1 GENERAL INTRODUCTION

Sharks are included in the class Chondrichthyes, a very ancient clade that dates from at least ~400 Million years ago during the Paleozoic Era (Hubbell 1996). Sharks are very important apex predators in modern oceans and they include some of the most ancient vertebrates still around today (Cione et al. 2007). In the geologic record, shark teeth are the most abundant vertebrate fossils present worldwide (Hubbell 1996). The presence of fossil shark teeth in different localities around the world allows determination of the composition of ancient marine faunas.

Numerous fossil shark species have been found at different Miocene localities worldwide. These discoveries are essential to understand the ecology of the fauna during that particular period of time. During the Pliocene about 4 million years ago, the Panamanian Isthmus was formed by the closing of an oceanic gateway that had been open since the Mesozoic (Cronin and Dowsett 1996). Before this closure, marine warm shallow waters (Teranes et al., 1996) covered southern Central America forming the Central America Seaway.

In this non-traditional thesis, fossil sharks are the main subject of study. This work is divided in two main components; the first is the scientific component and the second is a broader impact deliverable

Scientific Component

Woodring (1957, 1959, 1964) described the invertebrates of the Tertiary Caribbean Fauna Province. Within this Caribbean Province, different fossil shark teeth have been recorded in a few publications. These findings reveal the composition of the Caribbean Miocene shark faunas from Panama (Blake 1862, Gillette 1984, Pimiento et al. 2010), Venezuela (Aguilera, and Rodríguez de Aguilera, 2002, 2004) and Ecuador (Longbottom, 1979).

Related to these occurrences, in order to further elucidate the fossil record of sharks from Panama, particularly from the Gatun Formation, all relevant fossil shark tooth material known were reviewed and re-described in this research. Additionally, new specimens were collected and identified to add to the record. The additional new specimens were also compared to the original material collected and described (Gillette 1984). In this research, a better census of the ancient selachian biodiversity during the late Miocene of Panama was completed, expanding our knowledge of ichthyofauna of the Gatun Formation. This work is described in Chapter 2 and is currently under revision to be published on our very own Bulletin of the FLMNH.

Based on the work mentioned above and other studies on different areas, the Gatun is a highly fossiliferous Neogene formation located in the Isthmus of Panama (Figure 1-1) with a diverse fauna of sharks. It was located within the marine Sea Way (Central America Sea Way) that connected the Pacific Ocean and the Caribbean Sea during the late Miocene (~10Ma) [8]. Studies of different taxa indicate that it was a shallow-water ecosystem (~ 25 m depth) with higher salinity, mean annual temperature variations, seasonality and productivity relative to modern systems in this region.

From the shark species found in the Gatun Formation, Megalodon (*Carcharocles megalodon*) has generated curiosity in both the scientific community and among fossil collectors. The reason for this is because this extinct lamnoid shark is the biggest predator that ever lived, exceeding estimated body sizes attributed to even the largest carnivorous dinosaur. A single *C. megalodon* tooth can reach 168 mm in height, and studies have estimated that an adult could reach more than 15 m of total length (Gottfried et al. 1996).

Even when sharks are apex predators in the oceans, juveniles are preyed by larger individuals during the first years (Heithaus 2007). In order to protect their offspring, females lay

their eggs, or give birth in shallow and productive zones called “nursery areas” for juveniles to use these environments as a refuge from larger predators (Heupel et al. 2007). In this research, I hypothesize that of Panama was used as a paleo-nursery area during the late Miocene for the juveniles of *C. megalodon*.

Nursery areas for *C. megalodon* have been proposed based on anecdotal records in a few previous publications. In this study, *C megalodon* teeth were collected and measured from the Gatun Formation of Panama. Surprisingly, large teeth are uncommon with specimens recovered having crown heights ranging between 16 to 72 mm, far smaller than the range of variation seen in collections of *C. megalodon* that span an expected size range to include juveniles and adults. In this research, tooth sizes from the Gatun were compared with specimens from different, but analogous localities. Additionally, from these measurements the total lengths of the individuals from the Gatun were calculated. The results obtained allowed to determine the age class/size of individuals that inhabited the shallow-water habitats of the late Miocene Gatun Formation, ~10 million years ago, and to support the hypothesis that Panama was used as a nursery area for young *C. megalodon* during the late Miocene. This work is described in Chapter 3 and will be soon submitted to the PLoS Biology Journal. In addition, it was presented to the Society of Vertebrate Paleontology 69th Annual meeting, where it received media attention from the Discovery Channel [<http://news.discovery.com/animals/megalodon-nursery-prehistoric-sharks.html>].

Broader Impact Component

After investigating ancient sharks of the Neotropics, one may wonder why it is so important to create knowledge and do science? Science is a powerful enterprise that can improve the lives of human beings in fundamental ways. It requires not only the work of scientists,

engineers and doctors, but also journalists, teachers, politicians, and everyone that can contribute to the great enterprise of science (Michaels et al. 2008).

The development of science for young learners allows them, among other things, to think critically, giving them power to become members of society rather than mere observers (Michaels et al. 2008). Evaluations in museums have revealed that fossil sharks are very attractive for young learners (MacFadden, 2006). Fossil shark teeth permit the understanding of the composition of ancient faunas as well as the environmental conditions that allows us to comprehend the climate changes that have occurred in earth's history. Therefore, the history of fossil sharks in Panama facilitates understanding several important concepts of natural sciences such as biology, ecology, geology and paleontology. This topic sparks young learners' curiosity and in turn leads to the acquisition of science knowledge.

The Internet offers a new way to teach science, particularly with the interactivity of Web 2.0 technology. Contrary to the static textbooks, with the Internet, scientific concepts can be communicated in a dynamic and creative way, which is closer to how science really works. This turns out to be more attractive and less intimidating for both students and teachers and does not ignore fun (Sanders 2009).

For this Masters research, and in collaboration with STRI and the FLMNH, approximately 400 new fossil shark teeth specimens from the Miocene Gatun Formation of Panama, were collected. This large collection has a great potential to be used not only for scientific proposes, but also as a teaching tool for young learners. The objective of the broader impact component of this research is to develop of a kid-friendly and bilingual website about fossil sharks from Panama to engage young learners to science. This website, hosted by the STRI kids webpage [<http://www.stri.org/kids>], is described in Chapter 4. It will be a novel model for education using

the Internet as a tool, and will promote science and technology to society, particularly for the next generation.

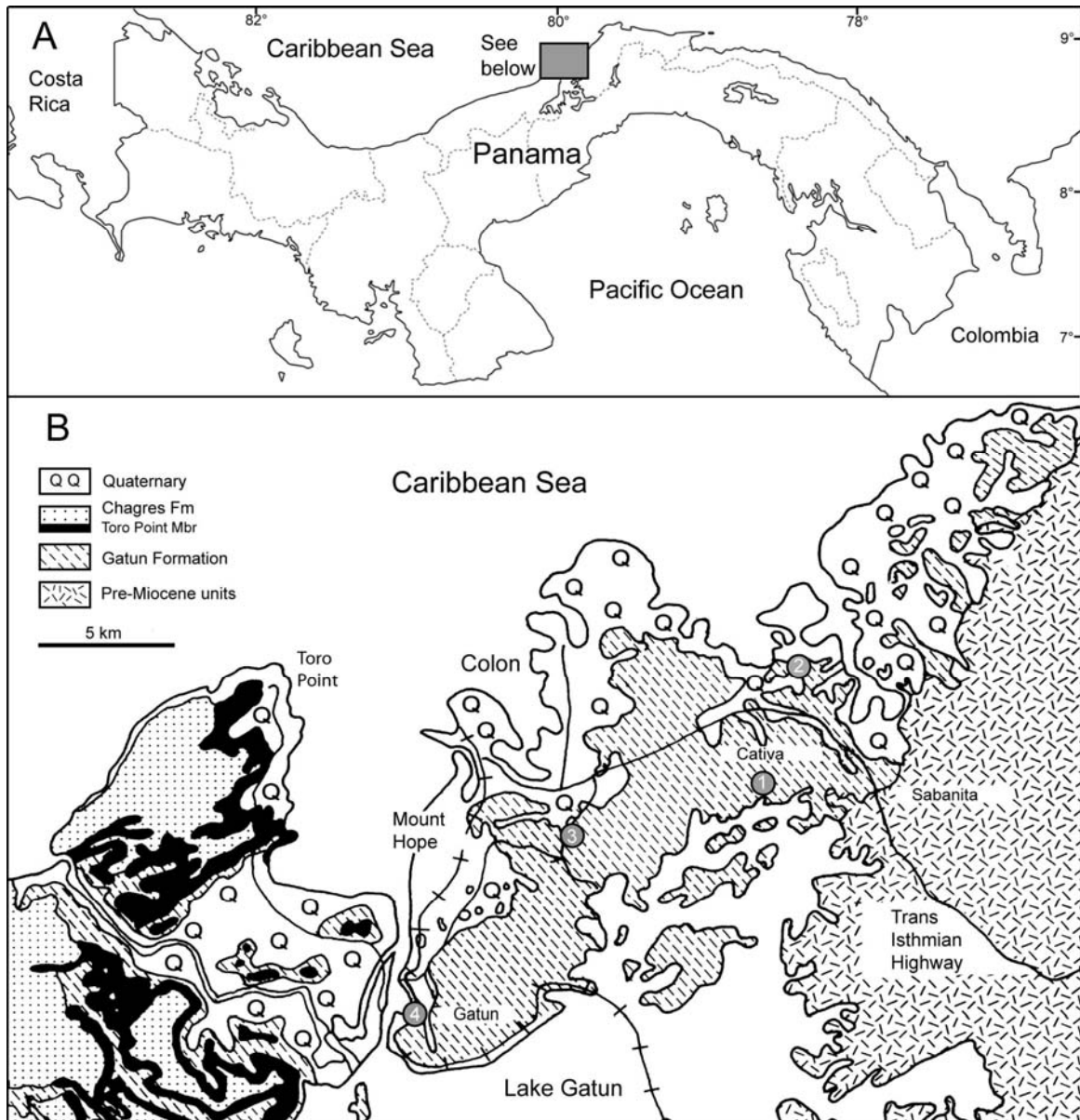


Figure 1-1. Area of study. A. Location of Gatun Formation (shaded box) in northern Panama. B. Expanded geological map (from “See Below” shaded box in Figure A) showing exposures of the Gatun Formation and surrounding rock units (modified from Coates et al., 1992). B. The four fossil localities collected from the Gatun Formation during this study include: (1) Las Lomas, (2) Isla Payardi, (3) Cuatro Altos, and (4) Banco EE.

CHAPTER 2
LATE MIOCENE SHARKS (CHONDRICHTHYES, ELASMOBRANCHII, SELACHII)
FROM THE GATUN FORMATION, PANAMA

Introduction

Shark teeth are the most commonly collected vertebrate fossils found in shallow-water marine sediments worldwide. Of relevance to this report, despite their abundance in space and time, Neogene sharks are poorly known in the literature from the circumtropical oceans of the Neotropics (American tropics). The late Miocene Gatun Formation consists of a series of highly fossiliferous exposures that outcrop in the Isthmus of Panama with a highly diverse fauna, including macro- and micro-invertebrates (Woodring 1957, 1959, 1964; Borne et al. 1996; Collins 1996; Jackson et al. 1996; Hecht, work in progress). Previous studies of different taxa of the Gatun Formation indicate that during the late Miocene, this area was a shallow-water seaway (the Central America Seaway) that supported a neritic environment and connected the Pacific Ocean and the Caribbean Sea (Teranes et al. 1996). Therefore, the Gatun marine faunas existed during a time of active transoceanic interchange and dispersal before the time of the full closure of the Isthmus about 3.5 to 4 million years ago (Coates & Obando 1996; Gussione et al. 2004; Huag et al. 2001). This closure was a key vicariance event for tropical biotic evolution (Cronin & Dowsett 1996) that resulted in increased of habitat and biogeographic complexity (Jackson & Budd 1996).

Blake (1862) reported three fossil shark species from the Miocene deposits at Panama in a very short publication. Since that time, Gillette (1984) has published the only other work on fossil sharks from Panama. Based on the screenwashing of sediments in 1978 and 1979 at the *Sabanitas* (=Las Lomas in this study) locality in the Gatun Formation, he described the marine ichthyofauna, which included 11 shark taxa. In order to further elucidate the shark fossil record

of the Gatun Formation, I reviewed and re-described all relevant fossil shark tooth material known. Additionally, we collected and have identified 247 new specimens to add to the record.

The additional new specimens, which we collected between 2007 to 2009 by surface prospecting, were also compared to the original material collected and described (Gillette 1984) from the Gatun Formation. In doing so we sampled the different tooth size classes that regularly result when using these two different field techniques. Therefore a better census of the ancient selachian biodiversity during the late Miocene of Panama was completed, expanding our knowledge of ichthyofauna of the Gatun Formation.

Over the past 20 years, the Gatun Formation localities have been extensively used to extract sediment for construction. During the past 5 years, these extraction activities have increased substantially. Based on observations made while surface prospecting, I predict that these outcrops will soon likely be excavated completely. The objective of this work is to reconstruct the Gatun Formation shark fauna based on the study of the new fossil material collected, the fossil material from previous work and the information available on extant related species. Using this information I will then evaluate the, ecology, taxonomic longevity, sizes and habitat preferences of the Gatun sharks to better understand the marine faunas of the ancient Neotropics prior to the formation of the Isthmus of Panama during the Pliocene.

Geological, Paleontological, and Paleoecological Context

The fossil shark teeth described in this Chapter were collected from Neogene marine sediments of the Gatun Formation. This formation crops out in a broad area of north-central Panama (Figure 1-1) extending along the northern shore of Lake Gatun ca. 15 km northward to the Caribbean Sea, and east and west of Colon, within the Panama Canal structural basin. In the current study area, the gently dipping (i.e., 5 to 10°) Gatun Formation, overlies either unnamed

Cretaceous volcanics or the upper Oligocene sediments and volcanics of the Caimito Formation depending upon the specific location (Woodring 1957; Coates et al. 1992; Coates 1996a).

The Gatun Formation, with a composite outcrop and subsurface thickness of 500 m, consists of three described members. Of relevance to this research, most of the fossils collected during our study, and likely those of Gillette's (1984) from Sabanitas (= Las Lomas, also see detailed locality information below), occur within the lower member of the stratotype (section 1, Sabanita-Payardi) and referred sections (Coates 1996a, Text-fig. 4; 1996b). The lithology of these sections characteristically consists of massive, gray-green clayey siltstone and interbedded, more indurated concretions. This part of the Gatun Formation is highly fossiliferous, with diverse molluscan (up to 259 genera and 359 species listed for the middle Gatun, Jackson et al., 1996) assemblages that are classically described in the literature (e.g., Woodring 1957, 1959 & 1964). At some localities within the Gatun Formation (e.g., Las Lomas located ~12 km southeast of Colon in Figure 1-1 the highly fossiliferous nature of the sediments exposed along weathered bedding planes results in pavements of macrofossils, i.e., primarily consisting of bivalves and gastropods. Within this taphonomic context, vertebrate macrofossils recovered by surface prospecting consist mostly of shark teeth and ray tooth plates, although osteichthyan (e.g., barracuda *Sphyraena*) teeth and turtle fragments are also common. In addition, screenwashing of the clastic sedimentary matrix yields rich microfossil assemblages, including ostracods (Borne et al. 1996; Hecht, work in progress), benthic foraminifera (Collins 1996), bony fish otoliths (Aguilera & De Aguilera 1996), and many of the smaller shark taxa reported by Gillette (1984).

Multiple lines of biostratigraphic evidence from the rich marine invertebrate fauna indicate that the Gatun Formation is late Miocene in age, with a total range represented by the composite stratigraphic section spanning from about 12 until 8.4 million years ago (Coates 1996a). In terms

of comparisons with other similarly diverse and relatively well-sampled marine faunas in the coastal regions in the western hemisphere, several faunas bracket those of the Gatun Formation: (a) Older, early-middle Miocene assemblages containing sharks include the Pungo River (Ward & Bohaska 2008), Agricola Fauna, Florida (Morgan 1994), Calvert Fauna, Maryland (Tedford et al. 2004); Domo de Zaza, Cuba (MacPhee & Iturralde-Vinent 1994); the Cantaure Formation, Venezuela (Léxico Estratigráfico de Venezuela 1997); the Grand Bay Formation of Carriacou, the Grenadines, Lesser Antilles (Donovan et al. 2003) and the Uscari Formation, Costa Rica (Pizarro 1986); (b) roughly contemporaneous late Miocene assemblages include the Love Bone Bed Local Fauna (L.F.) and McGehee L.F., Florida (Hulbert 2001), St Marys Formation, Maryland, the Canímar Formation, Cuba (Iturralde-Vinent, 1969) and the Rio Banano Formation, Costa Rica (Taylor 1975); and (3) younger, early Pliocene assemblages include the Yorktown, North Carolina (Ward & Bohaska 2008), Bone Valley, Florida (Morgan 1994; Tedford et al. 2004), upper Pisco, Peru (De Muizon & DeVries 1985) and the Cubagua Formation, Venezuela (Léxico Estratigráfico de Venezuela 1997).

With regard to paleoecology and paleogeography of the Gatun Formation, the foraminifera (Collins 1996), ostracodes (Borne et al. 1996), and fish otoliths (Aguilera & De Aguilera 1996) all indicate a shallow-water marine shelf neritic environment with a depth between 20 to 40 m (Teranes et al., 1996). Studies of oxygen isotope ratios preserved in mollusk shells from the Gatun Formation indicate that salinity, annual temperature variations, relative seasonality and productivity were more pronounced during the late Miocene relative to those of today (Teranes et al. 1996). The Gatun Formation and its faunas were located in a productive shallow marine seaway that connected a broad and unified fauna province during the late Miocene, ~10 million years ago. Thus, the Gatun marine faunas existed during a time of active transoceanic

interchange and dispersal (Collins et al. 1996; Newkirk & Martin 2009) within the Central American Gateway (e.g., Gussione et al. 2004) or Central American Seaway (Newkirk & Martin 2009) before the time of the full closure of the Isthmus about 3.5 to 4 million years ago (Coates & Obando 1996; Gussione et al. 2004; Huag et al. 2001). It is well documented in the literature that the closing of the Isthmus resulted in the Great American Interchange on land (Stelhi & Webb 1985), as well as biogeographic separation (vicariance event) of the once continuous marine distribution, resulting in the precursors of the modern-day Caribbean and Pacific marine faunal provinces.

Methodology

Materials

Relevant specimens from the UF and SMU vertebrate paleontology collections were examined during this study. The following codes are used in the text: UF locality YPA017, Las Lomas (9°21'15.66"N, 79°50'11.34"W); YPA020, Banco EE (9°17' 59.11"N, 79°55' 5.36"W); YPA021, Isla Payardi (9°22'57.18"N, 79°49'16.50"W); YPA022, Cuatro Altos (9°20'7.08"N, 79°52'58.80"W).

The UF material was collected by surface prospecting from the late Miocene Gatun Formation, Panama, between August 2007 and March 2009 from four different localities (Figure 1-1) by the Panama Canal Project Field Team of the Center of Tropical Paleobiology and Archaeology of STRI, as well as by UF scientists. In total, 247 isolated shark teeth were collected by UF-STRI Panama Canal Project Field Team and are designated with a UF catalogue number, with each number corresponding to one specimen, which are also available in our online data base [<http://www.flmnh.ufl.edu/databases/VP/intro.htm>].

The material borrowed from the SMU Vertebrate Paleontology collection was recovered in 1978 and 1979 in an exposure that measured ~200 x 400 m from a single locality (equivalent to

Las Lomas (YPA017)) also called “Sabanitas.” This collection method consisted of screenwashing ~900 kg of sediment using traditional wet-sieving methods (for more detailed information see Gillette, 1984). A total of 157 isolated shark teeth were borrowed and studied from SMU, every tooth is designated with a SMU catalogue number, however, several teeth have been designated to the same number, i.e., they were catalogued as lots.

Given the fact that surface prospecting was done by the research team, and also that the SMU specimens that were collected by screenwashing (Gillette 1984) were studied, the different size classes that regularly result from these two different field techniques have been sampled and therefore better census ancient selachian biodiversity during the late Miocene of Panama was constructed.

Updated distribution and age range data for each extinct taxa were taken among other scientific references, from the Paleobiology Database [www.paleodb.org], as listed in the Systematic Paleontology section below. Likewise, distributional data from extant selachians were taken from Compagno, 1984 and FishBase [<http://www.fishbase.org>].

Thus, a total of 387 isolated teeth from both UF and SMU collections from the Gatun Formation were identified and studied. Specimens were first identified using comparative collections available at UF. Our identifications were then verified with the collaboration of Dr. Gordon Hubbell in his private collection in Gainesville, Florida. Tooth terminology follows the work of Shimada (2002). Appendix A describes the relevant diagnostic characters used to identify the material as well as the measurement dimensions. Tooth measurements (in millimeters) can be seen in Table 2-1. These measurements were compared with previous works on the Neogene sharks of the Pungo River Formation (middle Miocene) and the Yorktown Formation (early Pliocene) at Lee Creek Mine, North Carolina (Purdy et al., 2001), which are

respectively younger and older than Gatun. Common names were taken from Cocke (2002) for extinct species and Compagno (1984) for extant species so this study can also be useful for fossil collectors.

Sampling Strategy

Fossil shark teeth are oftentimes collected casually and as such do not represent a systematic sampling that is necessary to understand and reconstruct, to the best of our ability, the ancient taxonomic biodiversity represented in the fossil record. The goal of this study is to assess ancient selachian biodiversity as fully as possible.

In doing so, a total of 387 isolated shark teeth were collected and identified from the late Miocene Gatun Formation in Panama. Of the 159 teeth recovered from Gillette's (1984) work (screenwashing, 1 locality), I identified 8 shark taxa. In addition, from the 230 teeth collected by our team (surface prospecting, 4 localities) I identified 13 shark taxa (Table 2-1) for a total of 16. Both methods proved useful in find certain taxa (Figure 2-1). Small teeth such as those from *Rhizoprionodon* sp. and *Sphyrna lewini* were only found when screenwashing. Taxa with a broad tooth size range such as *Sphyrna* sp, *Carcharhinus* sp. and *Negaprion brevirostris*, were found with both screenwashing and surface prospecting techniques. The remaining taxa (the largest teeth) were found only when surface prospecting.

Comparisons with the SMU collections were important for the identification of 3 taxa. In contrast, by surface prospecting I was able to identify approximately 80% of the total selachian fauna. By combining these two methodologies, I am reducing the collecting bias. On the other hand, since shark teeth do not distribute uniformly in the sediment (as opposed to rays) (O. Aguilera, Pers. Comm., 2009), I highly recommend surface prospecting rather than screenwashing when collecting shark teeth.

Systematic Paleontology

Class CHONDRICHTHYES Huxley 1880

Subclass ELASMOBRANCHII Bonaparte 1838

Order ORECTOLOBIFORMES Applegate 1974

Family ORECTOLOBIDAE Jordan & Fowler 1903

Genus GINGLYMOSTOMA Müller & Henle 1838

†GINGLYMOSTOMA DELFORTRIEI Daimeries 1889

Common name: Extinct nurse shark

Referred specimens: Three isolated teeth; indeterminate position: SMU 76460 and SMU 76470. Described in Gillette (1984).

Specific locality: YPA017.

Distribution: Miocene, from Costa Rica and Florida; early Miocene of Venezuela and Guinea; and middle Miocene of France and Portugal, late Miocene of Panama (Cappetta 1987; Gillette 1984; Laurito 1999; Aguilera & De Aguilera 2001; Hulbert et al. 2001).

Description: The only unbroken *G. delfortriei* tooth from the Gatun Formation measures 5.0 mm in CH and 8.4 mm in W (Figure 2-2). For a detailed description see Gillette, 1984.

Discussion: The dentition of *G. delfortriei* is adapted for clutching, which is useful for feeding on fish, mollusks, corals, sea urchins and tunicates (Kent 1994). Extant species of the genus *Ginglymostoma* are reef associated, near-shore, bottom dwelling sharks that inhabit temperate and tropical waters at a depth range of 0 - 130 m. They also nurse in estuarine or near-shore shallow environments (McCandless et al. 2007).

Order LAMNIFORMES Berg 1958

Family OTODONTIDAE Glückman 1964

Genus †CARCHAROCLES Jordan & Hannibal 1923

†CARCHAROCLES MEGALODON Agassiz 1843

Procarcharodon megalodon megalodon (Gillette 1984:176)

Carcharodon megalodon (Blake, 1862:316)

Carcharodon megalodon (Aguilera & De Aguilera, 2004:370)

Common name: Megalodon

Referred specimens: 16 isolated teeth; upper anteriors: UF 237898, UF 237949, UF 237955 – 237955 and UF 242804; lower anteriors: UF 237950 and UF 237959; upper laterals: UF 237914, UF 237951 – 237952 and UF 242802 – 242803; lower lateral: UF 237953; upper posterior: UF 237957; lower posterior: 237956; indeterminant position: UF 242801.

Specific localities: YPA017 and YPA021.

Distribution: Cosmopolitan, ranges from the Miocene to the Pliocene, including the Miocene of Japan, USA (Florida, Maryland, New Jersey, California, Virginia, North and South Carolina), Madagascar, Australia (Victoria), India, Slovakia, Austria, Italy, Portugal (Lisbon Province), France (Aquitaine Region), South Africa (KwaZulu-Natal), Mexico (Baja California), Chile, Panama, Venezuela, Peru, Ecuador, Costa Rica, Cuba, Puerto Rico, The Grenadines and Jamaica. Pliocene of Australia (Victoria), USA (Florida and North Carolina), and New Zealand (Hawera) (Blake 1862; Longbottom 1979; Gillette 1984; De Muizon and DeVries 1985; Long 1993; Iturralde-Vinent 1996; Laurito 1999; Aguilera and De Aguilera 2001; Donovan and Gunter 2001; Hulbert et al. 2001; Nieves-Rivera 2003; Portell et al. 2008; www.paleodb.org, 26 March 2009, using the name *Carcharodon megalodon*).

Description: The diagnostic characters of *C. megalodon* teeth include large size, triangular shape, broad serrated crown, lingual face convex, labial face flat, large neck, robust, thick, angled or U-shaped root with dispersed foramina. Juvenile teeth of *C. megalodon* can present

cusplets (Ward & Bonavia 2001). *C. megalodon* differs from *C. carcharias* by lacking a labiolingually flattened crown (Purdy et al. 2001), having larger roots and finer, more regular and lobed serrations (Nyberg et al. 2006) and the presence of a neck. The *C. megalodon* teeth from the Gatun Formation range in size from 16.0 to 54.2 mm in CH and from 16.1 to 47.7 mm in W. Anterior teeth are symmetrical (Figure 2-3A and C), whereas the laterals are distally inclined (Figure 2-3B), UF 237914 also presents lateral cusplets indicating a juvenile stage.

Discussion: *C. megalodon* is the largest macropredatory shark to have ever lived and is among the largest known fishes. Teeth from *C. megalodon* can reach 168 mm in CH and TL is estimated to have been over 15 m (Gottfried 1996). The teeth from the early Pliocene Yorktown Formation at Lee Creek Mine range in size from 60.0 to 150.0 mm in CH (Purdy et al. 2001). *C. megalodon* has a wide occurrence in tropical to temperate latitudes of the ancient oceans, with an apparent preference for coastal habitats (Gottfried et al. 1996).

Purdy (1996) proposed nursery areas for *Carcharocles* based on the abundance of juvenile teeth accompanied by primitive odontocete and small mysticete skulls in Chandler Bridge Formation of South Carolina. Based on the extant white shark and fossil evidence, Purdy (1996) also inferred that they used warm-water areas for nurseries. The relatively small size of *C. megalodon* teeth from the Gatun Formation (Figure 2-3) compared with other localities is notable; Blake (1862) also noticed this in his publication and will be the topic of another study (Pimiento et al., in progress).

Order CARCHARHINIFORMES Compagno 1977

Family HEMIGALEIDAE Compagno 1984

Genus HEMIPRISTIS Agassiz 1843

†HEMIPRISTIS SERRA Agassiz 1843

Common name: Snaggletooth shark

Referred specimens: 54 isolated teeth; uppers: UF 237919 - 237948, UF 241803 - 241808, UF 241835 and UF 242810 - 242817; lowers: UF 241801-241802, UF 242805 -242809 and SMU 76467.

Specific localities: YPA017, YPA020 and YPA022.

Distribution: Miocene to Pliocene. Miocene of USA (South Carolina, New Jersey, Virginia and Maryland), Italy, Germany, Fiji, Saudi Arabia, India, Pakistan, Madagascar, Australia, Java, Zaire, Japan, Venezuela, Cuba, Peru (Ica), Costa Rica, Panama, The Grenadines, Mexico (Baja California and Yucatan), Argentina (Entre Rios), Saudi Arabia, India, Pakistan, Madagascar, Australia, Java, Zaire and Japan. Pliocene of USA (Florida and North Carolina), Angola and Zanzibar (Cappetta 1987; Iturralde-Vinent et al. 1996; Laurito 1999; Purdy et al. 2001; MacPhee et al. 2003; Aguilera & De Aguilera 2001, 2004; Portell et al. 2008; www.paleodb.org, 6 April 2009, using the name *H. serra*).

Description: Teeth of *H. serra* from the Gatun Formation demonstrate diagnostic characters of the species such as dignathic heterodonty (Figure 2-4).

Upper Teeth: Crown curved distally, oblique coarse serrations, serrations do not continue to the apex, mesial cutting edge rectilinear at its base, distal cutting edge concave and with fewer serrations; root high and compressed with a lingual protuberance forming a Z-shape. Teeth are generally broader than the corresponding lowers (Figure 2-4A and B).

Lower Teeth: Long pointed crown, lingually slanted or inclined, labial face convex, no serrations on the crown, small serrations or cusplets near the base, bilobated root with a lingual protuberance (Figure 2-4C and D)

Upper teeth of *H. serra* differ from *Carcharhinus* by having a distinctively smooth apex and oblique serrations; lower teeth differ from the genus *Carcharias* by having incomplete cutting edges on both mesial and distal side margins that are limited to approximately the apical third of the crown (Kent 1994).

The dentition of *H. serra* differs from adult females of the extant species, *H. elongatus*, by having more straight crowns in their upper teeth (Purdy et al., 2001). This species is very common from the Gatun Formation selachian fauna and vary greatly in size, from 5.4 to 21.6 mm in CH and 5.2 to 29.0 mm in W (Figure 2-4).

Discussion: The large size of *H. serra* teeth (up to 45.0 mm) suggests that this species reached total lengths much greater than the living *H. elongatus*, perhaps up to 6 m (Kent 1994). Based on its large upper teeth (presumably analogous to those of the tiger shark, *Galeocerdo cuvier*), *H. serra* was able to catch large prey (Kent 1994). *H. serra* seems to increase in size through its evolutionary history (Purdy et al. 2001). Adult teeth of *H. serra* teeth from Pungo River Formation range between 14.1 and 29.1 mm in CH and from 12.3 to 35.5 mm in W (Purdy et al. 2001) as opposed to the teeth from the Gatun Formation which are much smaller.

With regard to the ecology of *H. serra*, it is particularly abundant in neritic deposits containing warm-water faunas and scarce in deposits with cold-adapted species (Cappetta 1987). The extant *H. elongatus* is a tropical coastal shark that inhabits in-shore and off-shore waters from 1 to 30 m depth (Compagno 1984).

Family CARCHARHINIDAE Jordan & Evermann 1896

Genus GALEOCERDO Müller & Henle 1837

GALEOCERDO CUVIER Peron & Lesueur 1822

Common name: Tiger shark

Referred Specimens: 18 isolated teeth; indeterminate position: UF 237901 – 237907, UF 241809 – 241812, UF 242818 – 242822, SMU 76456 and SMU 76466.

Specific Locality: YPA017.

Distribution: Miocene to recent. Miocene of USA (North Carolina and Florida), Brazil, Venezuela and Panama (this study). Pliocene of Italy, South Africa, and USA (North Carolina and Florida). Pleistocene of Celebes and Pleistocene of USA (Georgia). Extant *G. cuvier* has a cosmopolitan distribution (Compagno 1984; Cappetta 1987; Purdy et al. 2001; Aguilera & De Aguilera, 2001 2004; Dos Reis 2005; www.paleodb.org, 31 March 2009, using the name *G. cuvier*).

Description: The diagnostic characters of *G. cuvier* teeth include large and robust size and crown or apex slightly slanted; mesial edge rounded, with serrations at the base of crown, which is basally and apically straight, forming an obtuse angle; distal edge has a pronounced notch, coarser serrations on the heel and base; V-shaped root, no central foramen (Figure 2-5).

G. cuvier teeth are similar to those from *Physogaleus aduncus*, but have a broader and larger crown and a more strongly convex mesial cutting edge. *G. cuvier* teeth differ from *Physogaleus contortus* by the absence of very pronounced transverse groove and a thicker crown. *G. cuvier* teeth from the Gatun Formation measure 7.4 to 17.8 mm in CH and from 14.4 to 24.5 mm in W. A transverse groove is present in some, but not all teeth.

Discussion: Extant *Galeocerdo cuvier* can reach lengths up to 7.5 m TL (Compagno 1984). Based on fossil material, *G. cuvier* probably grew to less than half this length in the past (Kent 1994). The teeth collected in the Yorktown Formation, at Lee Creek Mine, North Carolina range from 13.5 to 29.1 mm in CH and 24.4 to 33.0 mm in W (Purdy et al. 2001), which are larger than those found in the Gatun Formation.

Regarding its ecology, *G. cuvier* is an opportunistic feeder; it eats a wide variety of marine life as well as taking carrion and a variety of inedible objects (Compagno 1984). Prey items vary from fish, marine reptiles, sea birds, marine mammals, and mollusks (Compagno 1988). Morphological features of its teeth, including its coarse serrations, are likely adaptations for slicing and ripping (Frazzetta 1988).

G. cuvier is a coastal-pelagic tropical and warm-temperature shark (Compagno 1988), with tolerance for different marine habitats at depths from 0 to 140 m (Compagno 1984). It is very common in shallow waters during the night (Randall, 1992). Extant *G. cuvier* use shallow near-shore and offshore and estuarine waters as nursery areas (McCandless et al. 2007).

Genus PHYSOGALEUS Cappetta 1980

PHYSOGALEUS CONTORTUS Gibbes 1849

Galeocerdo contortus (Gillette, 1984:177.)

Galeocerdo contortus (Purdy et al. 2001:146)

Common Name: Longtooth tiger shark

Referred Specimen: One isolated tooth; indeterminate position: UF 237908.

Specific Locality: YPA017.

Distribution: Early to middle Miocene of USA (North Carolina, Maryland, Florida and Virginia), Italy (Marsili, 2007) and Panama (Cappetta, 1987; Gillette, 1984; Hulbert et al., 2001; www.paleodb.org, 6 April 2009, using the name *G. contortus*).

Description: Teeth are very similar to the genus *Galeocerdo* with finely serrated, long, thick and warped crowns, pronounced notch and small serrations on heel of distal side; undulating margin and fine serrations on mesial edge; U-shaped root with prominent protuberance on lingual face and transverse groove (Figure 2-6).

P. contortus differs from the genus *Galeocerdo* by having a very prominent and bulging root with the deep notch. From lateral view the expansion is much more erect in *P. contortus* teeth than *Galeocerdo* teeth (Leder 2005). *P. contortus* differs from *P. aduncus* in having a narrower, more apically erect and slightly twisted cusp and finer distal serrations; a very large lingual protuberance and a flat basal surface on the tooth (Ward & Bonavia 2001). The *P. contortus* tooth from the Gatun Formation is 11.1 mm in CH and 15.5 mm in W.

Discussion.— *P. contortus* from Pungo River at Lee Creek Mine, North Carolina, range from 12 to 19 mm in CH. This species always occurs with *Galeocerdo* in Neogene localities along the east coast of the United States. Counts of specimens collected in Lee Creek Mine indicate that it is twice as common as *Galeocerdo* (Purdy et al. 2001). This is very different from the Gatun Formation where only one specimen has been identified. The occurrence of this species within the Gatun Formation extends its temporal range into the late Miocene.

Purdy et al. (2001) compared the dentition of both *P. contortus* and *Galeocerdo* sp. and concluded that both species inhabited the same environments but did not compete for the same food resources. Both probably fed on a variety of bony fishes and rays, similar to lemon sharks (*Negaprion*), while the *Galeocerdo* fed on larger animals.

Genus CARCHARHINUS Blainville 1816

CARCHARHINUS SP.

Referred Specimens: 160 isolated teeth; uppers: UF 237990 – 237999, UF 238001 – 238018, UF 238020 – 238025, UF 238032, UF 241823 – 241825, UF 241827, UF 242825 – 242826, UF 242829, UF 242832, UF 242871; lowers: UF 241828, UF 241831 – 241832, UF 242823 – 242824, UF 242827 – 242828, UF 242830 – 242831, UF 242833, UF 242836, UF 242871, UF 237992, UF 237995, UF 237998 – UF 237999; lateral: SMU 76475; indeterminate

position: UF 238019, UF 241826, SMU 76457 - 76459, SMU 76463, SMU 76465, SMU 76469 and SMU 76472 – 76475

Specific Localities: YPA017, YPA020, YPA021 and YPA022.

Distribution: The range of this genus extends from the early Eocene to Recent. Eocene of Pakistan, USA (Texas) and Egypt. Oligocene of USA (Florida) and Australia (Victoria). Miocene of Colombia (Pimiento, personal observation) Europe, North and West Africa, USA (California, Virginia, Maryland and Florida), Australia (Victoria), Japan (Shimane Prefecture), Panama, Mexico (Baja California), Argentina (Entre Rios), Peru (Ica), Venezuela (Falcon) and India (Gujarat). Pliocene of Australia (Tasmania), Peru, Brazil, Pleistocene of USA (Florida, California, and Georgia) Recent in all tropical and temperate seas (Cappetta 1987; www.paleodb.org, 1 April 2009, using the name *Carcharhinus* sp.).

Description: Diagnostic characters of upper teeth of the genus *Carcharhinus* include triangular shape, straight crown in anterior teeth and curved in laterals, flat labial face, slightly convex lingual face, serrated cutting edges, cusps separated or not from heels; root can present a clear transverse groove in small forms (Figure 2-7A and B). Lower teeth have narrower cusps, crown well separated from heel, cutting edges serrated, with a clear transverse groove (Figure 2-7C).

Lower teeth of the genus *Carcharhinus* differ from *Negaprion* by having serrated cutting edges, *Carcharhinus* teeth differ from *Sphyrna* by having a thinner root and the lack of an expanded lingual heel. *Carcharhinus* differs from *Galeocerdo* by the absence of a strongly contorted crown, the lack of a large difference between mesial and distal cutting edge thickness and lengths, the absence of coarse serration in heels, and a thinner and non-bulged root. This

genus is abundant in the Gatun Formation with teeth ranging greatly in sizes, from 1.9 to 12.9 mm in CH and 4.1 to 17.6 mm in W (Figure 2-7).

Discussion.— Most species of *Carcharhinus* have teeth adapted for cutting and grasping (Kent 1994). Much taxonomic confusion exists within this genus (Purdy et al., 2001). The identification of individual *Carcharhinus* species based solely on isolated teeth is extremely difficult given the degree of convergence in tooth morphology. This problem is particularly acute in lower teeth, which are very similar among most species (Kent 1994). Factors influencing variation in tooth shape within the genus *Carcharhinus* include: variation among species, variation within a species, differences within individuals of a species (Naylor & Marcus 1994) and within a tooth row. Upper teeth have been documented up to 20 mm in CH (Cappetta 1987).

CARCHARHINUS FALCIFORMIS Bibron 1841 (in Muller & Henle 1839-1841)

Common name: Silky shark

Referred Specimens: One isolated upper tooth: UF 241817.

Specific Locality: YPA017.

Distribution: Middle Miocene to Recent. Middle Miocene of USA (North Carolina). Miocene of Costa Rica and Panama (this study). Extant *C. falciformis* has a circumtropical distribution (Compagno 1984; Laurito 1999; Purdy et al. 2001; www.paleodb.org, 2 April 2009, using the name *C. falciformis*).

Description: UF 241817 displays diagnostic characters including triangular, narrow cusp, distal edge with angular notch perpendicular to the base with fine serrations; mesial edge is straight with a gap lacking serrations at mid point, coarser serrations at the base, finer serrations at the apex, and root with well developed transverse groove (Figure 2-8).

C. falciformis differs from other species of *Carcharhinus* by having a gap lacking serrations at the mid point of the mesial cutting edge. The *C. falciformis* specimen from the Gatun Formation is 7.2 mm in CH and ~6.4 mm in W. Even when this specimen has the edges a bit broken, it is possible to distinguish a serrations gap (Figure 2-8) at the base of mesial side confirming the identification of this tooth as *C. falciformis*.

Discussion: Purdy (2001) reported this species from the middle Miocene Pungo River Formation at Lee Creek Mine, North Carolina. The only tooth described measured 14.2 mm in CH and 15.0 mm in W, which is twice as large as the Gatun specimen. Teeth in extant individuals vary in morphology, with some individuals not exhibiting the mid point gap discussed above (Figure 2-8) (Purdy et al. 2001).

Regarding the ecology of extant *C. falciformis*, it is a large epipelagic shark that inhabits near shore, warm-shallow waters, from 18 to 500 m depth (Compagno 1984; Purdy et al. 2001). Females use shallow coastal waters as nursery areas (Alejo-Plata 2007). This species feeds mostly on bony fishes (Compagno 1984).

CARCHARHINUS LEUCAS Valenciennes 1839 (in Muller & Henle 1839-1841)

Common name: Bull shark

Referred Specimens: 25 isolated teeth; uppers: UF 237979 – 237989, UF 237981, UF 237983 – 237989, UF 241829 – 241830 and UF 242838; lowers: UF 237980, UF 237982 and UF 237984.

Specific Localities: YPA017 and YPA022.

Distribution: Middle Miocene to Recent. Middle Miocene of USA (North Carolina and Florida). Late Miocene of Panama (this study). Pliocene of USA (Florida and North Carolina). Pleistocene of USA (Florida and Georgia). Extant *C. leucas* with a circumtropical distribution

(Compagno, 1984; Hulbert et al., 2001; www.paleodb.org, 2 April 2009, using the name *C. leucas*).

Description: *C. leucas* teeth exhibit diagnostic characters including triangular, finely serrated crowns, serrations that become progressively coarser near the base of crown, mesial edge straight or slightly convex with a shallow or absent notch; distal edge more concave with a shallow notch, U-shaped root (Figure 2-9).

C. leucas differs from other *Carcharhinus* species in having a more equilateral crown shape. *C. leucas* differs from *C. longimanus* by having a less elongated and thinner crown in the upper teeth and by having more symmetrical lower teeth. Some teeth have a well developed transverse groove. Lower teeth have thick crowns and cutting edges are finely serrated (Purdy et al. 2001). *C. leucas* from the Gatun Formation measure 7.5 to 10.7 mm in CH and 13.6 to 14.2 mm in W.

Discussion: *C. leucas* from Pungo River Formation at Lee Creek Mine, North Carolina ranges from 17.0 to 20.0 mm in CH and 16.0 to 22.0 mm in W. These probably belong to individuals that were 2 to 3 m TL (Purdy et al., 2001), which are larger than individuals from the Gatun Formation.

The extant *C. leucas* is a large epipelagic shark that is widespread in warm oceans, and also rivers and lakes (Compagno 1988). It inhabits shallow (> 30 m depth) tropical and subtropical waters and feeds on bony fishes (Compagno 1984). *C. leucas* use shallow, low salinity, freshwater environments and estuaries as nursery areas (Steiner et al. 2007).

CARCHARHINUS OBSCURUS Lesueur 1818

Common name: Dusky shark

Referred Specimens: Seven isolated teeth; uppers: UF 237915, UF 237917– 237918 and UF 241818; lowers: UF 237916 and UF 242839.

Specific Locality: YPA017.

Distribution: Early Miocene to Recent. Early Miocene of Venezuela, the Grenadines and Cuba. Middle Miocene of USA (Florida). Late Miocene of Panama (this study). Early Pliocene of USA (North Carolina). Late Pleistocene of USA (Florida and Georgia). Extant *C. obscurus* is distributed in the Western and Eastern Atlantic Ocean, the Mediterranean, Indo-West Pacific Eastern Pacific: southern California, USA to Gulf of California (Hulbert et al. 2001; MacPhee et al. 2003; Portell et al. 2008; www.paleodb.org, 2 April 2009; www.fishbase.org, 3 of April 2009, using the name *C. obscurus*).

Description: *C. obscurus* teeth exhibit diagnostic characters including upper teeth with basal crown serrations coarser than the apex, nearly vertical distal cutting edge, distal edge concave with convex apex and inclined distally (Figure 2-10). Lower teeth with erect crowns and straight or moderately arched root lobes.

C. obscurus differs from other species of *Carcharhinus* by having coarser serrations at the base of the crown. *C. obscurus* have a thick root with a transverse groove and a broad crown. The lingual surface is flat whereas the labial surface is convex and they do not have cusplets. *C. obscurus* from the Gatun Formation measure from 7.7 to 10.1 mm in CH and from 11.2 to 16.28 mm in W.

Discussion: *C. obscurus* from Yorktown Formation at Lee Creek Mine, North Carolina measure 17 to 22 mm in CH and from 18 to 25 mm in W. In extant individuals, sharks with corresponding tooth sizes are ~3 m TL (Purdy et al. 2001), suggesting that *C. obscurus* from the Gatun Formation were smaller in size.

Regarding the ecology of this species, *C. obscurus* is common in coastal and pelagic, inshore and offshore, warm - temperate and tropical shark of the continental and insular shelves and oceanic waters of 0 - 400 m of depth and feeds on bony fishes, other sharks, and invertebrates (Compagno 1984). Nursery areas are in shallow near-shore environments and occasionally estuaries (McCandless et al. 2007).

CARCHARHINUS PEREZI Poey 1876

Common name: Caribbean reef shark

Referred Specimens: 24 isolated teeth; uppers: UF 241819- 241820, UF 241822, UF 242840 – 242842, UF 242844 – 242846, UF 242848 – 242853, UF 242855 - 242857; lowers: UF 242845- 242846; indeterminate position: UF 241821, UF 241843, UF 241847 and UF 241854.

Specific Localities: YPA017, and YPA022.

Distribution: Early Miocene to Recent. Miocene of Brazil and the Grenadines. Early Miocene of Venezuela. Middle Miocene and USA (North Carolina). Late Miocene of Panama (this study). Early Pliocene of USA (North Carolina). Its extant distribution is restricted to the Caribbean (Compagno 1984; Dos Reis, 2005; Portell et al. 2008; www.paleodb.org, 2 April 2009, using the name *C. perezii*).

Description: *C. perezii* teeth demonstrate diagnostic characters that include high, narrow crown; distal edge inclined, well developed angular or rounded notch; mesial edge straight or slightly convex, medium to coarse serrations (Figure 2-11). Lower teeth with straight crowns, finely serrated cutting edges and nearly straight root edges.

C. perezii differs from other *Carcharhinus* species by having a coarsely serrated crown, an inclined distal side, and a straight mesial side. *C. perezii* have straight or oblique crowns, no cusplets, transverse groove weakly present. Some lateral teeth are slightly straight making them

difficult to differentiate from lower teeth. *C. perezii* from the Gatun Formation range between 5.8 to 10.8 mm in CH and from 10.6 to 16.9 mm in W.

Discussion: *C. perezii* from Lee Creek Mine, North Carolina measure 13.0 to 18.0 mm in CH and from 13.0 to 22.0 mm in W, which corresponds to sharks of 2 m TL (Purdy et al. 2001). This difference suggests that *C. perezii* from the Gatun Formation were represented by smaller individuals.

Regarding the ecology of this species, extant *C. perezii* feeds on bony fishes (Purdy et al. 2001). They are reported from tropical waters found inshore of continental and insular shelves down to at least 30 m depth (Compagno 1984). *C. perezii* uses insular shallow reef systems as nursery areas (Garla et al. 2006).

CARCHARHINUS PLUMBEUS Nardo 1827

Common name: Sandbar shark

Referred Specimens: Five isolated teeth; uppers: UF 242858 - 242862

Specific Locality: YPA017.

Distribution: Early Miocene to Recent. Early Miocene of Saudi Arabia. Middle Miocene of USA (North Carolina and Florida). Late Miocene of Panama (this study). Early Pliocene of USA (North Carolina). Early Pleistocene of USA (Florida). Extant *C. plumbeus* has a circumtropical distribution (Compagno 1984; Hulbert et al. 2001; www.paleodb.org, 3 April 2009, using the name *C. plumbeus*).

Description: *C. plumbeus* teeth exhibit diagnostic characters including: broad narrow crown, apically convex, fine to moderate serrations on edges, distal edge inclined with a well developed angular or rounded notch; mesial edge straight or slightly convex and thick root (Figure 2-12).

C. plumbeus teeth are very similar to those from *C. obscurus*, but differ in having apical convexity in cutting edges (Purdy et al. 2001). *C. plumbeus* differs from *C. albimarginatus* by the absence of a hook at the apex (Purdy et al. 2001). *C. plumbeus* differs from *C. perezii* by having finer serrations and apical convexity.

C. plumbeus may present a well developed transverse groove or a central foramen and a U-shaped root. Specimens from the Gatun Formation measure 6.8 and 10.6 mm in CH and 10.3 and 6.1 mm in W respectively.

Discussion: *C. plumbeus* teeth from the Lee Creek Mine, North Carolina measure 14.0 to 19.0 mm in CH. Teeth of this size correspond to sharks of 2 m TL (Purdy et al. 2001). This suggests that *C. plumbeus* from the Gatun Formation were represented by smaller individuals.

Regarding the ecology of this species, extant *C. plumbeus* individuals are coastal-pelagic sharks of warm temperate and tropical waters, found in insular and continental shelves and deep waters adjacent to them; and range from intertidal waters to 280 m in depth (Compagno 1984). *C. plumbeus* use estuarine or near-shore shallow warm waters for nurseries (McCandless et al. 2007).

Genus NEGAPRION Whitley 1940

NEGAPRION BREVIROSTRIS Poey 1868

Negaprion eurybathrodon (Aguilera & De Aguilera, 2004:735)

Common name: Lemon shark

Referred specimens: 63 isolated teeth; indeterminate position: UF 237961 – 237978, UF 241813 – 241816, UF 241833- 241834, UF 242863- 242867, SMU 76455, SMU 76458 – 76459, SMU 76465, SMU 76469 and SMU 76474 – 76475.

Specific localities: YPA017, and YPA020.

Distribution: Eocene to Recent. Eocene of Pakistan and USA (Georgia). Miocene of Cuba, Italy, Saudi Arabia and USA (North Carolina and Florida), Nigeria, France, Portugal Venezuela, Ecuador and Panama (this study). Pliocene of USA (North Carolina, Georgia and Florida). Extant *N. brevirostris* is distributed in the Atlantic, including the Gulf of Mexico and the Caribbean, and Eastern Pacific (Longbottom 1979; Cappetta 1987; Aguilera & De Aguilera 2001 and 2004; www.paleodb.org, 3 April 2009, using the names *N. brevirostris* and *N. eurybathrodon*; www.fishbase.org, 5 April 2009, using the name *N. brevirostris*).

Description: Teeth of *N. brevirostris* from the Gatun Formation demonstrate diagnostic characters including: a T-shaped, narrow crown perpendicular to the root, crown not serrated, flat roots and transverse groove present. Moderate ontogenetic heterodonty is observed in this species with smaller specimens lacking serrations on heels (Figure 2-13) while larger individuals exhibit them (Compagno 1984; Purdy 2001).

Lower teeth of *N. brevirostris* differ from *Carcharhinus* by not having serrations on the crown. *N. brevirostris* can also demonstrate a slightly curved, inclined crown, elongated root lobes, strongly obtuse basal root angle, lingual face flat and labial face slightly convex. *N. brevirostris* from the Gatun Formation measure 3.7 to 13.7 mm in CH and from 4.3 to 16.3 mm in W.

Discussion: Cappetta (1987) established the maximum crown height of for *Negaprion* to be 20 mm. Purdy (2001) reported teeth in Lee Creek Mine, North Carolina measuring from 14 to 21 mm in CH and stated that in extant *N. brevirostris* teeth of this size are found in sharks 2.1 to 3 m TL, which is the size range for mature adults according to Compagno (1984). This suggests that sharks from the Gatun Formation were juveniles. In addition the lack of serrations on the heels of some specimens corroborates this hypothesis.

Regarding the ecology of this species, *N. brevirostris* inhabits inshore tropical and temperate estuarine and marine waters (Kent 1994). It occurs in intertidal zone down to at least 92 m depth. Prey items include bony fishes, stingrays, sea birds and invertebrates (Compagno 1984). This is a reef-associated species that occurs on continental and insular shelves. *N. brevirostris* uses estuarine or near-shore, shallow, warm waters such as swamps or mangroves for nursery areas (McCandless et al. 2007).

Genus RHIZOPRIONODON Whitley 1929

Isistius sp. (Gillette, 1984:179)

Common name: Sharpnose shark

Referred specimens: Three isolated teeth; indeterminate position: SMU 76461, SMU 76464 and SMU 76475.

Specific Locality: YPA017.

Distribution: The range of this genus goes from the Eocene to Recent. Eocene of Pakistan, Egypt, Jordan and USA (Alabama, Georgia). Oligocene of USA (Florida). Miocene of USA (North Carolina), Venezuela and Costa Rica. Pliocene of USA (Florida). Recent species' distributions in western Atlantic (including the Caribbean), eastern Atlantic and eastern Pacific (Compagno 1984; Laurito 1999; Hulbert et al. 2001; Aguilera & De Aguilera 2004; www.paleodb.org, 6 of April 2009, using the name *Rhizoprionodon* sp.).

Description: *Rhizoprionodon* sp. teeth display diagnostic characters including: a slightly recurved crown, cutting edges finely serrated or smooth, mesial edge curved, distal heel with a notable notch, roots straight, low with a deep, transverse groove present (Figure 2-14).

Rhizoprionodon sp. differs from *Sphyrna* by having a notch in distal heel and shorter crown. *Rhizoprionodon* sp. from the Gatun Formation measures between 2.5 and 3.3 mm in CH and 3.9 and 5.6 mm in W.

Discussion: Cappetta (1987) stated that teeth from *Rhizoprionodon* are less than 4 mm in CH. Although, teeth from Lee Creek Mine measured 3.2 to 5.2 mm in CH and from 4.3 to 5.7 mm in W (Purdy et al. 2001). Total length in extant adult individuals averages about 1 m TL (Compagno 1984). This genus shows marked sexual dimorphism in body size, even though tooth morphology is not affected (Cappetta 1987). Species of this genus are mainly distributed in the Atlantic Ocean (together with the Caribbean Sea), including *R. lalandii*, *R. porosus*, and *R. terranoenovae* (Compagno 1984).

Regarding the ecology of this genus, based on the extant *R. terranoenovae*, it inhabits coastal warm, temperate, and tropical waters, usually less than 10 m in depth (Compagno 1984). Nursery areas for this species are estuarine, near-shore, warm, shallow environments (McCandless et al. 2007).

Family SPHYRNIDAE Gill 1872

Genus SPHYRNA Rafinesque 1810

SPHYRNA SP.

Common name: Hammerhead shark

Referred specimens: 16 isolated teeth; upper: UF 242868; lower: UF 238020; indeterminate position: UF 242869 - 242870, SMU 76459, SMU 76463, SMU 76465 and SMU 76475.

Specific Locality: YPA017.

Distribution: The range of this genus goes from the Paleocene to Recent. Paleocene of USA (Maryland). Eocene of Pakistan and Togo. Miocene of USA (Florida, Maryland), Australia, Saudi Arabia, Mexico (Baja, California), Austria, India (Orissa), Brazil, Venezuela and Panama (this study). Pliocene of USA (California) and Australia (South Australia). Recent distribution in all temperate and tropical seas (Cappetta 1987; Aguilera & De Aguilera 2004; Dos Reis 2005; Adnet et al. 2007; www.paleodb.org, 5 April 2009, using the name *Sphyrna* sp.).

Description: *Sphyrna* teeth demonstrate diagnostic characters including crown labio-lingually flattened, finely serrated crown, apex inclined or slanted distally, acute notch, thick, bulky root, deep transverse groove (Figure 2-15).

Sphyrna sp. differs from *Carcharhinus* by having a thick bulky root. The mesial cutting edge of *Sphyrna* sp. is generally convex and slightly sigmoid. Cusps are slender and almost needlelike. *Sphyrna* sp. from the Gatun Formation has a thicker crown than the *S. lewini* and weaker serrations. This taxa's measurements range from 3.1 to 8.9 mm in CH and 7.4 and 10.6 mm in W.

Discussion: Cappetta (1987) established the maximum tooth size for this genus to be 20 mm in CH. This suggests that individuals from the Gatun Formation were small. Extant species inhabit all temperate and tropical seas. They are found mostly in coastal waters and have a diet consisting of skates, rays, small sharks and bony fishes (Compagno 1988).

SPHYRNA LEWINI Griffith & Smith 1834

Sphyrna zygaena (Gillette, 1984:179)

Common name: Scalloped hammerhead shark

Referred specimens: Four isolated teeth; uppers: SMU 76454, SMU 76458 and SMU 76462; lowers: SMU 76449.

Distribution: Middle Miocene to Recent. Middle Miocene of India. Late Miocene of Panama (this study). Pleistocene of USA (North Carolina). Extant *S. lewini* has a cosmopolitan distribution (Compagno 1984; www.paleodb.org, 06 April 2009, using the name *S. lewini*).

Description: *S. lewini* displays diagnostic characters including: stout to slender crown, cutting edges either smooth or weakly serrated, thick and bulky root and a deep transverse groove (Figure 2-16).

S. lewini is differentiated from other *Sphyrna* species by having smooth to weakly serrated cutting edges. The *S. lewini* specimens from the Gatun Formation have a well-developed notch on the distal edges and the crowns are inclined. The teeth measurements range between 2.7 and 5.4 mm in CH and 5.2 to 11.0 mm in W.

Discussion: This species is probably the most abundant hammerhead shark that occurs in coastal warm-temperate and tropical seas, ranging from the surface to at least 275 m in depth (Compagno 1984). Juvenile *S. lewini* usually occur close inshore (Compagno 1984). Juveniles use estuarine or near-shore warm shallow waters as nurseries (McCandless et al. 2007).

SPHYRNA MOKARRAN Rüppell 1837

Common name: Great hammerhead shark

Referred specimens: Four isolated teeth; uppers: UF 237909 – UF 237912.

Specific Locality: YPA017.

Distribution: Early Miocene to Recent. Early Miocene of Cuba. Late Miocene of Panama (this study). Extant *S. mokarran* has a circumtropical distribution (Compagno 1984; www.paleodb.org, 6 April 2009, using the name *S. mokarran*).

Description: *S. mokarran* exhibits diagnostic characters including: triangular shaped, increasingly oblique crown, strongly serrated cutting edges, thick and bulky root, and deep transverse groove (Figure 2-17).

S. mokarran differs from other species of *Sphyrna* by having one heel more pronounced than the other. *S. mokarran* teeth from the Gatun Formation measure 7.6 to 9.4 mm in CH and from 9.6 to 16.4 mm in W.

Discussion: This species is not well documented in the fossil record. It has only previously been reported from the Miocene of Cuba, although there is no description of the specimens (MacPhee 2003).

Regarding its ecology, this species inhabits coastal-pelagic and semi-oceanic, tropical habitats. Nursery areas for *S. mokarran* are typically shallow and warm, estuarine or near-shore waters (McCandless et al. 2007).

Discussion

While our identifications are consistent with those of Gillette (1984), there are a number of key differences and additions that expand our knowledge of ichthyofauna of the Gatun Formation.

The presence of *Ginglymostoma delfortriei*, *Carcharocles megalodon*, *Hemipristis serra*, *Carcharhinus sp.* and *Physogaleus contortus* are in agreement with the descriptions of Gillette (1984). While no other *Ginglymostoma* teeth were collected during the present study, the SMU specimens confirm their presence in the Gatun Formation and agree with other reports from the Caribbean (Aguilera & De Aguilera 2001; Laurito 1999). The fact that no other teeth were recovered during this study is not surprising, considering that these teeth are small and not typically found during surface collecting.

Additional *C. megalodon* specimens were collected in the Gatun Formation during this study. The cosmopolitan nature of the species is documented by the presence of *C. megalodon* teeth worldwide (Cappetta 1987; Purdy 1996; Purdy et al. 2001) including the Neotropics (Iturralde-Vinent 1996; Laurito 1999; Donovan & Gunter 2001; Nieves-Rivera 2003; Aguilera & De Aguilera 2001; Portell et al. 2008). The relatively small size of all the specimens found in Panama is notable, and will be addressed in future research (Pimiento et al., in progress).

H. serra teeth are one of the most common shark fossils in the Gatun Formation; this is also consistent with other records for the species, which is abundant in the Miocene and Pliocene of the Atlantic and Pacific basins (Cappetta 1987; Iturralde-Vinent et al. 1996; Laurito 1999; Purdy et al. 2001; MacPhee et al. 2003; Aguilera & De Aguilera 2001, 2004; Portell et al. 2008). The most common shark fossils found in the Gatun belongs to the genus *Carcharhinus* sp.; which is also reported in Venezuela (Aguilera & De Aguilera 2001) and Jamaica (Underwood & Mitchell 2004). This genus varies greatly in size and morphology being difficult to identify it to the species level.

The presence *Physogaleus (Galeocerdo) contortus* as reported by Gillette (1984) was confirmed by the collection of another specimen in this study. It should be noted, however that the specimens described in Gillette's work were not present in the SMU collection for comparison. This species is not very common in the Neotropics, although it has been reported in Cuba (Iturralde-Vinent et al. 1996) and the genus *Physogaleus* in Costa Rica (Laurito 1999). All of the species reported in this study that are consistent with Gillette (1984), are also consistent with other Miocene assemblages in the Caribbean Region.

There are a number of key differences and additions to the ichthyofauna of the Gatun Formation resulting from this study. Gillette (1984) identified one white shark (*Carcharodon*

carcharias) tooth, describing it as being highly worn, missing its edges and serrations. However, this specimen was also missing from the SMU collection and I was unable to confirm his identification. Regardless, the presence of a white shark tooth in the late Miocene is unlikely, because *C. carcharias* specimens do not become common in the fossil record until the Pliocene (Ehret et al. 2009). Without being able to view the specimen, it is difficult to speculate what species is represented by this tooth. The original description lacks enough detail to be confident, but it could be also attributable to a small *C. megalodon* or perhaps *Cosmopolitodus* (*Isurus*) *hastalis*, although the latter species lacks serrations. The current hypothesis regarding the evolution of the white shark places *C. hastalis* as an ancestral taxon to *C. carcharias*. One of the most obvious morphological differences between the taxa is the lack of serrations in *C. hastalis* and the presence of coarse serrations in *C. carcharias*. Transitional forms between the two are found throughout the Pacific Basin during the latest Miocene (De Muizon & DeVries 1985; Ehret et al. In Prep.). In the Neotropics during the Miocene, *Cosmopolitodus* (*Isurus*) *hastalis* has been reported in the Cuba (Iturralde-Vinent et al. 1996); *Isurus* sp. in Venezuela (Aguilera & De Aguilera 2001), *C. retroflexus* in Costa Rica (Laurito 1999) and *I. oxyrinchus* in the Grenadines (Portell et al. 2008). However, neither *Cosmopolitodus* nor *Isurus* has been recovered from Panama. The absence of this taxon in the shallow-water Gatun Formation may be due to the bathyal or mesopelagic depth range of this species (Aguilera & De Aguilera 2001).

Additional omissions in our study relative to Gillette's (1984) original description include the absences of the species *Physogaleus* (*Galeocerdo*) *aduncus*, *Sphyrna arambourgi*, *Sphyrna zygaena*, and *Isistius* sp. These differences reflect the reanalysis and re-description of the original materials. The teeth from the SMU collection were not catalogued until this study, making the identification of the individual specimens described by Gillette (1984) somewhat problematic.

The teeth that Gillette (1984) referred to as *S. arambourgi* and *S. zygeana* have been re-identified as *S. lewini* in this study. The shape and characteristics of these fossil teeth are more consistent with *S. lewini* than either *S. arambourgi* or *S. zygaena*.

Finally, the presence of *Isistius* sp. in the Gatun Formation is refuted. The specimens referred to *Isistius* sp. by Gillette (1984) belong to the sharpnose shark, *Rhizoprionodon*. While lower *Isistius* teeth are present in the Miocene of Venezuela (Aguilera & De Aguilera 2001) and in the Pliocene of North Carolina (Purdy et al. 2001) and Florida (G. Hubbell, Pers. Comm., 2009), no upper teeth have been described from the fossil record, which may be related to their weaker mineralization (Cappetta 1987). The re-identification of these teeth to *Rhizoprionodon* is also more consistent with the habitat reconstruction of the Gatun Formation. *Rhizoprionodon* has been reported from the Miocene of the Caribbean (Aguilera & De Aguilera 2004; Laurito 1999); in addition, it inhabits coastal, warm waters, whereas *Isistius* tends to be an oceanic, epipelagic to bathypelagic shark (Compagno 1984; Purdy et al. 2001). Therefore, given what is known of the other taxa of invertebrates and sharks, its presence in the Gatun Formation would be highly irregular.

Additional species that have been identified from the Gatun Formation of Panama (see * in Table 2-2) are mostly shared with other Miocene assemblages in the Caribbean region and include: *G. cuvier*, also reported in the Miocene of Venezuela (Aguilera & De Aguilera 2001); *C. falciformis*, also reported in Costa Rica (Laurito 1999); *C. leucas*; *C. obscurus*, also reported in Cuba (Iturralde-Vinent et al. 1996; MacPhee et al. 2006) and the Grenadines (Portell et al. 2008); *C. perezi*, also reported in the Grenadines (Portell et al. 2008); *C. plumbeus*; *Negaprion brevirostris*, also reported in Venezuela (Aguilera & De Aguilera 2001) and Cuba (Iturralde-Vinent et al. 1996; MacPhee et al. 2006); *Sphyrna* sp., also reported in Venezuela (Aguilera &

De Aguilera 2001); *S. lewini* and *S. mokorran*, also reported in the Miocene of Cuba (Iturralde-Vinent et al. 1996; MacPhee et al. 2006).

Based on the time distribution of the taxa found in the Gatun Formation, their teeth measurements (Table 2-1) and their ecology (Table 2-2); different assumptions can be made regarding their longevity, sizes and habitat preferences.

Taxonomic Longevity

Within the 16 taxa identified (Table 2-2) from the ~10 million years old late Miocene Gatun Formation, four species are now extinct (see † in Table 2-2) and the remaining 12 still exist today; the latter indicating the presence of relatively long-lived taxa. Sharks are very successful group that have been common in our oceans for 400 million years (Hubbell 1996). Some of the genera represented in the Gatun Formation first appear in the fossil record in the Paleocene (~65 Ma), others in the Eocene (~55 Ma) and the largest number have been around since the Miocene (~20 Ma). Those taxa have not changed for several million years and at least their tooth morphology remains similar to extant individuals.

The closure of the Isthmus of Panama ~4 million years ago resulted in a major geographic and environmental changes, and consequent vicariance of once continuous faunas. This was a key event for tropical biotic evolution, allowing for the interchange of terrestrial species between North and South America and also isolating Pacific and Atlantic marine organisms (Cronin & Dowsett 1996). The late Miocene Gatun Formation is represented by many long-lived shark species that survived the formation of the Isthmus of Panama, as opposed to several other species of that became extinct due to the effects of this event (O'dea et al. 2007; Budd et al. 1996).

Size

The tooth-size comparisons were made when possible with measurements of specimens from two formations within the Lee Creek Mine, Aurora, North Carolina (Purdy et al. 2001): The

Pungo River Formation (middle Miocene) and the Yorktown Formation (early Pliocene; Ward & Bohaska 2008). These formations are respectively older and younger than the late Miocene Gatun Formation age range (12-8.4 million years ago; Coates 1996a), and consequently reduce any potential variation arising from macroevolutionary shifts in body sizes through time.

Based on the size of the isolated teeth found within the Gatun Formation, I interpret that the sharks inhabiting Panama during the late Miocene were small overall. Extant related species use shallow environments similar to the late Miocene Gatun Formation as nursery area (Table 2-2); however, I cannot conclude they were all juveniles using this area as a nursery ground without studying the ontogenetic changes of every species (i.e. lateral teeth of juvenile *Hemipristis serra* have reduced or no serrations in the mesial edge and an unserrated tip (Compagno 1988)).

Habitat Preferences

Previous studies of the Gatun Formation indicate that this area was a shallow-water seaway between the Pacific Ocean and the Caribbean Sea, with depths between 20 to 40 m and salinity conditions similar to those found in large bays (Coates & Obando 1996; Teranes et al. 1996). Based on depth preferences of extant and related shark species to those occurring in the Gatun Formation, I also believe that this area was a shallow environment during the late Miocene (Figure 2-18). Many of the shark species that inhabited this environment occurred in the neritic zone, below 150 m depth (dashed line). Taxa with depth preferences deeper than 150 m are not commonly found in the Gatun Formation including *C. falciformis* (1 specimen), *C. obscurus* (6 specimens), *C. plumbeus* (5 specimens), and *S. lewini* (4 specimens). In addition, the absence of other pelagic fauna commonly found in Miocene assemblages of the region such as *Alopias*, *Cosmopolitodus* and odontaspids (Portell et al. 2008; Aguilera & De Aguilera 2001; Ward &

Bonavia 2001; Iturralde et al. 1996; Laurito 1999) in the Gatun Formation also supports the hypothesis of the shallow-water seaway.

Studies of benthic foraminifera (Collins et al. 1996) from the Gatun Formation show a strong Caribbean affinity. However, most of the shark genera found in the Gatun Formation have related modern species that are found in both the Pacific Ocean and the Caribbean Sea (Gillette 1984). On the other hand, one species described here (*C. perezii*) is currently restricted to the Caribbean Sea (Compagno 1984). This same trend is also apparent in *Rhizoprionodon*; the genus has extant representatives mainly distributed in the Atlantic Ocean (*R. terranova*, *R. lalandii*, and *R. porosus*) (Compagno 1984). These sharks inhabited the shallow seaway that was located in what is today Panama during the late Miocene and were able to move freely between the Caribbean and the Pacific. After the formation of the Isthmus of Panama during the early Pliocene, ~3.5 to 4 million years ago they then became restricted to the Caribbean Sea.

The closure of the isthmus was not a single event and its biological effects on marine organisms are likely to have occurred over several million years (Coates & Obando 1996). After the formation of the Isthmus of Panama, diversification influenced by the increase of the habitat complexity associated with this event occurred (Jackson & Budd 1996). In this study, 16 fossil taxa that lived in the shallow seaway that was located in Panama during the late Miocene were identified. Today, approximately 46 shark species are found on both sides of the Isthmus of Panama (data retrieved from FishBase, see Appendix 1). The results shown in this study significantly improve our knowledge on the Neotropic's shark fauna and provide a guideline to address further questions about the sharks' biodiversity of Neotropics and the effects of the formation of the Panamanian isthmus on sharks' fauna.

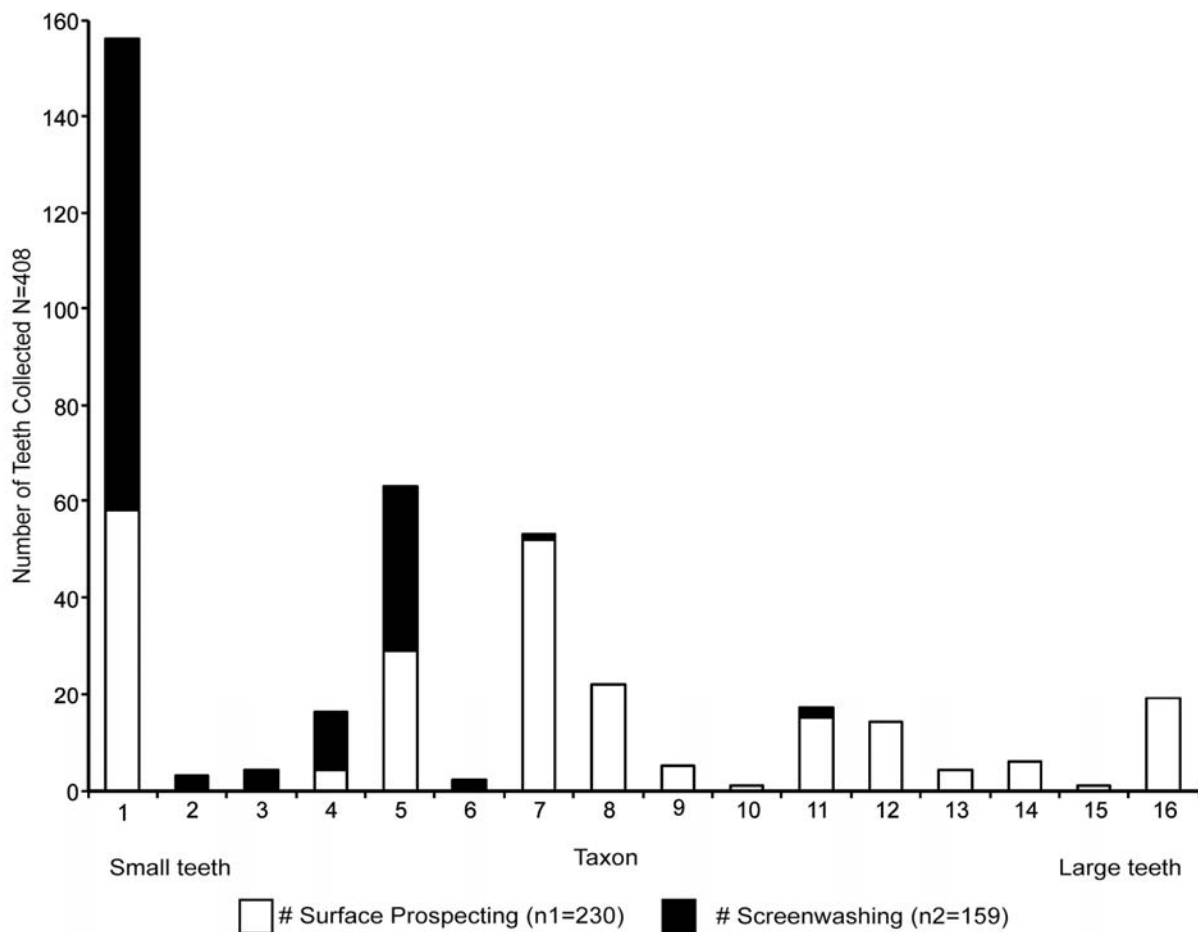


Figure 2-1. Graph showing the number of teeth collected in the Gatun Formation using 2 different techniques. Every number in the x-axis represents a taxon (see Table 2-1) ordered from the smallest to the larger teeth. White columns are the teeth collected by surface prospecting. Black columns are the teeth collected by Gillette (1984) using screenwashing.

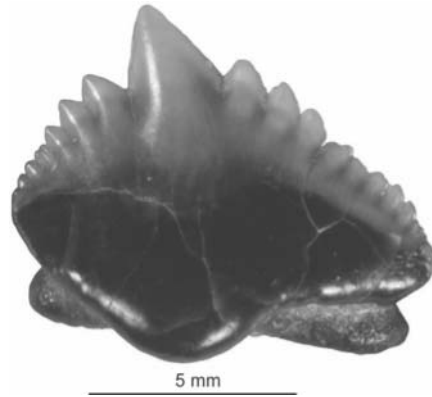


Figure 2-2. *Ginglymostoma delfortriei* from the late Miocene Gatun Formation, Panama, SMU 76470, indeterminate position.

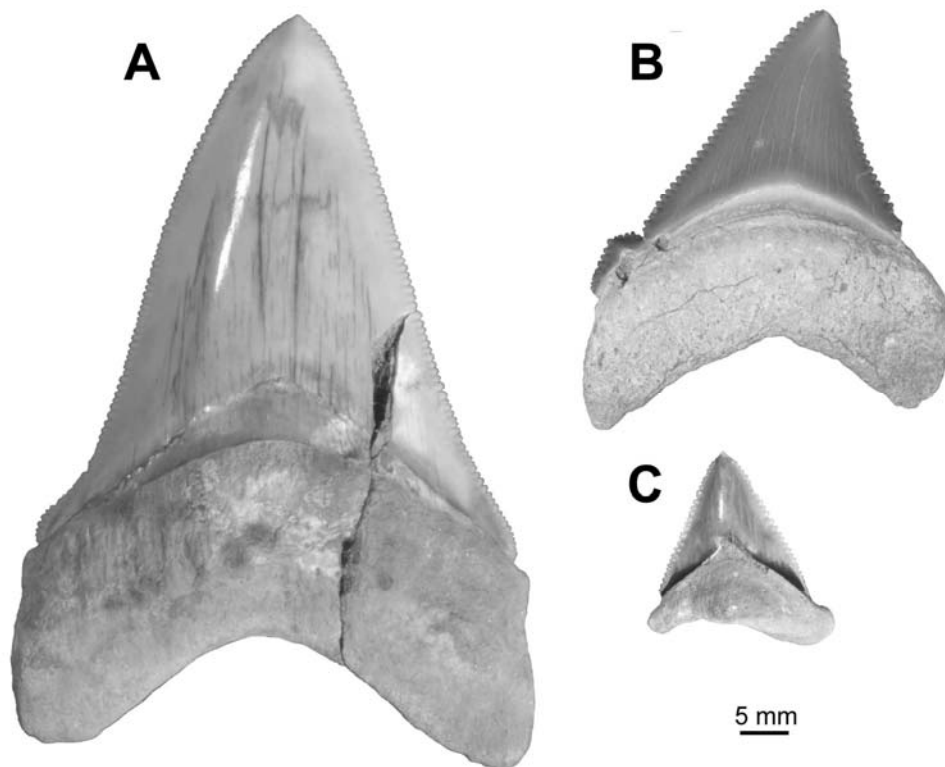


Figure 2-3. *Carcharocles megalodon* from the late Miocene Gatun Formation, Panama. A. UF 237950, largest anterior tooth. B. UF 237914, lateral tooth of a juvenile (with cusplets). C. UF 237959, smallest anterior tooth.

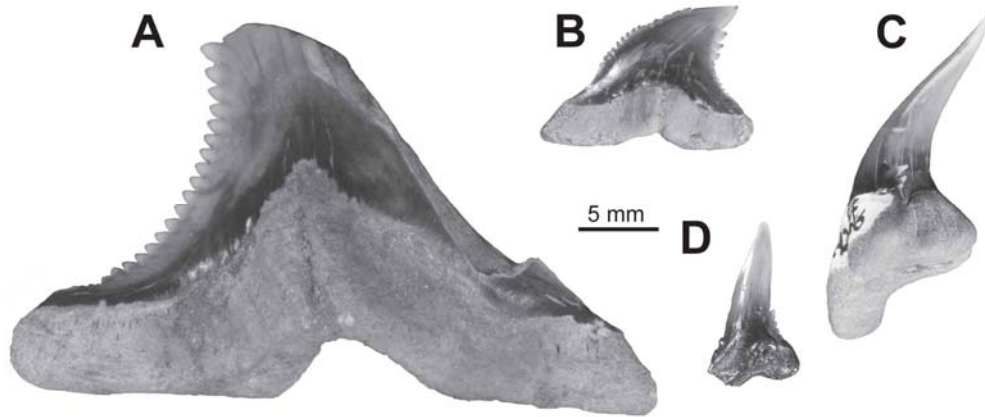


Figure 2-4. *Hemipristis serra* from the late Miocene Gatun Formation, Panama. A. UF 237941, upper largest tooth. B. UF 237924, upper smallest tooth. C. UF 242806, largest complete lower tooth. D. SMU 76467, smallest lower tooth.

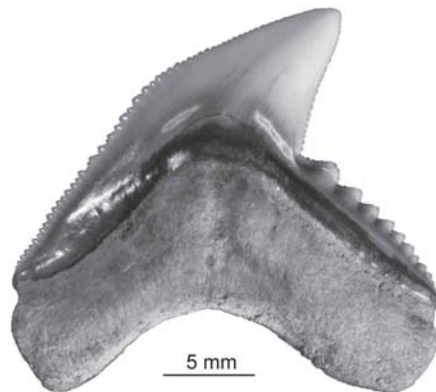


Figure 2-5. *Galeocerdo cuvier* from the late Miocene Gatun Formation, Panama, UF 237902, indeterminate position.

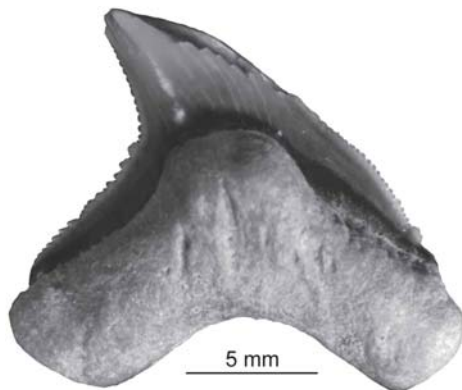


Figure 2-6. *Physogaleus contortus* from the late Miocene Gatun Formation, Panama, UF 237908, indeterminate position.

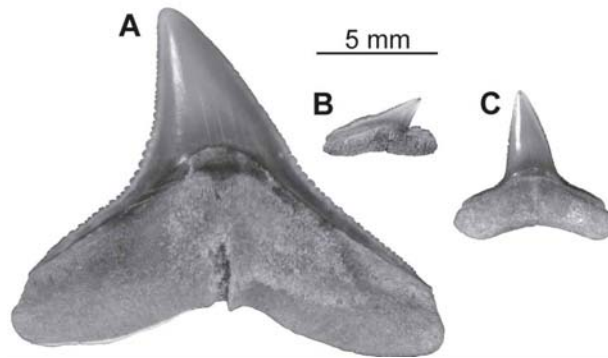


Figure 2-7. *Carcharhinus* sp. from the late Miocene Gatun Formation, Panama 1. UF 232004, upper tooth. 2. SMU 76475, smallest tooth (lateral). 3. UF 281828, lower tooth.

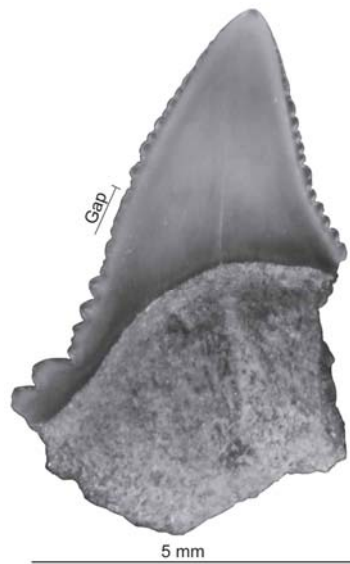


Figure 2-8. *Carcharhinus falciformis* from the late Miocene Gatun Formation, Panama, UF 241817, upper tooth. Gap of serrations in mesial side is diagnostic for this species.

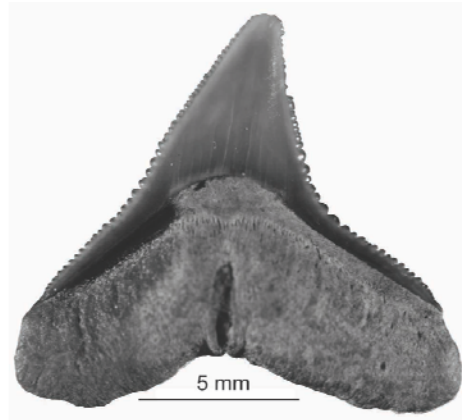


Figure 2-9. *Carcharhinus leucas* from the late Miocene Gatun Formation, Panama, UF 241829, upper tooth.

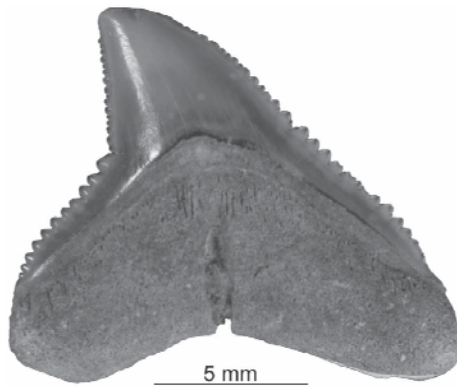


Figure 2-10. *Carcharhinus obscurus* from the late Miocene Gatun Formation, Panama, UF 242839, upper tooth.

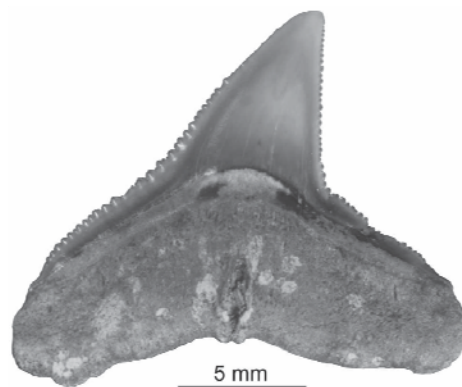


Figure 2-11. *Carcharhinus perezii* from the late Miocene Gatun Formation, Panama, UF 242851, upper tooth.

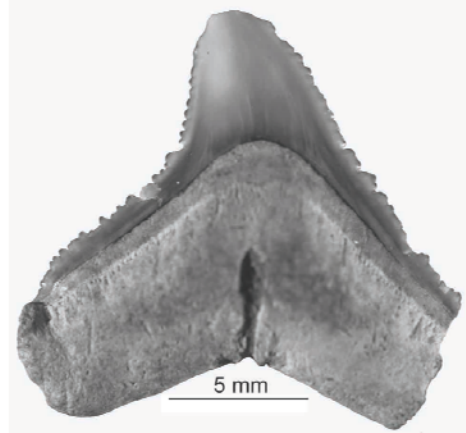


Figure 2-12. *Carcharhinus plumbeus*, from the late Miocene Gatun Formation, Panama, UF 242860, upper tooth.

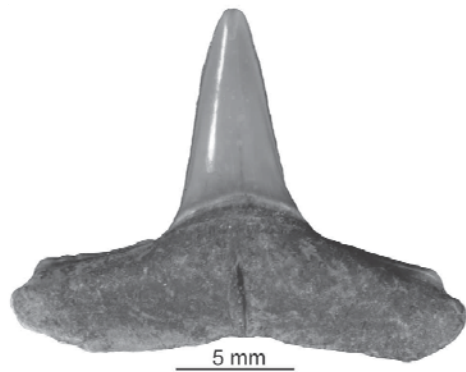


Figure 2-13. *Negaprion brevirostris* from the late Miocene Gatun Formation, Panama, UF 241814, indeterminate position.

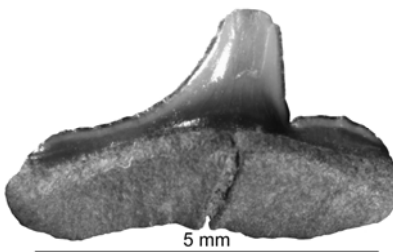


Figure 2-14. *Rhizoprionodon* sp. from the late Miocene Gatun Formation, Panama, SMU 76475, indeterminate position.

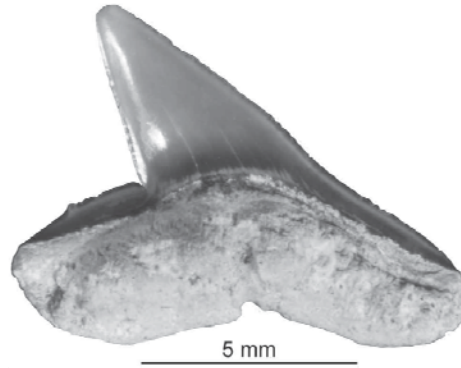


Figure 2-15. *Sphyrna* sp. from the late Miocene Gatun Formation, Panama, UF 242868, upper tooth.

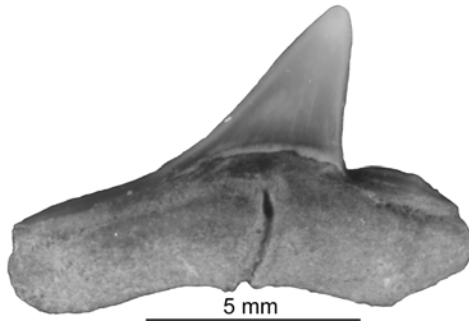


Figure 2-16. *Sphyrna lewini* from the late Miocene Gatun Formation, Panama, SMU 76458, upper tooth.

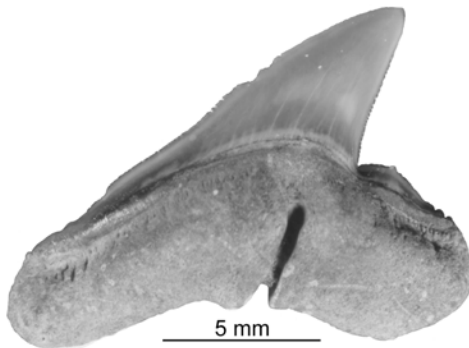


Figure 2-17. *Sphyrna mokarran* from the late Miocene Gatun Formation, Panama, UF 237912, upper tooth.

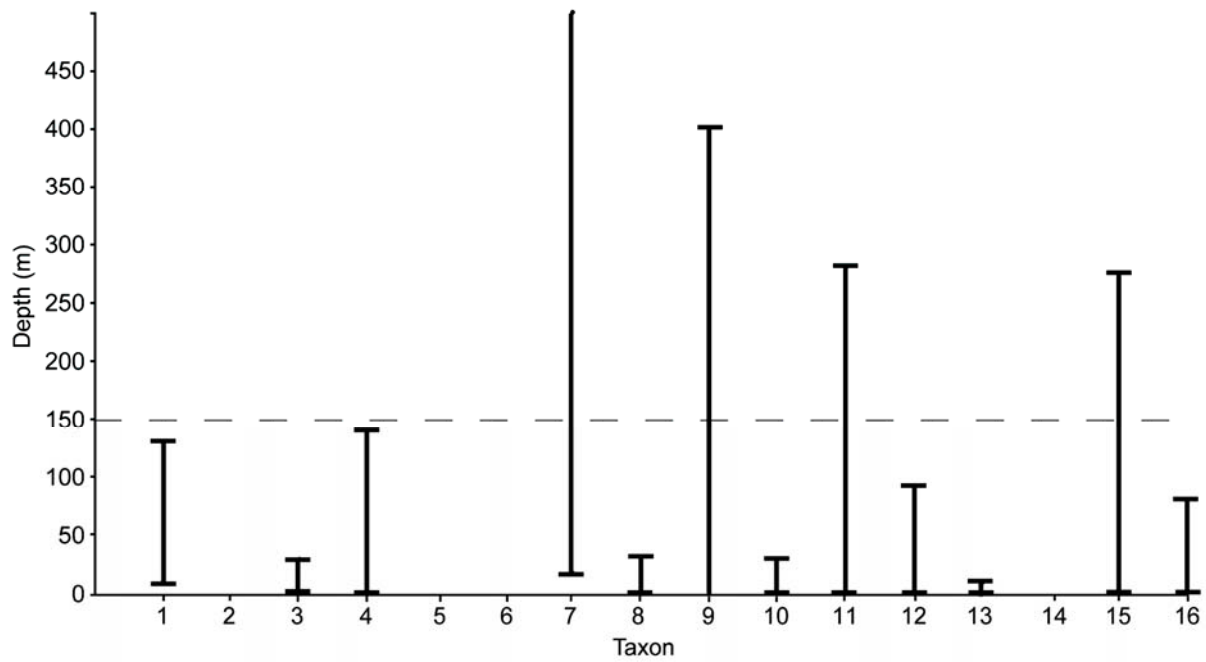


Figure 2-18. Estimated paleodepth of the Gatun Formation based on depth preferences of extant and related shark species. Many of the shark species occurred below the 150 m (dashed line), i.e., all in the neritic zone. Taxon number refers to the numbers in Table 2-2 ordered as appear in text.

Table 2-1. Number of specimens when two different collection methods employed in relation with teeth CH.

	Taxa	CH Size range (mm)	# Prospecting	# Screenwashing	Total
1	<i>Carcharhinus</i> sp.	1.9-12.9	58	98	156
2	<i>Rhizoprionodon</i> sp.	2.5 - 3.3	0	3	3
3	<i>Sphyrna lewini</i>	2.7 - 5.4	0	4	4
4	<i>Sphyrna</i> sp.	3.1 - 8.9	4	12	16
5	<i>Negaprion brevirostris</i>	3.7 - 13.7	29	34	63
6	† <i>Ginglymostoma delfortriei</i>	5	0	3	3
7	† <i>Hemipristis serra</i>	5.4-21.6	52	1	53
8	<i>Carcharhinus perezii</i>	5.8 - 10.8	22	0	22
9	<i>Carcharhinus plumbeus</i>	6.8 - 10.6	5	0	5
10	<i>Carcharhinus falciformis</i>	7.2	1	0	1
11	<i>Galeocerdo cuvier</i>	7.4-17.8	15	2	17
12	<i>Carcharhinus leucas</i>	7.5-10.7	14	0	14
13	<i>Sphyrna mokarran</i>	7.6 - 9.4	4	0	4
14	<i>Carcharhinus obscurus</i>	7.7 - 10.1	6	0	6
15	† <i>Physogaleus contortus</i>	11	1	0	1
16	† <i>Carcharocles megalodon</i>	16-54	19	0	19
	Total		230	157	387

Taxa numbers ordered from the smallest to the largest teeth

Table 2-2. Paleocology and inferred habitats of the elasmobranch fauna from the Gatun Formation; late Miocene of Panama.

	Taxa	Time Distribution	Ecology	
			Habitat	Nursery areas
1	† <i>Ginglymostoma delfortriei</i>	Miocene	Near-shore, 0 to 130 m	Estuarine or near-shore, shallow environments
2	† <i>Carcharocles megalodon</i>	Miocene to Pliocene	Coastal habitats	Warm-water areas
3	† <i>Hemipristis serra</i>	Miocene to Pliocene	Neritic, warm waters, 1 to 30 m	Not known
4	<i>Galeocerdo cuvier</i> *	Miocene to Recent	Coastal-pelagic, warm waters, 0 to 140 m	Shallow near-shore and offshore and estuarine waters
5	† <i>Physogaleus contortus</i>	Early to middle Miocene	Coastal-pelagic, warm waters, assumed to be same as <i>G. cuvier</i>	Not known or assumed to be same as <i>G. cuvier</i>
6	<i>Carcharhinus</i>	Early Eocene to Recent	Shallow waters	Not applicable
7	<i>Carcharhinus falciformis</i> *	Middle Miocene to Recent	Epipelagic, near shore, warm-shallow waters, 18 to 500 m	Shallow coastal waters
8	<i>Carcharhinus leucas</i> *	Middle Miocene to Recent	Epipelagic, rivers and lakes, warm waters, 0 to 30 m	Shallow coastal waters
9	<i>Carcharhinus obscurus</i> *	Early Miocene to Recent	Coastal and pelagic, warm waters, 0 - 400 m	Near shore, shallow environments and occasionally estuaries
10	<i>Carcharhinus perezii</i> *	Early Miocene to Recent	Inshore of continental and insular shelves, warm waters, 0 -30 m	Insular shallow reef systems
11	<i>Carcharhinus plumbeus</i> *	Early Miocene to Recent	Coastal-pelagic, warm waters, 0 - 280 m	Estuarine or near-shore, shallow, warm waters
12	<i>Negaprion brevirostris</i> *	Eocene to Recent	Inshore, estuarine and marine waters, 0 - 92 m	Estuarine or near-shore, shallow, warm waters such as swamps or mangroves
13	<i>Rhizoprionodon</i> *	Eocene to Recent	Coastal warm waters, usually less than 10 m	Estuarine, near-shore, warm, shallow environments
14	<i>Sphyrna</i> *	Paleocene to Recent	Coastal waters	Not applicable
15	<i>Sphyrna lewini</i> *	Middle Miocene to Recent	Coastal warm waters, 0 - 275 m	Estuarine or near-shore shallow, warm waters
16	<i>Sphyrna mokarran</i> *	Early Miocene to Recent	Coastal-pelagic and semi-oceanic, warm waters 1 - 80 m	Estuarine or near-shore shallow, warm waters

* Indicates new reports for Panama. Taxa numbers ordered in phylogenetic order as it is in text.

CHAPTER 3
ANCIENT NURSERY AREA FOR THE EXTINCT GIANT SHARK MEGALODON
(*CARCHAROCLES MEGALODON*) IN THE MIOCENE OF PANAMA

Introduction

Sharks, especially large species, are highly mobile organisms with a complex life history and wide distribution. During their lifetime they generally utilize three types of areas: adult feeding, reproduction and nurseries (Plata et al. 2007). In modern species, nursery areas are historically defined by the presence of gravid females and free-swimming neonates. It is also an area that can be shared by several shark species, where young sharks spend their first weeks, months or years (Castro 1993). More recent studies have defined nursery areas as geographically discrete essential zones for shark survival that provides them with two types of benefits: protection from predation (mainly larger sharks (Castro 1993)); and abundant food resources (Heupel et al. 2007). Productive, shallow-water ecosystems thus provide sharks significant protection from larger predators and/or abundant food (Heithaus 2007).

The Gatun is a highly fossiliferous Neogene formation located in the Isthmus of Panama (Figure 1-1) with a diverse fauna of sharks (Blake 1862; Gillette 1984; Pimiento et al. 2010). Studies of different taxa, including the exceedingly diverse molluscan fauna, indicate that it was a shallow-water ecosystem (~ 25 m depth) with higher salinity, mean annual temperature variations, seasonality and productivity relative to modern systems in this region (~10Ma) (Coates 1996a). Studies of different taxa indicate that it was a shallow-water ecosystem (~ 25 m depth) with higher salinity, mean annual temperature variations, seasonality and productivity relative to modern systems in this region (Collins et al. 1996; Coates & Obando 1996; Teranes et al. 1996; Gussone et al. 2004; Haug et al. 2001). Over the past 20 years, the Gatun Formation localities have been extensively used to extract sediment for construction. During the more recent years, these extraction activities have increased substantially. Based on our observations

made during the two past years of fieldwork, we predict that these outcrops will soon likely be excavated completely. Therefore it is timely and urgent to study the fossils occurring in these outcrops before they are no longer available to science.

Fossil sharks were first reported from Panama in 1862 (Blake 1862). In 1984, the first description of the elasmobranchs from the Gatun Formation was published (Gillette 1984). More recently, the biodiversity of the fossil sharks from the Gatun is documented on a large new collection consisting of 16 recognizable taxa. This work also included paleoecological and paleodepth analyses that supported the interpretation of the paleoecology of the Gatun Formation as shallow-water habitat (Pimiento et al. 2010).

Although is not very common, the extinct *Carcharocles megalodon* (Agassiz 1843) is one of the species that occurs in the Gatun Formation. The taxonomic assignment of this species has been debated for nearly a century, and there are three possible interpretations: (1) Some authors place *C. megalodon* and other megatoothed sharks with the extant white shark (*Carcharodon carcharias*) in the same genus (*Carcharodon*) and therefore the same family (Lamnidae) (Applegate & Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996). (2) Other authors place *C. megalodon* and megatoothed sharks in a different genus (*Carcharocles*) and family (Otodontidae) (Jordan & Hannibal 1923; Casier 1960; Gluckman 1964; Cappetta 1987, Ward & Bonavia 2001; Nyberg et al. 2006; Ehret et al. 2009). Although minority points of view, some workers recognize (3) megatoothed sharks as a series of chronospecies of the genus *Otodus*, and place all megatoothed sharks except *C. megalodon* in this genus. Furthermore, *C. megalodon* is assigned to the genus *Megaselachus*, based on the loss of lateral cusplets (Zhelezko & Kozlov 1999). Of relevance of this study, we follow the second hypothesis; that *Carcharocles megalodon* and *Carcharodon carcharias* belong to separate genera in different families.

However, both species belong to the order Lamniformes, and in the absence of living members of the Otodontidae, *C. carcharias* should be regarded as an analogous species to *C. megalodon*. We base this analogy on the presumed similarities in body shape, feeding habits, and overall tooth and vertebral centrum morphology.

C. megalodon is widely regarded as the largest shark to have ever lived. Based on tooth crown height (CH), this giant reached a total length (TL) of more than 16 m. One single tooth can exceed more than 168 mm of total height (Gottfried et al. 1996). The diagnostic characters of *C. megalodon* teeth include: large size, triangular shape, fine serrations on the cutting edges, a convex lingual face, a slightly convex to flat labial face, and a large neck (Pimiento et al. 2010). Juvenile specimens of *C. megalodon* can have lateral cusplets (Applegate & Espinosa-Arrubarrena 1996), or not (Ward & Bonavia 2001). The size and shape of the teeth vary within the jaw: Anterior teeth are large and symmetrical whereas the latero-posterior teeth are asymmetrical with slanted crowns. Moving antero-posteriorly through the jaw, there is a slight initial increase in size on either side of the mid-line, followed by a progressive decrease that continues to the last tooth (e.g. Purdy et al. 2001) (Appendix C). Fossil teeth of *C. megalodon* range in age from 17 to 2 Ma (middle Miocene to Pleistocene) and have a cosmopolitan distribution (Pimiento et al. 2010; Gottfried et al. 1996; Purdy 1996).

It has been suggested the megatoothed *Carcharocles* used warm-water areas for nurseries (Purdy 1996). Two nursery areas have previously been proposed for this genus: the late Oligocene Chandler Bridge Formation of South Carolina, based on the abundance of juvenile *Carcharocles* teeth, accompanied by fossils of presumed prey species (Purdy 1996); and the Paleocene Williamsburg Formation of South Carolina, based on the presence of juvenile *C. orientalis* teeth in a shallow marine environment (Purdy 1998). However, neither of the

collections from these two localities have been rigorously analyzed and thus the presence of paleo-nurseries remained anecdotal until the present report.

Previously proposed nursery areas for the mega-toothed *Carcharocles* have been mainly assigned based on the presence of juvenile teeth along with small odontocete and mysticete skulls, which are assumed to be their prey species (Purdy 1996). Despite extensive field collecting, marine mammals have not been found in the Gatun Formation so far. Thus I assert that the small size of teeth found in the Gatun Formation may also relate to the absence of large prey species that would have likely been required for larger individuals to have existed in this shallow-water habitat.

The presence of mammals as potential prey does not represent an evidence of a shark nursery area. As is known from modern studies of sharks, the main purpose of the nursery areas is not feeding (Castro 1993; Heithaus 2007; Heupel et al. 2007; Plata et al. 2007). Studies have shown that some shark species do not consume large quantities of food during their juvenile stages (Bush & Holland 2002; Lowe 2002). Even when nursery areas provide ample food resources for juvenile sharks, some species select these habitats more for predator avoidance and not food consumption (Heupel et al. 2007; Heithaus 2007). Furthermore, some shark species (Lowe et al. 1996; Yamaguchi & Taniuchi T 2000; Ebert 2002; McElroy et al. 2006) present an ontogenetic shift in its feeding patterns. For example, the lamnoid white shark (*C. carcharias*) (Tricas & McCosker 1984; Estrada 2006) feeds on fishes during their juvenile stage and on mammals during their adult stage. Marine mammals have not been found in the Gatun Formation so far. On the other hand, bony fish otoliths are abundant and represent a food source for the marine fauna that lived in this diverse environment (Aguilera & De Aguilera 1996).

In this study, *Carcharocles megalodon* teeth were collected and measured from two localities within the Gatun Formation of Panama. Surprisingly, large teeth are uncommon with specimens recovered having crown heights ranging between 16 to 72 mm. The objective of this work is to determine if the late Miocene Gatun Formation was used as a nursery area by young *C. megalodon*. Accordingly, we compared the tooth sizes from the Gatun Formation with those found in older and younger formations to determine if the smaller size distribution observed is unique to the species during the late Miocene. In addition, we compared these sizes with tooth sets from individuals of different life stages to determine if the small size observed is related to age, or position within the jaw. Finally, we calculated the total length of all *C. megalodon* individuals based on tooth crown height from the Gatun Formation to estimate the life stage based on overall body size. The results obtained in this study from tooth measurement comparisons and individual total length estimates allowed us to determine the age class/size of individuals that inhabited the shallow-water habitats of the late Miocene Gatun Formation, ~10 million years ago.

Materials and Methods

Carcharocles megalodon teeth are relatively rare in the Gatun Formation. Of more than 400 teeth of fossil sharks collected from the Gatun Formation between 2007 and 2009 representing 16 taxa, a total of 28 specimens (Appendix D) of *C. megalodon* have been collected. Fossils do not provide a record of life as complete as when studying living organisms. For that reason and also because of the rarity of this species in the area of study, we consider our sample size adequate. In addition, it is urgent to study the fossils of a formation that will soon disappear due to the increasing excavations.

The two localities studied in the Neogene marine sediments of the Gatun Formation of Panama (Figure 1-1), crop out in a broad area in north-central Panama and has been proposed to

be late Miocene, spanning from about 12 to 8.4 Ma (Collins et al. 1996). The materials were collected mainly by surface prospecting by the Panama Canal Project Field Team of the Center of Tropical Paleobiology and Archaeology (CTPA) of the Smithsonian Tropical Research Institute (STRI), as well as the University of Florida (UF) scientists. Some of the specimens collected are deposited in the Florida Museum of Natural History (FLMNH) and are designated with a UF catalogue number which are available in its database:

<http://www.flmnh.ufl.edu/databases/VP/intro.htm>. The remaining specimens are designated with a CTPA or AT number and are part of the STRI collection.

Crown height (CH) and width (W) of all specimens were measured in millimeters (Figure 2-1, Table 3-1). In order to calculate dimensions of incomplete specimens, W vs. CH measurements were plotted and a line regression was calculated (Appendix E). Measurements were then compared with isolated teeth from geologically younger and older collections and finally the specimens' total lengths were calculated based on their CH.

Temporal Comparisons of Similar Faunas

Isolated teeth from the younger Bone Valley Formation, Florida (early Pliocene, ~5 Ma) (Morgan 1994; Tedford et al. 2004), from the Vertebrate Paleontology Collection at the FLMNH in Gainesville, Florida; were measured (Appendix F) and compared with the Gatun teeth. Additionally, isolated teeth from the older Calvert Formation, Maryland (middle Miocene, ~14 Ma) (Morgan 1994), from the Vertebrate Paleontology Collection at the NMNH, in Washington, D.C.; were also measured (Appendix G) and then compared with the Gatun Formation teeth.

Life Stage Comparisons

Two *C. megalodon* associated tooth sets of different life stages from the Hubbell collection at Gainesville, FL were measured and compared with tooth sizes of the Gatun isolated teeth. The juvenile tooth set is from the Bone Valley Formation, Florida (early Pliocene) (Morgan 1994;

Tedford et al. 2004) (Appendix H). The adult tooth set is from the Yorktown Formation, North Carolina (early Pliocene) (Ward & Bohanska 2008) (Appendix I).

Total Length Estimates

As described above, the extant white shark (*Carcharodon carcharias*), has been used as a general morphological analog for the extinct *Carcharocles megalodon*. Likewise, previous studies have asserted that teeth of *C. carcharias* can be used to estimate the total length of *C. megalodon* (Gottfried et al. 1996; Shimada 2003). Based on *C. carcharias* tooth height and total length ratios, I have measured *C. megalodon* crown height to extrapolate its total length estimates based on the work of Shimada (2006), where every tooth position in the jaw corresponds to one regression equation that calculates its body size (Appendix J). I assigned a range of possible positions to the Gatun teeth and estimated the TL of every specimen by calculating it from the average among the different positions where every tooth could have belonged (Mean TL, Table 3-1). Furthermore, I inferred the life stage of every *C. megalodon*, by extrapolating it from the relationship between body size and life stage in *C. carcharias* following Gottfried et al. (1996). I based our *C. megalodon* estimates on extrapolations from the extant *C. carcharias* given their similarities in body shape, feeding habits, and tooth and vertebral morphology. In addition, both species belong to the same order (Lamniformes), and in the absence of living members of *C. megalodon*'s family (Otodontidae), *C. carcharias* is the only analogous species available.

Results and Discussion

Temporal Comparisons of Similar Faunas

In many clades represented in the fossil record, animals oftentimes show a general tendency to become larger through time, i.e., also called “Cope’s Rule” (MacFadden 1992; Hone & Benton). For example, there is a trend towards increasing size of species within the genus

Carcharocles from *C. auriculatus* to *C. agustidensis* to its larger form, *C. megalodon* (Purdy 1996). However, there is no evidence of such a microevolutionary trend in the single species *C. megalodon* through time, as is shown below.

In order to know if the small size observed in the fossil *C. megalodon* from the Gatun Formation is a special feature during the late Miocene in a potentially chronoclinally evolving species, we performed tooth size comparisons through time within other marine faunas that have sufficiently large numbers of specimens of *C. megalodon*. Given the fact that the *C. megalodon* from the Calvert Formation of Maryland are older (~14 Ma) and the *C. megalodon* from the Bone Valley Formation of Florida are younger (~5 Ma), comparing these populations with *C. megalodon* from the Gatun Formation can determine if there is a long-term, chronoclinical trend for size increase, or if *C. megalodon* from the Gatun Formation are unusually small. Figure 3-1 shows that both large and small tooth sizes are found in the faunas older and younger than the Gatun Formation, and thus there is no observed microevolutionary trend for increased size in *C. megalodon* over time. I therefore assert that the small size observed in the Gatun Formation is not related to microevolutionary shifts in body size. Consequently, I demonstrate stasis in body size within the species *C. megalodon*, which provides us important context in which to compare ancient populations from the localities described above.

Life Stage Comparisons

Is it known that within an individual, *C. megalodon* teeth vary in size within the jaw (e.g. Applegate & Espinosa-Arrubarrena 1996; Purdy 1996; Purdy et al. 2001) (Appendix C). It could therefore be argued that the small size observed in the Gatun Formation is related to tooth position, rather than juvenile life stage of the individuals. In order to test this, we compared tooth sizes of the Gatun Formation specimens with associated tooth sets from individuals of different life stages (juvenile and adult) from other localities. Our results indicate that most teeth from the

Gatun Formation are close to the observed range of a juvenile dentition (Figure 3-2), regardless of tooth position within the jaw.

Comparing the Gatun's isolated teeth with tooth sets of individuals from different life stages helps to determine if the tooth size observed is related with tooth position. Nevertheless, in order to determine the life stage of those animals were neonates, juveniles or adults; it is necessary to establish total length estimates as well, as presented below.

Total Length Estimations

The tooth size comparisons made in this research suggest that the small size of *C. megalodon* teeth from the Gatun Formation is not related to temporal differences within a chronoclinally evolving species (as described above), but rather they may belong to juvenile sharks. When only the teeth of a shark species are preserved, life stages of individuals can be predicted in two different ways: (1) studying morphological features of the teeth during juvenile stages; and (2) extrapolating total length using the relationship between body size and crown height.

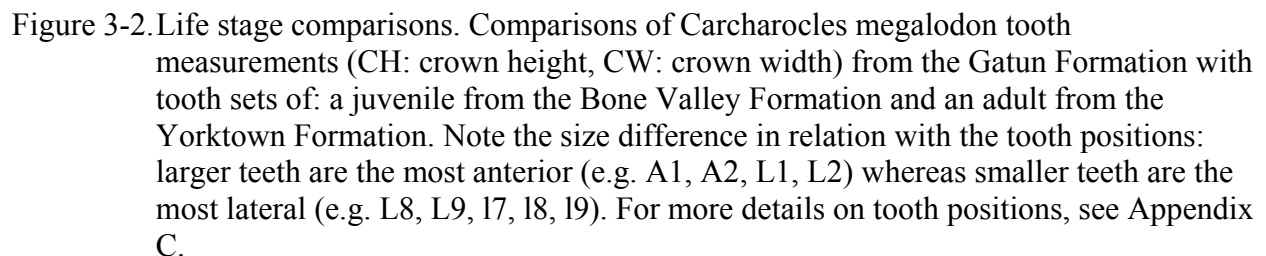
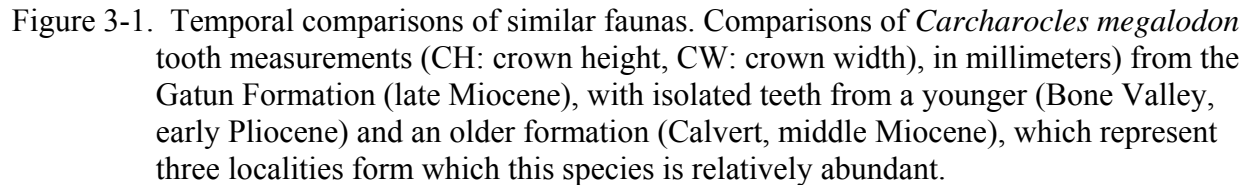
(1) In *C. megalodon*, teeth of juveniles sometimes demonstrate lateral cusplets (Applegate & Espinosa-Arrubarrena 1996; Ehret et al. 2009). For example, UF 237914 (a lateral tooth) exhibits lateral cusplets and is assumed to be from a juvenile. On the other hand, UF 237959 (a lower anterior tooth) and UF 237949 (an upper anterior) are both very small teeth that exhibit no lateral cusplets (Appendix D). The latter teeth are thick, heart-shaped, and are considered to represent embryonic Megalodon teeth (G. Hubbell, pers. communication). These teeth retain the morphology of the species even at small sizes and do not demonstrate lateral cusplets (Ward & Bonavia 2001).

(2) Gottfried et al. (1996) made inferences about the skeletal anatomy of *C. megalodon* based on comparisons with ontogenetic trends in the white shark, *C. carcharias*. They deduced that a *C. megalodon* fetus could reach ~ 4 m, juveniles ~14 m, and adults ~17 m. Based on crown heights and following the work of Shimada (2003), I estimate the total lengths of *C. megalodon* specimens from the Gatun Formation (Table 3-1). Based on Gottfried et al.'s inferences, the total length estimations made in this research suggest that the *C. megalodon* specimens from the Gatun Formation represent mostly juveniles, with total lengths less than 14m, while one specimen is interpreted as an adult, with an estimated total length of 17m (Figure 3-3).

Concluding Remarks: Nursery Area Hypothesis

In this study I show that the small tooth size observed in *C. megalodon* from the Gatun Formation is not related to its temporal position within a chronoclinally evolving species, or paucity of large prey species. Thus, the *C. megalodon* from the Gatun Formation indicates the dominant juvenile life stage of individuals present from this fossil locality. The *C. megalodon* and associated marine invertebrate and vertebrate faunas from the late Miocene Gatun Formation of Panama presents the typical characteristics of a shark nursery area: a shallow, productive environment that contains juveniles and neonates. I therefore propose the Miocene Gatun Formation, as a nursery area that offered juvenile *C. megalodon* protection from larger predators and ample food resources (i.e. fishes).

This study represents the first definitive evidence of an ancient shark nursery area from the Neotropics. Sharks are a very successful group that has been common in our oceans for at least 400 million years (Hubbell 1996). This research presents evidence that sharks have used nursery areas since ancient times, i.e., for at least 10 million years, and therefore extends the record of this behavior and adaptive strategy based on fossil evidence. Nursery areas are critical habitats for the success of extant shark species (Heithaus 2007). Currently, several sharks' populations



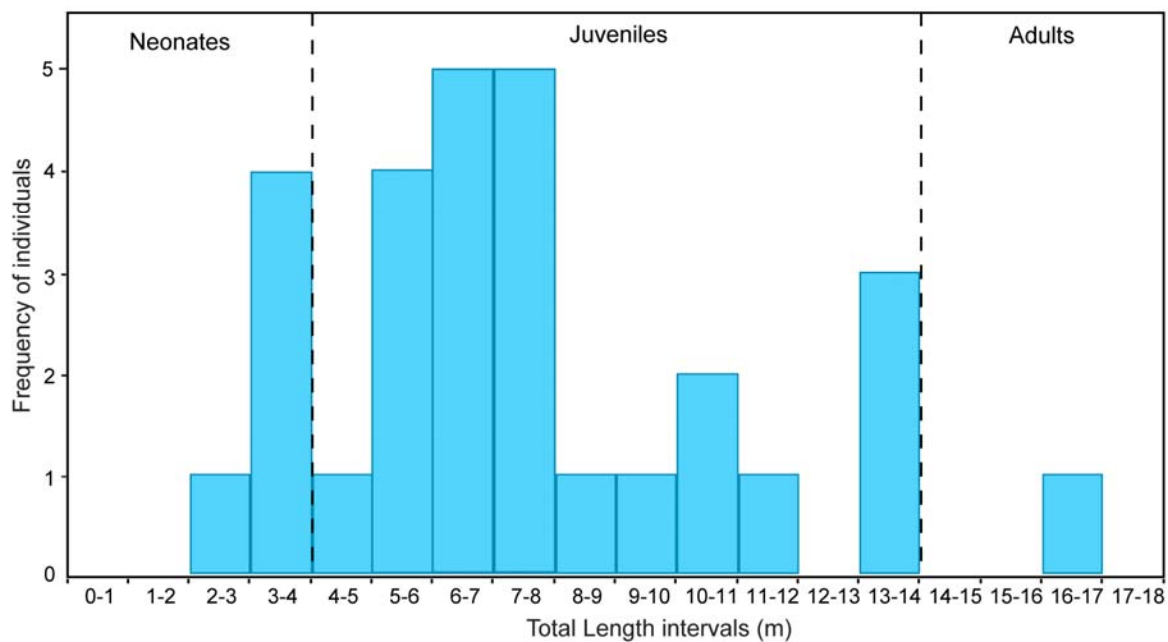


Figure 3-3. Total length histogram. Frequency of *Carcharocles megalodon* individuals at different life stages based on Gottfried et al [14]. Neonates of *C. megalodon* reach until 4 m; juveniles until 14 m, and adults more than 17 m.

Table 3-1. *Carcharocles megalodon* isolated teeth from the Gatun Formation, Panama

Specimen	CW (mm)	CH (mm)	Position**	Mean TL (m)***
UF 237898	53.0	50.0*	A1-A2	5.9
UF 237914	31.4	46.4	L1-L5	8.0
UF 237949	35.7	32.9	A1-A2	3.9
UF 237950	47.7	54.2	a2	7.3
UF 237951	26.8	17.6	L1-L5	3.1
UF 237952	43.2	31.3	L1-L5	5.4
UF 237953	30.9	24.5	l1-l5	7.2
UF 237954	41.7	41.2	A1-A2	4.9
UF 237955	28.4	28.5	A1-A2	3.4
UF 237956	44.9	28.1	l4-l6	16.8
UF 237957	26.7*	19.4	L6-L9	13.8
UF 237959	16.1	16.0	a1-a2	2.2
UF 242801	31.2	27.5*	L1-L5, l1-l5	6.4
UF 242802	45.1	41.0	L1-L5	7.1
UF 242803	40.8	34.7	L1-L5	6.0
AT04-17-1	43.2	43.8	a1-l2	6.2
AT04-41-2	60.3	56.4	A1-A2	6.7
AT06-9-1	57.7	60.1	A1-A2	7.1
UF 245844	20.6	11.2	l5-l7	10.0
UF 245852	73.2	70.9*	L2-L4	10.8
UF 245885	39.6	36.6	L1-L3	5.2
UF 245886	45.6	40.5	L1-L5	7.0
UF 245996	31.8*	25.9	l3-l6	13.1
UF 245995	62.2	63.2	a3	11.0
UF 246002	35.0	24.5	L7-L9	11.5
UF 246003	52.4	45.4	L1-L3	6.4
UF 245925	23.2	19.2*	L6-L9	13.7
CTPA 6671	74.7	72.3	A1-A2	8.6

* Incomplete specimens. Measurement predicted using the line equation: $y=mx+b$ (see Appendix E).

** Range of possible positions where every tooth could have belonged (see Appendix C for position details).

*** Mean TL estimated based on Shimada (2003) (see Appendix H). Mean calculated from the average among the different positions where every tooth could have belonged.

CHAPTER 4
BROADER IMPACT COMPONENT: ENGAGING YOUNG LEARNERS IN SCIENCE
THROUGH A WEBSITE ON FOSSIL SHARKS FROM PANAMA

Introduction

After the above studies on the ancient sharks of the Neotropics, one may wonder: why is this subject important? As scientist, we know that understanding the past can help us to comprehend the present and predict the future. We also know that science knowledge seeks to improve human life in fundamental ways; e.g. developing treatment for diseases, technologies for distributing clean water in arid environments, building systems for enhancing national security and building computers models that help track the impact of human behavior on the environment (Michaels et al. 2008). What we do not necessarily know quite well as scientists is how to convey scientific knowledge to the general public, and particularly children, nor how to create appropriate opportunities to engage young learners in the scientific enterprise.

But why is it important to engage young learners in science? Generating scientific productivity requires the workforce not only of scientist, but also journalists, teachers, politicians, and the broader network of people who make critical contributions to science. It is essential to engage children to science, not only because they will be the scientists, journalists, teachers and politicians of the future; but also because science is a critical factor in maintaining and improving the quality of life; we live in a scientific and technological driven society and its population will need to be functionally literate in science (Michaels et al. 2008).

Engaging young learners in authentic science allows the development of a foundation for continued science learning. Young learners who learn to communicate with their peers in a scientific way (following logical connections among ideas, and evidencing and criticizing them) may use these skills in other professional fields (Michaels et al. 2008). Science learning also provides children the opportunity to think critically, giving them tools to become functional

members of society rather than mere observers. In summary, science is a resource of becoming better citizens.

Problem

Even when sometimes, scientists do not know how to engage young learners to science; parents, teachers and the general population do not either. Sometimes, the media do not send the right message to young learners. In television (the greatest source of information for children), the image of a scientist is often the mad scientist, neglected, reclusive, and in a white lab coat (usually a white male), whose job is to invent things without application. Other times, the scientist is a wicked man, whose discoveries or inventions are evil for humanity (Massarini 1999). That is a negative view of science and is not engaging at all.

As an example of the disengagement to knowledge, statistics from the UNESCO reveal that in Panama for instance, about 98% of children receive primary education. However, only 65% continue their secondary education; 45% of young people continue to higher education and of these, less than 8% have level of expertise or PhD (UNESCO. Institute for statistics 2009). Today, the Internet has become a growing and powerful communication medium that provides new opportunities as a teaching tool for the citizens of the future.

Objective

The objective of this work is to develop a kid-friendly and bilingual website about fossil sharks from Panama hosted by the STRI kids webpage, to engage young learners to science learning. This website will promote science and technology and young learners will:

- Learn what species of sharks existed in Panama before the formation of the Isthmus 4 million years ago,
- Learn about the present and future of extant shark species.
- Learn concepts on biology, ecology, geology and paleontology.

Background

Learning is more than the transfer of knowledge from teacher to student in a formal learning environment. It is also a social process that includes on different individuals with different experiences and social environments (Vygotsky 1978). Beyond the schools, there are several opportunities for learning informally. Each year, tens of millions of Americans of all ages, explore and learn about science by visiting informal learning institutions, participating in programs, and using media to pursue their interests (NRC, 2009). The purpose of informal science education programs is to help the public to improve their understanding of science and to promote lifelong learning.

But, does people actually learn science on informal settings? The Committee on Learning Science in Informal Environments of the US National Academic Council (NRC) concluded that in everyday experiences, designed settings, and programs, individuals of all ages learn science. Today, popular media, in the form of radio, television and the Internet, make science information gradually more available to people across venues for science learning. These media are shaping people's relationship with science and are providing new means of supporting science learning.

Unlike the formal programs (in classrooms), informal programs focused on a much broader and diverse audience (different age ranges, ethnicities, scientific training, etc.), (Wheaton and Ash 2008). This is why it is very important to recognize the richness and complexity of the audience before designing a program of informal education as a website. For instance, preconceptions (prior learning that can act as barrier to learning) needs to be known given that it will significantly shape how they make sense of what they are taught. Preconceptions are a powerful support of for further leaning and if they are not addressed properly, they will memorize the content rather than understand it (NRC, 2000).

Studies in learning theory (Screven 1990) have indicated that audience interviews during front-end evaluation before beginning the design of an informal program will generate essential information to guide the development of the program. For instance, is important to evaluate audience's knowledge, which is what visitors consciously know, and their engagement, excitement and involvement in science (Friedman 2008).

Moreover, other research has shown that the use of two languages in informal education is very useful for students to access science (Wheaton and Ash 2008). In the case of Panama, bilingual schools teach science in English, while some young learners speak Spanish at home. Conversely, other schools teach classes in Spanish and young learners learn science in their native language; however, these young learners also need to learn a second language. In the case of young learners learning science in English, bilingual education programs provide them informal opportunities to join their knowledge in both languages and thus improve their vocabulary; in the case of young learners learning science in Spanish, they can also learn vocabulary and reinforce and/or learn English.

Young elementary school children reason biologically, rather than exclusively psychologically (Evans et al. 2009). Studies have shown that even the youngest have sophisticated ways of thinking about the natural world: Based on experience with the environment and in their pursuit of understand the world around them; children develop scientific ideas. Moreover, young learners who attend informal education programs (online or traditional) are more predisposed to form scientific skills (Michaels et al. 2008).

The Internet offers a new way to teach science so that young learners can learn both science ideas and skills. The interactivity of Web 2.0 technologies allows children to create, share and edit scientific content as well as to comment about it. Contrary to the static textbooks

that teach science in a linear fashion, with the Internet, scientific concepts can be communicated in a dynamic and creative way, which is closer to how science really works. This turns out to be more attractive and less intimidating for both students and teachers and does not ignore fun (Sanders 2009).

The findings from current research of the importance of the Internet in supporting informal learning have resulted in recommendations to create quality online experiences (Soren 2004, Soren and Network 2005, Alwi, A and McKa, E. 2009), for both adults and children of all ages. The recommendations include for example, to share information, learn through experience, explore databases, exchange ideas, offer significant content, and use friendly formats that facilitate comparisons with different learning styles.

With the advent of Web 2.0, the Internet is more than pages with information young learners read. It provides children the opportunities to become Web-creators; they publish their thoughts, respond to others, post pictures, share files, and contribute to the content available online, that is, they are part of the Read/Write Web and they have fun doing so. Young learners are building vast social networks with no adult guidance, and teachers and parents on the other hand, have been slow in to adapt to these new tools and potentials (Richardson 2009).

There are a growing number of Web 2.0 tools that young learners are using every day that have great potential for science education. In this project, different Web 2.0 tools are used to integrate children to the content of the website. They are among others (Richardson 2009):

- Social Networks: Web spaces where people can connect with friends and friends of their friends [e.g. www.facebook.com and www.twitter.com].
- Online photo galleries: Web-based communities where photographers share their photos, ideas and experiences [e.g. www.flickr.com].
- Blogs: It is an easily created, easily updateable, Websites that allows authors to publish instantly to the Internet, like a journal [e.g. www.blogger.com].

- Wikis: It is a collaborative Web space where anyone can add or edit content [e.g. www.wikipedia.com].
- Podcasts: Sites where people can easily produce and publish audio and videos [e.g. www.youtube.com].

Fossil Sharks from Panama as a Science-Engaging Tool

Why Fossil Sharks?

In the geologic record, shark teeth are the most abundant vertebrate fossils present worldwide (Hubbell 1996) and today they fascinate collectors, scientists, and the general public. Evaluations of audience preferences in museums have revealed that fossil sharks are very attractive for young learners as well (MacFadden 2006) (Figure 4-1) Fossil shark teeth permit the understanding of the composition of ancient faunas as well as the environmental conditions that helps to comprehend the climate changes that have occurred in earth's history. Thus the history of fossil sharks allows understanding numerous important STEM areas of natural sciences such as biology, ecology, geology and paleontology. Fossil sharks causes young learners' curiosity and in turn leads to education in the sciences.

Why Panama?

The Isthmus of Panama was completely formed in the Pliocene (~ 4 Ma) (Cronin et al. 1996) separating the Caribbean Sea and Pacific Ocean. Before this event, the two seas converged in the region forming the Central America Seaway (Collins 1996). The abundant fossil record in this area indicates that before the formation of the isthmus, during the Miocene, numerous shark species inhabited the area (Gillette 1984, Pimiento et al. 2009).

For this Masters research, and in collaboration with STRI and the FLMNH we collected approximately 400 new fossil shark teeth specimens from the Miocene Gatun Formation of Panama. Over the past 20 years, the Gatun Formation localities have been extensively used to

extract sediment for construction and we predict that these outcrops will soon likely be excavated completely. We therefore capitalized on this current opportunity before these fossils are no longer available for collection in the field.

This large collection has a great potential to be used not only with scientific proposes, but also, as a teaching tool for young learners. Panamanian young learners would be more appealing to learn about fossil sharks from Panama. This is what is called placed-based learning; an educational philosophy that promotes learning that is rooted in what is local. One of the strengths of this type of education is that it can adapt to the exclusive characteristics of particular places and in this way, it helps to overcome the disjuncture between school and real life (Smith G. A. 2002). Given the fact that a large percentage of young learners from Panama are bilingual, the science-engaging product should be bilingual as well, and therefore, more attractive for a broader audience around the world, which is a great advantage. English is the most used language in the Internet with 478 million users, and Spanish the third most used with 138 million users.

Another advantage of Panama is the collaboration with STRI (Smithsonian Tropical Research Institute). STRI is a bureau of the Smithsonian Institution based in Panama, dedicated to understanding biological diversity. The institute not only offers unique opportunities for long-term ecological studies in the tropics, but also different informal educational programs, including “Punta Culebra”.

Punta Culebra Marine Center is a hands-on and open-air museum for kids that is focused mainly on marine science, education, conservation and interpretation of marine coastal environments. More than 700,000 students and visitors have visited Punta Culebra since it opened in 1996, and hundreds of schools have taken part in its educational program.

The Marine Center is a place where individuals can increase their awareness and appreciation of coastal and marine environments in Panama and nearby regions of South and Central America. Its goal is to increase public understanding of Panama 's past and present coastal environments, promoting their conservation. It is also meant to show how scientific discoveries improve our understanding and deepens our appreciation of the natural world [http://www.stri.org/english/visit_us/culebra/].

STRI also offers an engaging Website, including a site specially for young learners [www.stri.org/kids] where kids can learn about the Panamanian biodiversity by doing experiments and playing games.

Front-End Evaluation: Learning from and about the Audience

Research indicates that in developing informal learning experiences, front-end evaluations can provide important information about the learners' knowledge and also gauge the program's development. Young learners from 3 to 15 years old were randomly chosen from two bilingual schools in Panama City (Figure 4-2): The Isaac Rabin and The Balboa Academy. In each school and were involved in focus groups interviews. In each school, principals asked parents for permission to have their students involved. After they received parental consent, around 10 groups of 4-6 learners answered a survey (Appendix B); their answers were archived with a voice recorder.

All questions inquired to investigate the state of knowledge on the issues intended to be addressed in the Website, what they would like to know, their misconceptions, how to make the Website attractive to them and the group of ages the Website should be addressed to. It should be noted, however, that information was not used to conduct statistical analyses in a research. The data from these surveys was used to improve the design and learning goals of the Website and are described as follows:

Young learners want to learn, by using:

- Short text
- A lot of photos and figures
- A lot of videos
- Fun fonts for texts
- Brilliant colors
- Accurate and specific information (to the point)
- A character (avatar) that can guide young learners throughout the site.
- Other linked resources, for example, Wikipedia and National Geographic

What they already know:

- What a fossil shark
- Fossil sharks teeth look darker than living sharks teeth
- What is a fossil shark
- Sharks are marine animals
- Sharks live in the sea
- Extinction is the end of a species
- Dinosaurs became extinct 65 Ma
- Megalodon is an ancient shark
- Fossil shark teeth have different colors as opposed to living sharks
- Shark skeletons are composed of cartilage
- Scientist know about ancient species because they can find their fossils

What they want to know about fossil sharks:

- How long did a shark lived?
- Different shark tooth morphologies
- How many fossil sharks are found in Panama?
- Are extant sharks in danger?
- What do sharks eat?
- What did Megalodon eat?
- Ancient shark's sizes
- Do sharks eat people?
- How did fossil sharks loose their teeth?
- How big was Megalodon?
- Who was the first shark?
- How old is the first shark?
- Where did Megalodon live?
- Where do fossil sharks come from?

Misconceptions:

- Sharks eat people
- Sharks eat only meat
- Geologic time goes to trillion years
- Evolution=improvement
- Humans are responsible for Megalodon extinction
- Dinosaurs appeared before sharks
- Fossil sharks go extinct
- Fossil means in the time of dinosaurs
- Fossils are 1000-3000 years old
- Evolution=Evolution of humans
- Sharks have infinite number of teeth
- Fossil shark teeth are 10 years old
- Fossils shark teeth are from living organisms
- Fossils shark teeth are no older than 90 years old

Websites young learners visit:

- Youtube
- Facebook
- Wikipedia
- Google
- National Geographic

Grades range: Young learners are more interested in fossil shark teeth from 2nd grade to 6th grade. Kindergarteners and 1st graders did not show too much interest. Even when older kids (from 6th to 9th grade) were interested on the subject, they were not on learning on a Website for especially made for kids. Based on this finding, in this study, the target audience is young learners from 2nd to 6th grade.

Title for the website: The title young learners like the most was: “Fossil Sharks from Panama”

Website Design**Formative Evaluation**

After the focus groups survey, I designed the four main sections in paper. STRI graphic designer (Ricardo Chong) prepared all graphs, while STRI Webmaster (Marisol Lopez) put all

the material together in a digital offline format. This first draft was then shown to a group of 6th graders after a class field trip to one of Gatun Formation's localities, where they collected and identified several fossil shark specimens. The young learners pointed out the main issues they considered could be a problem when using the Website (Figure 4-3). Some of these issues were difficulties to find some of sections and lack of guidance while navigating on the Website. Particular attention was made to their reaction when finding two languages in each text; young learners found it advantageous for their learning. Negative issues were addressed and the Website was developed [<http://stri.org/english/kids/sharks/>].

Web 2.0

Facebook: The Website is connected to Facebook throughout a page called “Fossil Sharks of Panama” with information and news about the fossil sharks and news about the Website in general. In this page, young learners also can post anything they want, including thoughts, videos, photos, songs, notes, etc. Young learners can become fans of this page; then other young learners see that in the newsfeed of their friends, and become fans as well, thus increasing the number of participants accessing the Website. Therefore, the Fossil Sharks of Panama Facebook page is also a way to promote the Website. This page is completely bilingual.

Blog: The Website has its own Blog hosted by Google. In this Blog, news about the site is posted, and young learners can respond to it with ideas, recommendations and complaints. They can also start a new subject to be discussed. The name of the Blog is: Fossil Sharks of Panama and is completely bilingual.

Wiki: The Website is linked to a Wiki hosted by Wikispaces. This is a tool where young learners can add or edit information that is also found in the Website. The idea is to have little information in the Wiki so young learners can complete it using the Website as a source of information. This Wiki called sharkspanama is also a great tool to be used in formal educational

settings (i.e. can be used as a fun assignment for kids to complete at home, for group project or as classroom activity). The Wiki have some pages in English and others in Spanish.

Youtube: Several videos are part of the Website content. All these videos are downloadable via Youtube.

Flickr: Several images are part of the Website content. All these figures and pictures are posted in Flickr where young learners can comment about them and also share them with their friends. Flickr is therefore a tool to promote the Website.

Website Sections

Every Website section covers different subjects on fossil sharks from Panama. However, all sections have common design elements, including: a cartoon (avatar) who will guide young learners while navigating on the Web; key words linked to Wikipedia; a self-assessment questionnaire where the target audience will test what they have learned, and also, questions that encourage them to do more research; links with more information and finally, video-interviews to experts in each subject. The content of each section was chosen based on the front-end survey.

Geologic time

The objective of the section is the target audience to realize the magnitude of the geologic time and recognize major evolutionary events so they can properly place in temporal context the rest of the content of the Website. This was selected as the first section because the majority of misconceptions were related with this issue. In this section, young learners will learn about the different forms of life that exist in the fossil record through the geologic time from the earliest forms that appear in the Cambrian, to the more complex forms (i.e. humans) that first appear during the Quaternary. Young learners will learn the dimension of the geologic time by comparing it with a virtual trip through the Panama Canal (Figure 4-4), where every number in

the tour represents a period; by clicking on every number, images of the forms of life that appear in these periods will be displayed.

Fossil sharks

In this section, the target audience will learn about the sharks species inhabited Panama when it was covered by water before the formation of the isthmus. The section is divided into 2 main parts. The first is an introductory section where the target audience learns about fossils in general (i.e. what they are, how they form and how they are found) (Figure 4-5A). The second section is more like a cyber-exhibit where young learners some fossil sharks taxa that have been discovered in the Gatun Formation from Panama (Figure 4-5B). Here, young learners will learn about their teeth morphology, maximum total length and diet. In addition to this, this section has a picture of a tooth of every species, a picture of the shark if it is an extinct species, or a video of the animal if it is an extant species (Figure 4-5C).

Megalodon

This section is about the biggest sharks that have ever lived: Megalodon (*Carcharocles megalodon*). The study of this species was a very important research component of this thesis. Furthermore, the front-end evaluation indicated that it is also the species that kids are more interested. In this section young learners will learn the most important facts about this fascinating creature and will clarify some misconceptions that young learners and general public may have regarding this species. The content of this section will answer the following questions: How big was it? When did it live? How long did it live? What did it eat? What did it do in Panama? Why did it become extinct? and Why is it important? (Figure 4-6).

Present and future

The objective of this section is to bring young learners back to the present and look “outside the box” to the future. Here the target audience will learn important facts about living

sharks in general, but also, they will be able to realize how threatened sharks are currently due to the harmful activities of humans. An additional and also most important objective of this section is to clarify that sharks are not man-eaters. The content of this section will answer the following questions: What is a shark? What is the origin of sharks? Where do sharks live? How do they reproduce? What do they eat? Are they dangerous to humans? and Are humans dangerous to sharks? (Figure 4-7).

Recommendations and Best Practices

In this project, I built a Website specially made for young learners. In the process, I learned a lot about this new way to communicate science, especially about 4 main issues:

Communication with the Team

As recommended by Soren (2004), the constant communication with every member of the team, helped to the appropriate development of the Website. It is important for every member to be in the same line of thinking, so the different parts of the Website are showed in a integrated way, and not like if every person had a different version of how the website should be. To avoid this, regular meetings were held at different stages of the development of the Website. During these meetings we discussed our ideas and each time a product was completed, team members were engaged in reviewed before moving to the next phase.

Keep it Simple

For the development of the Website, the simple we kept the design, the better. When doing the front-end and formative evaluations, I noticed that young learners appreciated when the format was kept simple, rather than too sophisticated. For example, when just one click reveals the question they want to answer, rather than a whole path of different clicks.

Short Texts

Keeping the texts short, was a quite a challenge. From the evaluations I learned that young learners would not read more than a paragraph and that they would prefer looking at the graphs and other pictorial presentations. In order to give them all the information in one paragraph or less, I limited that information to what I learned during the front-end evaluation about what they actually wanted to know about fossil sharks. When extra information was pertinent, the Website provided two types of links: one with more information about that topic in the segment “More info” of every section, and other to Wikipedia when I considered they needed a definition of certain word.

Evaluations Mean Everything

To know the audience’s preferences was essential for the development of this website. The interviews to young learners gave us beneficial information (such as what questions they have about sharks, what they already know, how they want to website to be, etc). This information was used to shape the design and content of the site. Without this information, I would do a completely different version of the site such for example; I would focus more on morphology of the fossil teeth. We simply do not know what young learners want, we simply cannot think as a young learner, therefore the information needed will have to be elicited from using such methods as focus groups interviews

The Future of the Website

The objective of this section of my master thesis was to present the process of developing a fun, kid-friendly and bilingual Website on fossil sharks from Panama. My goal was to achieve the broader educational impact of an activity that integrates the research and educational content of my thesis. However, this project as an outreach activity will continue to foster young learner’s curiosity and provide continued information.

Even when the website will be self-promoted throughout the different social networking applications, other plans for continuity will include a dissemination campaign to be conducted via presentations to teachers, students and parents from different schools in Panama so they can know about the site and also how to use it. A teacher's guide will be prepared with the help of middle-school educators so they can use the Website as part of their curriculum. I will also give talks about this project at professional scientific, educational, and /or museum meetings. And finally, press releases in different newspaper will be done to promote this activity.

The website will be permanently displayed in the "Culebra Nature Center." Here a panel is devoted to fossils from Panama and young learners play as paleontologists, digging out fossils and then identifying them. In the case of fossil shark teeth, they use the Website to identify the species they found and to answer guided questions, which at the same time a great venue for further research.

Summative evaluations after young learners use the Website will be conducted to reflect and evaluate the successes of the Websites for online users. Based on the findings of these evaluations, I am planning to write a manuscript to be published in a specialized journal. In addition, user statistics, feedback messages and blog, wiki, and networking activity will be a Website assessment. In addition, it will likely be necessary to update content, building different generations of sections, connect the Website with the Web 2.0 applications of the future, and to offer different levels of design to ensure that users keep coming back to the Website

A.



B.



C.



Figure 4-1. Young learners find collecting fossil sharks a fascinating subject. Families and school groups often go to collect fossil sharks teeth at Las Lomas, a well-known locality in the Gatun Formation. A. Three 4th grade learners from the Balboa Academy find a fossil shark tooth. B. Two 4th grade girls also from the Balboa Academy look for fossil sharks. C. A young enthusiast finds a shark tooth when looking for fossils with his family.

A.



B.



C.



Figure 4-2.A-C. Young learners from the Isaac Rabin School answered a survey after they observed a fossil shark tooth. They were allowed to take the tooth home.



Figure 4-3. Formative evaluation: A draft of the Website was showed to 6th grade young learners from the Balboa Academy. The children pointed out the main issues they considered could be a problem when using the Website.



Figure 4-4. Geologic Time. A virtual trip thru the Panama Canal, as an analogy of the geologic time. Every number represents a period, where 1 is the Cambrian and 11 is the Quaternary period. By clicking on every number, images of the forms of life that appear in these periods will be displayed (<http://stri.org/english/kids/sharks/tiempo.html>).

A.

1 ¿QUÉ ES UN FÓSIL?
WHAT IS A FOSSIL?

Fossils are the remains of long-dead plants and animals that were buried under many layers of earth. They have remained in the ground since. There are three types of fossils. Fossils may be the remains of the organism itself, such as a bone or piece of shell. Another type of fossil is an impression left by an organism in the ground, such as a footprint or the print of a leaf. A third type of fossil is a trace made by an animal when it was alive, a burrow made by a worm, for example.

Los fósiles son restos de plantas y animales que han quedado atrapados por muchas capas de tierra. Han permanecido en el suelo desde entonces. Hay tres tipos de fósiles. Los fósiles pueden ser restos de un animal, organismo, fragmentos de hueso por ejemplo, o el molde de un hueso hecho por los organismos cuando estaban vivos.

2 ¿CÓMO SE FORMAN LOS FÓSILES?
HOW ARE FOSSILS FORMED?

Para que la fosilización ocurra, el organismo lo parte de (a) debe ser rápido por el agua hasta enterrarse. Rápidamente en el sedimento. Luego ocurren diferentes procesos que hacen que el fósil sea diferente. Los fósiles se forman de tres maneras diferentes. (b) El organismo se convierte en un molde en el sedimento. (c) El organismo se convierte en un molde en el sedimento. (d) El organismo se convierte en un molde en el sedimento.

Un fósil puede ser un hueso, diente, caparazón o huella. (a) El organismo se convierte en un molde en el sedimento. (b) El organismo se convierte en un molde en el sedimento. (c) El organismo se convierte en un molde en el sedimento. (d) El organismo se convierte en un molde en el sedimento.

For fossilization to occur, the organism (part of it) has to be buried quickly in the sediment. This might happen during a flood or when a volcano erupts and covers a lot of land. Then chemical alterations occur. For many years, minerals are added or removed, helping to preserve the remains.

Let's think about a shark's tooth. Sharks lose their teeth as they grow new ones. The tooth falls out into the sand or mud, where it may disintegrate (a) or get buried (b). Chemical processes may dissolve the tooth and it would not become a fossil (c). Or the mineral from the sediment or water might fill empty spaces in the tooth, which would cause the tooth to turn to rock and become a fossil (d). This process takes thousands of years. The tooth can be different colors depending on which minerals are absorbed. After many years, if the ground where the tooth is buried is eroded, we might find the fossil tooth.

3 ¿CÓMO LOS ENCONTRAMOS?
HOW CAN WE FIND FOSSILS?

Por lo general, los fósiles de dientes de tiburón se encuentran en sedimentos arenosos, limosos o arcillosos en el mar. En Panamá, los fósiles de dientes de tiburón se encuentran en el mar. En Panamá, los fósiles de dientes de tiburón se encuentran en el mar. En Panamá, los fósiles de dientes de tiburón se encuentran en el mar.

Generalmente, los fósiles de dientes de tiburón se encuentran en sedimentos arenosos, limosos o arcillosos en el mar. En Panamá, los fósiles de dientes de tiburón se encuentran en el mar. En Panamá, los fósiles de dientes de tiburón se encuentran en el mar.

When you're looking for a fossil shark tooth, you have to look all over the area, looking closely at the ground. Sometimes, you can get a tooth because it is shiny.

B.



C.

TIBURÓN TORO
BULL SHARK

"*Carcharhinus leucas*"

15 Million years ago to present
Millones de años al presente

Fossil Teeth/Dientes Fósiles: Triangular, finely serrated crowns; serrations become coarser near the base of crown. U-shaped root/Triangular, corona finamente aserrada, serraciones más gruesas en la base de la corona, raíz en forma de U.

Length/Tamaño: 3.5 m max

Diet/Dieta: Smaller sharks and other fishes/Tiburones pequeños y otros peces

Bull Sharks
★★★★★

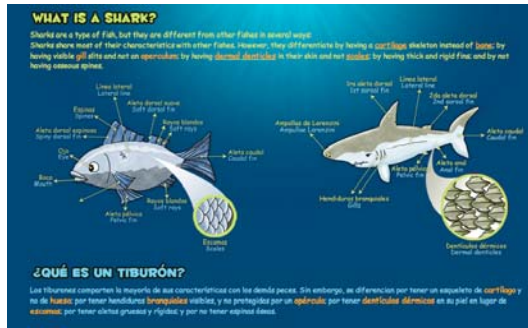
0:00 / 2:52

Figure 4-5. Fossils. A. In this section young learners learn what is a fossil, how they are formed and how can they be found. B. Some of the 16 taxa that were identified in the Gatun formation during this research. C. Information about every species: time range, tooth morphology, maximum total length and diet (http://stri.org/english/kids/sharks/acerca_fosiles.html).

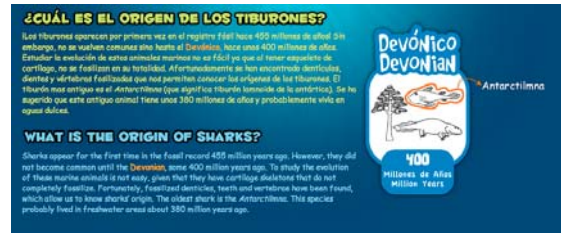


Figure 4-6. Megalodon. A. Size. B. Time Range. C. Longevity. D. Diet. E. Nursery Area in Panama. F. Extinction. G. Importance (http://stri.org/english/kids/sharks/megalodon_intro.html).

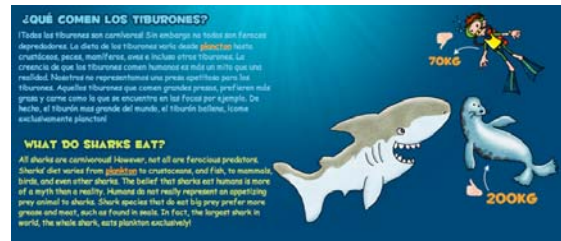
A.



B.



D.



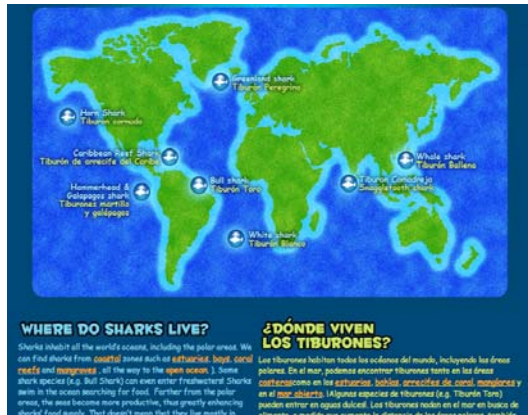
C.



F.



E.



G.



Figure 4-7. Sharks Present and Future. A. Definition. B. Origin. C. Reproduction. D. Diet. E. Habitats. F. Danger to humans. G. Threats
(http://stri.org/english/kids/sharks/presFut_intro.html).

CHAPTER 5

GENERAL CONCLUSIONS

This study contributes to the understanding of the ancient selachian biodiversity during the late Miocene of Panama, expanding our knowledge of the ichthyofauna of the Gatun Formation. Our field discoveries, further analysis of existing collections and taxonomic identifications, indicate that the sharks from this unit consist of a relative diverse assemblage of at least 16 taxa, including four species that are extinct today.

The remaining portion of the total selachian biodiversity has taxonomic affinities with modern taxa, and indicate relatively long-lived species. These taxa demonstrate stasis for several million years and at least their tooth morphology remains similar to extant individuals. They survived the formation of the Isthmus of Panama, as opposed to several other species of that became extinct due to the effects of this event.

Based on the known habitat preferences for modern selachians analog assemblages, the Gatun sharks were primarily adapted to shallow waters (i.e., between about 20 to 40 m depth) within the neritic zone. This paleodepth assessment is also consistent with previous interpretations based on the extensive marine invertebrate fauna from the Gatun Formation. Furthermore, in comparison with modern species, we infer that the Gatun shark fauna has mixed Pacific-Atlantic (Caribbean) biogeographic affinities due to its central location between two ancient ocean basins. However, one species (*Carcharhinus perezii*) became restricted to the Caribbean Sea after the Isthmus closed.

The comparisons of Gatun dental measurements with older and younger formations containing similar biodiversity suggest that many of the species have an abundance of small individuals. This discovery is very interesting because based on extant species, juvenile sharks

use shallow environments as nursery areas similar to those interpreted to have existed in the late Miocene Gatun Formation.

Although not very common, one of the species present in the Gatun Formation, *Carcharocles megalodon* has surprisingly small fossil teeth. This extinct shark was the biggest shark that ever lived. In this study I carefully studied *C. megalodon* dentition found in the Gatun Formation and calculated the total length of all *C. megalodon* individuals based on their crown height to estimate the life stage based on overall body size. These results confirm that the *C. megalodon* individuals from Gatun were mostly juveniles and neonates, with estimated body lengths between 2 and 14 meters. I therefore propose the Gatun Formation as a paleo-nursery area for young *C. megalodon*.

Previous paleo-nursery areas proposed for this species were mostly anecdotal and based on the presence of juvenile fossil teeth accompanied by fossil marine mammals. However, none of these were subjected to rigorous analyses. In contrast, the life stage of Gatun's individuals was not only inferred based on their body lengths in this study, but also the tooth sizes from this formation was compared with those found in older and younger formations to determine if the small size observed is unique to the species during the late Miocene.

I found that there is no tendency for increased size in *C. megalodon* over time, and that the small size observed in the Gatun Formation is therefore not related to microevolutionary shifts in body size or with the tooth position within the jaw. Finally I conclude that *C. megalodon* from the Gatun Formation fed on the abundant fishes occurring in this shallow environment and that the small size observed is not due to a scarcity of large prey items.

The results obtained in this research, along with previous knowledge of the paleoecology of the Gatun Formation (a shallow-water productive marine environment) demonstrate that the

Gatun Formation was used as a nursery area during the late Miocene by *C. megalodon*, and consequently show that sharks have used nursery areas for millions of years as an adaptive strategy during their life histories; extending the timing of this behavior based on the fossil record.

For this Masters research, and in collaboration with STRI and the FLMNH we collected a total of approximately 400 new fossil shark teeth specimens from the Miocene Gatun Formation of Panama. This large collection has the great potential to be used not only for scientific research, but also as a teaching tool for young learners. Evaluations of audience preferences in museums have revealed that fossil sharks are very attractive for young learners. Additionally, fossil shark teeth permit the understanding of the composition of ancient faunas as well as the environmental conditions that helps the public to comprehend the climate changes that have occurred during earth history, and therefore allows understanding numerous important STEM concepts of natural sciences.

In addition to the scientific research conducted during this master project, a broader impact deliverable was produced. A kid-friendly and bilingual website about fossil sharks from Panama: “Fossil sharks from Panama” [<http://stri.org/english/kids/sharks/>], was developed with a target audience of young learners to engage them to science. The site was designed to create a quality online experience based on evaluations to different-aged young learners and following the best practices.

The website incorporates different Web 2.0 applications, as well as four main sections that covers different subjects on fossil sharks from Panama. All sections have common design elements, including: a cartoon (avatar) who guides young learners while navigating on the Web, key words linked to Wikipedia, a self-assessment questionnaire, links with more information and

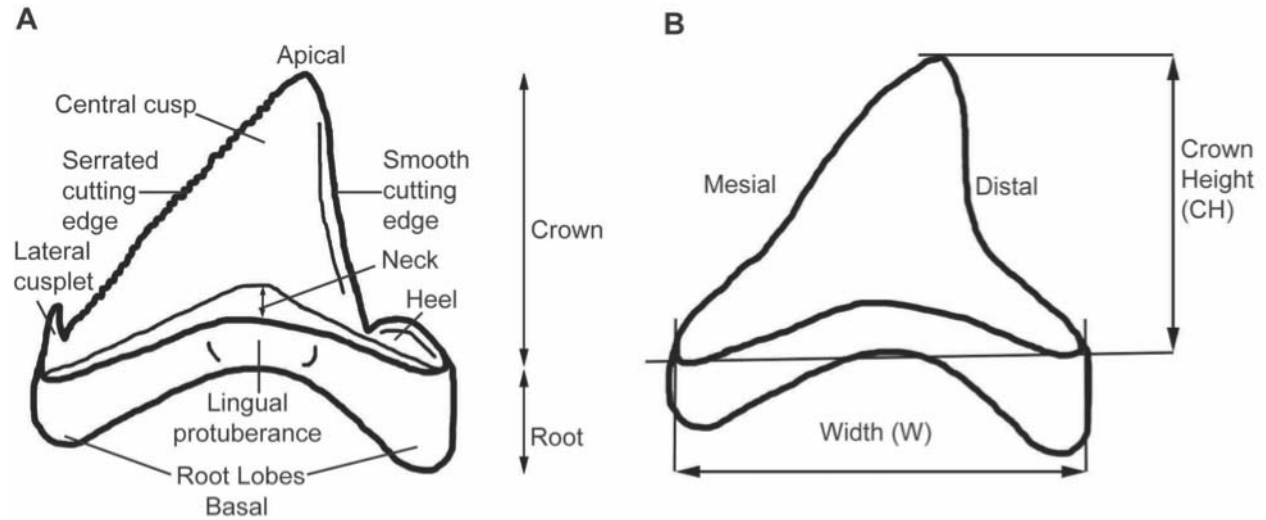
finally, video-interviews with experts in each subject. In the different sections, young learners learn about: (1) geologic time, (2) major evolutionary events, (3) general concepts about fossils, (4) ancient sharks that inhabited Panama before the formation of the isthmus (teeth morphology description, total length of the animal and diet), (5) important facts about Megalodon (what it ate, how big was it, how long did it lived, why did become extinct, etc.), and (6) living sharks (what is shark, what do they eat, how they reproduce, etc.).

In summary, this master's research contributes to the understanding of the systematics, paleobiology, and paleoecology of late Miocene sharks from panama and integrates an educational component, conveying scientific knowledge to the general public, and particularly children, hopefully engaging them in science learning.

APPENDIX A
CHAPTER 2 TOOTH DIAGNOSTIC CHARACTERS AND DIMENSIONS

A. Tooth diagnostic characters as these pertain to the fossil sharks described in this study.

B. Tooth measurement codes and dimensions.



APPENDIX B
CHAPTER 2 DATA

Extant shark species occurring in Isthmus of Panama. * Indicates species also present in the Gatun Formation fossil record.

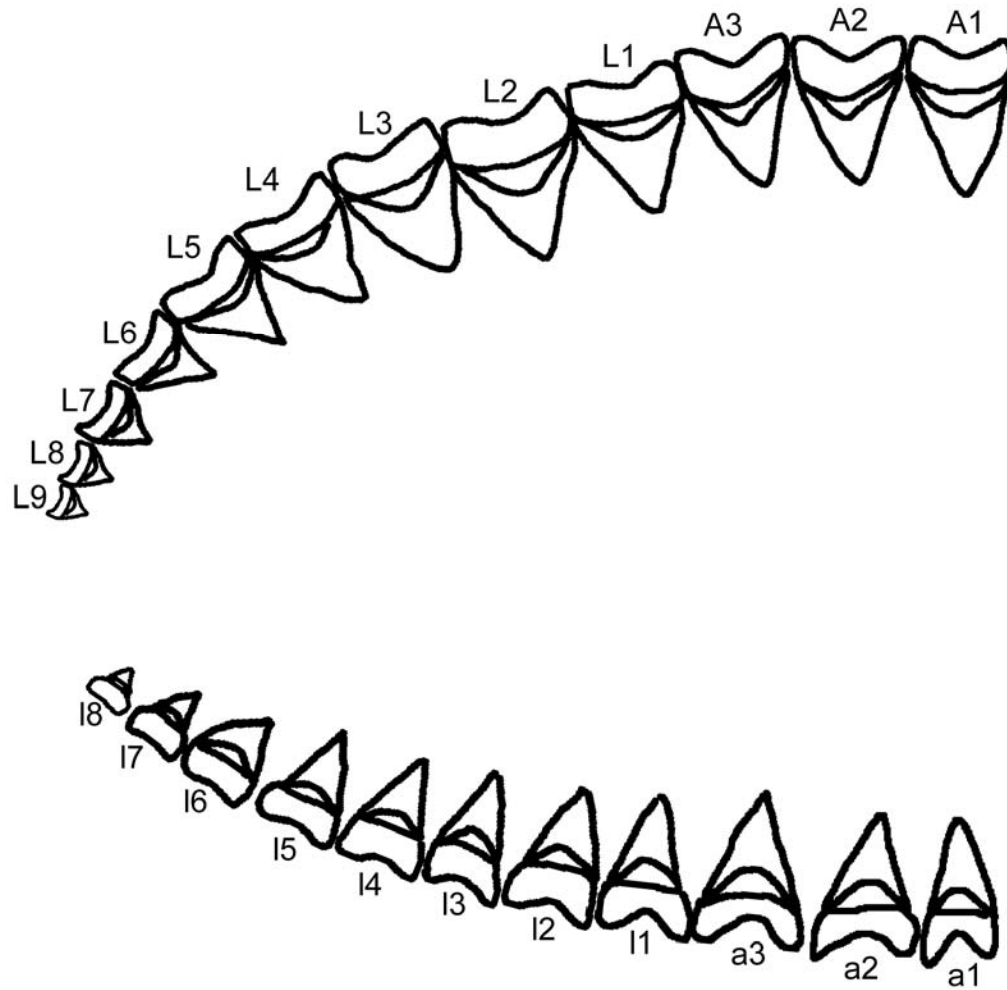
Species	Common name	Distribution
<i>Alopias pelagicus</i>	Pelagic thresher	Pacific
<i>Alopias superciliosus</i>	Bigeye thresher	Caribbean/Pacific
<i>Alopias vulpinus</i>	Thresher shark	Caribbean/Pacific
<i>Carcharhinus acronotus</i>	Blacknose shark	Caribbean
<i>Carcharhinus albimarginatus</i>	Silvertip shark	Pacific
<i>Carcharhinus altimus</i>	Bignose shark	Caribbean
<i>Carcharhinus falciformis</i> *	Silky shark	Caribbean/Pacific
<i>Carcharhinus galapagensis</i>	Galapagos shark	Pacific
<i>Carcharhinus leucas</i> *	Bull shark	Pacific/Caribbean
<i>Carcharhinus limbatus</i>	Blacktip shark	Pacific and Caribbean
<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	Pacific and Caribbean
<i>Carcharhinus obscurus</i> *	Dusky shark	Pacific/Caribbean
<i>Carcharhinus perezii</i> *	Caribbean reef shark	Caribbean
<i>Carcharhinus porosus</i>	Smalltail shark	Caribbean/Pacific
<i>Carcharhinus plumbeus</i> *	Sandbar shark	Caribbean/Pacific
<i>Carcharias taurus</i>	Sand tiger shark	Caribbean
<i>Carcharodon carcharias</i>	Great white shark	Caribbean/Pacific
<i>Galeocerdo cuvier</i> *	Tiger shark	Pacific/Caribbean
<i>Ginglymostoma cirratum</i>	Nurse shark	Pacific/Caribbean
<i>Heptranchias perlo</i>	Sharpnose sevengill shark	Caribbean/Pacific
<i>Heterodontus mexicanus</i>	Mexican hornshark	Pacific
<i>Heterodontus quoyi</i>	Galapagos bullhead shark	Pacific
<i>Isurus oxyrinchus</i>	Shortfin mako	Caribbean/Pacific
<i>Mustelus canis</i>	Smooth dogfish	Caribbean
<i>Mustelus dorsalis</i>	Sharptooth smooth-hound	Pacific
<i>Mustelus minicanis</i>	Houndshark	Caribbean
<i>Mustelus norrisi</i>	Narrowfin smooth-hound	Caribbean
<i>Mustelus lunulatus</i>	Brown smooth-hound	Pacific
<i>Nasolamia velox</i>	Whitenose shark	Pacific
<i>Negaprion brevirostris</i> *	Lemon shark	Pacific/Caribbean

Appendix B Continued.

Species	Common name	Distribution
<i>Odontaspis ferox</i>	Smalltooth sand tiger	Caribbean/Pacific
<i>Prionace glauca</i>	Blue shark	Caribbean/Pacific
<i>Pseudocarcharias kamoharai</i>	Crocodile shark	Caribbean/Pacific
<i>Rhincodon typus</i>	Whale shark	Caribbean/Pacific
<i>Rhizoprionodon lalandei</i>	Brazilian sharpnose shark	Caribbean
<i>Rhizoprionodon longurio</i>	Pacific sharpnose shark	Pacific
<i>Rhizoprionodon porosus</i>	Caribbean sharpnose shark	Caribbean
<i>Rhizoprionodon terraenovae</i>	Atlantic sharpnose shark	Caribbean
<i>Sphyrna mokarran</i> *	Great hammerhead	Caribbean/Pacific
<i>Sphyrna tiburo</i>	Bonnethead	Caribbean/Pacific
<i>Sphyrna tudes</i>	Smalleye hammerhead	Caribbean/Pacific
<i>Sphyrna zygaena</i>	Smooth hammerhead	Caribbean/Pacific
<i>Sphyrna corona</i>	Scalloped bonnethead shark	Pacific
<i>Sphyrna lewini</i> *	Scalloped hammerhead shark	Caribbean/Pacific
<i>Sphyrna media</i>	Scoophead shark	Caribbean and Pacific
<i>Triaenodon obesus</i>	Whitetip reef shark	Pacific

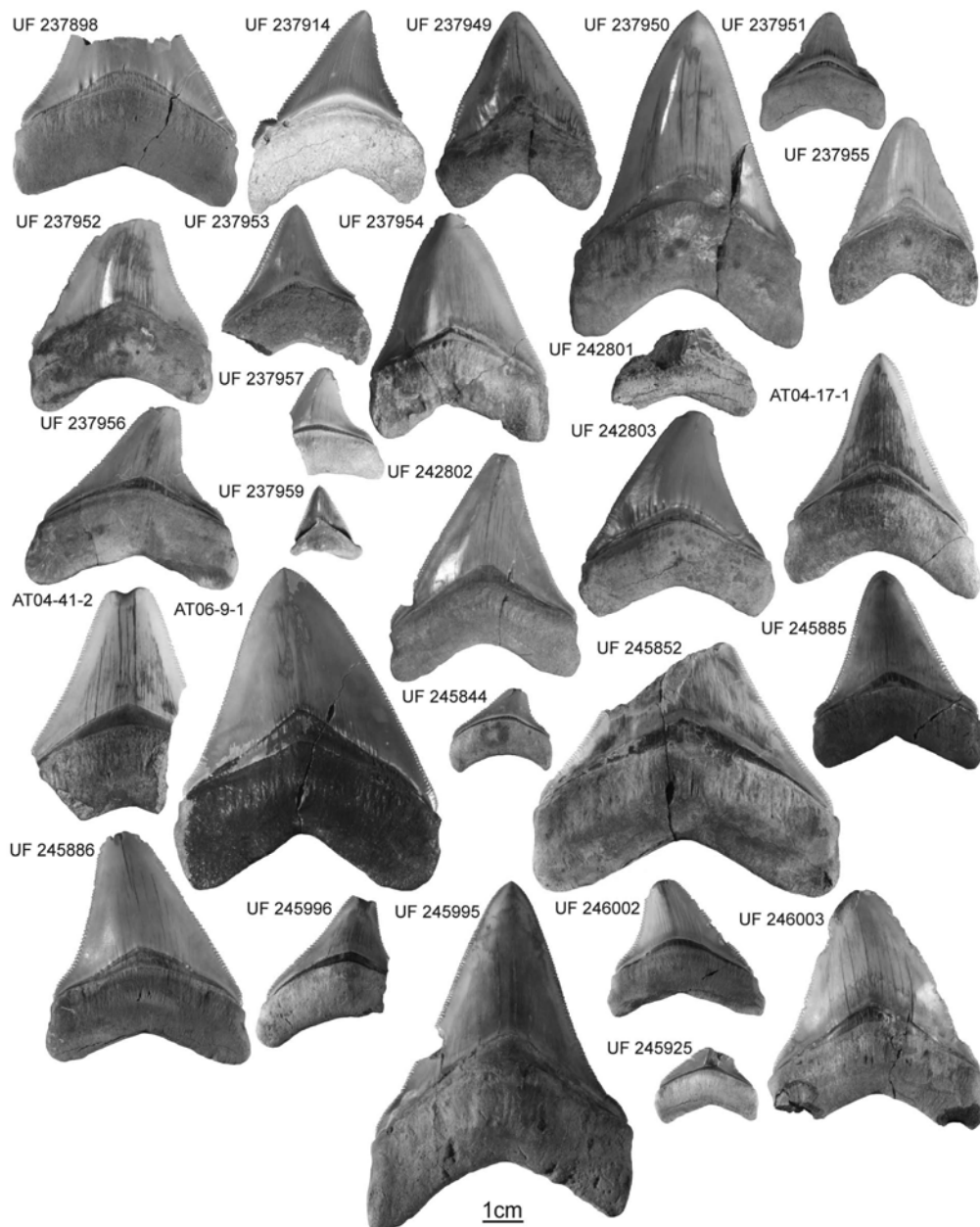
APPENDIX C
CHAPTER 3 REPRESENTATION OF A *CARCHAROCLES MEGALODON* DENTITION

Tooth size and shape varies greatly within the jaw. Left side, adapted from Gottfried et al. (1996).



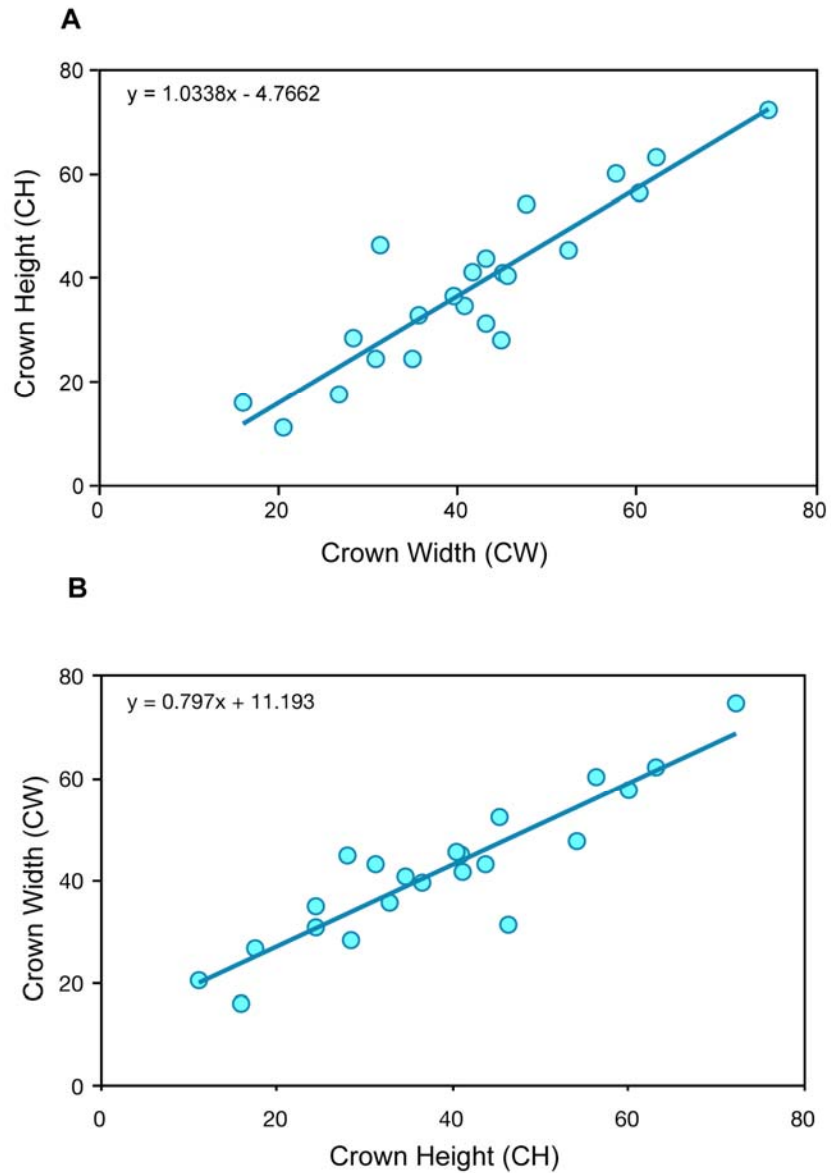
APPENDIX D CHAPTER 3 *CARCHAROCLES MEGALODON* COLLECTION FROM THE GATUN FORMATION

The 28 *Carcharocles megalodon* specimens collected with its collection number. CTPA 6671 was not available to photograph.



APPENDIX E
CHAPTER 3 LINE REGRESSIONS FOR TOOTH MEASUREMENTS.

A. Known CW. Line regression calculated when is possible to measure the CW (i.e. CW in the x or independent axes) but the CH is unknown due to fossil preservation. B. Known CH. Line regression calculated when is possible to measure the CH (i.e. CH in the x or independent axes) but the CH is unknown due to fossil preservation.



APPENDIX F
CHAPTER 3 MEASUREMENTS FROM BONE VALLEY FORMATION

Carcharocles megalodon isolated teeth measurements, from the Bone Valley Formation,
Florida, USA.

Specimen	CW (mm)	CH (mm)
UF 217225	69.8	67.3
UF 300	70.7	73.7
UF 234583	79.8	81.1
UF 217140	78.7	75.2
UF 209170	59.8	55.8
UF 228480	56.5	50.6
UF 17850	53.4	49.4
UF 17980	44.0	47.0
UF 17850	48.9	46.1
UF 228479	46.1	42.8
UF 209164	46.4	40.7
UF 17839	37.2	32.5
UF 17839	33.7	30.8
UF 24715	46.4	45.9
UF 24715	41.4	44.6
UF 24715	43.1	41.3
UF 24715	38.4	38.2
UF 24715	33.2	35.6
UF 24715	43.7	31.9
UF 17872	54.0	45.8
UF 17872	44.9	38.3
UF 17872	40.0	31.4
UF 17872	36.2	33.6
UF 17872	46.2	36.1
UF 17872	34.1	35.4
UF 17872	31.9	20.8
UF 17872	25.8	24.6
UF 17872	26.6	23.4
UF 17872	31.5	31.7
UF 55973	38.7	35.2
UF 55973	35.1	29.6
UF 17840	46.9	42.1
UF 17840	33.2	27.0

Appendix F Continued.

Specimen	CW (mm)	CH (mm)
UF 17840	40.3	35.0
UF 17840	21.8	16.6
UF 132595	33.3	35.2
UF 132588	31.7	29.4
UF 132593	30.3	33.4
UF 229807	33.4	33.7
UF 229804	29.9	20.8

APPENDIX G
CHAPTER 3 MEASUREMENTS FROM THE CALVERT FORMATION

Carcharocles megalodon isolated teeth, from the Calvert Formation, Maryland, USA.

Specimen	CW (mm)	CH (mm)
USNM 457364	32.2	26.9
DJB 2152	55.8	36.0
USNM 494369	44.4	45.0
USNM 489141	55.5	47.1
USNM 475347	52.3	48.8
USNM unnumbered	67.7	63.9
USNM 489136	86.8	68.1
USNM 494370	102.6	71.8
DJB 1029	27.1	26.6
DJB 1566	29.4	26.2
USNM 489137	43.9	45.6
DJB 850	57.3	55.5
DJB 1860	64.5	52.7
DJB 1933	62.2	79.9
DJB 1766	36.8	34.6
DJB 1061	36.0	29.8
DJB 1564	35.6	33.9
ACC NO. 418873	30.1	19.8
ACC NO. 413905	43.6	35.6
DJB 1975	59.8	55.6
DJB 934	26.9	21.4
DJB 2009	25.0	17.5
R.O. 411148	32.3	21.3
USNM unnumbered	47.1	33.5
USNM 475303	34.4	38.1
USNM 475306	39.8	30.5
USNM 475299	30.4	33.0
USNM unnumbered	23.7	24.8
USNM 475304	30.7	36.8
USNM 473302	31.3	30.2
USNM 475290	30.6	27.4
USNM475297	34.0	19.3
DJB 2090	67.8	68.8
USNM4 95294	39.5	38.1
PAL 535357	32.1	27.6

Appendix G Continued.

Specimen	CW (mm)	CH (mm)
USNM 26189	36.3	39.8
USNM 171153	59.7	47.6
USNM 171156	73.8	50.8
USNM 24956	23.8	22.1
USNM 24956	61.2	52.7
USNM 171182	35.9	31.3
USNM 337208	39.1	26.4
USNM 171170	22.3	14.8

APPENDIX H
CHAPTER 3 MEASUREMENTS JUVENILE TOOTH SET

Juvenile *Carcharocles megalodon* associated tooth set, from the Bone Valley Formation,
Florida, USA.

Position*	CW (mm)	CH (mm)
A1	82.7	82.3
A2	78.8	75.4
A3	76.7	80.2
L1	77.6	79.2
L2	77.5	87.8
L3	73.7	81.6
L4	68.2	71.7
L5	53.7	62.2
L6	36.3	50.6
L7	32.2	48.2
L8	19.9	34.1
L9	14.2	21.0
a1	68.7	59.8
a2	72.0	67.9
a3	74.0	64.7
l1	67.2	63.0
l2	67.7	66.8
l3	63.1	65.8
l4	55.8	63.9
l5	46.7	58.8
l6	34.4	48.4
l7	21.3	32.8
l8	10.8	22.2

* For position details, see Appendix C

APPENDIX I
CHAPTER 3 MEASUREMENTS ADULT TOOTH SET

Adult Carcharocles megalodon associated tooth set, from the Yorktown Formation,
North Carolina, USA.

Position*	CW (mm)	CH (mm)
A1	107.3	104.6
A2	105.6	102.2
A3	103.5	99.3
L1	114.3	100.2
L2	112.3	97.8
L3	110.4	98.3
L4	109.0	95.7
L5	109.5	85.6
L6	89.7	64.6
L7	63.7	37.5
L8	56.8	28.3
L9	40.9	14.8
a1	84.5	81.8
a2	96.7	85.5
a3	95.0	91.0
l1	96.2	88.0
l2	90.5	83.6
l3	89.6	81.0
l4	90.0	75.5
l5	79.8	59.3
l6	62.3	39.0
l7	49.3	31.1
l8	39.3	15.6

* For position details, see Appendix C.

APPENDIX J
CHAPTER 3 TOTAL LENGTH

Total length regression based on CH of every tooth position, Shimada (2003).

Position	Regression Equation (x=CH)
A1	TL= 5.234+11.522x
A2	TL= -2.16+12.103x
A3	TL= 19.162+15.738x
L1	TL= 5.54+14.197x
L2	TL= 4.911+13.433x
L3	TL= 0.464+14.550x
L4	TL= 5.569+17.658x
L5	TL= -5.778+26.381x
L6	TL= -71.915+50.205x
L7	TL= -8.216+14.895x
L8	TL= -7.643+13.597x
L9	TL= -10.765+17.616x
a1	TL= -8.216+14.895x
a2	TL= -7.643+13.597x
a3	TL= -10.765+17.616x
l1	TL= 9.962+17.437x
l2	TL= 1.131+19.204x
l3	TL= -30.947+25.132x
l4	TL= -51.765+35.210x
l5	TL= -73.120+55.262x
l6	TL= -117.456+96.971x
l7	TL= -64.732+138.350x
l8	TL= -137.583+231.411x

APENDIX K
CHAPTER 4 FOCUS GROUP SURVEY

Objectives

1. To identify what they know about fossil sharks and misconceptions.
2. To know what misconceptions and knowledge do they have regarding concepts such as biodiversity, extinction, evolution, conservation and the nature of science.
3. To realize what to the want to know about fossil sharks
4. To find out the appealing features of the website that will cause they to enter.
5. To receive additional unanticipated (open-ended) feedback from the children as a result of the focus group brainstorming.

Assent Script—Parent or Guardian of Minor

My name is [insert interviewer's name] and I am conducting a survey about web site on fossil sharks that I'm planning to develop for the summer of 2009. Can I ask you some questions?

This survey should take about 5 minutes to complete. All questions are answered anonymously.

You do not have to answer any questions that you do not wish to answer. This is a voluntary survey, so you may withdraw from it at any time without consequences.

Procedure

Receive parental approval

Select various groups of 3-5 kids from different ages.

Record the ages and grade.

Give them a fossil shark tooth.

Ask:

1. What is it? If don't know, explain it is a fossil shark teeth [O1]
2. What is a shark? [O1]
3. Where do they live? [O1]
4. What do sharks eat? [O1]
5. What is a fossil shark? [O1]
6. How old do you think are these teeth? [O1]
7. What comes to your mind when you hear the world evolution? [O2]
8. What came first dinosaurs, sharks or humans? [O2]
9. Why do scientists say that some sharks are in danger of extinction? [O2]
10. How scientists know that? [O2]

11. What do you like to know about fossil sharks? [O3]
12. What you think is cool about fossil sharks? [O3, O4, O5—also elsewhere]
13. Where do you learn about fossil sharks? In the web? [O4]
14. What web sites do you visit? Why? [O4, O5]
15. I am developing a kids' web site on fossil sharks—what do you think I should have on it?
16. What should it be called? [O4]

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BIOGRAPHICAL SKETCH

Catalina Pimiento is a Colombian biologist. She has worked with sharks since 2002; first in Mexico, where she did her undergraduate thesis on the population ecology of the whale sharks that occur in the Contoy National Park in the Mexican Caribbean. For the last 5 years, Catalina has worked in Panama at the Smithsonian Tropical Research Institute, where she first worked at the Naos Marine Laboratory studying the migration patterns of whale sharks in Las Perlas Archipelago and the Central Pacific Ocean; and then at the Center for Archeology and Paleoecology (CTPA) as a laboratory assistant. Catalina is currently a biology graduate student at the University of Florida with a minor in Science Education. She works as a researcher-curator of Florida Museum of Natural History. Her current research has two main components, in one she studies the paleoecology of fossil sharks from Panama and in the other component, she develops Internet tools to engage children to science. After attending her first paleontology meeting, the Discovery Channel News Website published a report about her research on the nursery area for the Megalodon in the Miocene of Panama. After she finishes her master, Catalina is looking forward to keep working not only on shark's paleoecology, evolution, biodiversity, development, migrations routes, and conservation; but also on the delivering scientific information to children.