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Leann Michele Hubiak

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Porters Landing, Effingham County, Georgia

by

Leann Michele Hubiak

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Abstract

Porters Landing is an early Miocene fossil site located on the Savannah River in Effingham County, Georgia. Two fossiliferous units have good outcrops at Porters Landing, the Marks Head Formation and the Porters Landing Member of the Parachucla Formation, both within the Hawthorn Group. An age of 23 to 18 million years has been determined for Porters Landing. The Porters Landing Member, the older of the units, has an Aquitanian age (23 to 21 Ma). The Marks Head Formation is upper Burdigalian (18 Ma).

The site is rich in vertebrate fossil material, especially cartilaginous and bony fishes (Chondrichthyes and teleosts, respectively). The chondrichthyans are represented by 20 taxa including 14 taxa of sharks. The most abundant sharks are *Carcharhinus* spp., *Physogaleus latus,* and *Rhizoprionodon terraenovae*. Of the 7 taxa of batomorphs (skates, rays, and guitarfish), *Dasyatis* sp. and *Rhynchobatus pristinus* are the most abundant. A total of 6 teleost taxa were identified, with cf. *Pogonias* sp. and *Sphyraena* sp. being the most abundant.

Porters Landing represents a subtropical to tropical nearshore marine. This is confirmed by comparisons with age-equivalent sites from the Atlantic Coastal Plain. Faunal similarity was calculated, using the Simpson Coefficient between Georgia and early

Miocene vertebrate localities from the following states: Delaware, Maryland, North Carolina, and Florida. The paleoecology of these sites corroborated with the findings at Porters Landing.

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Introduction

Introduction and Significance of the Study

Paleontological information is available for five early Miocene fossil vertebrate localities along the western Atlantic Coast from Delaware, Maryland, North Carolina, and Florida. Preliminary work at an early Miocene site in Georgia, Porters Landing, reported the presence of fishes, marine mammals and reptiles, and terrestrial mammals (Pratt and Petkewich, 1989). However, early Miocene vertebrate assemblages or paleoecology of such assemblages in coastal Georgia are essentially unknown. Therefore, there exists minimal information on early Miocene fish populations from the southeastern United States.

The early Miocene (approximately 24 to 16 million years ago) was a turning point in the climatic history of the earth. Changes in deep-water circulation were contributing to a cooling trend accompanied by the development of ice sheets (Kennett, 1995). Relatively warm, equable waters were becoming more temperate and relatively cooler. A study of the early Miocene in coastal Georgia contributes to the understanding of the impact of these climatic changes on the aquatic environment. Paleontological analyses of fossil fish from Porters Landing, Georgia will address issues of community composition, relative abundance of organisms, and environmental conditions during a time of climatic fluctuations. Studies of the Porters Landing fossils will supplement data from contemporaneous sites along the western Atlantic Coast.

Although extensive research has been done on fossil fish, the incomplete nature of the fossil record prohibits a full understanding of the evolution of these organisms. Fossils are the preserved remains or traces of formerly living organisms. Depositional conditions at the time of death and burial in sediments must be ideal, limiting degradation of the dead organism. Soft parts of the body (i.e. tissue, muscle, hair, feathers) are rarely preserved in the fossil record as these portions decay very quickly (Benton, 1997). Skeletal remains and other hard parts (teeth, dermal spines, dermal scales) are usually reinforced with inorganic materials which protect them against degradation.

Most of the specimens recovered from Porters Landing are either isolated (i.e. disarticulated and fragmented) teleost (bony fish) skeletal material or chondrichthyan (sharks, rays) teeth. Teleost teeth, vertebrae, and spines are often difficult to identify due to size, wear, and degree of similarity between species. Some taxa and elements are more diagnostic than others. It is these elements that comprise the identifiable fauna at Porters Landing. Chondrichthyan specimens are most often isolated teeth and occasionally vertebrae. Since chondrichthyans are the most abundant identifiable fossil elements at Porters Landing and comprise the major topic of this study, I have included a brief review of their fossil history.

The specific objectives of my research are four-fold: 1) Identify fossil fish specimens from Porters Landing, in particular chondrichthyans, to the lowest possible taxonomic level; 2) Quantify the relative abundances of identified taxa; 3) Analyze the paleoecology of Porters Landing; and 4) Make comparisons with age-equivalent sites along the western Atlantic Coast.

The Chondrichthyan Fossil Record

Chondrichthyans, including modern sharks and rays, have internal skeletons of hard, gristly collagen proteins (Lineaweaver and Backus, 1970). Their cartilaginous skeletons may be reinforced with minute crystals of calcium carbonate or calcium phosphate. Therefore, hard bony scales, spines, and teeth comprise the majority of the chondrichthyan fossil record (Lineaweaver and Backus, 1970). It is primarily the isolated but numerous, well preserved teeth that have contributed most to the study of fossil sharks and rays.

The outer surface of shark teeth is covered with enameloid, a highly mineralized, hard, shiny material similar in composition to enamel (Cappetta, 1987). The presence of enameloid on the surface of shark teeth protects them from degradation once they are shed. Additionally, the abundance of teeth produced by one shark from birth through maturation is quite numerous (Moss, 1967). This in part accounts for the large quantity of shark teeth in marine faunal assemblages.

In chondrichthyans, teeth develop on the medial surface of the jaw and are continually replaced throughout life (Applegate, 1965). They may increase in size and/or change in morphology as the shark ages, and teeth also vary in size according to position in the jaw. This type of morphologic change related to growth or development is known as ontogenetic heterodonty (Compagno, 1988). Naturally, it is common for sharks to possess relatively small teeth at early stages of ontogenetic development with each successive tooth becoming larger.

A file of each tooth type is housed in the mouth at one time. As teeth mature and are lost, the whole row of teeth (one tooth of each position) rotates into lateral position, similar to a conveyer belt (Figure 1). Nutrients are supplied to the tooth for up to a few weeks (Maisey, 1996). Eventually those nutrient supplies are cut off from the anchoring root, causing the surrounding gum tissue to die. Teeth fall out and are very quickly replaced. The continual replacement of teeth throughout the lifetime of an individual results in isolated teeth preserved in the fossil record. Isolated specimens are often found as beach float or are reworked, lacking associated strata for further evaluation (Gottfried, 1993). Fortunately, this is not the case at Porters Landing, as specimens have been preserved *in situ*. This is supported by identification of species that are restricted to the early Miocene plus lack of evidence of sediment reworking.

Some chondrichthyans, the Batomorphs, have a spine associated with their tail region. The spine is a core of dermal dentine covered with enameloid (Nelson, 1994). The enameloid preserves the spine from degradation just as it protects teeth. Spines are part of the batomorph fossil record but are not distinctive enough to be identified to species or even genus. In addition, most chondrichthyans are covered with microscopic dermal denticles that have been preserved (Nelson, 1994). Some batomorphs also have enlarged dermal ‘thorns’ of dentine and enameloid embedded in their skin. These can be common fossils but like the spine, denticles are not identifiable.

When doing a faunal analysis, not only is it important to determine the presence and abundance of an organism but it is necessary to evaluate the stratigraphic context from which the fossil was collected. To better understand the evolution of an organism and the history of the Earth, one must interpret the fossil record with great care. It is through efforts associated with extensive fossil recoveries that paleoecology of extinct species can be determined. Following meticulous analysis and examination, fossil chondrichthyans have been described, identified, and used to study phylogenetic relationships (Maisey, 1984; Cappetta, 1987).

Origin and Classification of Chondrichthyans

The two extant groups of jawed fishes are the classes Chondrichthyes and Osteichthyes. Chondrichthyans may have the earliest fossil record of the jawed fishes, dating to the late Ordovician Period (Maisey, 1996). Microscopic dermal scales indicate an origin of at least 450 million years before present (Ma). The fossil record of other jawed fish only goes back as far as the Silurian Period. Thus, chondrichthyans were widespread even before the Devonian Period, the so called "Age of Fishes".

The first great radiation of chondrichthyans (specifically early sharks)occurred in the Devonian, between 400 and 350 Ma. It was then that the Chondrichthyes diverged into the subclasses Elasmobranchii and Holocephali (Carroll, 1988). There have been additional chondrichthyan radiations, including one during the Carboniferous (Maisey, 1996). Chondrichthyans reached a level of modern evolution, as a group, in the late Cretaceous. However, the oldest record of modern chondrichthyan families are fossils recovered from lower and middle Jurassic rocks (Maisey, 1996). By the late Jurassic, approximately 200 Ma, most modern families were represented.

Skates, rays, and guitarfish are classified as batomorphs and may be the sister taxon to saw sharks (Family Pristiophoridae) (Nelson, 1994). They are a close relative to sharks, placed within the Superorder Batomorphii (same as Rajiformes of Nelson, 1994). Batomorphs evolved during the Jurassic (Maisey, 1996). Following the Jurassic, many new groups of skates and rays appeared during the Cretaceous and Paleogene. The four recognized orders are divided into 12 families and 62 genera with approximately 456 species (Nelson, 1994). Table 1 shows the classification of the batomorphs. Skates (Family Rajidae) first appeared in the early Cretaceous along with sawfish (Family Pristidae) (Maisey, 1996). The fossil record of stingrays (Family Dasyatidae) suggests that they first became abundant in the early Cretaceous. Eagle rays (Family Myliobatidae) were common by the Eocene (Maisey, 1996).

Based on a series of derived features, all living chondrichthyans (sharks, skates, rays) and some Mesozoic and Cenozoic fossil species are classified in the Subcohort Neoselachii (Table 1). Derived from an ancient group of Paleozoic chondrichthyans, neoselachians inhabited late Mesozoic waters and gave rise to modern genera (Carroll, 1988). Extant sharks, skates, and rays belong to nine recognized orders within the

Superclass Gnathostomata, Grade Chondrichthimorphi, Class Chondrichthyes, Subclass Elasmobranchii with nine recognized orders (Nelson, 1994). A classification of the orders identified at Porters Landing is given in Table 1. The estimated 1000 living species of sharks, skates and rays are classified into 164 genera and 42 families (Nelson, 1994). Due to discovery of new species plus reorganization of established taxa, classification is constantly changing.

The classification of elasmobranchs has been based primarily on the morphology of modern species, but their phyletic relationships are difficult to interpret. By comparing extinct to extant species, evolutionary trends can be identified. However, the limited nature of the chondrichthyan fossil record impedes cladistic analyses. Martin (1996) utilized molecular techniques to investigate lamniform relationships. He compared DNA sequences between six living species of sharks for degree of similarity. The results of Martin (1996) and other molecular studies (Fisher and Thompson, 1979; Fisher et al., 1980, 1981) supplement paleontological data of chondrichthyan phylogenetic relationships.

The classic phylogenetic interpretation is that sharks and rays are separate taxon based on differences in the location of gill openings, pectoral muscles and pectoral girdle (Nelson 1994). Shirai (cited by Nelson, 1994) concluded that Squalea, a monophyletic group of 4 shark orders plus the skates and rays, is a sister taxon to Galeomorphii (the shark orders Orectolobiformes, Lamniformes, Carcharchiniformes, and Heterodontiformes). Compagno (1973, 1987) proposed monophyly of sharks plus rays with sharks being paraphyletic without the inclusion of rays. This hypothesis has been generally accepted, resulting in a monphyletic group of living chondrichthyans called Euselachii (Maisey, 1984; Nelson, 1994).

Geology

Stratigraphy, Correlation, and Chronology of the Porters Landing Fossil Site

The Hawthorn Group underlies more than half of the Georgia Coastal Plain, including its continental shelf (Huddlestun, 1988) (Figure 2). Numerous geological units have been formally named within the Hawthorn Group. The two early Miocene formations recognized by Huddlestun (1988) throughout eastern Georgia are the Parachucla Formation and the Marks Head Formation. Specimens for this study were collected from both the Porters Landing Member of the Parachucla Formation and the Marks Head Formation along the Savannah River at the type section of the former unit. In the text the informal term 'Porters Landing' will refer collectively to the Porters Landing Member and the Marks Head Formation found in this general region.

The upper portion of the Parachucla Formation is formally called the Porters Landing Member. It was named for a boat landing along the Savannah River, 4.3 km southeast of the Screven-Effingham county-line in Georgia (Huddlestun, 1988). Areas along the river immediately adjacent to the boat landing were designated as its type locality. The Porters Landing Member is found exposed here along lower portions of bluffs from approximately river level to nearly 6 meters above water level.

The Porters Landing Member is identical to the combined Parachucla marl and shale of Sloan (1908: 273-274, 466). The dominant lithology of the Porters Landing

Member is argillaceous sand. In northern Effingham County it is thickly bedded, vaguely to massively stratified, usually noncalcareous and nonfossiliferous, fine-to-medium grained sand and clay (Huddlestun, 1988). In addition to the dominant quartz sand, other lithic components include calcite, phosphate, mica, zeolite, dolostone, and calcitic invertebrate shells. Clays of the Porters Landing Members can be found interstially among the sand grains or in discrete beds. It is the presence of clay beds that distinguishes the Porters Landing Member from the underlying Tiger Leap Member of the Parachucla Formation (Huddlestun, 1988).

Exposures in northeastern Effingham County are fossiliferous along a portion of the Savannah River near the named Porters Landing. Fossils may be found in outcrops of eroded sediments or subsurface in a sandy-shelly conglomerate. The site is only accessible during low water levels. At that time, layers of the Porters Landing Member are exposed as bluffs and beach along the bank of the Savannah River. Different sized sand and limestone grains, calcitic shells and fossils are exposed on the face of the bluffs. The presence of pebble-sized grains and water-worn fossils are indicative of a high energy regime as found in the fossil-bearing layer at the Porters Landing Member. At the time of deposition, the velocity of water was strong enough to eventually wear sediment particles and fossiliferous material to a smooth finish. This feature of the Porters Landing Member is distinct from the other Porters Landing sediments.

The Porters Landing Member is locally truncated in southernmost Screven County and seaward in southern Effingham County (Huddlestun, 1988). Calcareous lithofacies reappear in central Chatham County and underlie the coast of that county. Based on cores from Wayne, Coffee, Berrien, and Colquitt counties, the Porters Landing Member likely underlies most of the Southeast Georgia Embayment area and the Gulf Trough. To the west, the Porters Landing Member is known from southernmost Screven County southwestward through Emanuel, Dodge, and into Colquitt County. The southern limits of the Porters Landing Member are unknown. However, the south Georgia coastal area of Glynn County is underlain by Porters Landing. In northern Florida, strata along the upper Suwannee River (White Springs locality) have been correlated with the Porters Landing Member (Morgan, 1989,1993; Jones et al., 1993; Scott, 1988a). All strata that overlie the Suwannee Limestone and underlie the "unnamed dolostone, clay, and sand of the Hawthorn Group" (Huddlestun, 1988) were included in the Parachucla Formation by Morgan (1989).

Huddlestun (1988) proposed that the Porters Landing Member was deposited in a shallow, open circulation continental shelf region during the early Miocene. This is supported by planktonic foraminiferal species identified from cores containing the Porters Landing Member from the lower Savannah River area. Huddlestun (1988) correlated the Porters Landing Member with either upper Zone N4 or lower Zone N5 of Blow (1969). This places it in the Aquitanian, or lowermost Miocene. Berggren et al. (1995) assigned these zones a numeric age of 23 to 21 Ma.

Jones et al. (1993) dated several Oligocene and Miocene strata from Georgia and Florida using $^{87}Sr/^{86}Sr$ geochronology. An average age of 20.2 Ma was reported from the type locality of the Porters Landing Member. North Florida strata, referred to the Parachucla Formation by Morgan (1984) (White Springs locality), had a considerably older age of approximately 24.2 Ma.

The Marks Head Formation is the other early Miocene formation of the Hawthorn Group from Georgia and northern Florida (Huddlestun, 1988). The Marks Head Formation was named for a ravine in the floodplain of the Savannah River. The type section is known as the Marks Head Run and is 1.9 km northwest of Porters Landing (Huddlestun, 1988). The formation disconformably overlies the Porters Landing Member and is best exposed at Porters Landing in bluffs rising 30.5 meters above the Savannah River.

The lithology of the Marks Head Formation is primarily sand-sized quartz grains but some stratigraphic layers may be argillaceous or finely sandy clay. Huddlestun (1988) reported that sand grains decrease in size as the formation proceeds seaward. Other lithic components of the Marks Head Formation include mica, dolostone, zeolite, feldspar, phosphate, calcitic shells, and siliceous claystone. The clay content in the Marks Head Formation is variable. It may occur in stratified layers, thick beds, thins beds, streaks, and/or interstially between sand grains. The Marks Head Formation is the least fossiliferous formation of the Hawthorn Group. Exceptions are at its type section and where it overlies the Porters Landing Member along the Screven-Effingham County border. The Marks Head Formation has a higher content of phosphate, dolostone, silicon, is less fossiliferous, and has lighter clays than the Porters Landing Member (Huddlestun, 1988).

The Marks Head Formation has been identified as far north as Jasper County, South Carolina, eastward as part of the Georgia continental shelf, and south into northern Florida (Huddlestun, 1988). Scott (1988b) and Morgan (1993) reported that the Marks Head Formation is common in northern Florida, including the Brooks Sink locality, but is eroded away in other areas. The most western boundary of the formation is not known, but it has been described in western Wayne and Charlton counties in Georgia. Huddlestun (1988) reported that the formation is not found in Coffee, Berrien, or Colquitt counties, unlike the Porters Landing Member.

The depositional environment of the Marks Head Formation was open-marine, shallow insular shelf (Huddlestun, 1988). Using foraminifera, the formation has been placed in the Upper Burdigalian within Zone N6 of Blow (1969). According to Berggren et al. (1995), this is equivalent to a numeric age of about 18 Ma.

Ward (1998) used fossil mollusks to correlate lower Miocene formations along the Atlantic Coast. His results corroborated the previous reported ages of the Porters Landing Member and the Marks Head Formation. An age correlation chart for lower Miocene formations in Delaware, Maryland, North Carolina, Georgia, and Florida shows that the Porters Landing Member (Parachucla Formation) is equivalent to the Old Church and the Belgrade Formations (Figure 3). The Marks Head Formation is equivalent to the Kirkwood/Calvert and the Pungo River Formations.

Materials and Methods

Field and Laboratory

Field crews from Georgia Southern University (GSU) have collected fossiliferous matrix from the Porters Landing site over a ten year period. Collection began in 1988 under the direction of the late R.P. Petkewich, Associate Professor of Geology. Georgia Southern crews often included geology students, Dr. Ann Pratt (GSU Biology Department), and personnel from the Florida Museum of Natural History (FLMNH). The intent of the visits was to provide field experience for geology students as well as to conduct stratigraphic and paleontologic analyses.

The Marks Head Formation is exposed on the face of a near-vertical cliff that rises approximately 30.5 meters from the banks of the Savannah River. Collection of matrix (unsorted sediments and fossil material) was made possible by standing on a ledge about one-third up the cliff. Tightly woven bags (resembling plastic burlap) were filled and passed around the face of the cliff. Observations of lithography were noted prior to removal of matrix.

On outcrops of the Porters Landing Member, surface finds provided GSU crews with numerous fossils. The fossiliferous bed of the unit is normally below river level, which impeded collection of matrix and fossils. Only when water levels were below mean-low-water stage could the site be reached on foot.

Matrix and fossils were then transported to the Paleontology Laboratory at Georgia Southern University. Dry weights were recorded for all collected samples. Matrix from the various layers of the Porters Landing site were washed and sorted. Care was taken to prevent mixing of matrix from the different stratigraphic layers.

Matrix was prepared for washing following the separation techniques described in Johnson et al. (1994). Approximately eight milliliters of Calgon (a commercial form of sodium hexametaphosphate) per liter of water were used to break apart the clay sediments collected from the Marks Head Formation. The Calgon bath does not need to be changed and it may sit for several months without damaging the fossils.

A series of nested screens was used when washing Porters Landing matrix. Mesh size, in descending order, was 39 mm^2, 2 mm^2, and 1.1 mm^2. The edges of the screens were aligned to minimize loss of fossiliferous material during washing. The large washing sink was equipped with a sediment trap. Washing and agitation of screens (side-to-side back-and-forth movement) was continued until no noticeable sediment was being eliminated (Johnson et al., 1994). This sorting process resulted in concentrate of three sizes. The washed material was then dried in a rack with adequate ventilation and a fan for at least 24 hours. The washing/drying process was repeated two times for each series of screens. To reduce contamination of matrix between different layers or formations, screens were cleaned with a wire brush between washings.

Concentrate was sampled for fossiliferous material (skeletal material, teeth, dermal scales, dermal spines). The large concentrate was sorted with the unaided eye. The two smaller sizes of concentrate were sorted with the aid of a dissecting microscope, magnification depended upon size of specimens. A total of about 800 kg of dried matrix was picked for vertebrates.

Analytical Methods

Specimens were identified to the lowest possible taxonomic level based on morphological characters. Comparative specimens from the Vertebrate Paleontology and Zooarchaeology collections of the FLMNH were used in the identification process. Measurements were recorded for most of the teeth using digital calipers. Tooth height was measured from apex of crown to base of the roots. Width of tooth was recorded across the widest part of the root.

Number of identifiable specimens (NISP or NIS) (Badgley, 1986) were tallied for the individual geologic unit (the Porters Landing Member and the Marks Head Formation), for each stratigraphic layer within the Marks Head Formation, and for the Porters Landing locality (the Porters Landing Member plus the Marks Head Formation combined). Abundance relative to total identifiable material (i.e. relative abundance) was calculated to make quantitative comparisons. It is understood that the calculated values are not the actual relative abundances of the once living taxa (due to taphonomic bias and unquantifiable differences in tooth replacement rates), but do allow for a standard numeric estimate of specimens identified. This method was chosen as a numeric comparison due to minimal information on tooth replacement frequency in chondrichthyans (Moss, 1967).

A measure of faunal similarity was determined for North American early Miocene sites using the Simpson Coefficient. To determine this value, the number of shared taxa between two sites is divided by the number of taxa at the site with the fewest taxa. The value is similar to a percent of shared taxa, therefore, multiply by 100. These comparisons were calculated between the Porters Landing Member and the Marks Head Formation to asses similarity of Aquitanian and Burdigalian deposits within Georgia. The Simpson Coefficient was also calculated for the combined faunas of Porters Landing versus the combined faunas of each other region. In addition, calculations were done to compare the Aquitanian faunas with each other and the Burdigalian faunas with each other.

Abbreviations used are: **GSM**, Georgia Southern Museum; **FLMNH**, Florida Museum of Natural History; **NIS**, number of identifiable specimens; **MNI**, minimum number of individuals; **GA006**, the Porters Landing Member; **GA007**, the Marks Head Formation; **GA008**, Neural Spine/ Bone Bed Layer; **GA009**, Landslide/Bone Bed Layer; **GA024**, Dark Oyster Layer; **GA025**, Pebbly Layer; **GA026**, Lower Sand Layer/Sand below laminated sand and clay layer; **GA027**, Upper Pebbly Layer.

Discussion

Chondrichthyan Orders Present at Porters Landing

The sharks: Carcharhiniformes, Lamniformes, and Orectolobiformes

The Lamniformes and Carcharhiniformes together form a monophyletic clade within Galeomorphii. Their synapomorphies include: 1) characteristic tripod-shaped rostrum (Carroll, 1988); 2) lack of fin spines, instead dorsal fins supported by segmented cartilaginous dorsal basals; 3) reduced mesopterygium (Cappetta, 1987); and 4) separate foramen for the superficial ophthalmic nerve which exits the cranial cavity via orbital fissures (Compagno, 1988). All known members of the Lamniformes and Carcharhiniformes have heterodont dentitions composed of symphyseal (along the midline), anterior, intermediate, lateral, and posterior tooth groups (Applegate, 1965; Applegate and Espinosa-Arrubarrena, 1996). Tooth morphology reflects the diet and feeding style within these two taxa, with numerous instances of convergence.

Of the eight living orders of sharks the Carcharhiniformes is the largest with over 200 species, about 55 % of all extant species. These include the dusky (*Carcharhinus*), lemon (*Negaprion*), snaggletoothed (*Hemipristis*), and the sharpnose (*Rhizoprionodon)* sharks. The great diversity in carcharhiniform tooth morphologies reflects specialization into numerous feeding niches (Cappetta, 1987). Carcharhiniform teeth have a lesser degree of heterodonty than those of lamniforms, but usually have serrated edges (Cappetta, 1987). Most Carcharhiniform teeth have an open pulp cavity (the orthodont type). The largest carcharhiniform is the tiger shark (*Galeocerdo*) with a length of 3 to 4 meters. Most carcharhiniforms inhabit warm temperate to tropical waters with a concentration of species in the Pacific Ocean (Compagno, 1988). Most members of the group are generally found along insular shelves or the upper continental slope.

Lamniformes comprise about 5 % of all modern shark species, including some of the most familiar types (Compagno, 1988). The extant sand tiger (*Carcharias*), mako (*Isurus*), great white (*Carcharodon*), and thresher (*Alopias*) sharks all belong in the Lamniformes. Some very well known fossil chondrichthyans also belong in this order. Most lamniforms possess a tearing-type heterodont dentition characterized by the previously mentioned tooth types coupled with similar shaped upper and lower teeth (usually dagger-like). Lamniform teeth are usually osteodont, that is having the pulp cavity filled by osteodentine (Cappetta, 1987). Members of the Lamniformes generally exceed 2 meters in length with the great white shark exceeding 3 meters (Compagno, 1984). Most inhabit pelagic waters except in extreme north-south latitudes and have broad geographic distributions (Compagno, 1987). Their range extends from intertidal waters to depths exceeding 1200 meters and includes coastlines to pelagic areas.

The Orectolobiformes comprise less than 10% of all extant sharks with approximately 33 identified species (Compagno, 1988). They have a reduced rostrum supported by a cartilaginous rod, resulting in a shortened snout (Cappetta, 1987). This order also lacks dorsal fin spines and subsequently supports the fin with segmented dorsal basals. Orectolobiforms posses separate adductor and constrictor muscles of the jaw (Cappetta, 1987). Grooves and barbs found in the nasal region are unique to orectolobiforms. Otic capsules and preorbital wall are reduced and may be incomplete. Some members, including those within Ginglymostomatidae, have small spiracles as well as a distinct separation between the anal and the caudal fins.

Orectolobiformes are represented at Porters Landing by the nurse (*Ginglymostoma* and *Cantioscyllium*), bamboo (*Chiloscyllium*) and whale (*Rhincodon*) sharks (Kent, 1994). Orectolobiforms have little to no heterodonty, however, degree of asymmetry of teeth may reflect general position (see Systematic Paleontology Discussion of the genus *Ginglymostoma*). Although most orectolobiforms have a clutching-type dentition, members of the family Ginglymostomatidae display a crushing dentition (Cappetta, 1987). Teeth of this type have bulging crowns and are narrowly transverse.

As the common name of the order suggests, these carpet sharks dwell on or near the floor of the ocean. The orectolobiforms live on continental shelves and are often found resting in shallow water (Bigelow and Schroeder, 1948). They prefer subtropical to tropical Atlantic waters and are also found along the western coast of Mexico.

The rays, skates, and guitarfish: Myliobatiformes and Rajiformes

The Superorder Batomorphii includes the orders Rajiformes and Myliobatiformes (Cappetta, 1987) with over 450 named species (Nelson, 1994). The batomorphs share the following features: dorsoventrally flattened body, extension and fusion of pectoral muscles and fins to the head during secondary development (Bigelow and Schroeder, 1953), dorsal spiracle and eyes, and ventral mouth and gills (Maisey, 1996). Batomorphs differ from modern sharks in that they lack a nictitating membrane (Bigelow and Schroeder, 1953). Batomorphs also lack anal fins. Regardless of tooth morphology, teeth are arranged in a pavement across the surface of the jaw (Nelson, 1994) (Figure 4).

Rays are placed in the order Myliobatiformes and include *Dasyatis* (stingray), *Myliobatis* and *Aetobatus* (collectively called eagle rays), *Rhinoptera* (cow nose ray), and the extinct devilray, *Plinthicus*. The head region is distinct from the body in rays except *Dasyatis*. *Myliobatis* and *Aetobatus* have eyes and spiracles on the lateral edges of an elevated head (Nelson, 1994). The body and tail are sparingly covered with dermal denticles. Most species have a serrated tail spine in conjunction with a posterior poison gland (Bigelow and Schroeder, 1953). Myliobatiforms have a grinding-type dentition. Adults may be up to 2.5 to 3 meters in width (Bigelow and Schroeder, 1953). Rays are primarily benthic, often found resting on or buried in sand. Most are marine, although some can tolerate brackish or freshwater. Myliobatiforms prefer temperate to tropic waters and may be found along continental shelves (Bigelow and Schroeder, 1953).

Member of the Rajiformes includes *Rhynchobatus* and *Rhinobatis* (collectively called guitarfish) and *Raja* (the skates). There are approximately 45 species of guitarfish (Nelson, 1994). They have a shape that is intermediate between sharks and rays with two distinct dorsal fins and a caudal fin (Nelson, 1994). The midline of the body is armored with dermal denticles, but the tail spine is not serrated. Teeth are of the crushing type (Bigelow and Schroeder, 1953). Guitarfish prefer warm temperate to tropical waters. They are often seen hovering or swimming slowly above the ocean floor.

There are nearly 200 named species in the genus *Raja* (Nelson, 1994). In this genus, the head and body are flattened and the head is not distinct. The upper body and tail is covered with dermal denticles, but the tail spine lacks serrations (Bigelow and Schroeder, 1953). Tooth type is a crushing dentition. Large species may reach lengths of 90 cm to 2 meters with females approximately one-third larger than males (Bigelow and Schroeder, 1953). Skates are benthic, often laying buried in sand. *Raja* are common in warm temperate waters and a great number of species have been reported from equatorial latitudes. The genus is also found in the subartic regions of both hemispheres (Bigelow and Schroeder, 1953).

Issues of Naming and Recognizing Species

Some morphologic feature(s) of teeth are characteristic to chondrichthyan genera or species. The feature(s) can be used to identify fossil specimens. However, several factors may limit the usefulness of the feature(s). The diagnostic feature(s) may be lost or indistinct due to breakage and/or preservation. The feature(s) may not be helpful when identifying an isolated tooth. The independent evolution of a trait in different species minimizes its usefulness when identifying specimens.

For example, in carcharhiniform lineages acquisition of serrations has evolved independently several times in their tooth history. Therefore, serrations can be used to discriminate taxa at the familiar or generic level. Serrations evolved in the genus *Carcharhinus* starting in the early Neogene (Cappetta, 1987) yet serrations are not unique to this genus. In addition, the serrations are not helpful in identification to the species level.

Purdy (personal comn., 1998) discussed another problem in fossil fish identification. Tooth morphology is often indistinguishable between extant and extinct shark species. Lack of recognition of this fact has influenced the taxonomy of sharks. When tooth morphology is identical between extant and extinct species, some paleontologists will assign them different names thus confusing the identification and taxonomy. For example, *Negaprion brevirostris,* the modern lemon shark, has an identical tooth morphology to *Negaprion eurybathrodon*, the Neogene lemon shark. Some paleontologists (Case, 1981; Cappetta, 1987; Kent, 1994) refer Neogene specimens to *N. eurybathrodon.* Other paleontologists (Tessman and Webb, 1968; Tessman, 1969; Morgan and Pratt, 1988) use the modern name *N. brevirostris* for the same thing. It appears that the only thing separating *N. brevirostris* and *N. eurybathrodon* is geologic time. The similarity in tooth morphology supports that *N. eurybathrodon* is the same species as *N. brevirostris* beginning in the Neogene.

My methodology is to use the modern names for their identical fossil counterparts. This approach is supported in the naming of the alligator. Brochu (1999) stated that fossils indistinct from the modern alligator *Alligator mississippiensis* are described through the Pleistocene. Thus the modern species and the fossil Neogene species bear the same morphology and the same name.

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Superorder Galeomorphii Compagno, 1977
Order Carcharhiniformes Compagno, 1977
Family Carcharhinidae Jordan and Evermann, 1896
Genus *Galeocerdo* Muller and Henle, 1838
Galeocerdo aduncus Agassiz, 1843

Description: Tooth is asymmetrical with distally slanted crown and a strong distal notch where the crown and shoulder intersect (Figure 5). Upper and lower teeth are similar in morphology and represent a cutting dentition (Cappetta, 1987). Crown is broad and labiolingually compressed. Labial face of crown is flat or slightly convex, smooth, and often flush with root. Lingual crown face is smooth and slightly concave. Apex may be broad and blunt or narrow and sharp. Serrations on distal shoulder. Near the notch, serrations may be large enough to be cusplets but decrease in size distally. Both cutting edges fully serrated, often complex (i.e. primary serrations bear smaller serrations), but serrations become simpler and more petite apically. Mesial cutting edge is slightly convex.

Maximum tooth dimensions are 21 mm high and nearly 26 mm wide. Roots on anterior teeth are robust, compressed mesiodistally, slightly arched. Tip of lobes are slightly rounded to flat. Lateral teeth have roots that are less robust and compressed labiolingually. Cappetta (1987) described a short groove on the lingual root face. However, most Porters Landing specimens are water-worn, therefore, it is difficult to determine presence of a nutrient groove.

Geographic Distribution: In North America, *Galeocerdo aduncus* is found in lower to middle Miocene deposits of the Chesapeake Bay region of Maryland and Virginia (Kent, 1994). This species is present in Miocene marine faunas in Florida (Morgan and Pratt, 1988; Morgan, 1989). Additionally, *G. aduncus* was described from the Pungo River and Belgrade Formations of North Carolina (Case, 1980; Bourdon, 1998) and the Calvert Formation in Delaware (Purdy, 1998b). Longbottom (1979) listed records from South Carolina and New Jersey. He also compiled Miocene reports from Cuba and Baja California as well as South America including Ecuador and Argentina. A report of *G. aduncus* from the Miocene of Switzerland was listed by Cappetta (1987) and Cappetta (1970) described specimens from the middle Miocene of France.

Discussion: The chronologic range of this species is from the very late Oligocene or earliest Miocene through the Pliocene. Case (1980) reported what may be the oldest North American discovery from an Aquitanian formation in eastern North Carolina. Specimens from the Parachucla Formation of Georgia and Florida are of similar age.

Referred Specimens: From the Porters Landing Member: GSM 868; 870; 871; 872; 880. From The Marks Head Formation: GSM 830; 829 from GA025; GSM 845 from GA008; GSM 848 from GA009; GSM 852 from GA027.

Galeocerdo contortus Gibbes, 1849

Description: Tooth is asymmetrical with distally slanted crown. Crown is generally slender, tapers to a point and not compressed labiolingually (Figure 6). Unlike *Galeocerdo aduncus*, tooth lacks pronounced distal notch. Upper and lower teeth morphologically similar. Both cutting edges with simple serrations. Mesial cutting edge twists from apex to shoulder (Figure 7). Tooth is generally less than 17 mm tall and an average of 16 mm wide. Roots are bulky (robust), lobes form an acute angle. Tip of lobes are rounded and point apically. Lingual root face has pronounced protuberance with obvious nutrient groove.

Geographic Distribution: *Galeocerdo contortus* is restricted to the Miocene of North America, specifically the Gulf and Atlantic Coastal Plains; and is not found in Europe (Cappetta, 1987). *G. contortus* is characteristic of all Miocene deposits of the Chesapeake Bay area (Kent, 1994). It has also been found in Virginia and North Carolina (Case, 1980). The Calvert/Kirkwood Formations in Delaware (Purdy, 1998b) and from Florida (as *G. aduncus*) (Tessman, 1969).

Discussion: Both species of *Galeocerdo* identified from Porters Landing are extinct, possibly during the middle Miocene. The teeth of *Galeocerdo aduncus* and *Galeocerdo* *contortus* are distinguished by the mesial cutting edge. In *G. aduncus*, the edge extends from the apex to the shoulder without twisting (Figure 7); the twisted mesial cutting edge of *G. contortus* is the source of its species name. Serrations of *G. aduncus* are more complex than those of *G. contortus* and the former has a stronger distal notch. From neck to apex, the crown height of *G. contortus* is larger than *G. aduncus*.

Gottfried (1993) discussed several hypotheses for the co-occurrence of the two Miocene *Galeocerdo* phena. Obviously one hypothesis is that they are distinct species. However, because uppers and lowers are indistinguishable within both species, in has been hypothesized that *G. aduncus* represented upper teeth and *G. contortus* the lowers of a single, heterodont species (Tessman, 1969). Additionally, Gottfried hypothesized that the differences were the result of sexual dimorphism. This issue can only be resolved by studying upper and lower associated dentitions of Miocene *Galeocerdo* (Gottfried, 1993). Whatever the explanation for the two phena existing at the same geologic time, Cappetta (1987) noted that *G. contortus* is unique to Miocene deposits of the Gulf and western Atlantic Coastal Plains and has not been found with *G. aduncus* elsewhere. This supports the recognition of both species during the Miocene.

Referred Specimens: From the Porters Landing Member: GSM 869; 873; 874; 875; 876; 877; 878; 879; 881. From the Marks Head Formation: GSM 826 from GA008; GSM 827 from GA025; GSM 828 from GA007.

Genus *Negaprion* Whitley, 1940

Negaprion brevirostris (Poey, 1868)

Description: Crown is tall, narrow, triangular (Figure 8). Labial crown surface is flat while lingual face is slightly convex. Crown is compressed labiolingually but thick at the neck. Lateral view of the tooth shows a straight profile rather than sigmoidal. Enameloid extends to shoulders; enameloid extends labially along roots forming a straight line where gumline attachment is visible. Enameloid is often dimpled on labial crown face. Dimpling runs vertically between root lobes toward apex. Cutting edges extend from apex to shoulder. Upper teeth broader, shorter than lowers (Figure 8a). Upper laterals slant distally. Crown devoid of serrations. Upper teeth possess irregular serrations on both shoulders; upper anteriors devoid of serrations. Upper and lower anteriors differ from other tooth positions by the presence of a lingual protuberance, shorter shoulders, and are relatively thicker labiolingually. Lower teeth taller, narrower, more erect than uppers (Figure 8b). Crown of lowers remain erect in lateral positions, height becomes reduced. Apex considerably more blunt in laterals. *Negaprion* teeth range from 2.5 to 16.5 mm in height. Root lobes are expanded, may form a slight angle or be nearly straight. Lingual nutrient groove divides root into lobes, root tips are rounded.

Geographic Distribution: This species has been identified from the early Miocene of Maryland (Kent, 1994). Burdigalian formations in North Carolina and Florida have produced *Negaprion brevirostris* (Morgan and Pratt, 1988; Morgan, 1989). Purdy (1998b) described this genus from the Burdigalian of Delaware. Cappetta (1987) cited

Miocene discoveries from Ecuador, Portugal, and Southern France under the name *Negaprion eurybathrodon*..

Discussion: The chronologic range of this genus extends from the middle Eocene to the present. The earliest reports are from Georgia (Case, 1981) and Nigeria (cited by Cappetta, 1987). The geographic range in the western Atlantic tropical waters during the Neogene was similar to that of the modern species. This supports the philosophy of using extant names with fossil organisms when they are indistinguishable from each other (see Discussion, Issues of Naming and Recognizing Species).

Referred Specimens: From the Porters Landing Member: GSM 928; 929; 930. From the Marks Head Formation: GSM 896 from GA025; GSM 897 from GA007; GSM 899 from GA024; GSM 900 from GA008.

Genus *Rhizoprionodon* Whitley, 1929

Rhizoprionodon terraenovae (Richardson, 1836)

Description: Crown compressed labiolingually with some degree of distal slant (Figure 9). Convex distal shoulder forms a notch with the crown. Cutting edges and shoulders smooth, devoid of serrations or cusplets. Mesial cutting edge may be recurved. Maximum height is 6.2 mm; smallest tooth 1.8 mm tall. Roots usually wider than tooth is tall. Most specimens appear to have a lingual nutrient groove on roots, but this is difficult to distinguish on water-worn specimens.

Geographic Distribution: Previously reported from the Miocene along the Atlantic Coastal Plain of Maryland (Kent, 1994) and Delaware (Purdy, 1998a). Generic early Miocene reports have been listed for Florida (Morgan and Pratt, 1988; Morgan, 1989). Case (1980) described this species from the Aquitanian of North Carolina. Cappetta (1970) recorded this species from the middle and lower Miocene of Southern France, Portugal, and Belgium under the name *Rhizoprionodon fischeuri*.

Discussion: The oldest record of this extant genus is the early Eocene (Cappetta, 1987). An Eocene specimen from Georgia is among the oldest of this genus (Case, 1981). The fossil record indicates that *Rhizoprionodon terraenovae* has typically inhabited warm temperate to tropical waters along the Atlantic Coast. Currently it is abundant along the western Atlantic Coast including the Caribbean and the Gulf of Mexico (Compagno, 1984).

Sexual dimorphism is present in this genus (Cappetta, 1987; Compagno, 1988). Similarity in tooth size and generalized morphology makes identification at the species level difficult. Uppers of both sexes are virtually identical but lowers vary. Female lower teeth have a broader, more compressed crown than males. Lower male teeth have a more slender, erect crown as well as a root protuberance. Kent (1994) acknowledged that this distinction is often ambiguous on isolated fossil teeth.

A smooth distal shoulder devoid of serration is characteristic of this genus. *Galeorhinus*, *Paragaleus*, and *Physogaleus* all have similar sized teeth as *Rhizoprionodon*, but they possess varying degrees of serration on the distal shoulder (See Discussion of

Physogaleus for further distinction between these genera). *Rhizoprionodon*-like teeth from Porters Landing with broken shoulders could not be identified to genus.

Scoliodon is a generic name that is often synonymized with *Rhizoprionodon* based on similar morphologies. Many species currently placed in *Rhizoprionodon* were initially placed in *Scoliodon* (Case and Cappetta, 1990). For example, Case (1980) reported the species *R. terraenovae* under the genus *Scoliodon*. *Scoliodon* applies specifically to *S. laticaudus* while *Rhizoprionodon* is used for *R. terraenovae* (Compagno 1984).

The absence of *R. terraenovae* from the Porters Landing Member may reflect taphonomic sorting or collection biases since the smaller, finer material was collected less often at this location than at the Marks Head Formation.

Referred Specimens: From the Marks Head Formation: GSM 918 from GA007; GSM 831 from GA027.

Genus *Physogaleus* Cappetta, 1980
Physogaleus latus (Storms, 1894)

Description: Teeth of *Physogaleus* display great morphologic variation due to three factors: 1) sexual dimorphism; 2) morphological differences in uppers versus lowers, dignathic variation; and 3) differences between posterior teeth and anterior teeth, monognathic heterodonty. The crown of *Physogaleus* is relatively broad but never erect (Figure 10). Crown is oblique distally, degree of slant depends on gender and tooth position. Tooth may be compressed labiolingually. Some specimens a neck lacking enameloid. Distal shoulder shorter than mesial shoulder. Mesial cutting edge continuous with shoulder, concave, may twist apically. *Physogaleus* is characterized by regular distal shoulder serrations. Mesial shoulder serrations may be present in both male and female, usually irregular. Height ranges from 2.2 to 5.6 mm. Root tips rounded, base slightly arched. Some specimens may have bulky root with protuberance coupled with a deep nutrient groove dividing root into lobes. Other specimens have flatter roots, shallow groove.

Geographic Distribution: Case (1980) reported this species from the Belgrade Formation of North Carolina while Kent (1994) listed it from the Chesapeake Bay region. Kent (1994) also compiled reports of this genus from the Eocene to the early Miocene in Africa and the former U.S.S.R. South France and Switzerland provide middle Miocene records of *Physogaleus latus* (Cappetta, 1970).

Discussion: This genus has been recorded from the lower Eocene and persisted until the middle Miocene (Cappetta, 1987). *Physogaleus latus* is known from the early Oligocene, becoming extinct at the end of the Burdigalian, late early Miocene. Genus is known from the Eocene of Georgia (Case, 1981, as *Galeorhinus huberensis*). Cappetta (1987) named the genus *Physogaleus* with *P. latus* as its type species. Previously *P. latus* was included in *Galeorhinus* (Cappetta, 1970).

Similarity in tooth shape and size is known for several carcharhiniform shark genera including *Rhizoprionodon, Physogaleus,* and *Galeorhinus.* The distinctive character of *Physogaleus* is the short distal shoulder with regular serrations.

Rhizoprionodon lacks serrations on shoulders (Figure 11). *Galeorhinus* has distal cusplets that extend from the root to the apex, similar to *Hemipristis*.

Serrations were counted on both shoulders of specimens recovered at Porters Landing. Out of 353 teeth that had distal serrations intact, the mode was 3 with a range of 2 to 4 serrations. Of the 503 teeth counted for mesial serrations, 245 teeth (49%) were unrecognizable, 149 (30%) of the teeth had zero mesial serrations and the remaining 21% had between 1 and 6 serrations.

Referred Specimens: From the Marks Head Formation: GSM 919 from GA027; GSM 920 from GA025; GSM 921 from GA026.

Genus *Carcharhinus* Blainville, 1816

Carcharhinus spp.

Description: Similarity in tooth morphology, size, and serration patterns of isolated *Carcharhinus* fossil teeth prevents identification below the genus level. Morphological descriptions are for several phena that have been identified from Porters Landing. All upper teeth of *Carcharhinus* have serrated cutting edges, crowns are broad and triangular.

One phenon of *Carcharhinus* is represented by GSM #889 (Figure 12a). Broad, short crown is distally oblique. Enameloid extends to tips of the shoulders. Serrations are continuous from crown apex laterally across the shoulders. The mesial cutting edge is convex; distal cutting edge is straight to concave. Height of teeth is approximately 13 mm, 18 to 22 mm wide. Roots are compressed labiolingually, extend onto enameloid.

Roots have a relatively straight basal margin but may be concave on labial face. Root tips are recurved and lobes separated by nutrient groove.

Erect crown covered with petite, regular serrations (GSM #915; Figure 12b). Enameloid-covered shoulders bear simple to complex serrations. Serrations decrease in size toward root tip. Height may range from 6.8 to 9.0 mm. Width may be 7.2 to 9.2 mm. Roots extend high onto enameloid. Lobes are straight across basal surface with straight tips.

Crown, mesial edge, and shoulders covered with regular, small serrations (GSM #216 and GSM #217; Figure 12c). On distal shoulder, serrations decrease in size toward tip. Average measurements are about 5.8 mm tall, 6.0 mm wide. Roots appear block-like, are broad and wide mesiodistally with straight edges. Roots may also be broad and wide, slightly arched with rounded tips.

Geographic Distribution: North American Miocene reports of *Carcharhinus* are from Delaware (Purdy, 1998b), Florida (Morgan and Pratt, 1988; Morgan, 1989), North Carolina (Cappetta, 1987), and Maryland (Kent, 1994). Cappetta (1987) listed Miocene records of the genus from South France, Spain, New Zealand (as *Galeocerdo*), Australia, North Africa, Zaire, Italy, Malta, Belgium, and India. Numerous species have been reported from the Miocene. Two of the most frequently reported species are *Carcharhinus egertoni* and *Carcharhinus priscus.* Reports of *C. priscus* and *C. egertoni* were compiled by Longbottom (1979). *C. egertoni* is known from South Carolina while *C. priscus* is reported from Virginia, New Jersey, and Maryland (Kent, 1994).

Longbottom (1979) compiled South American records from Ecuador, Peru, Brazil, Argentina, and Portugal.

Discussion: The first appearances of this genus are from the middle Eocene of Egypt, Alabama, and South Carolina (Cappetta, 1987). The species *C. gibbesi* was originally assigned to *Negaprion* but belongs in *Carcharhinus* (Cappetta, 1987). It is known from the early Miocene of North Carolina (Case, 1980). The extinct and Recent distribution of this genus is global.

Identification of upper teeth is based on the presence of serrations. In this genus, serrations on upper teeth evolved during the early Miocene and are characteristic of Recent species of *Carcharhinus* (Cappetta, 1987; Kent, 1994). Lower teeth have more narrow, erect crowns devoid of serrations; this is a classic cutting-type dentition. Similarities exist between the uppers of all *Carcharhinus* phena as well as between lowers of *Carcharhinus* and various other sharks with cutting dentitions. Naylor and Marcus (1994) discussed the identification of isolated shark teeth in the genus *Carcharhinus*. They noted that uppers are easier to identify than are lowers and anteriors are easier to distinguish from other tooth positions. However, unless teeth are particularly distinct, it is still difficult to identify isolated teeth to species even if the position is known.

Referred Specimens: From the Porters Landing Member: GSM 917; 889. From the Marks Head Formation: GSM 915 from GA027; GSM 916 from GA009.

Family Hemigaleidae Hasse, 1879

Genus *Hemipristis* Agassiz, 1843

Hemipristis serra (Agassiz, 1843)

Description: A strongly diagnathic dentition is present in this genus with the uppers used for cutting, lowers for grasping (Figure 13). Uppers are broad triangles narrowing toward the apex, compressed labiolingually, may be flat or concave on the labial crown face. Crowns of lateral teeth bent distally. Upper anteriors are more erect, not compressed labiolingually. Serrations present on cutting edges but absent on apex. Serrations decrease in size along the distal cutting edge. Mesial cutting edge of *Hemipristis serra* marked by numerous serrations but do not cover entire cutting surface. Tallest upper tooth was greater than 26 mm; smallest was less than 8 mm. Roots possess a lingual protuberance, are high, labiolingually flat. Mesial root lobe tapers to a sharp point, distal lobe is rounded.

Lowers are dagger-like, distally bent. Crown not compressed labiolingually. Labial crown face is concave opposite lingual protuberance. Tooth is slightly sigmoidal in lateral view. Incomplete cutting edges extend from apex to two-thirds down the crown (Figure14). Teeth may have 2 to 3 cusplets at base of crown. Average height is 11.5 to 12 mm tall. Roots are bilobed with distal extremity shorter. Lobes are rounded at the ends.

Geographic Distribution: This species is known from the early to middle Miocene along both coasts of North and South America (Kent, 1994). *Hemipristis serra* has been found in all Miocene formations of the Chesapeake Bay region (Kent, 1994). In Miocene sites of the United States, *H. serra* is reported from Delaware (Purdy, 1998b), Florida (Morgan and Pratt, 1988; Morgan, 1989), and North Carolina (Bourdon, 1998). Cappetta (1987) compiled reports from the Miocene of Southern France, Germany, Europe, India, and Java. Longbottom (1979) listed *H. serra* from Ecuador, Argentina, Venezuela, Brazil, Africa, Australia, and the Caribbean.

Discussion: The abundance of *Hemipristis serra* in the fossil record increases throughout the Miocene while an older species, *Hemipristis curvatus*, becomes less frequent. Case (1980) hypothesized that *Hemipristis serra* replaced *Hemipristis curvatus* by the early middle Miocene. *Hemipristis serra* inhabited temperate waters, becoming abundant in Pliocene marine fauna. The species survived until the Pleistocene (Cappetta, 1987; Scudder et al., 1995).

Serrations on the mesial cutting edge of the upper teeth distinguish *H. serra* from *H. curvatus* (Case, 1980). Some of the smaller specimens of *Hemipristis serra* have worn mesial cutting edges and thus are difficult to identify. However, the size and number of serrations on *H. serra* teeth are greater than *H. curvatus* (Figures 15 and 16). See discussion section of *H. curvatus* for further distinction between the two species.

Referred Specimens: From the Porters Landing Member: uppers GSM 931; 932; lowers GSM 859; 857; 933. From the Marks Head Formation: uppers GSM 851 from GA024; GSM 836 from GA007; lowers GSM 833 from GA027.

Hemipristis curvatus Dames, 1883

Description: Uppers and lowers show slight heterodonty but are otherwise similar. Both possess a lingual protuberance. Generalized morphology of upper teeth is similar to uppers of *Hemipristis serra* except for the distinct mesial cutting edge and reduced size. The mesial cutting edge of *Hemipristis curvatus* supports weakly developed serrations (Figure 16) (see discussion). Additionally, at least 2 specimens had a noticeable indentation or concavity on mesial cutting edge. Average height is 5 mm. Roots possess a reduced lingual protuberance, are high, relatively compressed labiolingually.

Lowers resemble the uppers but are narrower, more erect. Lowers have serrations on both sides of the crown base. Only two lowers of *Hemipristis curvatus* were identified; they have an average height of 6.5 mm. *Hemipristis curvatus* lowers are similar to reduced upper anteriors of *Hemipristis serra*.

Geographic Distribution: Case (1980) reported the only previous Miocene account of *Hemipristis curvatus* in the Aquitanian of North Carolina. However, the Marks Head Formation has now produced the youngest record of this species (Burdigalian).

Discussion: *Hemipristis curvatus* was previously known, primarily, from the Eocene (Cappetta, 1987), including Georgia (Case, 1981) and Maryland (Kent, 1994). It is presumed that this species inhabited continental shelf regions in tropical waters from the Eocene through the early Miocene. This is also the geographic distribution of the modern species (Compagno, 1984). Porter Landing is the only reported occurrence of sympatry in the two *Hemipristis* species.

Hemipristis curvatus is the senior synonym of *Hemipristis wyattdurhami* White, 1956 (Cappetta, 1986; Cappetta and Case, 1990). *Hemipristis wyattdurhami* is the name more commonly used in North American literature when discussing Eocene sharks. The recognition of *Hemipristis curvatus* from Porters Landing is based on small size and weakly serrated mesial edges. *Hemipristis curvatus* specimens possess between 0 and 8 mesial serrations (n = 16). The mode was 0 serrations while only one tooth had a total of 8 serrations. The number of mesial serrations on *Hemipristis serra* is most often from about 9 to 14 (n = 57). For *H. serra*, the number of serrations are directly related to tooth size; the larger the tooth, the more serrations. Some teeth (GSM # 851 and GSM #856) had as many as 25 mesial serrations, considerably more than *H. curvatus.*

Referred Specimens: From the Marks Head Formation: uppers GSM 840 from GA007; GSM 862 from GA007; GSM 934 from GA025; lowers GSM 935 from GA025.

Order Orectolobiformes Applegate, 1972
Family Ginglymostomatidae Gill, 1862
Genus *Ginglymostoma* Muller and Henle, 1837
Ginglymostoma delfortriei Daimeries, 1889

Description: Upper and lower teeth resemble each other. Teeth have diagnostic three-dimensional morphology, appearing globular (Figure 17). Tooth triangular, singular main cusp flanked by cusplets. Tooth may be symmetrical with erect main cusp and cusplets, particularly in anteriors. In laterals, tooth asymmetrical with cusp and cusplets distally bent. Much variation exists in the number of cusplets on teeth. All tooth positions possess an apron of enameloid that extends labially onto the root, it may or may not reach basal level as seen from mesial view. Tooth width (mesiodistally) is generally wider than tooth breadth (measured labiolingually). Teeth generally taller that wide, may be as tall as 8.5 mm. Roots are flat and thin, broad under main cusp, tapering under cusplets.

Geographic Distribution: Cappetta (1987) established *Ginglymostoma delfortriei* as occurring from the early to middle Miocene. Miocene records have been reported from Florida (Morgan and Pratt, 1988; Morgan, 1989). Cappetta (1987) compiled early Miocene reports from Guinea Bissau and middle Miocene records from Southern France and Portugal.

Discussion: *Ginglymostoma serra* is the most common name used when identifying Atlantic Coast Miocene nurse sharks. However, *G. serra* is an Eocene species which has only been reported from Maryland (Cappetta, 1987). *Ginglymostoma delfortriei* seems to be restricted to the Miocene. It probably lived in subtropical to tropical waters along continental shelves, similar to the extant nurse shark (Bigelow and Schroeder, 1948).

It is thought that asymmetrical crowns are characteristic of *Nebrius*, another genus of nurse shark. However, personal observation of modern dentitions revealed that lateral *Ginglymostoma* teeth are increasingly asymmetrical and distally slanted. Mesial and distal cutting edges are indistinguishable, the only distinct feature is the labial apron. Measurements were recorded for Porters Landing specimens. The number of cusplets were recorded on the right and left sides of the main cusp with the apron situated labially

(Table 2). Height and width of each tooth were measured when possible. Mean tooth height, mesiodistal width, and labiolingual breadth were 4.0, 5.6, and 4.5, respectively. Most Porters Landing specimens of *Ginglymostoma delfortriei* have between 4 and 7 cusplets per side. It remains unclear whether teeth express paired or non-paired cusplets. Incidentally, non-paired cusplets refers to varying numbers of cusplet on both sides of the main cusp while asymmetrical means that the cusplets and main cusp slant in one direction.

Water-worn and incomplete specimens impeded the ability to gather useable data. Most specimens had broken or worn cusplets and therefore were difficult to analyze. The data was collected to extend the information available on early Miocene nurse shark genera; it is not impossible that both *Ginglymostoma* and *Nebrius* are present. Both genera had representative species inhabiting Miocene oceans (Cappetta, 1987).

Referred Specimens: From the Marks Head Formation: GSM 846 from GA009; GSM 849 from GA024; GSM 854 from GA024; GSM 902 from GA024.

Table 2. Number of cusplets on *Ginglymostoma* teeth. Number of individual teeth with 4, 5, 6, 7, 8, 9, or 10 cusplets on both sides (R = right side, L = left side) of the main cusp were recorded (frequency). When cusplets were difficult to enumerate due to wear or incompleteness, minimum (min) values were estimated. To the left of the apron, the greatest frequency was between 4 and 7. No teeth had less than 4 cusplets on either side.

# cusplets L of apron	**Frequency of teeth with that # of cusplets**	
	min # cusplets	range of cusplets
4	5	4 to 7
5	6	
6	4	
7	4	
8	2	
9	0	

# cusplets R of apron	**Frequency of teeth with that # of cusplets**	
	min # cusplets	range of cusplets
4	4	4 to 7, and up to 9
5	5	
6	7	
7	2	
8	2	
9	3	
10	0	

Order Lamniformes Berg, 1958
Family Lamnidae Muller and Henle, 1838
Genus *Carcharodon* Smith, 1838

Discussion: Much controversy exists concerning the systematics and phylogeny of this genus (Applegate and Espinosa-Arrubarrena, 1996; Hubbell, 1996). I support the use of *Carcharodon* Smith, 1838 for this genus. My primary reasoning is based on minimal degrees of variation within a standard, general tooth morphology of broad, fully serrated triangular crowns, at least 3 to 4 cm in height, and moderate to massive roots.

Numerous traits of *Carcharodon* teeth have been analyzed, including lateral denticles, serrations, root shape, and size (Hubbell, 1996; Applegate and Espinosa-Arrubarrena, 1996). Morphological descriptions of *Carcharodon carcharias* (Linnaeus, 1758) are the orthotype of the genus. Deviations from that orthotype must be objectively analyzed to eliminate construction of invalid genera. Phylogenetic (cladistic) studies of the above mentioned traits provide the most accurate analysis of relatedness. When the traits are considered in an evolutionary context, the overriding principle should be that ontogenetic variation exists in most shark species.

Ontogenetic transformation proceeds toward a terminal state of a character (Compagno, 1988). This type of change is essentially an embryonic evolution from juvenile through adult stages (Gould, 1977). Phylogenetic evolution of an organism is often reflected through its ontogenetic development. Ontogenetic transformation can also be understood as a process of specialization (Gould, 1977). At the lowest level of development many different organisms share a great degree of similarity. As each organism matures, the common features are replaced by specialized or adaptive traits for that organism. Presumably all members of a genus proceed through a series of characteristic ontogenetic changes thus defining its phylogenetic development.

When organisms are morphologically very similar, several phena may be recognized (Smith, 1994). Phena are usually defined by identifiable features which appear to be intermediate to other phena or species. Phena, therefore, are not considered true species because they may represent sexual dimorphism, developmental stages of an individual, or geographically distinct subspecies (Smith, 1994).

In the fossil record, identification can be complicated by phena and/or preservation of ontogenetic changes. Since sharks have dental ontogeny and a high rate of tooth replacement, it is inevitable that the fossil record will preserve these changes as phena. As teeth of the extant species *Carcharodon carcharias* develop with age, they take on a more "*Carcharodon megalodon*" appearance by losing lateral denticles (Applegate and Espinosa-Arrubarrena, 1996; Purdy, 1996). The loss of a trait may indeed be characteristic of an entire genus or species, or it may be an ontogenetic change in an individual. Obviously, teeth of various developmental stages should not be classified into different taxonomic categories. However, Cappetta (1987) divided the original genus, *Carcharodon,* into two additional genera, *Carcharocles* and *Palaeocarcharodon.* This division was based on the presence/absence of lateral denticles and/or serrations.

Kent (1994) used a similar argument, but at the species level. He recognized the three genera (*Carcharodon, Palaeocarcharodon, Carcharocles)*, and stated that tooth form may be markedly different between juvenile and adult stages within each taxon. Kent (1994) referred to these as allometric or size-related changes. Such changes are more often the rule than the exception for most species. Study of *Carcharodon carcharias* supports the idea that one genus exists with varying degrees of serration, size, and loss of lateral denticles with age.

As for phylogeny, *Carcharodon* is most closely related to either *Isurus* or *Cretolamna* (Cappetta, 1987; Applegate and Espinosa-Arrubarrena, 1996; Gottfried et al., 1996). Evidence in favor of a relationship with *Isurus* is supported by similar tooth shape and acquisition of serrations in *Carcharodon* (Cappetta, 1987; Kent, 1994). It is documented that only the Miocene *Isurus escheri* had fine serrations similar to *Carcharodon* specimens (Cappetta, 1987). Additionally, worn *Carcharodon* teeth resemble isurid teeth which are characteristically devoid of serrations.

Applegate and Espinosa-Arrubarrena (1996) rejected the isurid ancestry hypothesis as well as the divisions of the great white genus. They listed reasons of serration size, synonymies, and presence/absence of lateral denticles to reject *Carcharocles* and *Palaeocarcharodon* as valid genera. Applegate and Espinosa-Arrubarrena (1996) supported only the use of *Carcharodon* Smith, 1838.

Applegate and Espinosa-Arrubarrena (1996) defended a close phylogenetic relationship between *Carcharodon* and *Cretolamna* by comparing tooth anatomy of all those two genera plus *Isurus*. Few preserved, associated dentitions exist for fossil *Carcharodon, Isurus,* or the extinct *Cretolamna*, however, numerous workers have constructed artificial ones based on literature and isolated specimens (Applegate and Espinosa-Arrubarrena, 1996; Gottfried, et al., 1996; Purdy, 1996). Complete tooth sets of extant *Carcharodon* and *Isurus* are particularly similar except in the upper intermediate tooth. *Isurus* has a distally inclined intermediate while all *Carcharodon* species have a mesially inclined intermediate. Applegate and Espinosa-Arrubarrena (1996) provided even more support to this hypothesis when *Cretolamna* was described: mesially directed anteriors, presence of lateral denticles, possession of a dental band or neck above the root, and asymmetrical root shape in the lower anteriors. Purdy (1998a) used some of the same arguments when identifying a Paleocene fauna. These features provide a complete comparison with *Carcharodon* teeth and show a greater similarity between *Cretolamna* and the *Carcharodon* lineage than between *Isurus* and *Carcharodon*.

Carcharodon chubutensis (Ameghino, 1906)

Description: Broad, triangular teeth (Figure 18). Flat lingual crown face, convex labially. Slight thickness at the neck directly above root apex tapering toward crown, compressed labiolingually. Neck band present but may not be pronounced. Worn, regular serrations on all cutting edges. Possesses reduced, triangular lateral denticles that are finely serrated. Smallest specimen from Porters Landing is 19.5 mm tall by 21.5 mm wide.

Largest was incomplete but at least 68.6 mm tall. Massive roots, relatively compressed with straight edges. Root lobes form an acute angle often in the shape of a U or broad V.

Geographic Distribution: Ameghino (1906) described this species from the Miocene of Argentina. Kent (1994) reported early to middle Miocene specimens in North Carolina and from the Calvert and Choptank Formations of Maryland. Purdy (1998b) listed this species from the late early Miocene of Delaware. The species reported from a Florida Aquitanian fauna (Morgan, 1989) is most likely *C. chubutensis*.

Discussion: In addition to the controversy over fossil great white taxonomy at the genus level, debate also surrounds species names and their application. *Carcharodon auriculatus* first appeared in the middle Eocene while *Carcharodon angustidens* is known from the middle Oligocene (Applegate and Espinosa-Arrubarrena, 1996). *Carcharodon chubutensis* ranged from the early to early middle Miocene (Cappetta, 1987), it is also known as *Carcharodon subauriculatus* (Applegate and Espinosa-Arrubarrena, 1996). *Carcharodon megalodon* did not appear until the middle Miocene (Applegate and Espinosa-Arrubarrena, 1996). This species is often used for Miocene specimens. However, differences do exist between the two Miocene species. The teeth of *C. megalodon* are generally larger (between 60 and 80 mm tall), thicker labiolingually, has smaller serrations on cutting edges and no lateral denticles (Keyes, 1972). The genus is present at the Marks Head Formation but the specimens are not identifiable to species level.

Referred Specimens: From the Porters Landing Member: GSM 865; 866; 867.

Genus *Isurus* Rafinesque, 1810

Isurus desori (Sismonda, 1849)

Description: Triangular crown, narrow, elongate, tapers apically (Figure 19). Entire morphology is broader and more robust than *Carcharias* (Figure 20a and 20b). All *Isurus* teeth have complete, smooth cutting edges and a flat labial crown surface. Profile is strongly sigmoidal on large anterior teeth, erect on laterals. Crown is thickest at neck, becoming compressed labiolingually in the apical direction. Lingual crown face is convex. Juveniles possess lateral denticles. Specimens from Porters Landing are devoid of lateral denticles indicating a population of adult *Isurus*. On anteriors, teeth are asymmetrical, crown labiolingually recurved. Lateral teeth have shorter, broader crowns than anteriors, distally oblique. The average measurements of *Isurus desori* teeth are 28.2 mm tall and 22.3 mm wide. Roots vary with tooth position but none display a nutrient groove. Roots of anteriors are robust, tips taper and point toward gumline, concave labially. Lateral roots are flat, tips wide and blunt, may be rounded or pointed.

Geographic Distribution: Kent (1994) reported *Isurus desori* from all stages of the Maryland Miocene as well as personal observations in North Carolina, Virginia, and Florida. Kent (1994) stated that *Isurus desori* was present in the Pliocene but does not cite any specific records. Purdy (1998b) listed *Isurus desori* from the Burdigalian of Delaware. The type specimen was described from the Miocene of Italy (Cappetta, 1987). In addition, Cappetta (1987) compiled Miocene accounts from Southern France and Zaire.

Discussion: The fossil record indicates that the species was restricted to the Miocene (Cappetta, 1987). The modern species, *I. oxyrinhcus*, is found circumglobal, in temperate to tropical waters, generally near the shore (Compagno, 1984).

Referred Specimens: From the Porters Landing Member: GSM 891, upper lateral. From the Marks Head Formation: GSM 892, upper from GA008; GSM 890, upper lateral from GA024.

Family Odontaspididae Muller and Henle, 1839
Genus *Carcharias* Rafinesque, 1810

Description: Cutting-type dentition, heterodonty minimal within genus. Teeth possess one to three pairs of lateral cusplets. Enameloid may be striated or smooth, depending on species. However, striations on the crown of most specimens are masked by cracks in the enameloid. Sigmoid profile depends on tooth position; more lateral positions are less sigmoidal. Ridge exists at the union of the neck and root on the lingual face of the root.

Discussion: The systematics of odontaspids are unresolved at both the familial and generic levels which complicates relationships of genera and species. In 1987, *Carcharias* was resurrected as a valid genus on the Official List of Generic Names in Zoology (Bulletin of Zoological Nomenclature, 1987). This caused the genera used by Cappetta (1987) to become unavailable. Cappetta recognized *Synodontaspis* as a valid genus (type species *Carcharias taurus*) and included the Miocene species: *S. acutissima* and *S. cuspidata*. *Carcharias* (BZN, 1987) is now used for these fossil species. *Odontaspis* is still a valid genus for other species of sand tiger sharks (Purdy, 1998a). Other species are placed in the extinct genus *Striatolamna* (Kent, 1994; Cappetta, 1987).

Kent (1994) recognized three Miocene species of *Carcharias*: *Carcharias acutissima, Carcharias cuspidata,* and *Carcharias reticulata*. *C. acutissima* and *C. reticulata* have narrow crowns and lateral cusplets. *C. cuspidata* has the broadest crown of the three species and its lateral cusplets are aligned in a ridge. *C. reticulata* has only been reported among Miocene fossil sharks by Kent (1994). Case (1980; 1981) described *C. acutissima* and *C. cuspidata,* and stated that *C. acutissima* is the more common of the two early Miocene (Aquitanian) species but by the middle Miocene *C. cuspidata* was more common. Due to the infrequent report and lack of morphologic data on *C. reticulata*, my identifications focus on the other two species, *C. cuspidata* and *C. acutissima.*

Carcharias cuspidata (Agassiz, 1843)

Description: Species is characterized by smooth enameloid. Crown tall and broadest of the Miocene species (Figure 21). On anteriors, crown is widest at the neck, and gradually tapers apically. Crown is recurved lingually; labial face is flat. Cutting edges on anteriors extend from the apex to the base of the crown, rarely incomplete. Lateral cusplets present on both sides of the crown, usually one per side. Cusplets also recurved lingually. Anteriors averaged 20.4 mm tall with a mean width of 19.8 mm (n = 21). Roots are thick and broadly arched. Lingual protuberance bears deep nutrient groove which divides root into lobes. Lobes are rounded at the tips, may vary in length.

Crown is broader on laterals than anteriors, slants distally. Labial crown face is flat, lingual portion is only slightly concave. Profile is slightly sigmoidal. Cutting edges extend from the apex to the crown base. A lateral ridge of 2 or more cusplets is diagnostic of lateral teeth in this species. Some specimens are water-worn but the ridge is identifiable due to the length (as opposed to a single cusplet). Roots are thick and bulky, may have lingual protuberance. Vertical groove on the lingual surface of root divides into lobes.

Geographic Distribution: *Carcharias cuspidata* has been reported from numerous early Miocene sites along the Atlantic Coast including Delaware (Purdy, 1998b) and the Chesapeake Bay region (Kent, 1994). Case (1980) stated that this species is scarce in the early Miocene of North Carolina, but became more common in the middle Miocene. Miocene specimens from the former U.S.S.R and South France have been compiled by Cappetta (1987 and 1970).

Discussion: *Carcharias cuspidata* was widespread during the Oligocene through the Miocene (Cappetta, 1987), possibly being replaced in abundance by *Carcharias acutissima*. *C. cuspidata* has been identified from marine faunas in Europe, the former Soviet Union, and the United States (Cappetta, 1987).

Referred Specimens: From the Porters Landing Member: GSM 936. From the Marks Head Formation: GSM 843 and 844 from GA008.

Carcharias acutissima (Agassiz, 1844)

Description: Tall, narrow crown, severely recurved lingually (Figure 22). Tooth is narrower in the neck and crown than is *Carcharias cuspidata* (Figure 23). Kent (1994) described the enameloid as striated but in Porters Landing specimens, this is difficult to distinguish from enameloid cracks. Labial crown face is flat between cutting edges. Lingual face is strongly convex producing a strong sigmoid profile. Cutting edges are almost complete from apex to crown base but do not follow the outline of the tooth. Cutting edges extend onto the center of the labial face of the crown. Delicate lateral cusplets usually recurved lingually. One specimen had a second pair emerging, however, one pair is the norm for this species (Cappetta, 1987). The average height of specimens is 23.4 mm and 17.2 mm wide. Root has lingual protuberance with distinct vertical groove. Root lobes are greatly arched, tips are rounded.

Geographic Distribution: *Carcharias acutissima* is known from the early Miocene of North Carolina (Case, 1980). Case (1980) listed this species in marine deposits of Japan, New Zealand, Portugal, France and Belgium, Germany, and Italy. Cappetta (1987) listed it from the Miocene of Switzerland.

Discussion: *Carcharias acutissima* is the most common shark fossil from the early Miocene from the coastal plain of Georgia (Case, 1981). Fossils of this species are also very abundant in middle Miocene and Pliocene faunas. Younger specimens are very similar to the extant *Carcharias taurus* (Cappetta, 1987). The living species inhabits coastal warm temperate, tropical waters of the Atlantic Ocean (Compagno, 1984).

Referred Specimens: From the Porters Landing Member: GSM 898, upper. From the Marks Head Formation: GSM 838, anterior from GA007; GSM 839, upper from GA008.

Family Alopiidae Bonaparte, 1838

Genus *Alopias* Rafinesque, 1810

Alopias latidens (Leriche, 1909)

Description: Low, broad triangular crown (Figure 24). Enameloid extends onto shoulders. Flat labial and lingual surfaces. Mesial cutting edge straight and devoid of serrations. Distal cutting edge smooth and concave; apex points distally. Average height is 7.9 mm, 11.8 mm wide. Width measurement and root description is from the only specimen that had roots. Thin, petite roots, characteristically arched along basal margin. Lack nutrient groove on labial surface of root. Root tips are rounded.

Geographic Distribution: Kent (1994) reported this species from the Old Church, Calvert, and Choptank Formations of Maryland. Porters Landing specimens are the only Miocene record from Georgia. The genus is recognized in the late early Miocene of Delaware (Purdy, 1998b). Cappetta (1987) compiled reports of *Alopias latidens* from the late Oligocene of Belgium to the middle Miocene of North Carolina, Italy, and Southern France.

Discussion: This genus ranges from the late Eocene to the present (Cappetta, 1987). Cappetta (1987) listed several similarly aged species including *Alopias exigua, Alopias latidens,* and *Alopias superciliosus* from the same geographic regions during the lower

Oligocene to the middle Miocene. The latter species is probably the oldest of the three extant species. *Alopias* lives in oceans of the mid-latitudes circumglobal. Itt can be found in deep or coastal waters (Compagno, 1984).

Referred Specimens: From the Marks Head Formation: GSM 895 from GA008.

Superorder Batomorphii Cappetta, 1980
Order Rajiformes Berg, 1940
Suborder Rhinobatoidei Fowler, 1941
Family Rhynchobatidae Garman, 1913
Genus *Rhynchobatus* Muller and Henle, 1837

Discussion: Tooth morphology is greatly effected by position and wear. There is great variation in crown height, occlusal (grinding/crushing) surface of the tooth, and morphology of roots. Modern dentitions display a transverse crest (ridge) on the occlusal surface which divides the lingual from the labial surface (Cappetta, 1987). Crest or lingual bulge on crown is present on unworn teeth but absent on files that show wear. Additionally, the occlusal surface is flat, square and the crest is reduced on worn fossil specimens. Lack of ornamentation on occlusal surface of enameloid may be attributed to wear. On modern dentitions, morphology of the occlusal surface may be smooth or puckered, convex or concave.

Rhynchobatus pristinus (Probst, 1877)

Description: Dentition is of the crushing-type (Bigelow and Schroeder, 1953). An extension of the enameloid, called the lingual uvula, is present. Usually it is narrow and extends to or beyond the lingual notch of roots. On either side of the uvular protuberance are depressions in the lingual face. The depressions are the margino-lingual foramina. Teeth usually 3 mm wide (laterally) but may be as small as 1 mm wide. Roots equal to or less than lateral dimension of tooth. Roots never wider than crown, deep groove divides roots into 2 lobes. From the basal view, lobes narrow and slant lingually.

Geographic Distribution: Case (1980) described this species from the early Miocene of North Carolina. Porters Landing specimens corroborate the age of this species. Bourdon (1998) reported that this genus comprised nearly 80 % of the *Rhynchobatus*-like teeth from the Pungo River Formation in North Carolina. Cappetta (1987) listed numerous reports from the Miocene including early Miocene of Germany and the middle Miocene of France and Portugal.

Discussion: The chronologic range of *Rhynchobatus pristinus* appears to be restricted to the Miocene. The only North American records are from the Aquitanian of North Carolina and now Georgia. However, the genus is known from the late Eocene to the present (Cappetta, 1987). Present distribution of this genus is in the Atlantic, Indian, and Pacific oceans. It is rarely found in estuaries (Nelson, 1994).

Referred Specimens: From the Porters Landing Member: GSM 939. From the Marks Head Formation: GSM 937 from GA025; GSM 938 from GA027.

Suborder Rajoidei Garman, 1913
Family Rajidae Bonaparte, 1831
Genus *Raja* Linnaeus, 1758

Discussion: Sexual dimorphism is present in some species (Cappetta, 1987). If dimorphic, the male teeth are cuspidate while the female lack the cusp and are globular. When sexual dimorphism is lacking, both sexes are cuspidate. The specimens at Porters Landing lack noticeable sexual dimorphism.

Raja spp.

Description: All teeth cuspidate with a continuous, round apron. The cusp (apex) may extend upward from the center of the apron or from the lingual edge of the apron. Apex always points in a labial direction. From a lateral view, apex never extends beyond the labial edge of the apron. Apron overhangs labial face of the roots. Some teeth appear narrower than others while some taper to a shaper apex. Enameloid at the base of the crown may be smooth or have a single ridge extending from both sides to the edge of the apron. Range of height is between 1 and 2 mm but some are smaller. Roots are bilobed, narrowing labially. Roots are as wide, mesiodistally, as the apron. Basally roots are broad, flat, a well marked groove widens labially. Enameloid-coated dermal 'thorns' from the body and tail are often preserved (Nelson, 1994).

Geographic Distribution: Purdy (1998b) published the only true North American Miocene record of *Raja*. Bourdon (1998) indicated at least 7 phena from the Aquitanian of North Carolina. Cappetta (1987) compiled middle and late Miocene reports of two species, *Raja gentili* and *Raja olisiponensis*. The former is known from the middle Miocene of Switzerland and South France. *R. olisiponensis* is from the late Miocene of Portugal and South France. Cappetta (1987) noted that indeterminate species are present in the Miocene of Japan.

Discussion: This genus dates from the early Eocene to the present (Bigelow and Schroeder, 1948). Although few reliable accounts of this genus have been reported from North America, it is clearly present in the Miocene of Georgia. The characteristic smooth lingual apex, flat labial roots, and size confirms the identification as *Raja*. The Aquitanian report from Porters Landing supports the oldest record of *Raja* from the western Atlantic Coast. This genus presently inhabits all marine, tropical waters preferring pelagic regions (Cappetta, 1987).

Referred Specimens: From the Porters Landing Member: GSM 940. From the Marks Head Formation: GSM 943 from GA024.

Order Myliobatiformes Compagno, 1973
Superfamily Dasyatoidea Whitley, 1940
Family Dasyatidae Jordan, 1888
Genus *Dasyatis* Rafinesque, 1810

Discussion: A grinding dentition prevails in the teeth of myliobatiforms including *Dasyatis* (Bigelow and Schroeder, 1953). Sexual dimorphism exists within this genus. Variation of morphological features in *Dasyatis* may also be caused by wear, tooth position, or interspecific differences. The variation is seen in the enameloid, crown morphology, and roots.

Dasyatis spp.

Description: In male teeth, crown erect, apex comes to a sharp point (Figure 25). Apex may extend onto the labial visor becoming the labial zone. Tooth may be of two sizes, small or large. If small, tooth less than 2.5 mm tall. Labial visor may be bilobed or complete. If tooth is large, height is between 2.5 and 3.0 mm. Smooth labial visor, overhangs labial face of roots. Generally roots are bilobed with a narrow labiolingual groove separating them. Lobes are triangular, basally flat, slant lingually.

In females, enameloid may be smooth or ornamented with ridges. Occlusal surface consists of labial face of crown, labial zone, and median labial depression on the crushing surface (Cappetta, 1987). Lingual visor is distinct and of two forms: rounded and elongate or bilobed at lingual notch of root. Labial visor overhangs labial face of roots.

Some crowns are short between labial visor and labial zone, others elongate. Teeth are equal in height and width. May be up to 4 mm or as small as 1 mm. Roots are bilobed, usually thick, rounded and close together, like in the male. Some roots are deeply lobed, almost arch-like on lingual face of roots. Lobes are flat basally and compressed anterioposteriorly. *Dasyatis* has a serrated tail spine which often preserves well as well as dermal 'thorns' (Nelson, 1994).

Geographic Distribution: Two early Miocene species are known, *Dasyatis probsti* and *Dasyatis rugosa* (Cappetta, 1987). Two other Miocene species are recognized, *Dasyatis caveronsa* and *Dasyatis serralheiroi*. Generic Miocene reports have been described from Delaware (Purdy, 1998b), North Carolina (Bourdon, 1998), and Florida (Morgan and Pratt, 1988; Morgan, 1989). Case (1980) reported *D. cavernosa* from the Aquitanian of North Carolina. That species was previously reported from southwestern Germany as compiled by Cappetta (1987). He also listed that the two early Miocene species have been recovered from the Aquitanian of Southern France, southwestern Germany, Poland, and Portugal.

Discussion: Cappetta (1987) listed the range of this genus from the early Cretaceous to the present, with 18 extinct species. Descriptions of tooth morphology of *Dasyatis* species are limited despite the number of named species. Based on the age of the specimens from Porters Landing, they may be *D. probsti* or *D. rugosa*,. Extant members of this genus are found in shallow marine, brackish and/or freshwater associated with the Atlantic, Indian, and Pacific oceans (Bigelow and Schroeder, 1953; Nelson, 1994).

Referred Specimens: Male teeth from the Porters Landing Member: GSM 941. From the Marks Head Formation: GSM 944 from GA024. Female teeth from the Porters Landing Member: GSM 942. From the Marks Head Formation: GSM 945 from GA024.

Superfamily Myliobatoidea Compagno, 1973
Family Myliobatidae Bonaparte, 1838

Discussion: Dentition consists of plates that cover the surface of both jaws forming a pavement (Figure 4). Each row of plates is referred as a file (Cappetta, 1987). Some genera have a single file arranged in numerous rows or several files per row. Body devoid of dermal denticles but do possess a tail spine (Bigelow and Schroeder, 1953; Nelson, 1994).

Genus *Aetobatus* Blainville, 1816
Aetobatus arcuatus (Agassiz, 1843)

Description: Lingual face well marked with alternating grooves and laminae, less pronounced on labial face. Tooth may be very narrow labiolingually (anterioposteriorly) but roots always extend past the crown (Figure 26). *Aetobatus* does not have lateral tooth files but one elongated median file (Cappetta, 1987; Nelson, 1994). Lingual ridge present between crown and roots. Crown may be rounded, flat, or arched. Height of crown decreases with grinding action. Average height of roots and crown is 9.1 mm (n = 11) measured from lingual most edge of roots to labial edge of crown.

Morphology of uppers and lowers are different (Cappetta, 1987). Uppers are rectilinear, lateral edges curve distally decreasing in thickness. Roots on uppers always higher than crown, lingual displacement less pronounced. Number and width of root lobes is variable and difficult to determine due to breakage.

Lower files arched toward front of mouth, crown is tallest in middle of individual file (Cappetta, 1987). Entire file curves lingually. Roots are exaggerated, may be taller than crown, slant lingually, extend beyond crown at pronounced angle. Number and width of basal root attachments vary, breakage makes it difficult to describe.

Crown wear pattern is different on uppers than lowers. On uppers the wear occurs at distal tips of tooth plate creating an arch; the center of the file remains high. Lowers wear in the middle of the file. Wear is evident by thinner crown, depression, or a smoother surface and taller distal tips.

Geographical Distribution: Cappetta (1987) cited a Maryland Miocene recovery of *Aetobatus arcuatus*. Reports of the species are known from the Aquitanian of North Carolina (Case, 1980) and Florida (Morgan and Pratt, 1988). The genus is recorded from the late early Miocene of Delaware (Purdy, 1998b). *Aetobatus arcuatus* is common in middle and lower Miocene faunal deposits of Southern France (Cappetta, 1970).

Discussion: The genus is known from the early Paleocene to the present. The species is reported from the Eocene of Georgia (Case, 1981) and Egypt (Case and Cappetta, 1990). Recent species inhabit subtropical to tropical environments of the Atlantic, Indian, and Pacific Oceans (Cappetta, 1987).

Referred Specimens: From the Porters Landing Member: GSM 926; 927. From the Marks Head Formation: GSM 924 from GA027.

Myliobatis Cuvier, 1817

Myliobatis spp.

Description: Seven files per row, lateral files decreasing in length (Cappetta, 1987). Often the lateral files are pentagonal or hexagonal and broader than long. The center file is rectilinear and generally the longest. Some files are slightly arched. Labial transverse ridge separates crown from root. Labial and lingual faces have puckered enameloid. Crown height varies with each file and among files. Crown generally higher on labial edge, presumably wear is in lingual direction. Differences in length and width of the center files may be indicative of different species of *Myliobatis*. Width, in the labiolingual direction, of Porters Landing specimens ranges from 3.3 mm to 8.5 mm. The roots are composed of individual lobes for basal attachment. The number of root lobes is variable; some specimens had 16 lobes while others had up to 26 lobes. Data were recorded on complete or reconstructed center files only.

Geographic Distribution: Many of the Miocene species are indistinguishable from the modern species (Cappetta, 1987). Case (1980) reported this genus from the Aquitanian of North Carolina. This genus is present in the Miocene of Florida (Morgan and Pratt, 1988; Morgan, 1989). It is also known from the middle Miocene of Southern France (Cappetta, 1970).

Discussion: The chronologic range of *Myliobatis* is from the early Paleocene to the present (Purdy, 1998a). Cappetta (1987) listed Paleocene records from Morocco, West Africa, and Cabinda. Case and Cappetta (1990) reported several species from the Eocene of Egypt. Representatives of this genus are found in the coastal waters of the three main oceans often including shallow bays and estuaries (Bigelow and Schroeder, 1953).

Many species are named within this genus. The angle of roots, shape of crown, ornamentation on crown are thought to be diagnostic to species, although wear distorts these features. Case and Cappetta (1990) suggest a study of the cross-section of the crown and root to aid in the classification of specimens. In addition, detailed analysis may define differences between the morphologically similar genera *Myliobatis* and *Rhinoptera*. The latter genus is very common in Miocene faunas (Bourdon, 1998; Cappetta, 1970 and 1987; Purdy, 1998b). Both *Rhinoptera* and *Myliobatis* appear to be present at Porters Landing although the presence of *Rhinoptera* is inconclusive as it is based on incomplete specimens.

Referred Specimens: From the Porters Landing Member: GSM946.

Superfamily Mobuloidea Whitley, 1936
Family Mobulidae Gill, 1893
Genus *Plinthicus* Cope, 1869
Plinthicus stenodon Cope, 1869

Description: Crown fenestrated with embossed longitudinal grooves, higher than roots (Figure 27). Crown compressed labiolingually, rectilinear from occlusal view (Cappetta, 1987). The occlusal surface becomes jagged and recurved with wear. Some specimens possess transverse ridge on lingual surface of occlusal face. Grinding surface is concave, marked with raised labiolingual ridges. Crown wearing pattern is on labial edge of occlusal face. Labial face extends beyond roots, labial face concave. Lateral edges may be straight or rounded. Median and lateral files exist for both jaws forming a pavement in the mouth (Cappetta, 1987). If the crown has consistent height, the plate is from the median file. If crown height is higher on one side, plate is from a lateral file. Average height was 6.0 mm and 2.9 mm wide. Roots rounded, reduced, vary in number, extend lingually.

Geographic Distribution: Cappetta (1987) reported Miocene accounts from New Jersey and the middle Miocene of North Carolina and Maryland. *Plinthicus stenodon* is known from the Aquitanian of Florida (Morgan, 1989) and listed in the fauna of the Pungo River Formation of North Carolina (Bourdon, 1998). This species has been reported as rare in the lower and middle Miocene of Southern France (Cappetta, 1970).

Discussion: Morphology of this species is diagnostic and unique. *Plinthicus stenodon* is the only representative of this Miocene genus (Cappetta, 1987).

Referred Specimens: From the Marks Head Formation: GSM 922 from GA007; GSM 923 from GA025; GSM 925 from GA027.

Osteichthyes

Teleost remains are some of the most abundant fossil material recovered from vertebrate sites (Scudder et al., 1995). This is due in part to the vast numbers of fish species, extinct and extant, as well as the numerous hard parts that they possess (i.e. vertebrae, ribs, teeth, mouth parts, dermal scales, and spines). Unfortunately, identification of damaged or morphologically similar specimens can be difficult. Fossil fish reports often include a generic name, descriptions, photographs, references to related genera, and occasionally, a positive species identification (Webb and Tessman, 1968; Morgan, 1988; Morgan and Pratt, 1989; Hulbert and Pratt, 1998; Purdy, 1998b; Weems, 1998). This is the common state of fossil fish, and Porters Landing is no exception.

The quantity of fossil teleost material at Porters Landing is numerous, consisting primarily of vertebra, spines, and teeth. However, many are fragmented disassociated elements and are not identifiable. In addition, limited comparative material restricted identification. The identifications were made on recognizable mouth parts, jaws, and/or teeth. Even at that, generic or familiar levels were the lowest possible level of identification.

For example, pufferfish dentaries/premaxillaries (Superfamily Tetraodontoidea) could not be identified below Diodontidae. It is likely, though, that several species are present. The same situation exists for members of the drum genus *Pogonias* as is evident by different sized teeth and fragmented pharyngeal grinders.

Identifications have been supported by the presence of some of the same taxa at age-equivalent sites. From the Aquitanian of north Florida, *Pogonias* sp., *Sphyraena* sp., and *Sphoeroides* sp. (from the Superfamily Tetraodontoidea) have been reported (Morgan, 1989). *Lagodon* sp., *Pogonias* sp., *Sphyraena* sp., and Family Diodontidae were listed from the Marks Head Formation in northern Florida (Morgan and Pratt, 1988). Purdy (1998b) also listed *Lagodon* sp., *Pogonias* sp., and *Sphyraena* sp. from the Burdigalian of Delaware.

Fish are often adapted to a specific niche and, therefore, are indicators of that environment (Swift and Wing, 1968). The teleosts of Porters Landing are marine fishes that prefer subtropical to tropical waters (Table 3). More information concerning habitat preference is discussed in the Paleoecology section.

Relative abundances of bony fishes are most accurately assessed using minimum number of individuals (MNI), rather than NIS (Scudder et al., 1995). This is particularly true for paired cranial elements or even dermal scales. However, the identifiable elements from Porters Landing are primarily isolated teeth. As is the case with sharks, frequency of tooth replacement in fishes is unknown (see Introduction, Chondrichthyan fossil record). Due to the nature of the Porters Landing specimens, NIS is the best method to evaluate relative abundances. See Results section for a discussion on faunal composition at Porters Landing.

Results

The percent of total for identifiable fish specimens was calculated for identifiable taxa. For an individual taxa the total NIS were divided by the total number of identifiable teeth. The percent of total of specimensf was determined for the Porters Landing Member, the Marks Head Formation, and both units combined. Within the Marks Head Formation, percent of totals were calculated for several strata. These values do not necessarily indicate relative abundances of once living individuals as it is difficult to estimate minimum number of individuals based on isolated teeth (Moss, 1967). However, the values do allow for a general comparison of abundance. Shark percentages are based on the total NIS for sharks (3210), batomorph percentages on the total NIS for batomorphs (691), and teleost percentages on the total NIS for teleosts (796). To determine abundance of each taxa, NIS values were summed (NIS = 4697) and percentage of total of identifiable fish fauna was determined as above. Table 3 provides an overview of the fossil fish taxa present at Porters Landing.

A total of 20 taxa were identified from the Porters Landing Member(Table 4). Ten shark taxa were identified (NIS = 158, 67% of the total fish fauna from the Porters Landing Member). Of the shark fauna, the Carcharhiniformes represent 85.4% while the Lamniformes represent 14.6%. Four batomorph taxa (NIS = 33) comprise approximately 14% of the total identifiable fish fauna from the Porters Landing Member. The following taxa were identified: *Rhynchobatus pristinus*, *Raja* spp., *Dasyatis* spp., *Aetobatus arcutaus,* and *Myliobatis* spp. (personal observation has revealed the presence of *Myliobatis* spp. but no values were included from the Porters Landing Member). Five teleost taxa were identified (NIS = 44) for about 19% of the identifiable fish fauna from the Porters Landing Member.

Table 5 shows that 26 fish taxa were identified from the Marks Head Formation, 68% of the identifiable fish fauna is from 13 shark taxa (NIS = 3052). The Lamniformes and Orectolobiformes comprise less than 0.02% of the shark taxa.. Seven batomorphs taxa (NIS = 658, nearly 15% of identifiable fish fauna) and six teleost taxa (NIS = 752, approximately 17% of identifiable fish fauna) were identified from the Marks Head Formation.

Within the Marks Head Formation, there are 5 distinct stratigraphic layers (Table 6). In sequence from youngest to oldest they are: Upper Pebbly Layer (Unit 8), Dark Oyster Layer (Unit 7), Sand Layer (also known as the Lower Pebbly Layer, Unit 5), Laminated Sand and Clay (Unit 4), Sand below laminated sand and clay (also known as the Lower Sand, Unit 3). The 'Pebbly Layer' was established due to incomplete field notes, that is when 'upper' or 'lower' was not recorded. This general category undoubtedly includes specimens from both the Upper Pebbly Layer (Unit 8) and the Lower Pebbly Layer (Unit 5), but the distinction is unclear. Therefore, the fact that the Pebbly Layer had the greatest NIS (874; 18.61% of Marks Head identifiable fish fauna) does not provide adequate information about the Marks Head Formation stratigraphy.

Of the recognized layers at the Marks Head Formation, the Upper Pebbly Layer had the highest NIS (869;18.5% of Marks Head fauna). The composition of the fauna is 246 NIS of sharks, 307 NIS of batomorphs, and 316 NIS of teleosts. The Dark Oyster Layer had 816 NIS (17.37 % of Marks Head fauna): 567 NIS of sharks, 129 NIS of batomorphs, and 120 NIS of teleosts. The two youngest sediment layers have the richest fish fauna. This may be due to several factors, but the quantity of matrix collected was not a factor (Table 6). Elapsed time of burial of the Dark Oyster Layer and its specimens by the Upper Pebbly Layer may have been very short thus insuring the preservation of a large percentage of the specimens. Also, specimens may have been naturally concentrated in that former habitat. Taphonomic concentration may have been a result of a low energy regime at the time of deposition or minimal scavenging of specimens between the time of deposition and the recession of waters from the Porters Landing.

The combined fish fauna from the Porters Landing Member and the Marks Head Formation is 26 taxa (Table 7). This count includes 20 chondrichthyan taxa and 6 teleost taxa. Of the chondrichthyans, a total of 14 shark taxa have been identified (NIS = 3210, approximately 68% of the total identifiable fish fauna). The Carcharhiniformes represent about 98% of the shark fauna followed by the Lamniformes (1.40%) and the Orectolobiformes (0.65%). Six taxa of skates and rays were identified from Porters Landing (NIS = 691, approximately 15% of the total identifiable fish fauna). The bony fishes are represented by 6 taxa (NIS = 796, about 17% of the total identifiable fish fauna).

The most abundant fish at Porters Landing (from the Porters Landing Member and the Marks Head Formation) is *Carcharhinus* spp. (40.96%) followed in descending order by *Physogaleus latus* (11.33%), *Dasyatis* spp. (9.79%), *Rhizoprionodon terraenovae* (8.49%), cf. *Pogonias* sp. (5.75%), *Sphyraena* sp. (3.75%), *Negaprion brevirostris* (3.62%), *Megalops* cf. *atlantica* (3.36%), *Rhynchobatus pristinus* (3.15%) and *Lagodon* sp. (2.28%). The remaining taxa each represent less than 2% of the total fish fauna.

Paleoecology

Ward (1998) described a molluscan fauna that is intermediate in age between the Aquitanian aged Belgrade Formation of North Carolina and the Burdigalian aged Calvert Formation of Maryland. The fauna was recovered from the Kirkwood/Calvert Formations of Delaware. Its age is important for interpretation of the paleoecology along the Western Atlantic Coast during the lower Miocene. Ward (1998) listed bivalve and gastropod species from North Carolina, Virginia, Maryland, and Delaware. The similarity of faunas suggested similarity in age of the various formations. Indicator fossils of diatoms, bivalves, and gastropods have indicated correlations between many of the Atlantic Coastal Plain early Miocene formations (Figure 3). $^{87}Sr/^{86}Sr$ dating by Jones et al. (1998) confirmed the age of the formations and thus the correlations.

In addition, the mollusk fauna reveals marine conditions along the northern west Atlantic Coast (Ward, 1998). Some of these species preferred subtropical to tropical waters. A majority of the identified mollusks from the Kirkwood/Calvert Formations were shallow-water, nearshore marine species.

Most of the fossil fish species identified at Porters Landing also indicate a subtropical nearshore marine paleoecology. Table 3 shows the habitat of the Porters Landing chondrichthyan and teleost faunas based on similar studies by Bigelow and Schroeder (1948) and Compagno (1984, 1988).

Rhizoprionodon, Negaprion, and *Hemipristis* occur in warm waters of either inshore or continental shelf regions. *Carcharias, Ginglymostoma,* and *Galeocerdo* inhabit warm temperate to tropical waters and are often found near the coast (Bigelow and Schroeder, 1948). Members of the genus *Isurus* prefer temperate waters and are rarely found in water less than 60 degrees Fahrenheit. Reports state that *Carcharodon* is known to come into shallow bays or into continental shelf regions (Compagno, 1984).

The batomorph fauna from Porters Landing also reflects a marine, subtropical paleoenvironment. Members of each of the 5 genera (*Myliobatis, Aetobatus, Dasyatis, Raja,* and *Rhynchobatus*) are known to inhabit shallow, tropical waters (Bigelow and Schroeder, 1948). Extant guitarfish, skates, and rays can often be found hovering above the ocean floor or half buried in the sand.

The adults of *Sphyraena* sp. (barracuda) inhabit subtropical to tropical marine environments while the young live in estuaries. Likewise, adults in the family Diodontidae (pufferfish) prefer inshore waters while the young are pelagic (Nelson, 1994). Porters Landing supported a population of adult barracudas and pufferfish. *Pogonias* sp. is found in shallow temperate to subtropical waters, along shelf regions (Nelson, 1994). *Lutjanus*, a snapper, is described as a bottom-dweller in marine waters. They can be found nearshore or in waters as deep as 550 meters. Tarpons, *Megalops*, are predominately marine. Currently *M. atlantica* extends from Brazil to South Carolina but rarely north of the Carolinas (Nelson, 1994). There may be up to 6 fossil tarpon genera.

The teleost population at Porters Landing indicates a paleoenvironment of temperate to tropical marine waters. Several of the species identified from Porters Landing prefer coastal waters. This conclusion is congruent with the indicated paleoecology of the fossil chondrichthyans identifiaed from Porters Landing.

Low levels of oxygen isotopes indicate that the early Miocene was one of a few tremendous warming periods during the Neogene (Kennett, 1995). The earliest Miocene was a relatively warm age with minimal global ice development. This proceeded the late early Miocene (19.5 to 15 Ma), noted as the climax in Neogene warmth (Kennett, 1995). Kennett (1995) cited a previous study (Kennett and von der Borch, 1985) for paleontological evidence of this warm trend. He stated that, in what are now the modern temperate, southern latitudes, warm-subtropical foraminiferan and mollusk species prevailed. This hypothesis is supported by the foram fauna recovered from Porters Landing (Huddlestun, 1988) and the Calvert/Kirkwood molluscan population identified by Ward (1998). The identified fish fauna from Porters Landing also parallels the reports from Kennett (1995).

Comparisons of Porters Landing to other Atlantic Coast Miocene sites

The Simpson Coefficient was calculated to determine faunal similarity between early Miocene sites and to assess paleoecology of the Atlantic Coastal Plains (Table 8). The calculations were determined for sites in Delaware, Maryland, North Carolina, Georgia, and Florida. Number of identifiable specimens (NIS) of teleosts are difficult to interpret (Scudder et al., 1995) and NIS of batomorphs are rarely published, therefore, faunal comparisons were not calculated for these taxonomic groups. Records of shark teeth are often available and were the source of the Simpson comparisons. The higher the coefficient, the greater the similarity.

There is nearly three million years difference in age between the Parachucla and the Marks Head Formations. The taxa and abundances from these two geographically and chronologically similar units may reveal information about early Miocene paleoecology. The Simpson Coefficient for the Parachucla Formation versus the Marks Head Formation is 91.7. Essentially, the two localities share nearly 92% of their total shark population. During the time of deposition of the Porters Landing Member and the Marks Head Formation (21 to 18 Ma), little change occurred in the shark population. Likewise, the paleoecology may have been similar for this period of geologic time.

The Simpson Coefficient for the combined early Miocene shark fauna of Georgia and Florida is 87.5. Therefore, nearly 88% of all shark taxa were similar between the combined Parachucla and Marks Head Formations of Georgia and the combined Parachucla and Marks Head Formations of Florida. Morgan (1989) reported on the Parachucla Formation exposed at White Springs, north Florida. The coefficient for the two Aquitanian faunas for Georgia and Florida is 62.5. Morgan and Pratt (1988) described the fauna at Brooks Sink within the Marks Head Formation of north Florida. The similarity of the Burdigalian faunas is 100. Therefore, all shark taxa identified from the Marks Head Formation of Georgia were also identified from the Marks Head Formation of Florida. More faunal similarity exists between the Georgia/Florida Burdigalian sites than Georgia/Florida Aquitanian the sites. This also indicates that the Georgia/Florida coastal environments may have been quite similar during the late early Miocene.

Purdy (1998b) reported on a late early Miocene site from the Calvert/Kirkwood Formations of Delaware. The Calvert/Kirkwood Formations are contemporaneous to the Marks Head Formation (Figure 3). The faunal similarity between the Delaware Burdigalian and the Georgia Burdigalian is 53.3. Only about half of the shark taxa from Georgia have been identified from Delaware. Thus as expected, conditions may not have been as similar in these areas.

The Chesapeake Bay area of Maryland has prolific Miocene formations dating to the early Aquitanian (Calvert Formation) (Figure 3). Many middle and upper Miocene faunas are described in the literature (Kent, 1994, Cappetta, 1987, McLennen, 1971). The Simpson Coefficient was calculated between the entire early Miocene shark faunas of

Maryland and Georgia. The similarity is 78.6. Between the Aquitanian sites, the similarity is 66.7. The greatest similarity is between the Burdigalian sites from the Calvert and Marks Head Formations. Nearly 79% (78.6) of the shark taxa is the same. The combined faunas of Georgia and of Maryland have a similarity coefficient of 78.6. This value was calculated independently of the Burdigalian coefficient. The faunal similarity and paleoecology between Georgia and Maryland is greater than between Georgia and Delaware.

Case (1980) described an Aquitanian site in eastern North Carolina. It is evident that his fauna is derived from what is now called the Belgrade Formation. This formation is age-equivalent to the Parachucla Formation of Georgia and north central Florida (Figure 3). Probably one of the best known early Miocene sites is the Lee Creek Mine of North Carolina. The formation that has produced numerous marine fossils is the Pungo River Formation. This formation is equivalent to the Marks Head Formation. The coefficient was calculated between North Carolina and Georgia by combining the taxa for each state. The similarity between the early Miocene faunas is 92.9. A similarity of 77.8 was determined for the Aquitanian sites while the Burdigalian sites shared 64.2% of their shark fauna. A greater degree of similarity can been found when pooling the faunas between the two states. This also supports a similar paleoecology.

The greatest combined similarity (Aquitanian and Burdigalian) exists between the North Carolina and Georgia. The next greatest degree of similarity was within Georgia, between the Aquitanian and the Burdigalian faunas. Florida and Georgia shared over 87% of their shark fauna followed by Georgia and Maryland and finally Georgia and Delaware.

Of the Aquitanian formations, the greatest similarity was between Georgia and North Carolina followed by Maryland then Florida. Results of the Aquitanian comparison demonstrate a greater similarity between the geographically distant sites of Georgia and Maryland than between Georgia and Florida. It was presumed that Georgia would be more similar to Florida since the same geologic units are recognized in both states. The differences between the faunas of Georgia and Florida may be due to several factors. There may have been a sampling bias in the Florida fossil material. The level and/or accuracy of identification may contribute to the results. But more specifically, faunal reports from Southeastern Geological Society (Morgan and Pratt, 1988;Morgan, 1989) suggest that the localities were more terrestrial and possibly some distance from the shoreline. Thus a lesser degree of shark specimens would have been preserved.

Similarity in Burdigalian fauna was greatest between Georgia and Florida and the least similar between Georgia and Delaware. This is logical in that the sites closest geographically share the most faunal similarity. However, Georgia is more similar to Maryland than North Carolina. This conclusion may be a result of inadequate identifications and/or sampling.

The Simpson Coefficient has provided a quantitative evaluation of the identified shark taxa at age-equivalent sites. These values have also provided information on the paleoecology of these sites. The presence of indicator taxa aids in the assessment of paleoecology. The early Miocene shark faunas of the Atlantic Coastal Plains corroborate a paleoenvironment of a nearshore marine with subtropical to tropical waters.

Conclusions

Specimens were recovered *in situ* from Porters Landing. This detailed information has provided a wealth of paleontological data. Stratigraphic and paleoecology analyses and specimen identifications have been done on this site. A total of 26 chondrichthyans and teleosts taxa have been identified from the site. Of those taxa, 20 are chondrichthyans and 6 are teleost. The site produced the first Georgia Miocene record of 9 chondrichthyan taxa including the largest southeastern United States record of *Ginglymostoma* and the only Aquitanian report of *Aetobatus arcuatus* from North America. Of the identified chondrichthyan taxa, 12 are extinct.

In general, the fossil fish population at Porters Landing was a marine, subtropical to tropical nearshore community. It is difficult to compare modern relative abundances with fossil calculations due to insufficient records. However, the composition of the early Miocene population is very similar to the present population off the southern Atlantic Coast. The western Atlantic Ocean supported a rich diversity of Carcharhiniform sharks during this time. Prior to the early Miocene, especially during the Paleocene, Lamniforms dominated the western coast of the Atlantic (Purdy, 1998a). The Miocene fossil record shows the increasing dominance of Carcharhiniformes in the subtropical waters of the Atlantic.

The study of Porters Landing constitutes an important piece of a paleontological puzzle. Comparisons of taxa and paleoecology of early Miocene sites in the Atlantic Coastal Plain has supported climatic and ecological hypotheses associated with this time period. Fauna and stratigraphy from sites in Delaware, Maryland, North Carolina, and Florida confirm a nearshore marine environment with subtropical to tropical waters. Porters Landing fills the gap of early Miocene information between North Carolina and Florida in the southeastern United States and provides a thorough investigation of early Miocene fishes.

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Appendix

Table 1. Taxonomy of the Class Chondrichthyes, adapted from Cappetta (1987).

Subclass Elasmobranchii	
Cohort Euselachii	
Subcohort Selachii	
Superorder Galeomorphii	
Order Carcharhiniformes	
Family Carcharhinidae	Genus *Carcharhinus*
	Genus *Galeocerdo*
	Genus *Negaprion*
	Genus *Physogaleus*
	Genus *Rhizoprionodon*
Family Hemigaleidae	Genus *Hemipristis*
Family Scyliorhinidae	
Family Sprhynidae	
Family Triakidae	
Order Lamniformes	
Family Alopiidae	Genus *Alopias*
Family Anacoracidae	
Family Cetorhinidae	
Family Cretoxyrhinidae	
Family Lamnidae	Genus *Lamna*
	Genus *Isurus*
	Genus *Carcharodon*
Family Mitsukurinidae	
Family Odontaspididae	Genus *Carcharias*
Family Otodontidae	
Order Orectolobiformes	
Family Ginglymostomatidae	Genus *Ginglymostoma*
Superorder Batomorphii	
Order Rajiformes	
Family Rajidae	Genus *Raja*
Family Rhynchobatidae	Genus *Rhynchobatus*
Order Myliobatiformes	
Family Dasyatidae	Genus *Dasyatis*
Family Mobulidae	Genus *Plinthicus*
Family Myliobatidae	Genus *Myliobatis*
	Genus *Aetobatus*
	Genus *Rhinoptera*

Table 3. Modern habitat of fish found at Porters Landing. Information adapted from Bigelow and Schroeder (1948), Dahlberg (1975), and Compagno (1984, 1988). When possible each fish taxon identified from Porters Landing is represented by a modern taxon. Habitats are: T, temperate; Tp, tropical; S, subtropical; C, coastal; P, pelagic.

TAXA	**HABITAT**
CHONDRICHTHYANS	
Lamniformes	
Carcharias tauras	T, Tp, C
Isurus oxyrhichus	T, Tp
Carcharodon carcharias	T, S, Tp, C, P
Alopias vulpins	S, C, P
Orectolobiformes	
Ginglymostoma cirratum	S, Tp, C
Carcharhiniformes	
Negaprion brevirostris	T, Tp, C
Galeocerdo cuvier	T, Tp, C
Rhizoprionodon terraenovae	T, Tp, C
Carcharhinus sp.	T, Tp, C, P
Hemipristis elongatus	Tp, C
Rajiformes	
Raja sp.	T, Tp, C
Rhynchobatus sp.	T, Tp
Myliobatiformes	
Dasyatis sp.	T, Tp, C
Myliobatis sp.	T, Tp, C
Aetobatus narinari	T, Tp, C
Manta birostris (devilray)	S, Tp, C
Rhinoptera sp.	T, Tp, C
TELEOST	
Tetradontiformes	
Diodontidae	T, S, Tp, adults C, young P
Perciformes	
Lagodon rhomboides	T, S, Tp, C
Elopiformes	
Megalops atlantica	T, S, C
Lutjanus sp.	S, Tp, C, P
Pogonias cromis	T, S, C
Sphyraena sp.	S, Tp, young C

Table 4. Relative abundance of fish taxa from the Porters Landing Member at Porters Landing. Relative abundance is the total number of identifiable specimens (NIS) per taxon divided by the sum of NIS, multiplied by 100. Total NIS = 235.

Taxa	NIS	% of total
SHARKS	**158**	**67.23**
Carcharhinus spp.	17	7.23
Rhizoprionodon terraenovae	0	0.00
Galeocerdo aduncus	14	5.96
Galeocerdo contortus	17	7.23
Negaprion brevirostris	43	18.30
Hemipristis serra	34	14.47
Hemipristis cf. *curvatus*	0	0.00
Physogaleus latus	10	4.26
Ginglymostoma delfortriei	0	0.00
Carcharodon chubutensis	4	1.70
Isurus desori	4	1.70
Carcharias acutissima	3	1.28
Carcharias cuspidata	12	5.11
Alopias latidens	0	0.00
BATOMORPHS	**33**	**14.04**
Raja spp.	5	2.13
Rhynchobatus pristinus	4	1.70
Dasyatis spp.	20	8.51
Myliobatis spp.	0	0.00
Aetobatus arcuatus	4	1.70
Plinthicus stenodon	0	0.00

Table 4. Continued.

Taxa	NIS	% of total
TELEOSTS	**44**	**18.72**
Diodontidae	14	5.96
Lagodon sp.	5	2.13
Megalops cf. *atlantica*	7	2.98
Sphyraena sp.	6	2.55
Lutjanus sp.	0	0.00
cf. *Pogonias* sp.	12	5.11

Table 5. Relative abundance of fish taxa from the Marks Head Formation at Porters Landing. See Table 4 for description of terms. Total NIS = 3052.

Taxa	NIS	% of total
SHARKS	**3052**	**68.40**
Carcharhinus spp.	1907	42.74
Rhizoprionodon terraenovae	399	8.94
Galeocerdo aduncus	9	0.20
Galeocerdo contortus	6	0.13
Negaprion brevirostris	127	2.85
Hemipristis serra	23	0.52
Hemipristis cf. *curvatus*	16	0.36
Physogaleus latus	522	11.70
Ginglymostoma delfortriei	21	0.47
Carcharodon chubutensis	0	0.00
Isurus desori	3	0.07
Carcharias cuspidata	12	0.27
Carcharias acutissima	5	0.11
Alopias latidens	2	0.04
BATOMORPHS	**658**	**14.75**
Raja sp.	14	0.31
Rhynchobatus pristinus	144	3.23
Dasyatis spp.	440	9.86
Myliobatis spp.	18	0.40
Aetobatus arcuatus	8	0.18
Plinthicus stenodon	34	0.76

Table 5. Continued

Taxa	NIS	% of total
TELEOSTS	**752**	**16.85**
Diodontidae	70	1.57
Lagodon sp.	102	2.29
Megalops cf. *atlantica*	151	3.38
Sphyraena sp.	170	3.81
Lutjanus sp.	1	0.02
cf. *Pogonias* sp.	258	5.78

Table 6. Stratigraphic composition of the Marks Head Formation.

Sediment Layer	Unit	matrix collected (kg)	% of total, Marks Head Fm. matrix
Porters Landing South/the Marks Head Formation (GA007)		25.30	3.58
Upper Pebbly Layer (GA027)	8	79.98	11.33
Dark Oyster Layer (GA024)	7	195.46	27.69
Pebbly Layer (GA025)*		12.60	1.78
	6*		
Sand Layer (Lower Pebbly Layer)	5	49.65	7.03
Laminated Sand & Clay	4	67.50	9.56
Lower Sand (sand below laminated sand) (GA026)	3	94.80	13.43
Landslide/Bone Bed (GA009)*		67.50	9.56
Neural Spine Layer/Bone Bed (GA008)*		113.61	16.08

*Stratigraphic placement of these layers is indeterminate.

Table 7. Relative abundance of fish taxa from Porters Landing, combined from the Porters Landing Member and the Marks Head Formation. See Table 4 for description of terms. Total NIS = 4697.

Taxa	NIS	% of total
SHARKS	**3210**	**68.34**
Carcharhinus spp.	1924	40.96
Rhizoprionodon terraenovae	399	8.49
Galeocerdo aduncus	23	0.49
Galeocerdo contortus	23	0.49
Negaprion brevirostris	170	3.62
Hemipristis serra	57	1.21
Hemipristis cf. *curvatus*	16	0.34
Physogaleus latus	532	11.33
Ginglymostoma delfortriei	21	0.45
Carcharodon chubutensis	4	0.09
Isurus desori	7	0.15
Carcharias acutissima	8	0.17
Carcharias cuspidata	24	0.51
Alopias latidens	2	0.04
BATOMORPHS	**691**	**14.71**
Raja spp.	19	0.40
Rhynchobatus pristinus	148	3.15
Dasyatis spp.	460	9.79
Myliobatis spp.	18	0.38
Aetobatus arcuatus	12	0.26
Plinthicus stenodon	34	0.72

Table 7. Continued.

Taxa	NIS	% of total
TELEOSTS	**796**	**16.95**
Diodontidae	84	1.79
Lagodon sp.	107	2.28
Megalops cf. *atlantica*	158	3.36
Sphyraena sp.	176	3.75
Lutjanus sp.	1	0.02
cf. *Pogonias* sp.	270	5.75

Table 8. The Simpson Coefficient. A comparison of similarity can be determined using the Simpson Coefficient (the number of shared taxa at 2 sites divided by the number of taxa at the site with the fewest taxa). The coefficient was calculated for each site, using all recorded shark taxa. In addition, the coefficient was determined separately for the Aquitanian formations and for the Burdigalian formations.

Formation vs. Formation

	Delaware	Florida	Georgia	Maryland	North Carolina
Delaware		**75.0**	**53.3**	**75.0**	**75.0**
Maryland	**75.0**	**75.0**	**78.6**		**59.4**
North Carolina	**75.0**	**87.5**	**92.9**	**59.4**	
Georgia	**53.3**	**87.5**		**78.6**	**92.9**
Florida	**75.0**		**87.5**	**75.0**	**87.5**

Aquitanian vs. Aquitanian

	Florida	Georgia	Maryland	North Carolina
Maryland	**37.5**	**66.7**		**43.8**
North Carolina	**50.0**	**77.8**	**43.8**	
Georgia	**62.5**		**66.7**	**77.8**
Florida		**62.5**	**37.5**	**50.0**

Burdigalian vs. Burdigalian

	Delaware	Florida	Georgia	Maryland	North Carolina
Delaware		**83.3**	**57.1**	**60.0**	**65.0**
Maryland	**60.0**	**83.3**	**78.6**		**42.3**
North Carolina	**65.0**	**100.0**	**64.2**	**42.3**	
Georgia	**57.1**	**100.0**		**78.6**	**64.2**
Florida	**83.3**		**100.0**	**83.3**	**100.0**

Figure 1. Jaw of a Carcharhiniformes. The jaw of *Negaprion brevirostris* shows the development of several rows of fully developed teeth. Teeth are replaced every few weeks when nutrients to the roots are cut off. A fully mature row of teeth rotates laterally into place, similar to a conveyer belt.

Figure 2. Map of the Hawthorn Group. Taken from Hudlestun (1988), the shaded area of this map shows both subsurface and outcrops of the Hawthorn Group s. It covers nearly half of the Coastal Plain of Georgia, as far east as the continental shelf.

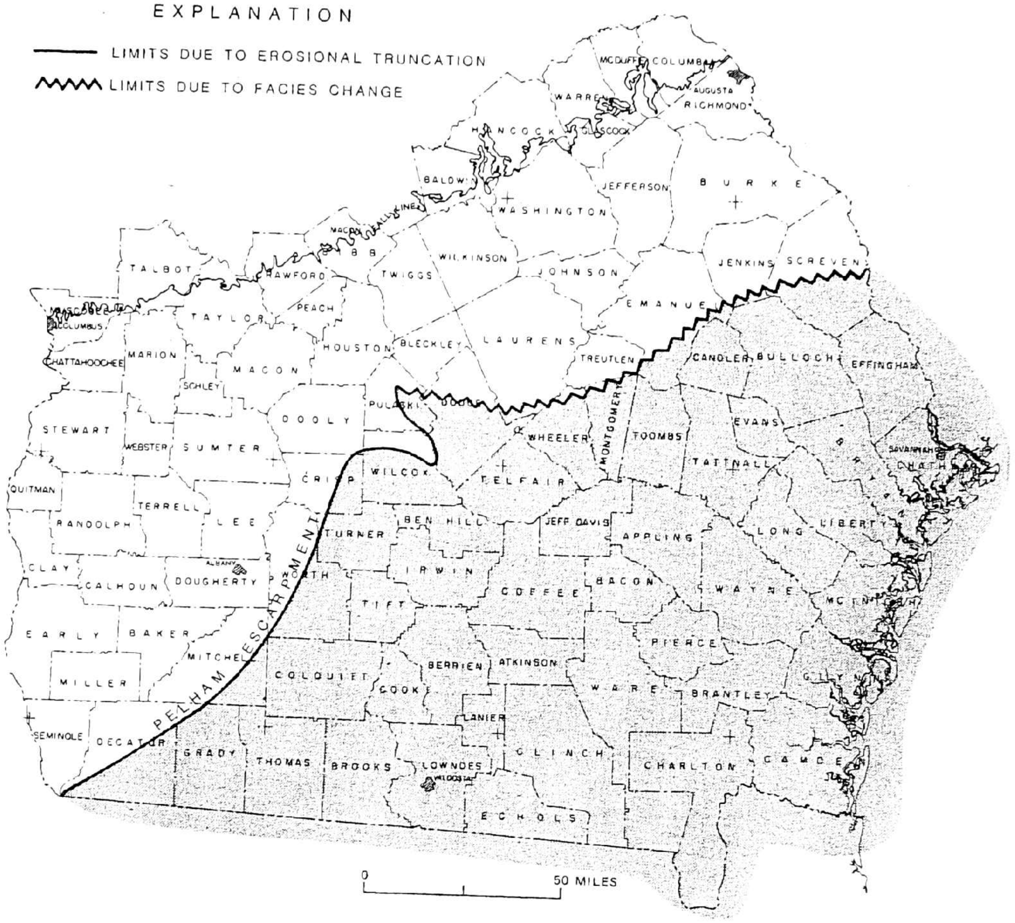


Figure 3. Correlation chart of early Miocene Atlantic Coastal Plain formations. Information adapted form Ward (1998).

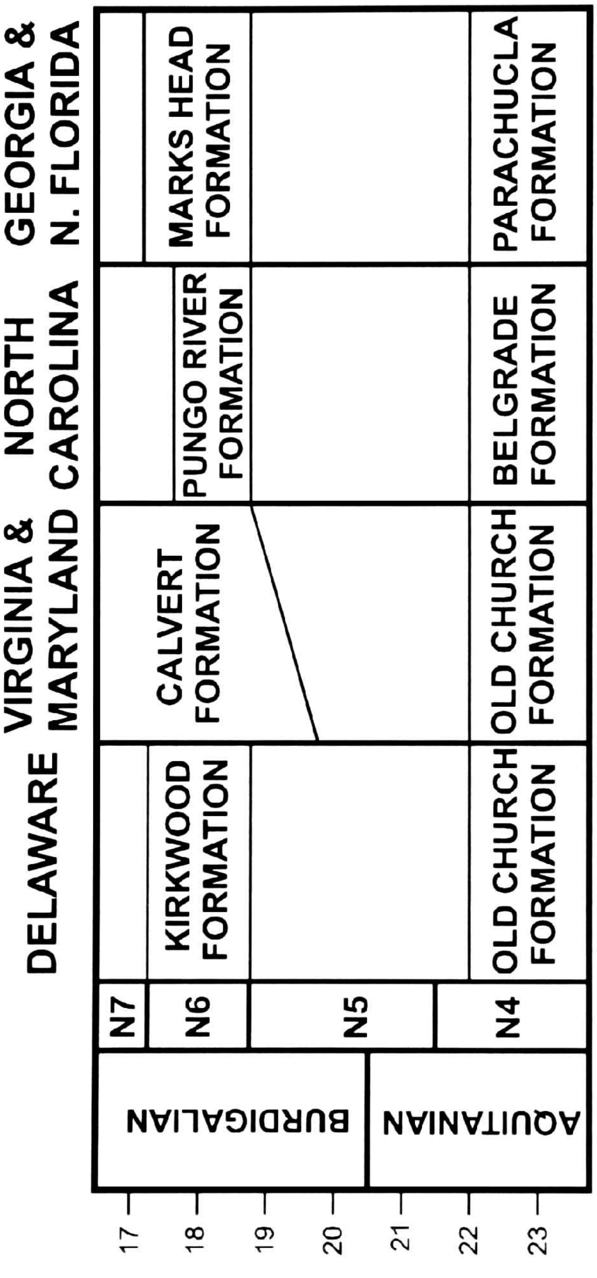


Figure 4. Tooth plate of a Batomorph. Skates and rays have a pavement of teeth that covers both the top and bottom jaws. The pavement provides a surface for grinding and/or crushing their prey. The number of files per row is often diagnostic to genus. This photo taken from Cappetta (1987) shows (A) the lower pavement and (B) the upper pavement of *Aetobatus*.

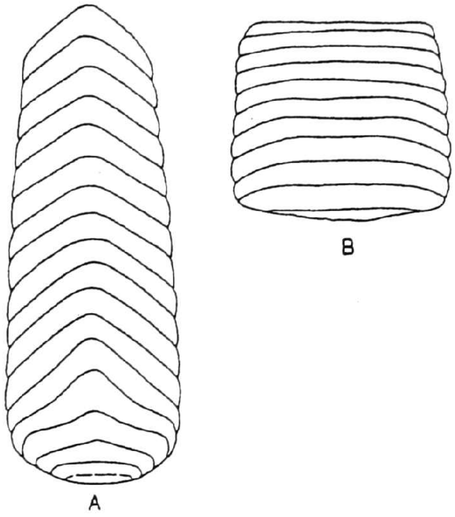


Figure 5. Lingual view of *Galeocerdo aduncus*.

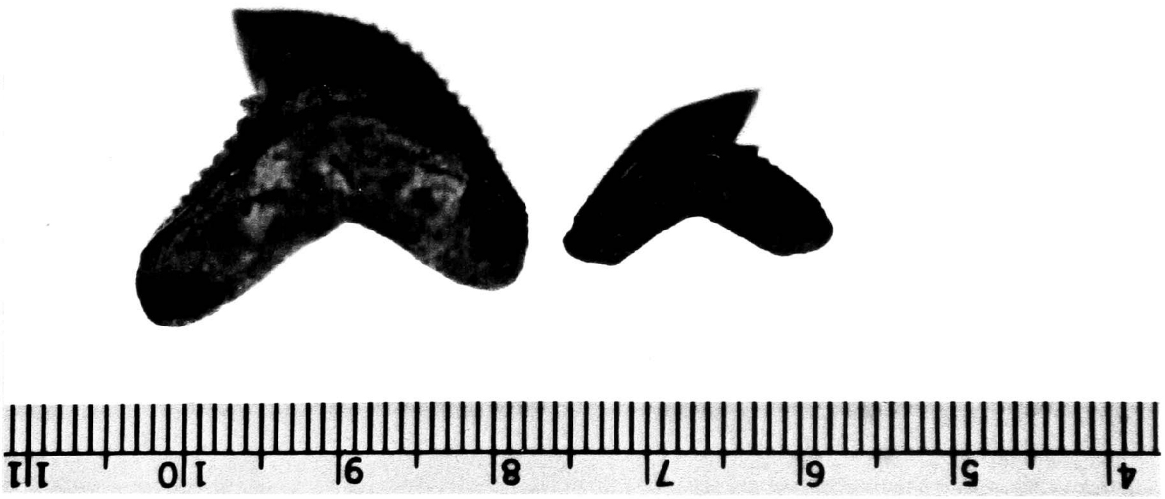
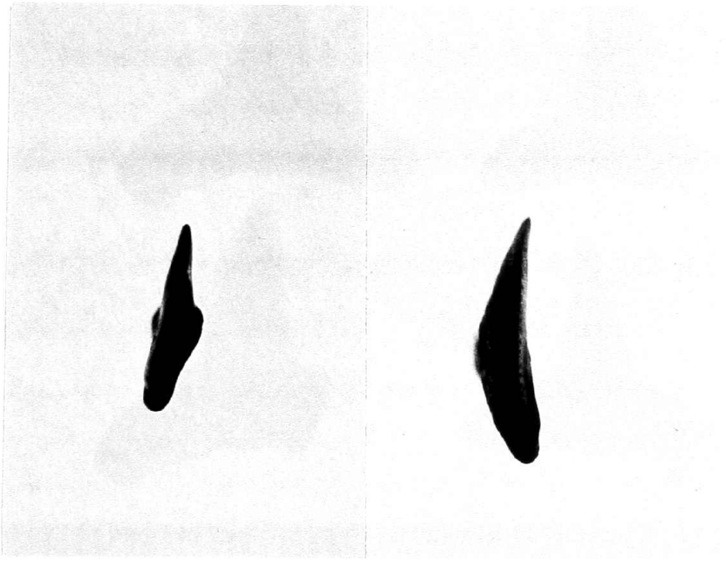


Figure 6. Lingual view of *Galeocerdo contortus.*

Figure 7. Mesial cutting edge of *Galeocerdo* spp. A distinguishing feature between the two early Miocene tiger shark species is the mesial cutting edge. Cutting edge twists apically from shoulder to crown tip on *Galeocerdo contortus* (A). Mesial cutting edge of *Galeocerdo aduncus* (B) is convex and straight from the shoulder to the apex.



A.

B.

Figure 8a. Upper teeth of *Negaprion brevirostris.* Shoulders are serrated on the upper teeth of the lemon shark.

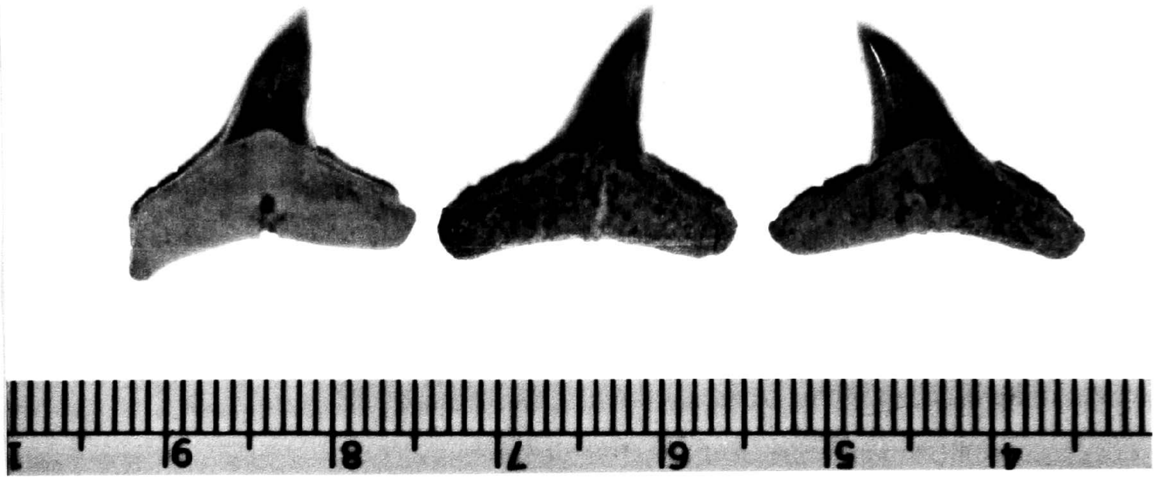


Figure 8b. Lower teeth of *Negaprion brevirostris.* Lower teeth are devoid of serrations and the crown is more erect than uppers.

Figure 9. Lingual view of *Rhizoprionodon terraenovae*. Distal and mesial shoulders of *Rhizoprionodon* are devoid of serrations.

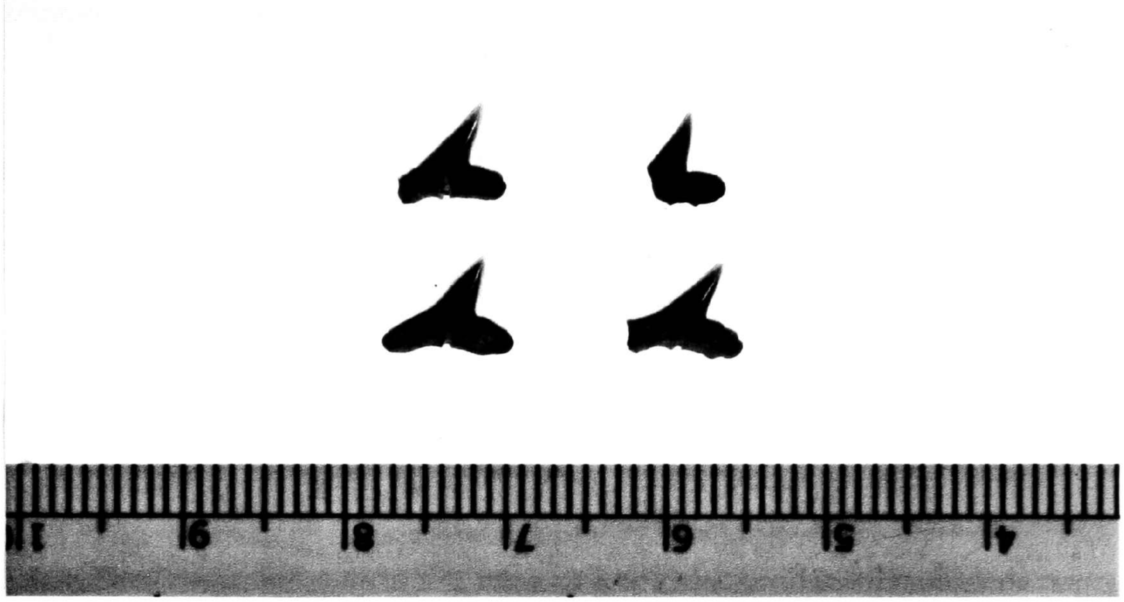


Figure 10. Lingual view of *Physogaleus latus*. The distinguishing feature between *Physogaleus* and *Rhizoprionodon* is the distal serrations. Distal shoulders of *Physogaleus* may possess 2 to 4 serrations.

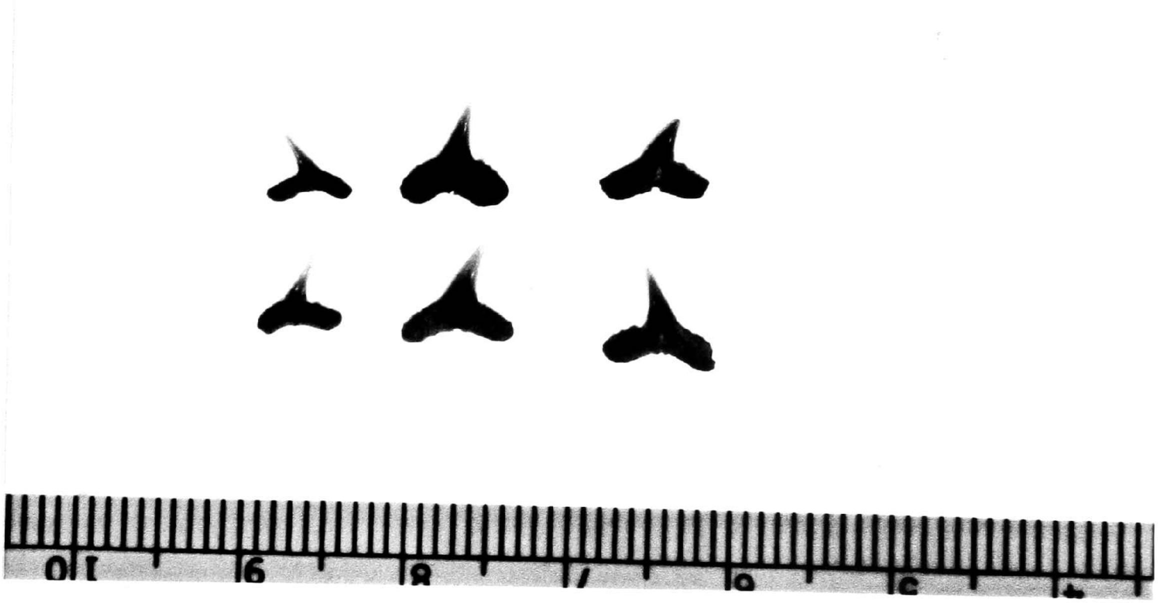


Figure 11. Lingual view of *Rhizoprionodon terraenovae* and *Physogaleus latus.* Teeth of *R. terranovae* are on the left while *P. latus* are on the right (note the presence of serrations on *Physogaleus*).

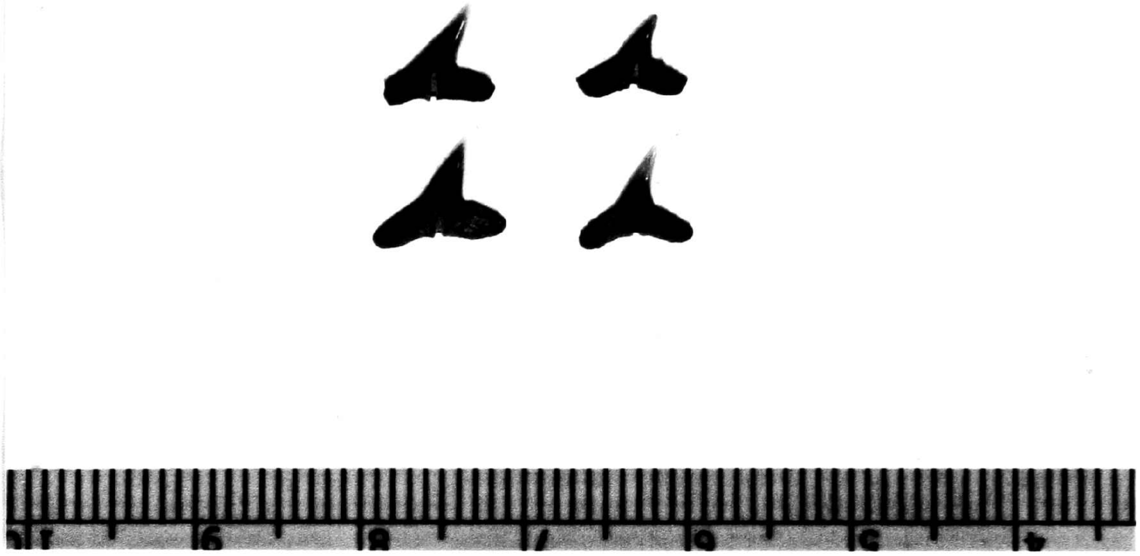


Figure 12. Lingual view of *Carcharhinus* spp. Distinct phena are recognizable presumably representing several species of *Carcharhinus* (see Systematic Paleontology, Description of *Carcharhinus* spp.). Specimens are (A) GSM #889; (B) GSM #915; (C) GSM #216 and GSM #217.

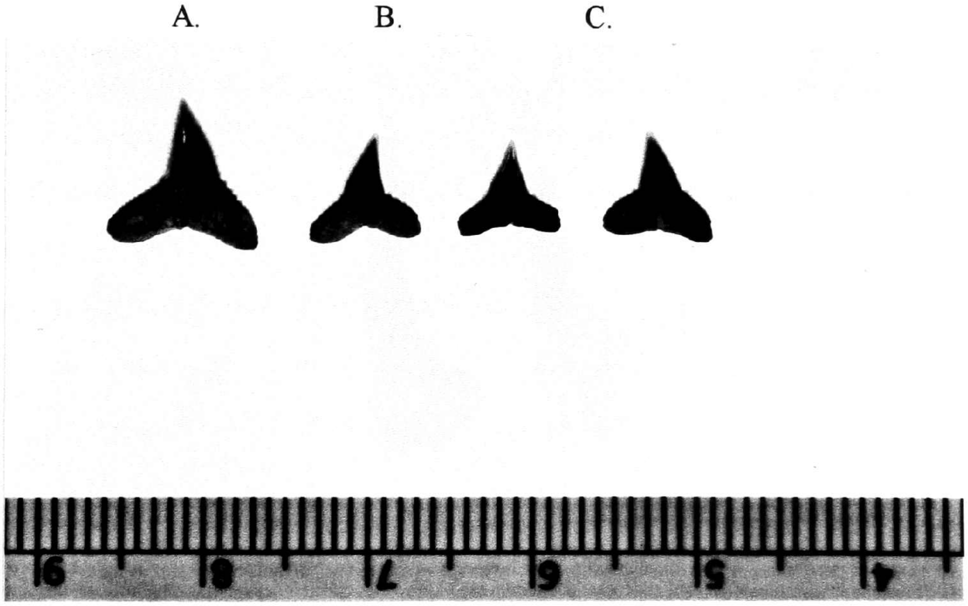


Figure 13. Diagnathic dentition of *Hemipristis serra.* The difference in appearance of lowers (A) and uppers (B) reflects their function. Uppers are used for tearing and/or shredding while the dagger-like lowers are for grasping.

Figure 14. Mesial comparison of *Carcharias cuspidata* and *Hemipristis serra.* Cutting edges of *C. cuspidata* are complete from the apex to shoulder (A). Cutting edges of *Hemipristis* extend approximately three quarters down the crown (B).

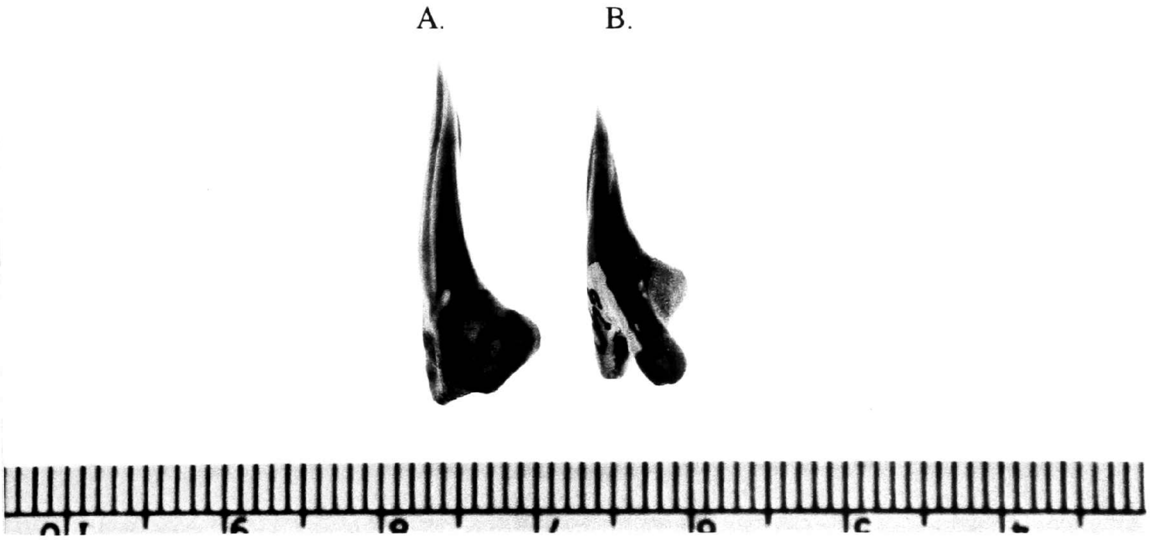


Figure 15. Lingual view of *Hemipristis serra.* Two upper teeth of *Hemipristis serra.* Size and number of mesial serrations is greater for *H. serra* than *Hemipristis curvatus.*

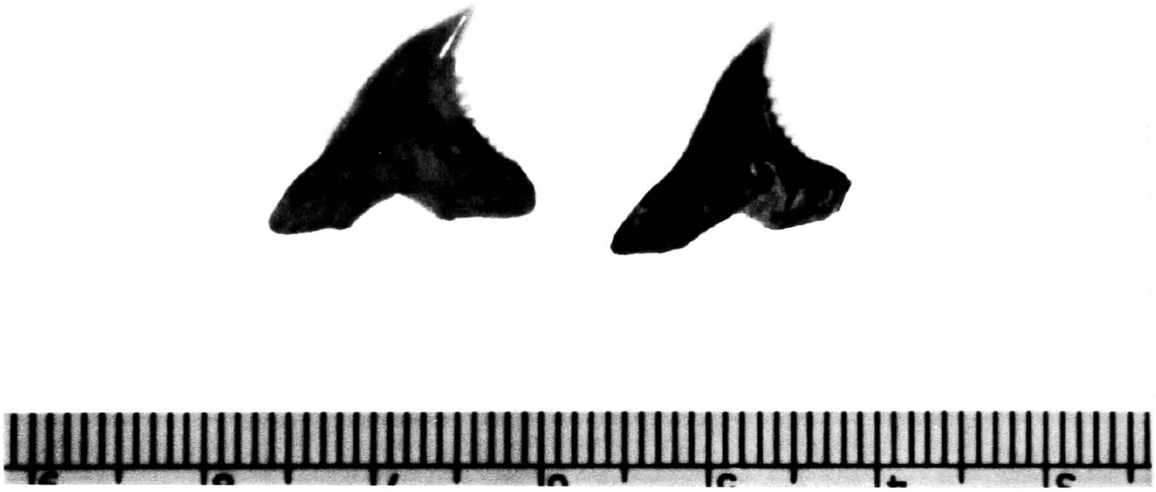


Figure 16. Lingual view of upper teeth from *Hemipristis curvatus*. Mesial serrations are fewer on this snaggletooth species than *H. serra.* In addition, reduced size distinguishes the two species.

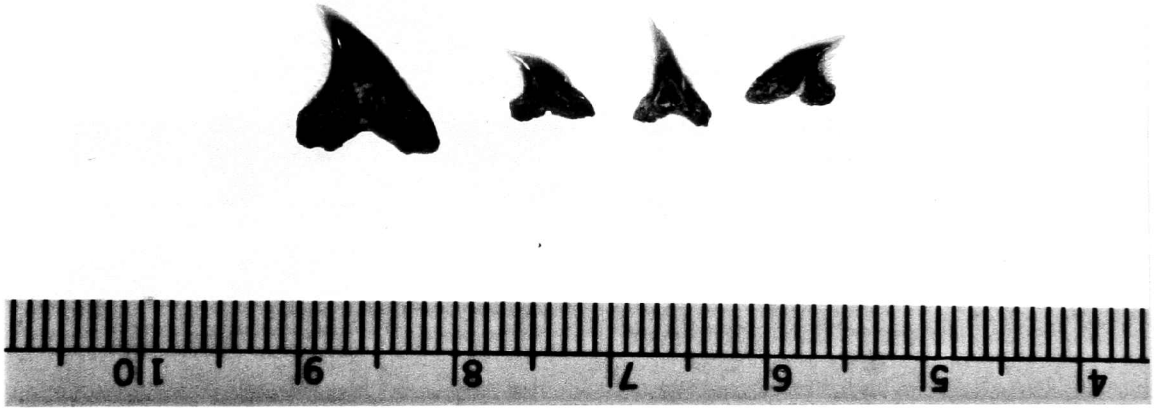


Figure 17. Labial view of *Ginglymostoma delfortriei*. Labial apron of enameloid has been preserved but breakage has distorted the serrations and details of the nurse shark teeth.

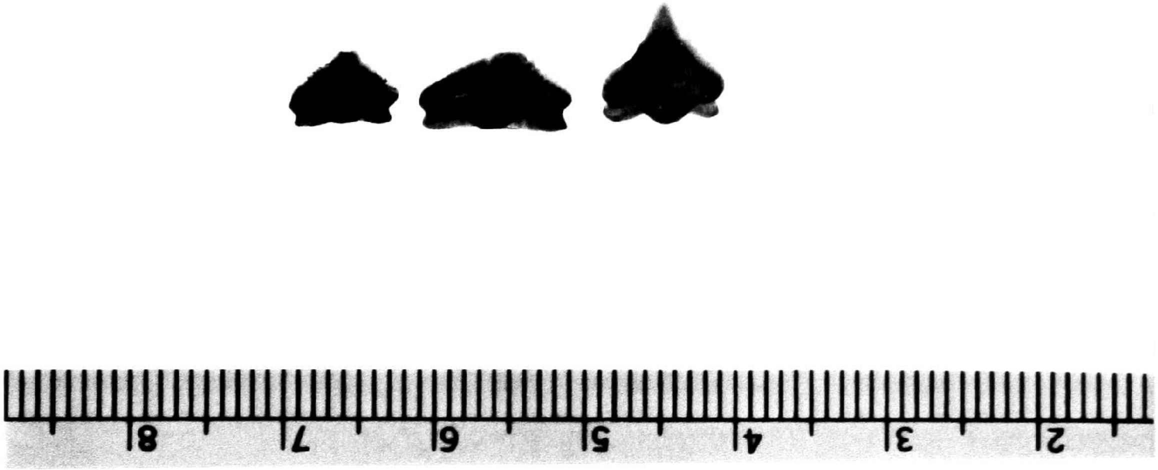


Figure 18. Lingual view of *Carcharodon chubutensis*. Presence of lateral cusplets and petit, regular serrations support the identification of this species.

Figure 19. Lingual view of *Isurus desori*. Slight variation in crown and root morphology reflects a monognathic dentition in *Isurus desori*.

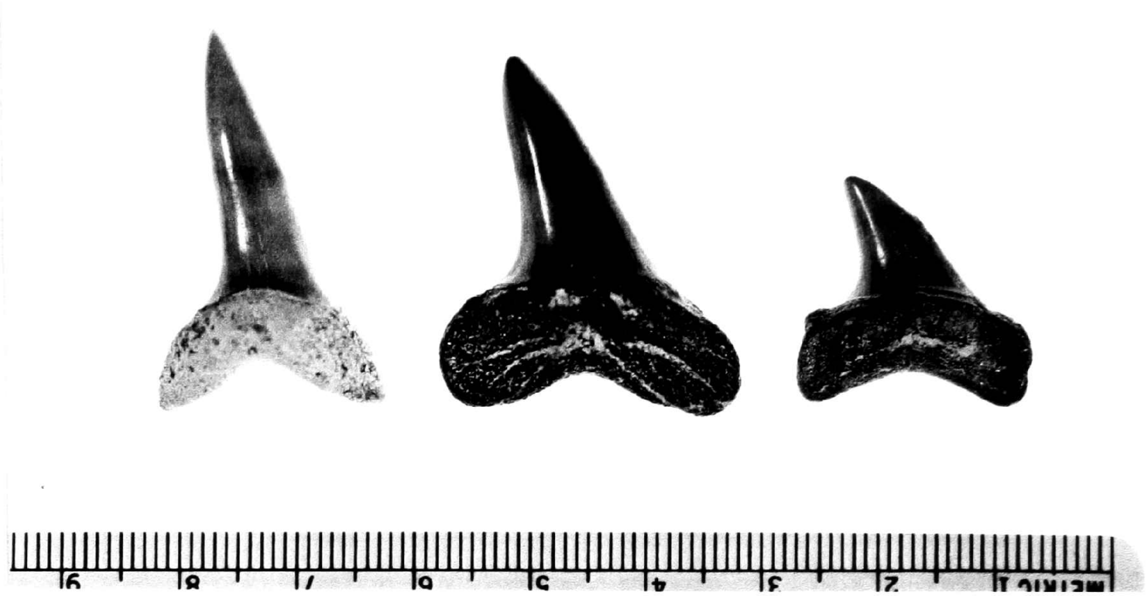


Figure 20a. Lingual comparison of *Isurus desori* and *Carcharias cuspidata*. Crown and roots of *C. cuspidata* (A) are narrower than *I. desori* teeth (B). In addition, *C. cuspidata* has a ridge of lateral cusplets.

Figure 20b. Lingual comparison of *Isurus desori* and *Carcharias acutissima*. Crown of *C. acutissima* (A) is narrower and roots are less robust than *I. desori* (B). In addition, *C. acutissima* has recurved lateral cusplets and a protuberance on the lingual surface of the roots. Only juvenile isurid teeth possess lateral cusplets.

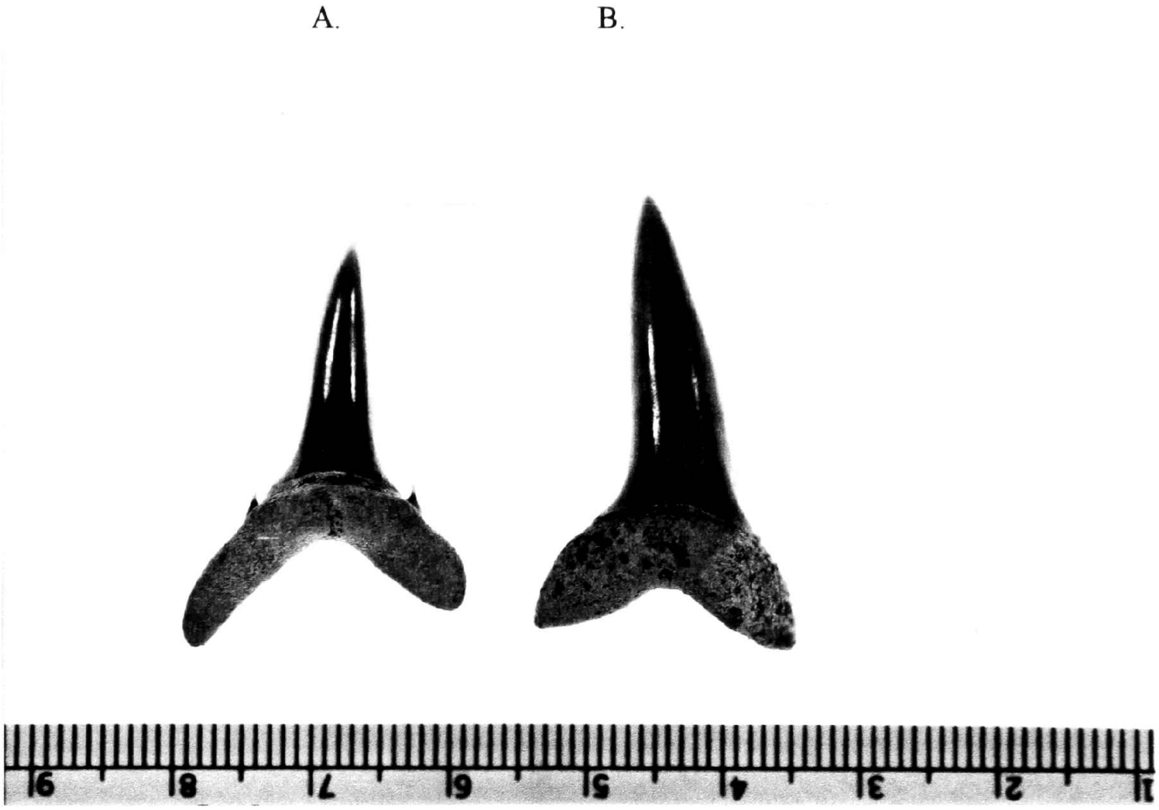


Figure 21. Lingual view of *Carcharias cuspidata*. *Carcharias cuspidata* is the broadest of the Miocene sand tiger shark species. Specimens are (A) an anterior tooth with single, recurved lateral cusplets and (B) a lateral tooth with a ridge of lateral cusplets.

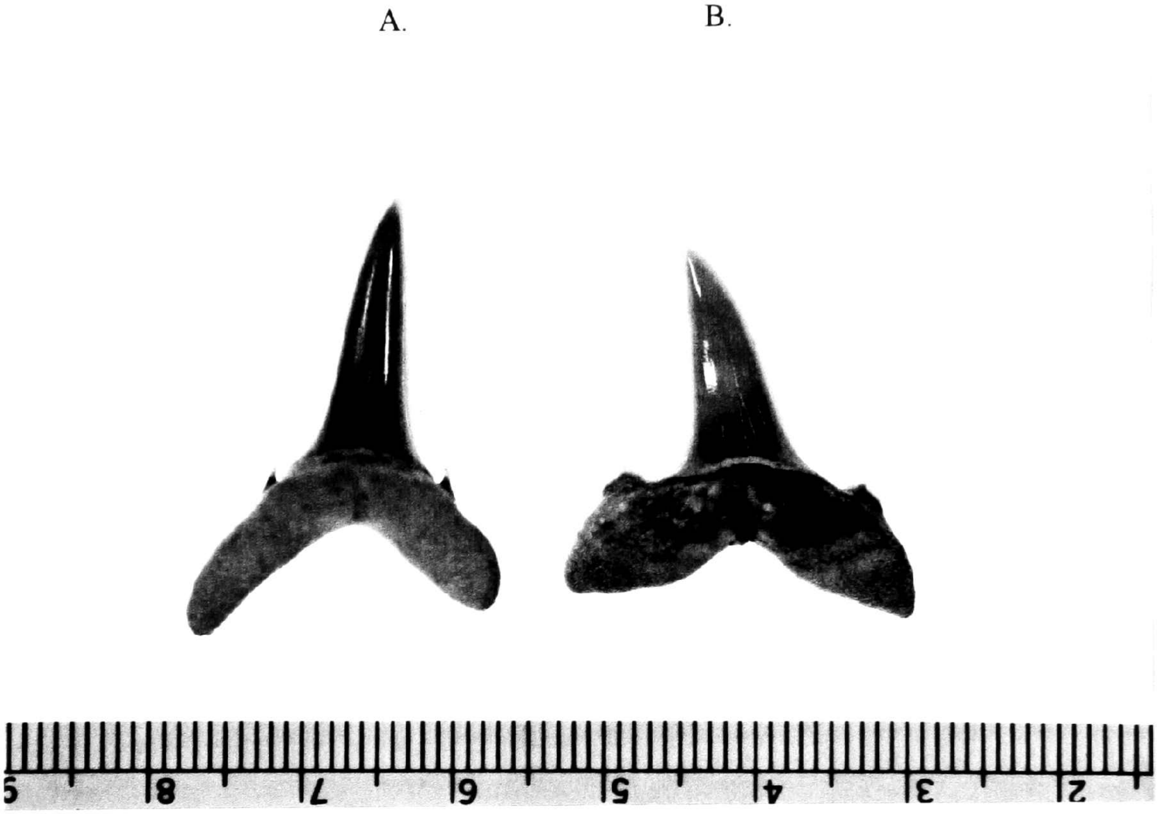


Figure 22. Labial view of *Carcharias acutissima*. Crown is narrower on *Carcharias acutissima* than *Carcharias cuspidata* (see Figure 21). All tooth positions of *C. acutissima* possess singular lateral cusplets.

Figure 23. Lingual view of *Carcharias cuspidata* and *Carcharias acutissima.* Specimens are (A) crown of *C. cuspidata,* GSM #844; (B) *C. acutissima,* GSM #838. The crown of *C. cuspidata* is broader than *C. acutissima.*

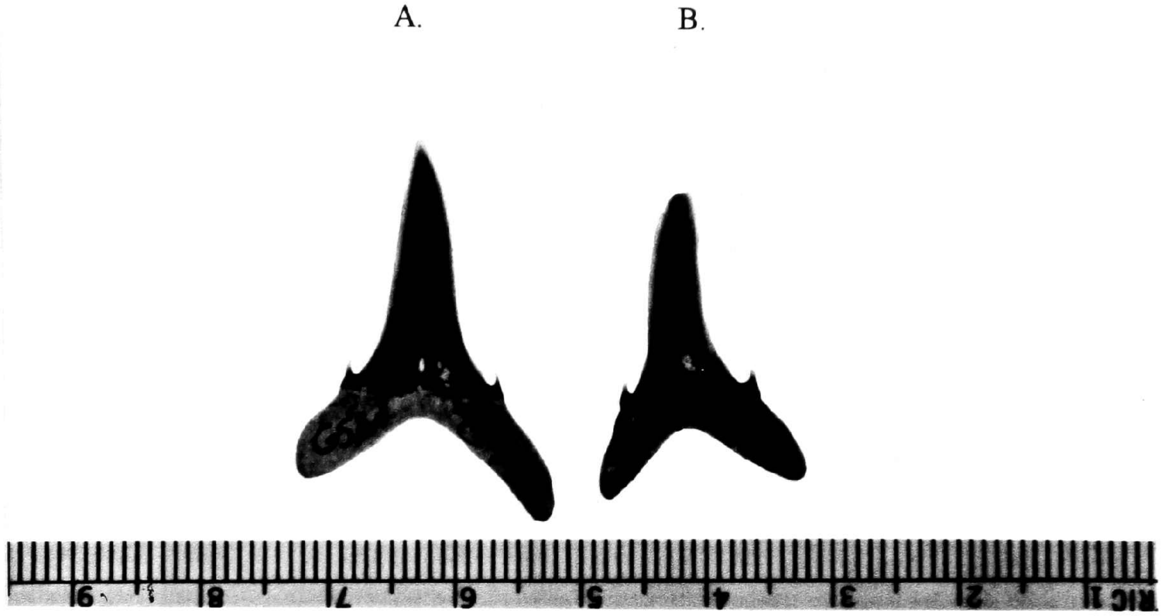


Figure 24. Lingual view of *Alopias latidens.* Identification of specimens is supported by diagnostic arched roots and crown devoid of serrations.

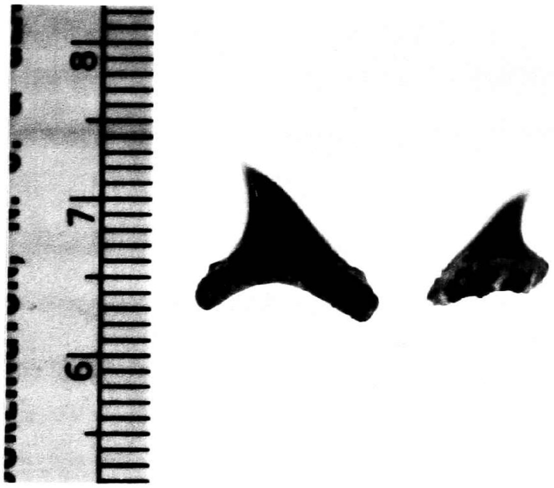


Figure 25. Two phena of *Dasyatis* spp. Scanning electron microscope (SEM) photographs reveal differences in the shape of the labial visor and the enameloid on *Dasyatis.*

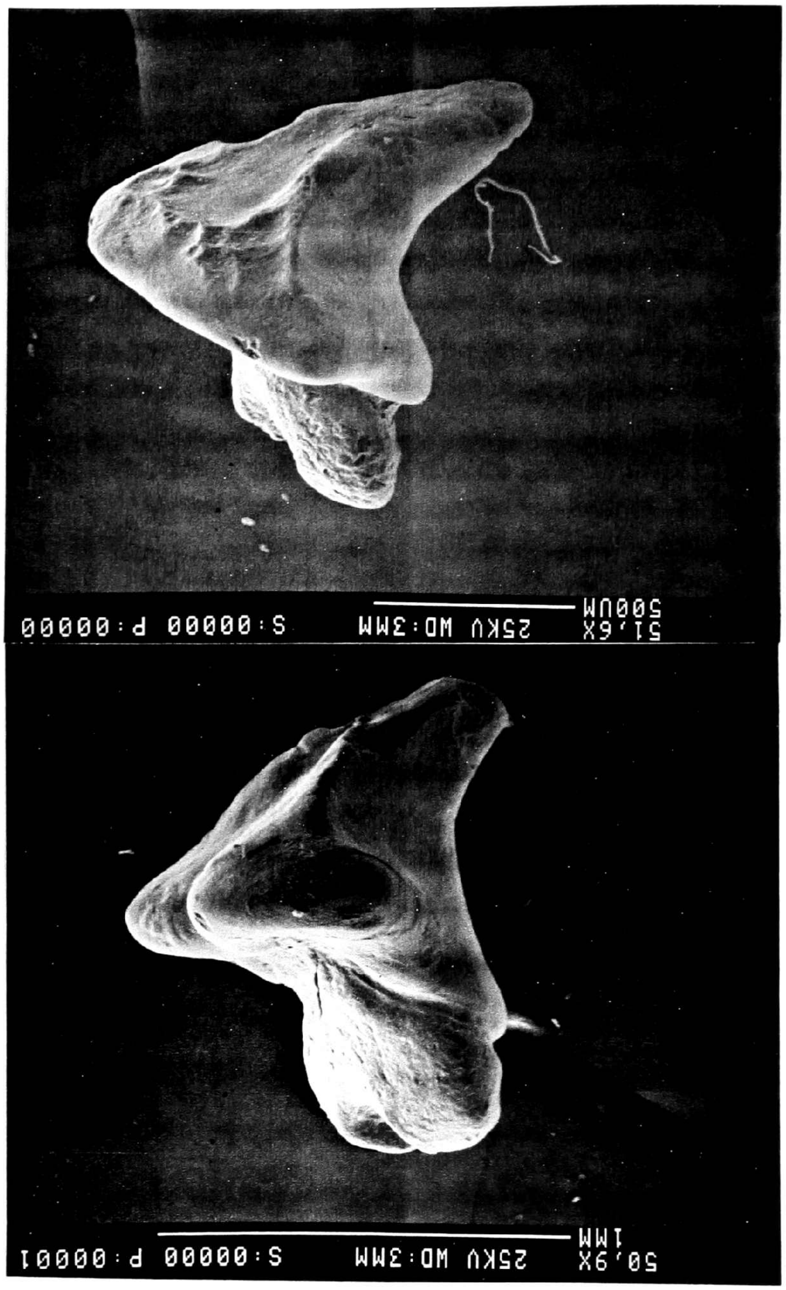


Figure 26. Occlusal view of *Aetobatus arcuatus*. Fragmented tooth files of *Aetobatus arcuatus*. Basal attachments extend past the edge of the crown and are distinct from other myliobatids.

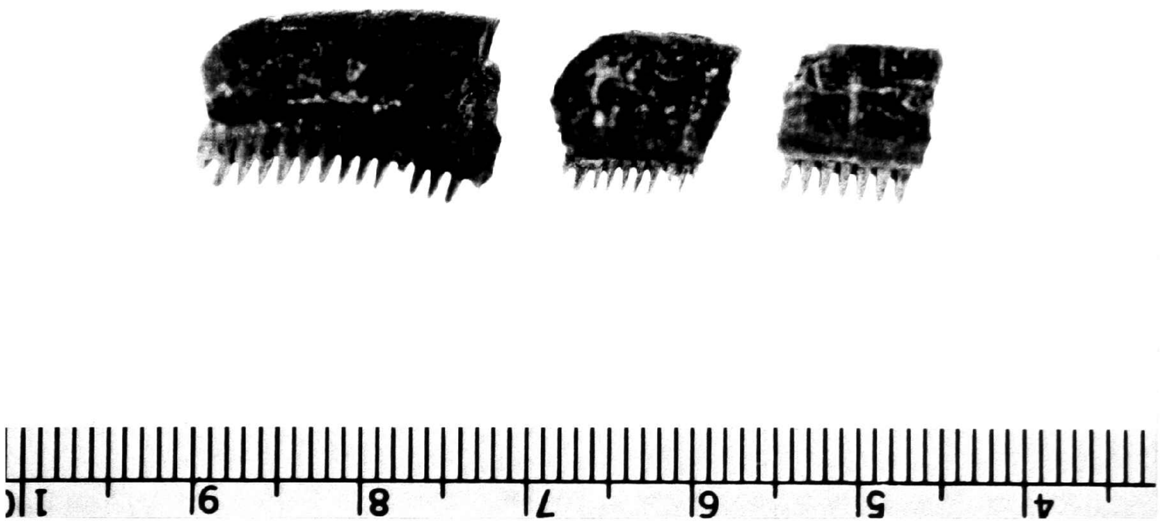


Figure 27. Tooth files of *Plinthicus stenodon*.. Tooth files are from an extinct devilray. (A) is from the labial view; (B) is from the lingual view.