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SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 100

The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland, USA

Edited by
Stephen J. Godfrey

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ABSTRACT

Godfrey, Stephen J., editor. The Geology and Vertebrate Paleontology of Calvert Cliffs, Maryland, USA. *Smithsonian Contributions to Paleobiology*, number 100, iv + 274 pages, 93 figures, 63 body restoration images, 11 tables, 2018.—The last comprehensive review of the fossil vertebrates from the Miocene of Calvert Cliffs was published more than 100 years ago. This volume is a collection of papers that updates some of the geological features of Calvert Cliffs and provides reviews of the fossil biota that include representatives from the following taxonomic groups: chondrichthyans (chimaeras, shark, skates, and rays), actinopterygians (ray-finned fishes), crocodilians (crocodiles), and sirenians (sea cows). Peter Vogt, Ralph E. Eshelman, and Stephen J. Godfrey document how the 20–40 m [65–130 ft] high Calvert Cliffs along the western shore of the Chesapeake Bay continue to yield insights into 18–8 MYA (Miocene) geology, marine and terrestrial vertebrate fauna, and the origin and evolution of Chesapeake Bay and Calvert Cliffs up to the present. These exposures rank high among the best-known fossiliferous deposits of any age. Bretton W. Kent describes the cartilaginous fish (the chondrichthyan) fauna, consisting of 54 species—3 chimaeras (ratfishes), 39 sharks, and 12 skates and rays—a fauna rich in large macrophagous sharks and large neritic rays. In an addendum to Kent's chapter, he and David J. Ward describe a new species of giant thresher shark with serrated teeth. Giorgio Carnevale and Stephen J. Godfrey present an account of the 38 actinopterygian taxa known from osteological remains and a diverse otolith assemblage of at least 55 taxa. These actinopterygians show an affinity for well-oxygenated muddy and sandy substrates dominated primarily by shallow-water species characteristic of the inner shelf and secondarily by epipelagic taxa. Robert E. Weems details the crocodilians referable to the tomistomine *Thecachampsa*. The closest living relative is *Tomistoma schlegelii*, the false gharial of Southeast Asia. Two species are present: *Thecachampsa sericodon* and *T. antiquus*. These tomistomines are found in shallow marine coastal deposits, indicating that they inhabited coastal waters. Daryl P. Domning reports that fossils of the Miocene marine fauna include rare sirenians of the family Dugongidae. Three taxa are known: the halitheriine dugongid *Metaxytherium crataegense*, the dugongine dugongid *Nanosiren* sp., and another dugongine, aff. *Corystosiren*. The St. Marys Formation contains remains that may be referable to *Metaxytherium floridanum*, but confirmation awaits the discovery of more complete specimens.

Cover image: Calvert Cliffs at Warrior's Rest Sanctuary; view looking north. These 12–15 million-year-old sediments from the Miocene epoch comprise the upper portion of the Calvert Formation and the overlying Choptank Formation. Photo by Stephen J. Godfrey.

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Contents

Introduction

Stephen J. Godfrey

The naturally eroding sea bluffs along Calvert Cliffs rank high among the best-known and long-studied fossiliferous deposits of any age on the planet, yet they continue to yield insights into the Miocene marine and terrestrial biota that thrived there between approximately 18 and 8 MYA (million years ago). Along the Potomac River on the Maryland side, and elsewhere in Virginia, the age of the Miocene sediments reaches back to 23 MYA (Kidwell et al., 2015). All of these shallow marine to coastal sediments comprise only a small part of the vast thickness of sediments that have been shed from the eroding Piedmont and Appalachian Mountains, an ongoing process that began with tectonic breakup of Pangaea and the consequent separation of North America from Africa ca. 175 MYA. At the time of the 1904 Maryland Geological Survey publication on the systematic paleontology of the Miocene deposits of Maryland (Case et al., 1904), the fossilized remains of more than 600 different species were documented, the majority of which were of marine invertebrates. Although a detailed survey of the invertebrate fossils found along the cliffs is beyond the scope of this volume, they, in addition to the vertebrate fossils reviewed here (more than 110 vertebrate species are reviewed in this volume), and the sediments in which they are entombed give us a picture of the environment and the organisms that lived in the Mid-Atlantic region of North America during the Miocene epoch.

The last comprehensive review of the fossil vertebrates from the Miocene of Calvert Cliffs was published more than 100 years ago, and since then, a great deal has been discovered, researched, and published. This volume updates some of the geological features of Calvert Cliffs and provides reviews for the following taxonomic groups from the Miocene Chesapeake Group: chondrichthyans (chimaeras, shark, skates, and rays), actinopterygians (ray-finned fishes), crocodilians, and sirenians (sea cows). It is anticipated that a second volume will include additional contributions on the geology of the cliffs as well as reviews of the other vertebrate groups known from the Chesapeake Group in Maryland and Virginia: turtles, birds, terrestrial mammals, seals, toothed whales, and baleen whales.

Upon hearing of my ambitious hopes to help compile, in a single volume, an update on the Miocene geology and vertebrate paleontology of Calvert Cliffs, David J. Bohaska (collections management, vertebrate paleontology, Smithsonian Institution) told me, “It will be wrong the day it’s published.” As a contributing editor to several of the *Geology and Paleontology of the Lee Creek Mine, North Carolina* volumes (Ray and Bohaska, 2001; Ray et al., 2008), he understood the nature of science and wanted my expectations to be realistic. (Thank you, Dave!) This effort is by no means the final word on the geology and vertebrate paleontology of Calvert Cliffs. It is a reflection of our collective curiosity

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that allows us to update what is currently known. Bohaska deserves special thanks for responding to countless requests from me for help and information throughout my 20 years here at the Calvert Marine Museum.

Daryl Domning of Howard University (and author of chapter 5) once said to me, “Do something now as opposed to everything never.” This volume is the “something now”; hopefully, it will inspire excellence in collecting and research so that future generations of paleontologists, both avocational and professional, can revise this work to further deepen our understanding of the world that used to be.

This work is dedicated to the landowners along Calvert Cliffs and along other tributaries flowing into the Chesapeake Bay, who have so generously allowed professional paleontologists to quarry fossils from their cliff-front properties. Permission to quarry is only half the equation, however. The majority of the finds along the cliffs are made by amateur/avocational collectors; they donate many of their finds to public museum collections—principally those of the Calvert Marine Museum (CMM) and the Smithsonian Institution’s National Museum of Natural History (NMNH). At the time of this writing, fully 70% of the fossils in the permanent paleontology collection of the CMM were donated by avocational paleontologists. Consequently, most of the fossils illustrated herein were also collected by amateurs. And so I extend the dedication of this volume to include avocational collectors, for without their generosity this volume would be poorer indeed. They are our eyes and scouts along the cliffs, regularly reporting the presence of newly exposed bones therein.

A WORD OF WARNING TO FOSSIL HUNTERS

“Digging in the cliffs is dangerous and is *prohibited* on all state and federal lands” without obtaining permits. “On private land, permission **must** be obtained from the owners before digging. If you see a skull, bone, or unusual fossil in the cliffs, please report it to the Calvert Marine Museum in Solomons, Maryland (410-326-2042). The museum appreciates getting this information and, if justified by the importance of the find, will make every effort to obtain the necessary permission and have trained personnel collect the specimen, giving full credit to the finder” and the property owner (Ashby, 1979:16).

ACKNOWLEDGMENTS

I express my gratitude to James O. Farlow, who first approached me during a coffee break at an annual meeting of the Society of Vertebrate Paleontology to ask if I had an interest in editing a volume on the geology and paleontology of Calvert Cliffs for Indiana University Press (IUP). And so the project began with guidance from Robert J. Sloan, editorial director at IUP. When it became obvious that the contributions far exceeded a single volume, he very graciously dissolved our agreement, allowing for submission to Smithsonian Institution Scholarly Press (SISP). Ginger Minkiewicz, director of SISP, was willing to publish this effort, and Stephanie Summerhays (formerly of SISP) cheerfully responded to many queries on my part; thank you both very much. Other members of the SISP team include Meredith McQuoid-Greason, Julie Beals, and Tshawna Byerly. I am very grateful for your attention to detail. This volume benefitted greatly from constructive reviews by Nicholas D. Pyenson (NMNH) and David J. Bohaska (NMNH).

I also express my appreciation to the contributing authors for their wonderful chapters and extraordinary patience. The artistic excellence of Tim Scheirer (CMM) is evident throughout; he has drawn all the life restorations of the Miocene vertebrates illustrated herein with the same expertise that characterizes all his work. John Nance (paleontology collections manager at CMM) also helped in many ways.

I am also indebted to C. Douglass Alves (former director, CMM) and Sherrod Sturrock (director of CMM) for also recognizing the value of a comprehensive work like this. Ralph Eshelman, first director (now research associate) at CMM, had the vision to create a curatorial position in paleontology at the fledgling CMM. He along with James A. Kaltenbach, David J. Bohaska, and volunteers including Norm Riker, Wally Ashby, and Linda McGilvery began the fossil collections that continue to grow with no end in sight. The curatorial position at CMM is made possible with funding from the citizens of Calvert County, Maryland, and the Calvert County Board of County Commissioners. Additional funding for the Department of Paleontology comes from the Clarissa and Lincoln Dryden Endowment for Paleontology at CMM.

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Calvert Cliffs: Eroding Mural Escarpment, Fossil Dispensary, and Paleoenvironmental Archive in Space and Time

Peter Vogt,[1,2] Ralph E. Eshelman,[2] and Stephen J. Godfrey[3]*

ABSTRACT. The Calvert Cliffs are a series of bayside bluffs, typically 20–40 m high, that form a 40 km long shoreline escarpment on the western shore of the Chesapeake Bay in Calvert County, Maryland. These cliffs expose fossil-rich shallow marine sediments deposited between about 18 and 8 MYA, during the Miocene epoch at times when relative sea level was higher than today. In ascending order, the Miocene strata exposed in the cliffs belong to the Calvert, Choptank, and St. Marys Formations. These formations are overlain along the southern portion of the cliffs by "upland gravels," fossil-poor fluvial deposits that accumulated at times in the latest Miocene or Pliocene when sea level was only slightly higher than today. The Calvert Cliffs we see today began to form about 5,000 years ago during the most recent rise of sea level that followed the last glacial event, called the Wisconsinan. The slopes of these cliffs, mostly between 45° and 60°, make them unstable and prone to collapse. Whenever the toe of a cliff becomes stabilized through formation of sand bars, sand spits, or human intervention, the overlying cliff face erodes back until it reaches a stable slope of about 30°–35°. Ongoing cliff erosion causes long-term shoreline retreat, which averages about 5–30 cm/yr along the central and northern cliffs where the semi-consolidated marl of the Plum Point Member is exposed at beach level. Erosion rates are much higher along the southern cliffs, where sandier, less consolidated Choptank and St. Marys Formation sediments are exposed at beach level. There the rate of shoreline retreat locally averages 50–100 cm/yr. The ongoing cycle of erosion and shoreline retreat exposes the abundant and diverse Miocene fossils entombed within the cliffs, which wash out and become scattered across the underlying beaches. The Calvert Cliffs constitute a regional scenic landmark with relatively high topographic relief very rare along the tidal shoreline between the northern New Jersey Highlands and Kill Devil Hills in North Carolina. They also are regarded as one of the three most important deposits of Miocene fossils in the world.

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INTRODUCTION

As the chapters in this volume demonstrate, the 20–40 m high Calvert Cliffs (Figures 1.1, 1.2) have yielded extremely significant insights into the Miocene world that was present in the region from approximately 18 to 8 mya. On the outcrop-poor Southern Maryland Coastal Plain, the Calvert Cliffs stand out as a premier example of local geology (Glaser, 1971) and paleontology (e.g., Ward and Powars, 1991). The Calvert Cliffs cap a 750 m thick stack of sediments near the landward edge of an enormous wedge of debris deposited on the eastern margin of North America since its breakup from Africa around 175 mya. Without an outcrop like the Calvert Cliffs, our knowledge of the Miocene world would be limited to what could be gleaned from a sediment core not more than 5 cm in diameter (e.g., Hansen and Wilson, 1984).

The cliffs expose the lower half of the Miocene Chesapeake Group, including much or all of the marine Calvert, Choptank, and St. Marys Formations (Figure 1.3). Shattuck (1904)

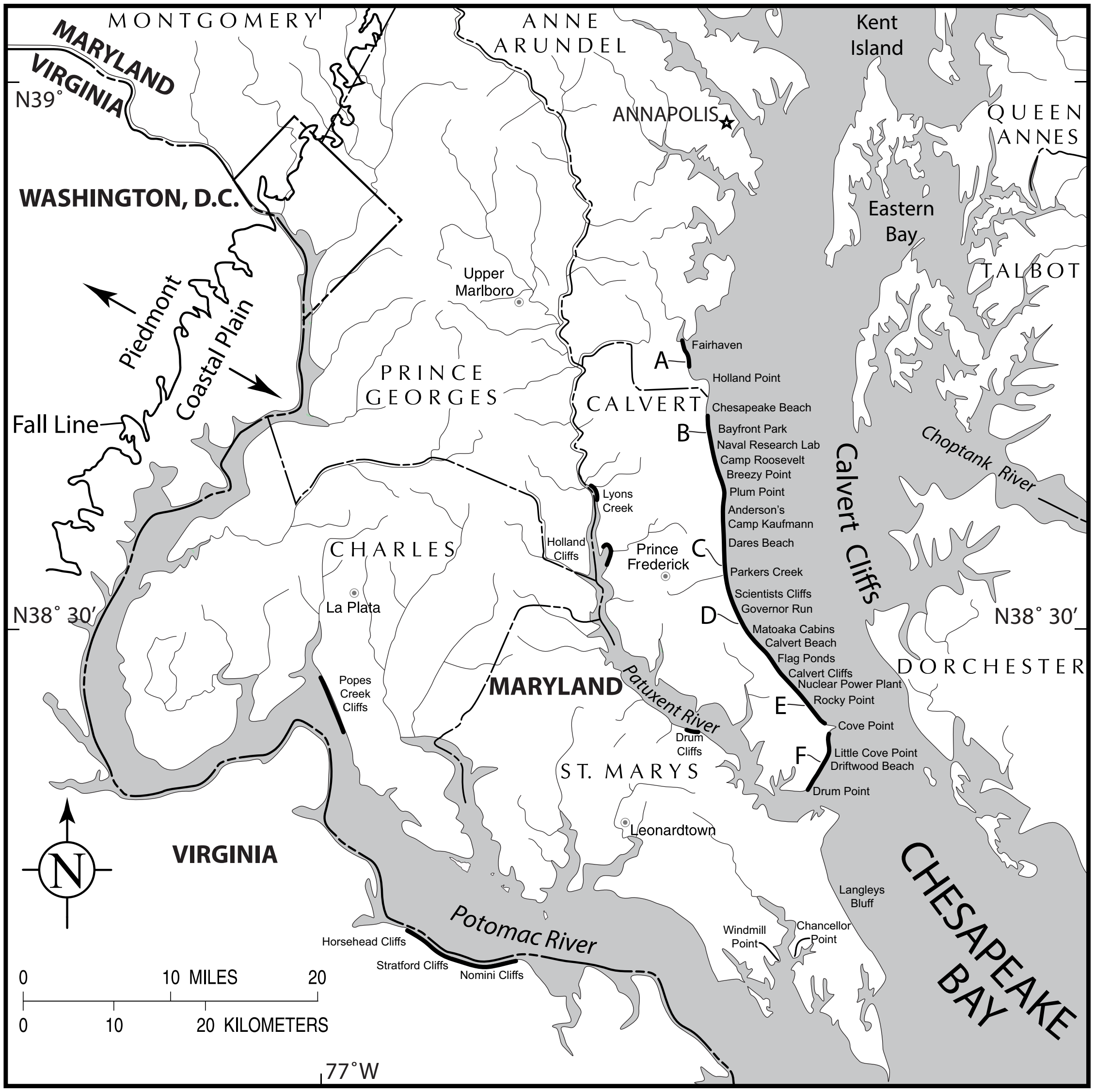


FIGURE 1.1. Chesapeake Bay region, showing the Calvert Cliffs, with its named communities, facilities, and beaches, and other coastal bluffs greater than 15 m high. Letters locate selected photos shown in Figure 1.2 of the Fairhaven Cliffs (Figure 1.2A) and the Calvert Cliffs (Figure 1.2B–F). The western border of the Atlantic Coastal Plain, marked by the Fall Line (Weems, 1998), is taken from Powars (2013).

subdivided the entire lower Chesapeake Group into two dozen "zones," which we here call "beds" to avoid confusion with paleontological zones. Shattuck's numbering system is still widely used today, with the exception of his zone 16, which later mapping has shown to be only a local unit. Overlying these shallow marine Miocene strata in the middle and especially the southern Calvert Cliffs are fluvial strata informally called upland deposits by Schlee (1957). With rare exceptions (e.g., McCartan et al., 1990), these upland deposits are nearly devoid of fossils and thus are not a focus of this volume. Although poorly dated, these sediments were generally deposited by the ancient Potomac and its tributaries during the late Miocene through Pliocene and perhaps early Pleistocene times. Even during maximum Pliocene warmth (Miller et al., 2012), however, the Atlantic did not return to the area of the Calvert Cliffs. Tidewater in the form of estuaries, producing the modern and earlier Calvert Cliffs by shoreline erosion (e.g., Hobbs, 2004; Vogt et al., 2010) only reappeared after the middle Pleistocene (since ca. 1 MYA). During repeated major glaciation and very low sea levels, rivers such as the Susquehanna carved deep valleys to enable formation of later estuaries and cliffs such as those described in this volume.

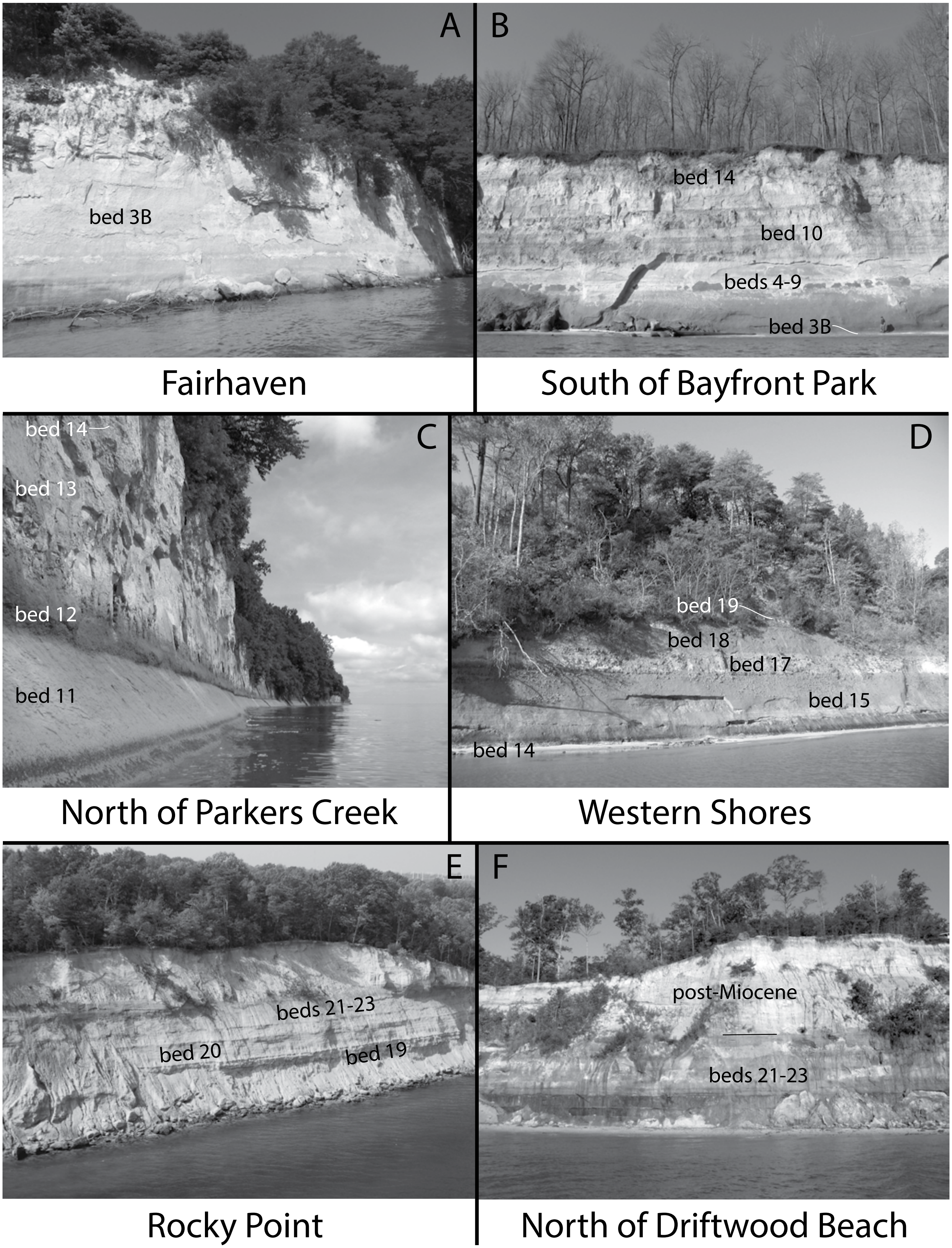
Calvert Cliffs expose shallow marine to coastal nonmarine sediments that were derived from the eroding Piedmont and Appalachians during the Miocene and probably Pliocene epochs. The marine Miocene exposures of the Calvert Cliffs rank among the best-known and longest-studied fossiliferous deposits of any age on the planet. Largely for this reason, the cliffs are among the 100 most significant geologic outcrops in northeastern North America (Vogt and Eshelman, 1987) and are extremely popular with amateur fossil collectors, including both serious museum volunteers and casual fossil hunters (e.g., Ashby, 1979; Powell, 1986; Dickas, 2012). Diverse species of invertebrate marine fossils—a review of which is outside the scope of this volume—are exposed in the eroding cliff faces, and abundant specimens of them litter the shoreline below the cliffs. As the following chapters in this volume demonstrate, the cliffs provide a window into not only the marine but also the terrestrial Miocene vertebrate faunas of the Mid-Atlantic region.

There are many other stories to be told about the 42 km long series of eroding coastal cliffs and intermittent stream valleys found along portions of the western shore of the Chesapeake Bay. They include conflicting human interactions with the cliffs and the role of the cliffs as regional scenic and recreational landmarks—the subject of photography, art, and fiction. Geomorphology and modern erosional processes (driven by wave erosion that is enabled by wind, exceptionally high tides during storms, and rising sea level) maintain the cliffs as ever-changing outcrops that are eroding back at rates typically ranging 0.1–0.5 m/yr. The cliffs also constitute an unusual ecological transition zone, called an ecotone, which is rich in ephemeral microhabitats lying between land and sea.

DIVERSITY OF FOSSILS FROM THE CALVERT CLIFFS

The nonvertebrate fossil record is readily subdivided into (1) the plant kingdom, (2) single-celled and other tiny animals best studied under the microscope, and (3) macroscopic invertebrates such as mollusks. Vertebrates, the focus of much early research (e.g., Whitmore, 1971b), include marine sharks, rays, chimeras, bony fishes, turtles, crocodilians, sea birds, and marine mammals, as well as occasional examples of freshwater and terrestrial vertebrates that washed into the Miocene sea. To reach out to a wider readership, we will use common English names for these Miocene creatures because most have modern relatives, at least at the family or genus level and in some cases even at the species level.

Microscopic plant remains from the Calvert Cliffs include diatoms (a major group of photosynthetic algae with at least 23 species identified to date; Andrews, 1978, 1988) and radiolarians (Shattuck, 1904), both of which have shells, called tests, which are made of silica. There are also abundant remains of many species of another biostratigraphically important phylum of single-celled organisms called dinoflagellates (De Verteuil and Norris, 1996), some of which can both photosynthesize and ingest other microbes. Microscopic pollen grains, although produced by macroscopic land plants, are another abundant component of the marine plant microflora that tells us most of what we know about the onshore flora. The pollen from the Calvert Cliffs remains largely unstudied, but Bryan Landacre (in Weems et al., 2017) reported pollen assemblages from beds of similar age in the nearby Westmoreland County cliffs of Virginia (Figure 1.1). These pollen assemblages (called palynofloras) come from the Plum Point Member of the Calvert Formation, the Choptank Formation, and the Little Cove Point Member of the St. Marys Formation. The palynofloras from all three of these units are dominated by species of oak (*Quercus*), hickory (*Carya*), and pine (*Pinus*). Secondary elements, however, can vary considerably from unit to unit. In the Plum Point Member, the secondary elements consist mainly of hardwood taxa such as alder (*Alnus*), ash (*Fraxinus*), elm (*Ulmus*), holly (*Ilex*), hornbeam (*Ostrya/Carpinus*), sweetgum (*Liquidambar*), and wingnut (*Pterocarya*, an exotic). Cypress trees (*Taxodium* type) are the most common and persistent warm-temperate to tropical taxon present in the Plum Point, followed by *Momipites* (an extinct exotic in the walnut family). In the Choptank Formation, the mix of secondary forest elements was somewhat different and consisted of ash (*Fraxinus*), beech (*Fagus*), birch (*Betula*), hornbeam (*Ostrya/Carpinus*), and sweetgum (*Liquidambar*). Cypress (*Taxodium* type) again is present throughout the Choptank Formation but in reduced numbers compared to the Plum Point time. Also represented in the Choptank Formation are grasses (Poaceae), sedges (Cyperaceae), and herbaceous taxa, including representatives of Amaranthaceae and Asteraceae. Yet another palynofloral assemblage is found in the Little Cove Point Member, where the



Fairhaven

South of Bayfront Park

North of Parkers Creek

Western Shores

Rocky Point

North of Driftwood Beach

FIGURE 1.2. (*Facing page*) (A) Cliffs south of Fairhaven, Anne Arundel County, Maryland (approximately 38°44′32.43″N, 76°33′23.75″W). (B) The Calvert Cliffs south of Bayfront Park, Calvert County, Md. (approximately 38°40′28.76″N, 76°31′52.22″W). (C) The Calvert Cliffs north of Parkers Creek, Calvert Co., Md. (approximately 38°32′33.23″N, 76°31′2.50″W). (D) The Calvert Cliffs at Western Shores, Calvert Co., Md. (approximately 38°29′31.62″N, 76°29′54.67″W). (E) The Calvert Cliffs at Rocky Point, Calvert Co., Md. (approximately 38°25′29.69″N, 76°25′41.37″W). (F) The Calvert Cliffs north of Driftwood Beach, Calvert Co., Md. (approximately 38°21′17.16″N, 76°23′31.02″W). Numbers in the photos indicate beds (zones) first defined by Shattuck (1904).

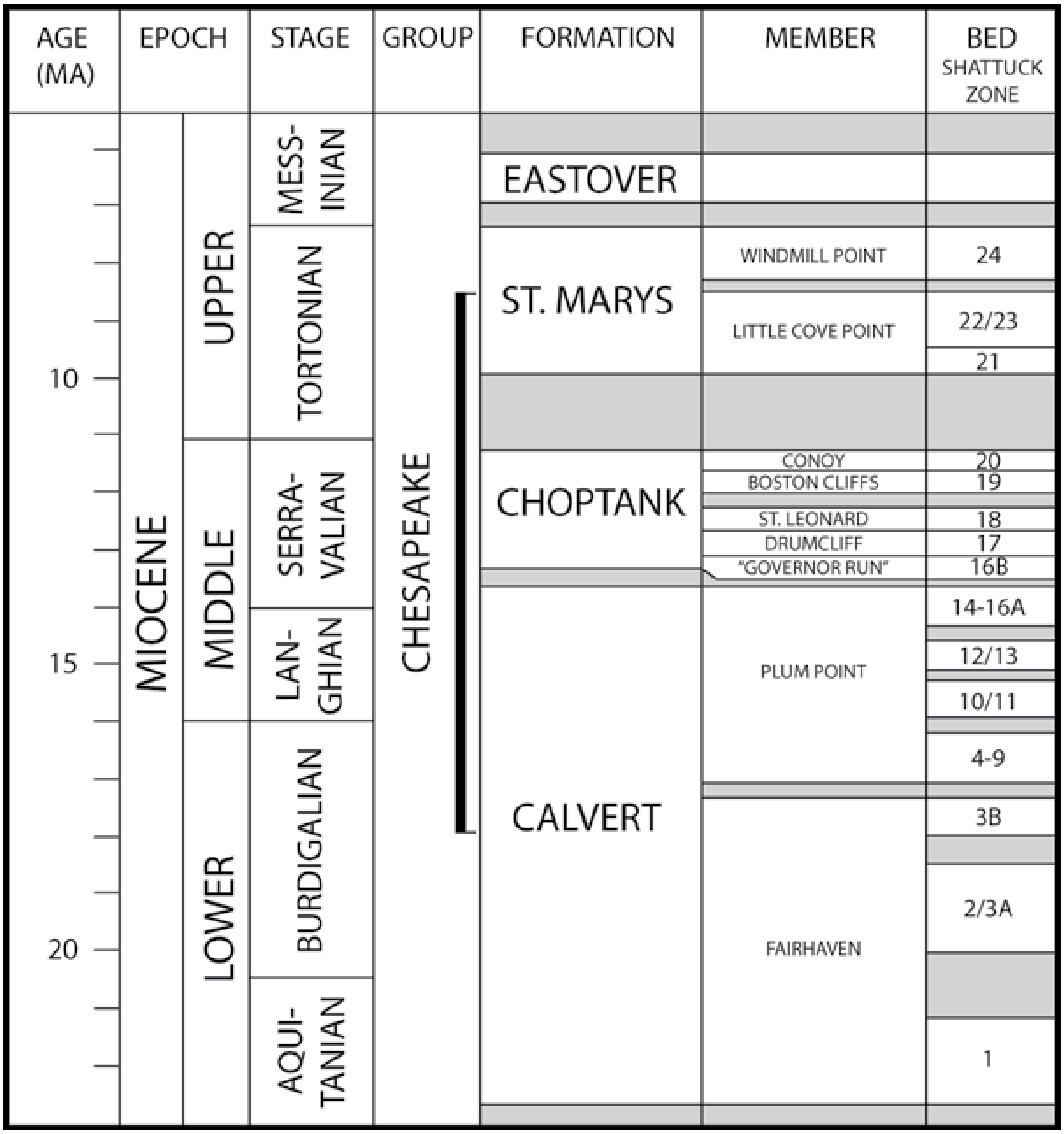


FIGURE 1.3. Ages and stratigraphic correlation chart for the Miocene part of the Chesapeake Group. The dark bracket within the group column designates the part of the Miocene Chesapeake Group represented by the sediments along the Calvert Cliffs. The Eastover Formation is preserved only in Virginia and northern North Carolina. Modified from R. E. Weems (Calvert Marine Museum, personal communication) and Powars (2013).

secondary hardwood forest elements include beech (*Fagus*), cypress (*Taxodium* type), hemlock (*Tsuga*), wingnut (*Pterocarya*), and sweetgum (Liquidambar). Grasses (Poaceae), sedges (Cyperaceae), and herbaceous taxa (Amaranthaceae and Asteraceae) again are well represented. All of the terrestrial palynofloras from the Westmoreland Cliffs have their greatest similarity to the palynofloras being produced today in Florida and the southern Atlantic and Gulf Coastal Plains.

Macroscopic remains of land plants include carbonized small logs, twigs, cones, fruits, and nuts of trees that originated from the nearby warm temperate to nearly subtropical coastal forests growing to the west. No modern comprehensive review of these plant remains has been undertaken; however, macrofossils from various kinds of pine (Stark, 1987), cypress, oak, and elm represent parts of forest associations that grew along nearby coasts and riparian venues (e.g., Berry, 1916). Vogt and Parrish (2012) suggested that rare erratic pebbles found in the Calvert Formation (along Calvert Cliffs) were rafted into the sea as 'driftwood dropstones' trapped in tree roots. These dropstones are most abundant in beds 12 and 14, both of which contain carbonized wood.

At least 23 species of foraminifera, tiny calcareous planktonic animals, have been identified to date (e.g., Shattuck, 1904; Gibson, 1983; Buzas and Gibson, 1990). Also known are calcareous shells from at least 25 species of ostracods (Malkin, 1953), which are tiny clam-like crustaceans. Larger invertebrates include echinoderms (Shattuck, 1904), with at least one species each of sand dollar (Kier, 1983), sea urchin, starfish, and brittle star; two hydrozoans (Shattuck, 1904); at least one species of coral (Shattuck, 1904); one brachiopod (Shattuck, 1904; superficially clamlike, they lived directly on the substrate); bryozoans (Shattuck, 1904; colonial organisms sometimes called moss animals); and several species of barnacles (Zullo, 1984) and other crustaceans, one of which is thought to have produced the abundant trace fossil *Gyrolithes* sp. (infilled helical burrows seen in vertical section along the cliffs; Uchmana and Hanken, 2013). Notable among many crabs collected is the giant spider crab *Libinia amplissimus* from the St. Marys Formation, which is nearly twice the size of its living relatives (Feldmann and Schweitzer, 2016).

Mollusks are by far the most common macrofossils found and are generally much more abundant on the beaches below the cliffs than are shells of modern species inhabiting the Chesapeake Bay (Figure 1.4). The paucity of shells of modern Chesapeake mollusks (such as oysters, mussels, and soft-shell and razor clams) is due in part to much lower abundance of these animals today than in the late nineteenth century. More than 400 Miocene species (e.g., Shattuck, 1904; Schoonover, 1941; Vokes, 1957; Ward, 1992; Petuch, 2005; Petuch and Drolshagen, 2010) are known from the Calvert Cliffs, including a scaphopod (a burrowing marine mollusk popularly known as a tooth or tusk shell), snails, clams, oysters, and pectens (scallops). The pectens are often especially well preserved, particularly in the Choptank Formation. Nance et al. (2015) recently reported on the presence of intact proteinaceous shell-binding material in *Ecphora* snail shells from along the Calvert Cliffs. These original proteins represent some of the oldest and best-preserved examples of proteins ever found in a fossil shell. Many of the mollusks found in the Calvert Cliffs are preserved in their life positions, a fossil association called a biocenosis. In contrast, most vertebrate remains are broken and scattered and often show bite marks made by sharks. Bone fragments are most abundant in the so-called Parkers Creek Bone Bed (bed 12), where they are typically found at 10–100 m intervals. This bed contains an association of remains typical of a fossil death assemblage (called a thanatocoenosis), but the remains are too scattered to qualify as a true "bone bed" because the bones, although abundant, are not tightly packed into dense clusters like they are at localities discussed in Rogers et al. (2007).

Fossil shark teeth (Figure 1.4; Kent, this volume) are probably the single greatest attraction the cliffs offer to the fossil-collecting public (e.g., Glaser, 1979; Powell, 1986; Kent, 1994; Dickas, 2012). Most shark teeth are found as "float" on the beach and, for some species, are abundant (Visaggi and Godfrey, 2010) because sharks continually shed teeth during their lifetimes. Miocene species—closely related to modern ones—include angel, bramble, bull (gray), cow, hammerhead, lemon, mako, sand tiger, sharpnose, snaggletooth, thresher, tiger, and whale sharks. The largest sharks in this fauna (*Carcharocles chubutensis, C. megalodon*, and *Parotodus benedenii*) are all now extinct. A front tooth of C. *megalodon* may measure more than about 13 cm (5 inches) on edge. For many collectors, the discovery of such a tooth is a find of a lifetime. *Carcharocles megalodon* traditionally has been considered to be related to the modern great white shark (Applegate and Espinosa-Arrubarrena, 1996), but now it appears likely that the modern great white shark is more closely related to *Carcharodon* (also known as *Isurus* or *Cosmopolitodus*) *hastalis* (Ehret et al., 2012; Kent, this volume), one of the extinct broad-toothed mako species found along the Calvert Cliffs. Shark vertebral centra also are occasionally found, but otherwise, the cartilaginous skeletons of sharks generally do not fossilize.

Other fossil fish remains include many species of skates and rays (Kent, this volume), as well as a wide variety of bony fishes (Leriche, 1942; Carnevale and Godfrey, this volume), including sturgeons, gars, bowfins, shad, freshwater and marine catfishes, hakes, cods, brotulas, toadfishes, anglerfishes, garfishes, sea robins, poachers, sea bass, tilefishes, bluefishes, cobias, pinfishes, scups, croakers, black drums, red drums, tautogs, stargazers, barracudas, wahoos, bonitos, tunas, blue marlins, sailfishes, lefteye flounders, burrfishes, and ocean sunfishes. Although some of the fossil fishes from the cliffs are different from living species (because of evolutionary change), others are practically indistinguishable from extant species and show how little many bony fishes have evolved in the last 10–20 million years.

Two amphibian taxa (both Caudata) have been reported from the Calvert Formation at the Pollack Farm fossil site near Cheswold, Kent County, Delaware (Weems and George, 2013), but as yet no amphibian fossils have been found along Calvert

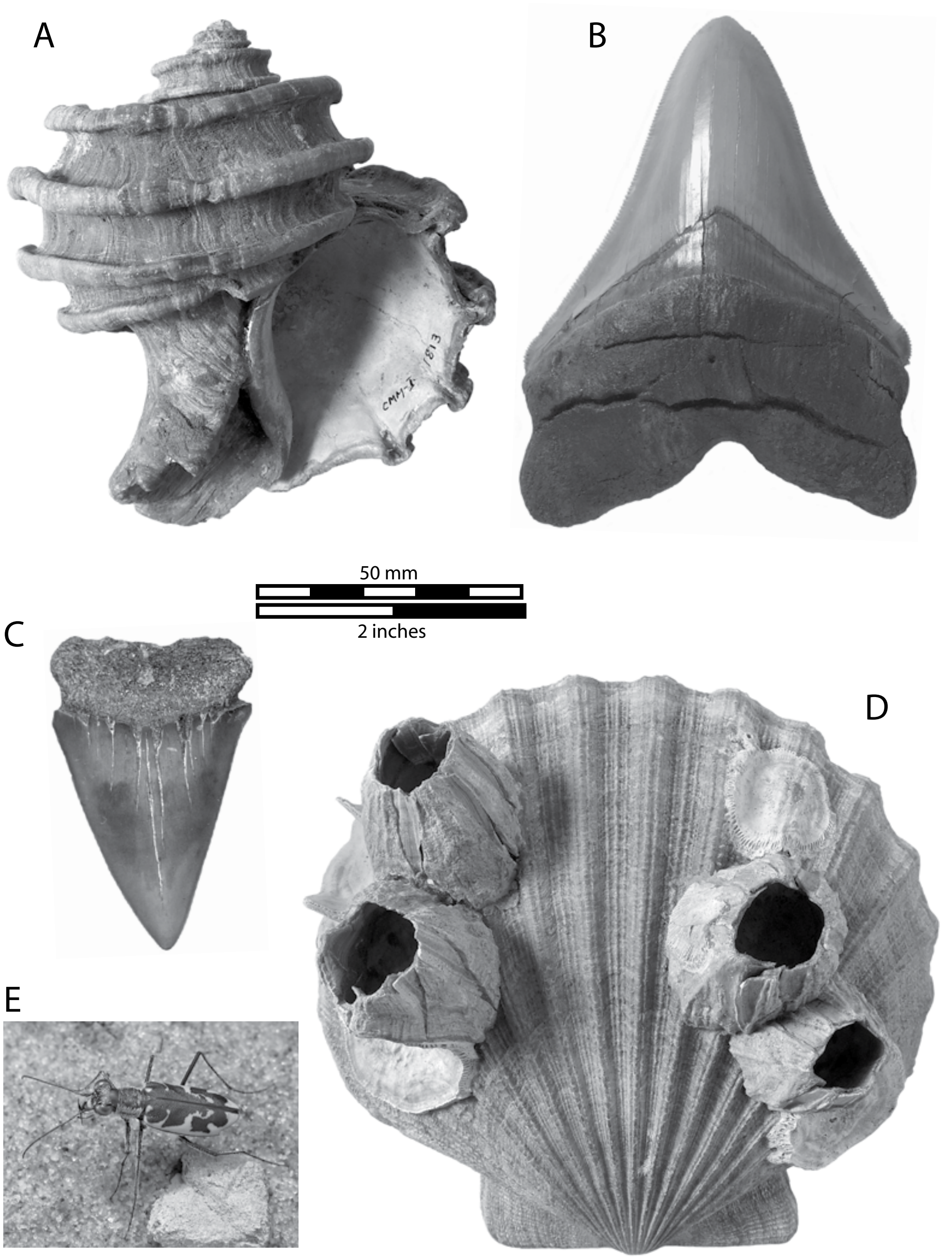


FIGURE 1.4. (A–D) Selected Miocene fossils and (E) the living Puritan tiger beetle. (A) The muricid gastropod *Ecphora gardnerae gardnerae*, Maryland's state fossil. (B) *Carcharocles megalodon* lower anterior tooth, lingual view. (C) *Carcharodon hastalis* upper anterior tooth in lingual view, showing where the base of the enameloid cutting edge was notched on both sides by Native Americans for use as a tool, projectile point, or pendant; this is one of four comparable shark teeth recovered from Wheatley Point midden site 18DO371 in Dorchester County, Maryland (Lowery et al., 2011: figs. 10–12). (D) Scallop shell (*Chesapecten nefrens*) festooned with barnacles (*Balanus concavus chesapeakensis*; Pilsbry, 1916; Zullo, 1984). (E) Extant tiger beetle (*Cicindela puritana*), federally listed as threatened, which requires eroding cliff in which to lay its eggs (Knisley, 2011); photo courtesy of B. Knisley.

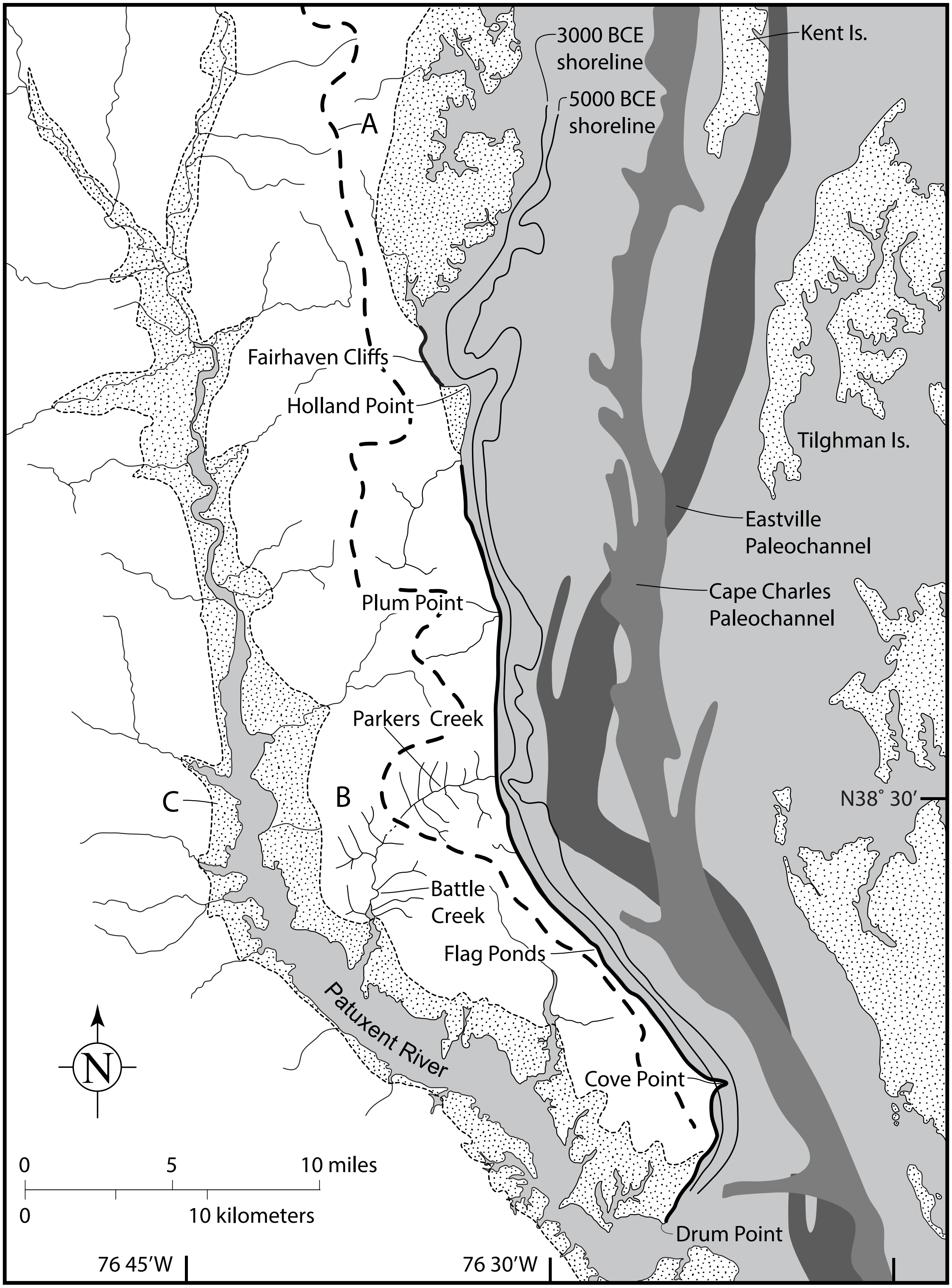

3000 BCE shoreline
5000 BCE shoreline
Kent Is.
A
Fairhaven Cliffs
Holland Point
Tilghman Is.
Eastville Paleochannel
Cape Charles Paleochannel
Plum Point
Parkers Creek
N38° 30′
C
B
Battle Creek
Flag Ponds
Patuxent River
N
Cove Point
0
5
10 miles
0
10 kilometers
Drum Point
76 45′W
76 30′W

FIGURE 1.5. (*Facing page*) The Calvert Cliffs region in relation to later Pleistocene and Holocene geomorphology, with estimated 3000 and 5000 bce shorelines indicated by thin dark lines. The modern Calvert Cliffs shoreline is indicated by the thick solid line. The thick dashed line (A) shows the present Chesapeake–Patuxent drainage divide that separates modern Battle Creek (B) from its previous headwaters, which were captured by the Susquehanna River and now flow in the opposite direction toward Chesapeake Bay as Parkers Creek (Vogt, 1991). The Last Glacial Maximum Cape Charles paleochannel (about 24,500 bce) and the MIS 6 Eastville paleochannel of the Susquehanna River (about 140,000 bce) are indicated (Colman et al., 1990). The location of a +6–7 m terrace (stippled area, C) shows areas that are now land but were submerged at the peak of the last interglacial (MIS 5e, 125,000 years ago). The landward edge of this terrace indicates MIS 5e shorelines, including "paleo" cliffs now covered by vegetated escarpments.

Cliffs. In contrast, sea turtles are represented by at least three species of cheloniid sea turtles plus a hefty leatherback turtle (Collins and Lynn, 1936; Weems, 1974; Lapparent de Broin, 2001; Chesi et al., 2007). Nonmarine turtles are very rare but include a side-necked turtle, a musk turtle, a painted turtle, a pond turtle, a slider turtle, two kinds of softshell turtle, and five kinds of tortoise from the Calvert and St. Marys Formations of Delaware, Maryland, and Virginia (Weems and George, 2013). Teeth and scutes of two species of presumably saltwater crocodiles (some of which produced some of the larger coprolites found in the cliffs) are prized finds (Weems, this volume). Among the known birds (Olson, 1984; Rasmussen, 1998) are two species of jaegers, two auks, a duck, three gannets, an albatross, several shearwaters, a loon, a tropic bird, a quail-like bird, a pheasant-like bird (the chachalaca), a turkey, and a dove. The most impressive bird remains are those of the giant false-toothed bird (*Pelagornis*), which is an extinct relative of the pelican and the world's largest marine bird with a wingspan up to about 6.4 m (21 ft; Mayr and Rubilar-Rogers, 2010). As many as three separate species of this flying marvel may have been present in the region of Maryland at one time or another during the Miocene.

Land animal remains (Emry and Eshelman, 1998; Eshelman et al., 2007; see also Dooley, 2007), presumably washed into the Calvert Sea as methane-inflated carcasses (known as "bloat and float" taphonomy), include an extinct wolf, a bear-dog, a large extinct cat, at least four species of peccaries, fanged deer, a protoceratid (an extinct group of antelope-like browsers with elaborate horns), at least two species of camel, a tapir, two species of rhinoceros, up to five species of three-toed horses, and a large elephant-like animal called a gomphothere. The odds were heavily stacked against the remains of any terrestrial animal being carried into the Miocene shallow marine environment. The vicissitudes of fossilization and preservation (the study of which is called taphonomy) mean that, for most of these prehistoric creatures, a few bones or teeth (but never entire skeletons) have been recovered. The Calvert Sea was well oxygenated, which was good for life but bad for fossilization. In contrast, the modern Chesapeake Bay has bottom waters that are often hypoxic or even anoxic because of wasteful and adverse human activities.

One of the world's richest records of fossil marine mammals has come from the Calvert Cliffs. It includes some of the world's oldest known true seals and also sea cow remains, representing at least three species (Kellogg, 1966; Domning, 1984, 2006, this volume). More than 30 species of cetaceans are known (Gottfried et al., 1994, and numerous references therein), including both baleen whales and toothed whales. Toothed whales include both large and small sperm whales, shark-toothed dolphins, and a variety of long- and short-snouted "dolphins." Representatives of the family Delphinidae, true dolphins, have never been found within the Calvert Cliffs.

HUMANS AND CALVERT CLIFFS

The actively eroding Calvert Cliffs as presently configured began to form about 5,000 years ago (Figures 1.5, 1.6). About that time, rising sea levels flooded the originally narrow freshwater lower Susquehanna River valley, inundating and eroding shorelines that caused the Chesapeake Bay to eventually lap up against cliffs abandoned when sea levels fell at the end of the last interglacial (marine isotope stage [MIS] 5e), around 125,000 years ago. The long-abandoned cliffs of the Chesapeake Bay that existed during the previous interglacial had by then been reduced by erosion to gentle forested escarpments in the more than 100,000 years that had passed. This means that the Paleo-Indian and early to middle Archaic natives that lived in this area prior to 5,000 years ago did not see the steep cliffs we see today because they did not yet exist.

In the absence of written records, we cannot know with any certainty how the earliest Native Americans interacted with the cliffs, but archeology confirms that fossil Miocene shark teeth were prehistorically traded (from around 500 bce to around 1300 ce) as far west as central Ohio (Lowery et al., 2011) and that at least some of these teeth probably were collected along the Calvert Cliffs. Examples have been found of fossil shark teeth that were modified into scrapers and projectile points (see Figure 1.4C), and possibly, others were collected simply as curiosities and ornaments.

It seems plausible that prehistoric Native Americans also herded game, notably white-tailed deer, over the Calvert Cliffs, where they could easily be killed on the beach below. Even today,

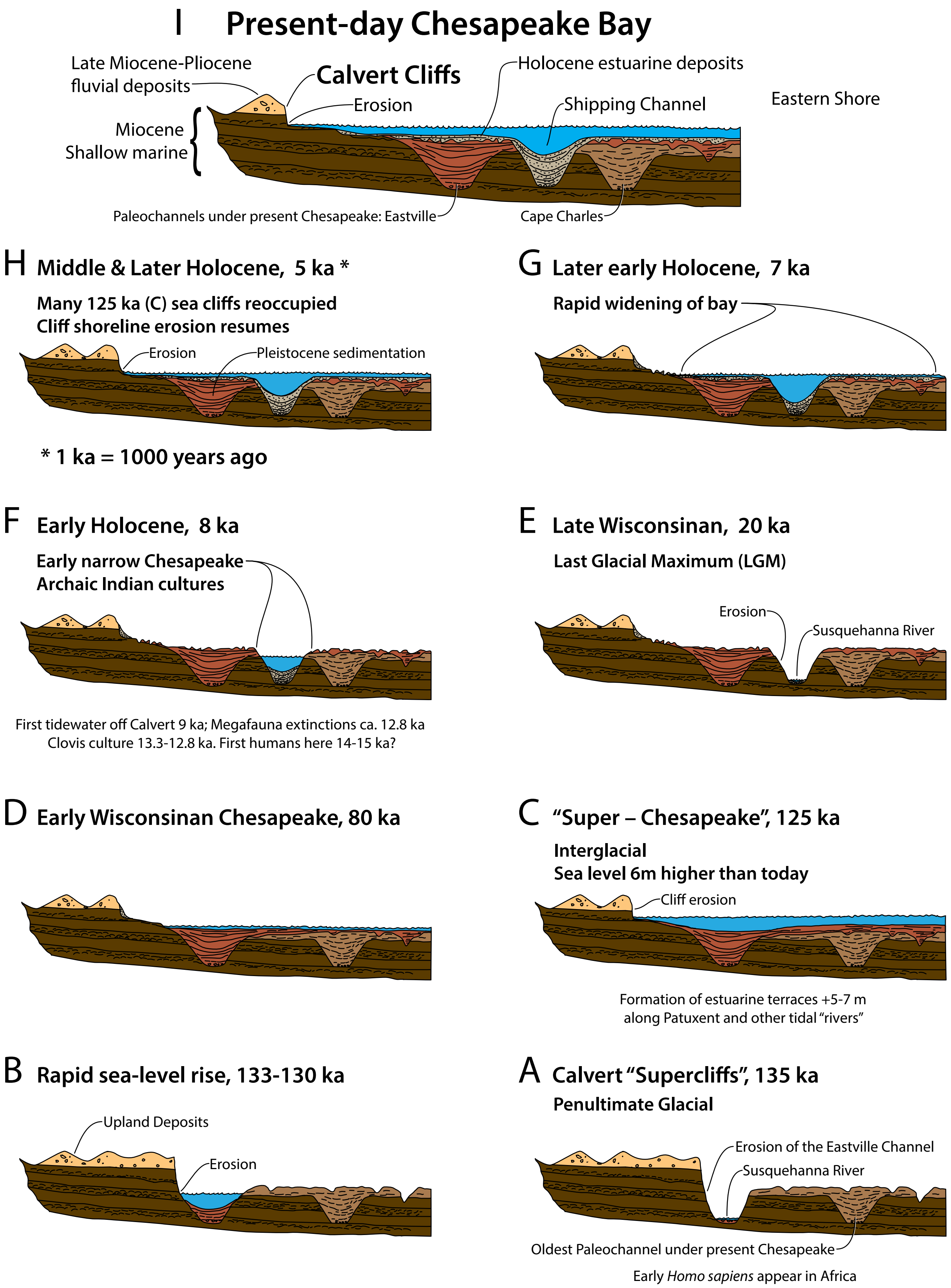

I Present-day Chesapeake Bay
Late Miocene-Pliocene fluvial deposits
Calvert Cliffs
Erosion
Holocene estuarine deposits
Shipping Channel
Eastern Shore
Miocene Shallow marine
Paleochannels under present Chesapeake: Eastville
Cape Charles
H Middle & Later Holocene, 5 ka *
Many 125 ka (C) sea cliffs reoccupied
Cliff shoreline erosion resumes
Erosion
Pleistocene sedimentation
* 1 ka = 1000 years ago
G Later early Holocene, 7 ka
Rapid widening of bay
F Early Holocene, 8 ka
Early narrow Chesapeake
Archaic Indian cultures
First tidewater off Calvert 9 ka; Megafauna extinctions ca. 12.8 ka
Clovis culture 13.3-12.8 ka. First humans here 14-15 ka?
E Late Wisconsinan, 20 ka
Last Glacial Maximum (LGM)
Erosion
Susquehanna River
D Early Wisconsinan Chesapeake, 80 ka
C "Super – Chesapeake", 125 ka
Interglacial
Sea level 6m higher than today
Cliff erosion
Formation of estuarine terraces +5-7 m along Patuxent and other tidal "rivers"
B Rapid sea-level rise, 133-130 ka
Upland Deposits
Erosion
A Calvert "Supercliffs", 135 ka
Penultimate Glacial
Erosion of the Eastville Channel
Susquehanna River
Oldest Paleochannel under present Chesapeake
Early Homo sapiens appear in Africa

FIGURE 1.6. (*Facing page*) Evolution of topography and sea level along an east–west profile across the central Calvert Cliffs from around 140 ka (when the Susquehanna River flowed in the Eastville paleochannel) to the present (A–I). Seismic reflection profiling mapped these paleochannels in the mid-1980s (Colman et al., 1990); higher-resolution but lower-penetration chirp sonar profiles show more detailed structure in the channel fill (e.g., Cronin et al., 2007; Shah et al., 2012). Late Pleistocene paleochannels like the two shown were carved during the major Laurentide ice sheet advances described by Balco and Rovey (2010). More speculatively, the southward shift of the Coastal Plain Susquehanna, Potomac, and Delaware rivers (e.g., Higgins et al., 1974) was possibly caused by southward migration of the forebulge of the first major glaciation (e.g., Balco et al., 2005).

dogs sometimes chase deer over the cliffs, causing broken bones and likely death for most of them. It is also highly likely that Late Archaic and Woodland Indians used the promontories on the cliff edges to scan the bay for friendly or hostile canoes. Similarly, earlier Archaic and Paleo-Indians must have stood on the edge of the remnant escarpment, east of the modern Calvert Cliffs, scanning the forested plain below for signs of game and perhaps also for enemy or friendly campfires near the Susquehanna River several kilometers to the east.

In 1525 the Spanish, under the pilot and explorer Pedro de Quexós, were likely the first Europeans to discover and enter the Chesapeake Bay, which they called Bahia de Santa María (Cumming, 1982:274). The first Europeans known to have explored the full length of the bay to its northern limits sailed on the 1588 Vicente Gonzales expedition (Cumming, 1982:278). That is likely to have been the first time the cliffs were seen by Europeans; however, no mention of them was made in the expedition's reports (see also Scisco, 1945, 1947). The cliffs were first definitely documented by Captain John Smith (Smith, 1986 [1608]) as he sailed north up the bay on his exploratory shallop voyage in June of 1608.

Upon departing Jamestown on the first of two discovery voyages, Smith and his men had been following the eastern side of the Chesapeake,

> but finding this easterne shore shallow broken isles, and maine for the most part without fresh water, we [sailed] for the weasterne shore. So broad is the bay here, that we could scarce perceive the great high Cliffes on the other side. By them, wee ancored that night, and called them Richards Cliffes. 30 leagues [about 167 km] we sailed more Northwards, not finding any inhabitants, yet the coast well watred, the mountains very barren, the vallies very fertile, but the woods extreame thicke, full of Woolves, Beares, Deare, and other wild beasts (Smith, 1986[1608], vol. 2:165).

It is not clear what "mountains very barren" meant, unless it was a change made by editors. Perhaps Smith was referring to the eroded, bare character of the cliffs, which would stand out in an otherwise thickly vegetated landscape. The Calvert Cliffs part of the Chesapeake shoreline was therefore largely or entirely uninhabited in 1608, and no archeological evidence for earlier Native American settlements—other than temporary hunting camps—has been discovered. However, it must be kept in mind that any evidence for settlement activity within roughly 100 m of the present cliff shoreline (including interspersed valleys where freshwater streams debouched into the bay) would have been destroyed over the last several centuries by cliff erosion, a process discussed elsewhere in this chapter.

The name "Richards" or "Rickards" Cliffs, after Smith's mother-in-law's family, obviously did not stick. Maps from the eighteenth to nineteenth centuries label the feature with names like "Clifts," "Cliffs," or "Cliffs of Calvert," with "Calvert Cliffs" eventually becoming standard in the twentieth century. However, since the Calvert Cliffs Nuclear Power Plant went into operation on the southern cliffs during 1975–1976, the term "Calvert Cliffs" is often used in reference to the power plant.

Smith may well have noticed the speckled white shell marl exposed in the cliffs, but if so he did not record this observation. However, in one of his accounts he did note "mountains of a diverse nature, Marle, Fuller Earth," which likely referred to materials he observed in the Calvert Cliffs. (Smith, 1986[1612:3]).

The first historical European notice of vertebrate fossils from the Chesapeake Bay area appears in John Winthrop's journal entry of 3 August 1636, reporting fossils found along the James River in southeastern Virginia (discussed in Hosmer, 1908:185–186):

> Samuel Maverick, who had been in Virginia near twelve months, now returned…It is strange, what was related by him and many others, that, above sixty miles [about 97 km] up James River, they dig nowhere but they find the ground full of oyster shells, and fishes' bones, etc; yes, he affirmed that he saw the bone of a whale taken out of the earth (where they digged for a well), eighteen feet [about 5.5 m] deep.

After English colonists, who first settled in Maryland at St. Mary's City off the Potomac River, had begun to cross the Patuxent River in the later 1630s and especially after the first plantations appeared along the Calvert Cliffs, probably starting in the later 1650s, locals surely explored the shoreline at the foot of the cliffs and collected fossils as curiosities. By the time of Augustine Herrman's 1670 (published 1673) map (available online at Library of Congress, https://www.loc.gov/item/2002623131/) of the Chesapeake Bay, the Calvert Cliffs shoreline is shown sprinkled with more than two dozen plantations. After Hugh Jones became minister and naturalist to Christ Church in Calvert County—not far inland from the central cliffs—he began to collect plant and animal remains starting in July of 1696 and also fossil remains that he shipped to collectors back in England. Out of all of the material that he collected, only his pressed botanic specimens, three tooth plates of the ray *Aetobatus*, and a partial odontocete atlas can be presently located (Reveal, 1987; Ray, 2001). Reverend Jones may well have collected fossils from the Calvert Cliffs or from the beaches along their base until his death in 1702.

Among the fossils that are found in the Calvert Cliffs is a four-ribbed extinct muricid snail called "*Ecphora*," which was long considered to be the earliest illustrated fossil from North America (supposedly in 1685; Shattuck, 1904). This attribution is now known to be incorrect (Ray, 1987; also see Conrad, 1832). More recent research suggests that the first illustrated fossil from North America came from Virginia (Figure 1.7B) and that the *Ecphora* illustration, probably dating from 1770, was drawn from a fossil collected by Hugh Jones from the Calvert Cliffs. The present location of this *Ecphora* shell is unknown, but a 1786 auction catalog of the Portland Museum (UK) lists item #3516 as "a very curious and rare species of Buccinum (a genus of snail) in a fossil state, having four high sharp ridges, from Maryland, very rare" (Lightfoot, 1786:137). *Ecphora* continues to be the most celebrated Miocene mollusk from the Calvert Cliffs. For example, the Calvert Marine Museum Fossil Club, the American Fossil Federation, and the Paleontological Research Institution include an *Ecphora* as part of their logos, and the state of Maryland adopted the *Ecphora* as its state fossil shell in 1985 (Figures 1.4A, 1.7A).

The earliest known reference to a vertebrate fossil from what is certainly the Calvert Cliffs is in Samuel Latham Mitchill's 1818 review of fossils from North America: "I remember, that petrified bones, apparently of a whale, were brought from the shore of the Chesapeake Bay, near the place where the river Patuxent enters it, to the City of Washington, by Mr. O'Neale" (Mitchill, 1818:394).

The well-known British paleontologist Thomas Say described fossil shells collected by John Finch (Finch, 1833) in 1824 from Maryland and Virginia. This pioneering work (Say, 1824) marks the beginning of scientific interest in the rich fossil deposits of the Atlantic Coastal Plain. One of us (REE) was privileged to view these fossils, which are still in the collections of the Natural History Museum in London (formerly the British Museum of Natural History). Say's 1824 observations are still appropriate today: "Many of these shells appear to the eye nearly perfect, in every respect, with the exception of color, as the recent ones of the coast, and not a few of the bivalves have both bivalves attached…; circumstances which indicate an undisturbed deposition in the waters in which they lived" (Say, 1824:124).

The American Timothy A. Conrad developed a keen interest in the molluscan fossils from the Chesapeake region. Beginning in 1830, Conrad published more than 30 scientific papers describing many fossils from the Calvert Cliffs (see, e.g., Conrad, 1832).

The first detailed geological description of the Calvert Cliffs (with measured stratigraphic sections) is that of the state geologist of Maryland, Julius Timolean Ducatel, whose *Report on the New Map of Maryland, 1836* (Ducatel and Alexander, 1837) devotes fully 25 of 59 pages to Calvert County (Figure 1.8). Ducatel's favorite geological outcrop was the short section of high cliffs between twentieth century developments at Governor Run and Scientists Cliffs. Ducatel (in Ducatel and Alexander, 1837:11) wrote,

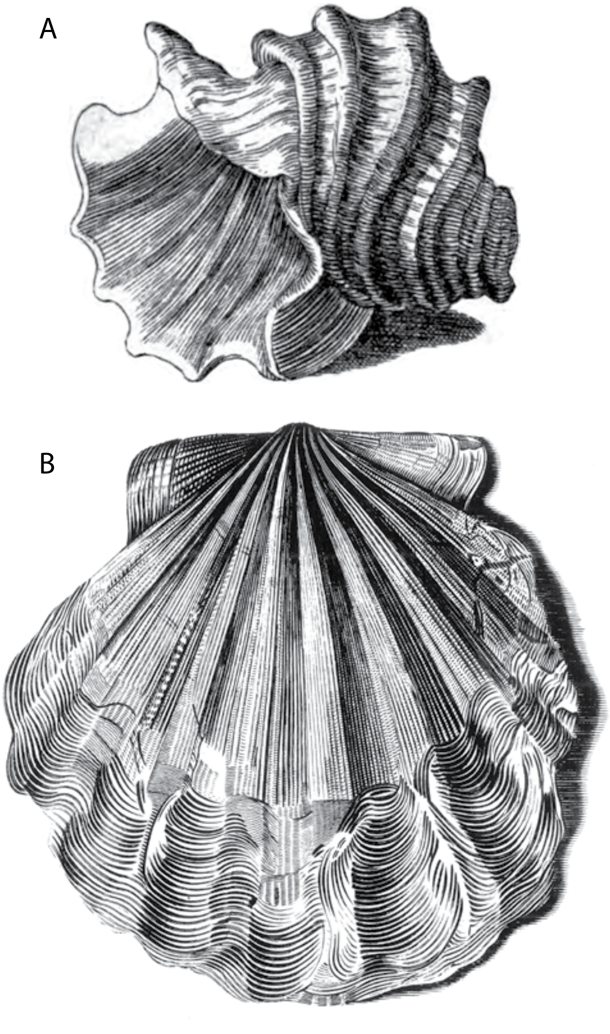


FIGURE 1.7. Two of the earliest illustrated fossils from North America. (A) "*Ecphora* sp., collector and formation unknown; from Maryland… (first published in… Lister, Huddesford edition, 1770, pl. 1059, fig. 2)" Ray (1987:3). (B) "*Chesapecten jeffersonius* (Say, 1824), right valve (thought to have been collected by John Banister from the Yorktown Formation of Virginia; first published in Lister, 1687, p. 167: . . . from Huddesford edition, 1770)." Ray (1987:4). Both images edited in Photoshop from Ray (1987).

> But perhaps the most interesting spot at which to determine the geological features of the county, is on the north side of Governor's [sic] Run, on the plantation of Mr. Frazier [probably either James or Charles Frazier]. In this locality the cliffs are upwards of one hundred feet [about 30.5 m] high and afford a luminous view of all the strata containing fossils [what later became known as zones 14, 17, and 19 of Shattuck, 1904] as well as many of the intermediary ones, thus furnishing useful directions for research of those beds that are sought after for marl.

Ducatel promoted the mining of fossil shells, outcropping also in deep ravines, for use by farmers to lime fields and to help sanitize outhouses. Referring to soil quality, Ducatel also noted "this good soil rarely extends beyond one mile [~1.6 km] from the bay side, after which it becomes very sandy and sour, throwing up a thick growth of pine." This observation shows that Ducatel recognized the connections between geological substrates and vegetation. From early colonial times through the first half of the nineteenth century, local farmers on occasion limed their fields with mollusk-rich fossil marl, as well as oyster shell mounds left by Native Americans (Ducatel and Alexander, 1837:9; Miller, 1907).

Richard Harlan (1842), sometimes characterized as America's first professional vertebrate paleontologist (Simpson, 1942), published the first formal scientific description of a fossil vertebrate from the Chesapeake Bay region, an extinct dolphin collected by Francis Markoe Jr. in 1841 from the southern end of the Calvert Cliffs. Timothy Conrad assisted Markoe in collecting these dolphin bones. Harlan named the dolphin *Delphinus calvertensis*, in recognition of the fact that the collection site was in Calvert County. Markoe was the cofounder and corresponding secretary of the National Institute for the Promotion of Science in Washington, the predecessor of the Smithsonian Institution.

Sir Charles Lyell (1845), the most famous geologist of his day, also published descriptions of the Miocene geology and fossils of Maryland. In 1867 the famous dinosaur hunter and vertebrate paleontologist Edward Drinker Cope placed Harlan's fossil dolphin in a new genus. That same year Cope (1867) described a fossil tooth from the Calvert Cliffs that he referred to as a shark-toothed whale. This specimen later proved to be a canine tooth from the extinct peccary *Cynorca*, now known from more diagnostic material (Wright and Eshelman, 1987). Although peccary bones might not have been expected in the Calvert Cliffs marine deposits, Harlan (1842) had already reported on the occurrence of a fossil proboscidean (gomphothere) tooth from the "Miocene of Maryland." Cope (Osborn, 1931:148) also surely knew that land mammal fossils sometimes turned up in Maryland Tertiary marine deposits, for he wrote in a letter to his father (1867),

> I accepted the invitation of a Marylander interested in science to examine with him the Eocene and Miocene beds in the South part of the state, between the Potomac and Patuxent. One object was to examine, and if possible to procure a collection of fossil vertebrata and Mollusks in possession of an old man [James T. Thomas] not far from the latter river. I examined the latter and found it of value to science. Of the vertebrates were remains of 26 or more species, of which seven are cetaceans. One is a whale of large size; among other parts is the whole lower jaw—7 ft. [about 2.1 m] long is there...and singularly enough two land vertebrates—a small peccary and a carnivore the size of a fox.

The relative importance of the Miocene vertebrate record from Calvert Cliffs, in contrast to outcrops in North Carolina and Virginia, is evident in the modern assessment by Ray (1983:8–9):

> Perusal of...publications on fossil vertebrates of the Chesapeake Series reveals very little on the Yorktown Formation and relatively little on North Carolina. The reasons are readily apparent; in spite of the occasional notice of large whale skeletons since early colonial times and the superabundance of invertebrates, natural exposures have produced an unreliable crop of vertebrate material. Of that, very little of adequate quality reached the hands of researchers, *as compared, for example, to the abundance of good specimens from the Calvert Formation of Maryland* [emphasis added].

Although good Miocene vertebrate remains have been recovered from the Lee Creek phosphate mine in North Carolina (Ray, 1983) and the Pollack Farm quarry in Delaware (Emry and Eshelman, 1998), the Calvert Cliffs remain unequaled in the abundance and quality of their fossil materials.

The historical era of Calvert Cliffs research can be thought of as terminating with the papers of Harris (1893) and particularly with Shattuck (1904), who published numerous drawings of vertebrate and invertebrate fossils (see also Vokes, 1957), and who, on the basis of measured sections along the cliffs, assigned numbers to the strata ("zones," here called beds) exposed in the cliffs and other areas. Shattuck's work is still referenced in modern publications, even though many of his taxonomic identifications have been revised and some of his stratigraphy refined or rejected (e.g., Vokes, 1957). With the close proximity of the cliffs to the Smithsonian Institution and the U.S. Geological Survey, it is not surprising that many curators and researchers from these institutions continued to conduct research at the Calvert Cliffs (Figure 1.9). Among them were Frederick W. True, C. Lewis Gazin, Alexander Wetmore, Remington Kellogg, Lauck W. Ward, and Frank C. Whitmore Jr.

THE CALVERT CLIFFS AS A MIOCENE PALEOENVIRONMENTAL ARCHIVE

The modern era of lithostratigraphic and biostratigraphic interpretation of the Miocene strata exposed along the Calvert Cliffs began with regional mapping of the Calvert Formation by Lincoln Dryden (1930, 1936), followed by Schoonover's (1941) stratigraphic study of mollusks in the Calvert and Choptank Formations. Renewed paleontological and paleoecological interest after World War II led to Gibson's (1962) study of benthic foraminifera

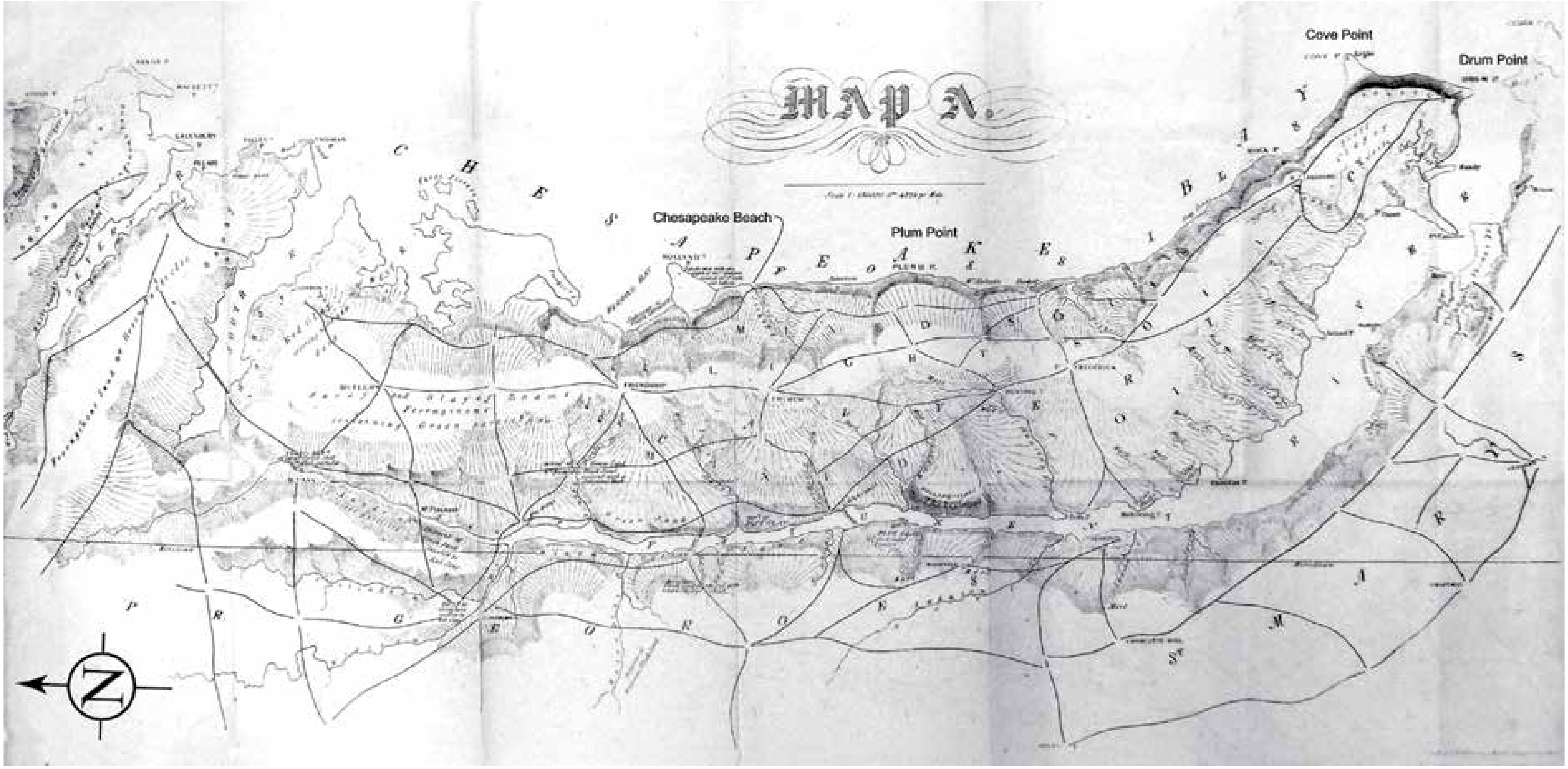


FIGURE 1.8. Ducatel's 1836 map (in Ducatel and Alexander, 1837) showing the topography of Calvert County with notes on local geology. Note indication of "fossils," "blue clay," "clayey loams," etc. North is to the left.

FIGURE 1.9. Smithsonian staff and affiliates conducting research at the Calvert Cliffs south of Plum Point, ca. 1905: from left to right, Norman H. Boss up on the cliff face, unknown individual digging, and William Palmer and his wife, Arminia Palmer, collecting fossils below the cliffs. Image courtesy of the Smithsonian Institution.

in the Mid-Atlantic middle Miocene, Gernant's (1970) study of the paleoecology of the Choptank Formation, Andrews' (1978, 1988) Calvert Cliffs and then regional study of Miocene diatoms, and Wetmore and Andrews' (1990) biostratigraphy of silicoflagellates and diatoms in the Mid-Atlantic Coastal Plain. Buzas and Gibson (1990) described the various foraminifera at the Calvert Cliffs Nuclear Power Plant site. The work of De Verteuil and Norris (1996) added dinoflagellates to the list of biostratigraphically important Miocene microfossils. Among the many studies of Mid-Atlantic middle Miocene mollusks, including those found in Calvert Cliffs, are the self-published works of Petuch (2005) and Petuch and Drolshagen (2010). Also important are the benchmark mollusk-based biostratigraphic syntheses of Ward (1992) and Ward and Andrews (2008) and also Kelley's (1983) attempt to test the theory of punctuated equilibrium using mollusks from the Chesapeake Group, including the Calvert Cliffs.

A comprehensive biostratigraphic and lithostratigraphic study was initiated by Susan Kidwell in her Ph.D. dissertation work conducted in the early 1980s, which focused mainly on the middle Miocene strata exposed in the Calvert Cliffs. Her work, later expanded and formally published (e.g., Kidwell, 1989, 1997), included along-strike profiles of the Calvert Cliffs that

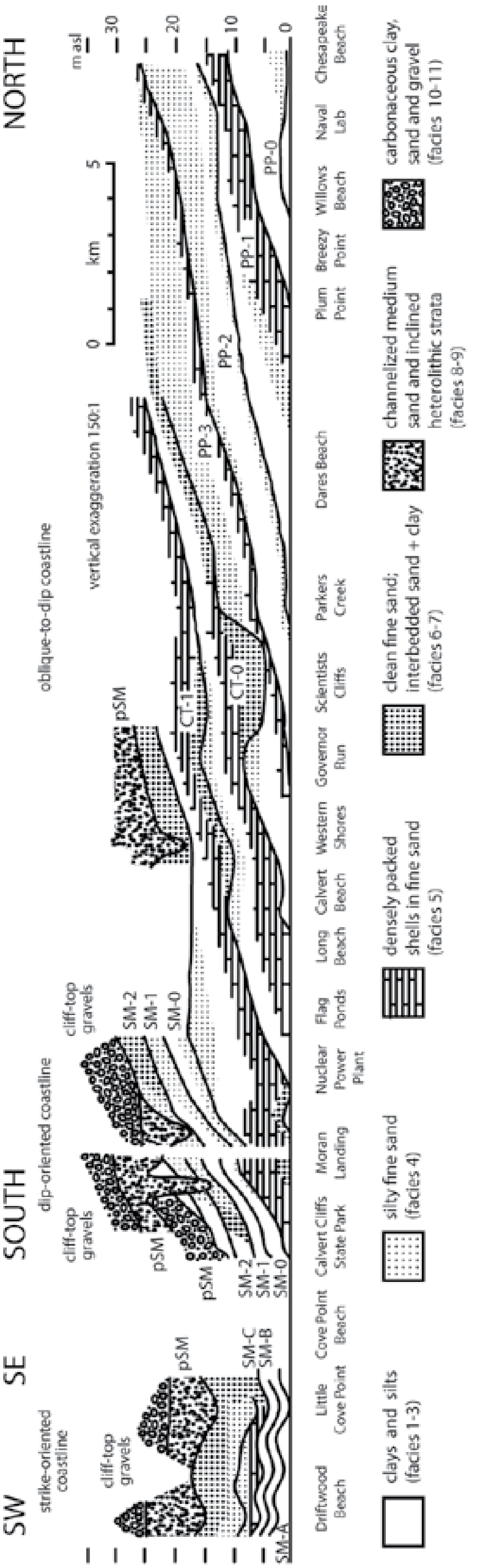


FIGURE 1.10. Along-strike (south to north) lithostratigraphic profile of the Calvert Cliffs based on Kidwell (1997) with the addition of the postulated Moran Landing reverse fault (see also Powars, 2013), which offsets the Chesapeake Group strata.

are shown here as Figures 1.10 and 1.11 Using Kidwell (1997) as their basis, Vogt and Parrish (2012) proposed that the Parkers Creek Bone Bed (bed 12) was deposited during the peak of the Middle Miocene Climatic Optimum and that the Governor Run channel of Kidwell (1997) at the base of the Choptank Formation was carved into the top of the Calvert Formation as the result of a significant sea level fall caused by Antarctic ice sheet expansion around 13.9 MYA.

Research has been undertaken to correlate the strata preserved in the Calvert Cliffs with core holes on the nearby New Jersey continental margin (Browning et al., 2006, 2008) and in the buried Chesapeake impact crater (Poag, 1999; Browning et al., 2009). Although the correlations proposed have not been universally accepted, they form the basis for incorporating the Calvert Cliffs stratigraphic record into a broader Atlantic margin stratigraphic record. As suggested by Boulila et al. (2011) and by Vogt and Parrish (2012), the New Jersey borehole sediment record may provide evidence for a 1.2 Ma obliquity modulation influence on Antarctic ice sheet volume and thus on global eustatic sea level fluctuations. Imprecise dating of sediments, however, currently limits the reliability of these correlations. Recently, a shorter-term, 405 ka Milankovitch cyclicity (controlled by orbital eccentricity) has been proposed as the explanation for the pervasive, fining-upward cycles that are seen throughout the Calvert Cliffs and age-equivalent Miocene strata in the Westmoreland County, Virginia, region (Weems et al., 2017). Should future work confirm this cyclicity, then exceptionally precise age control and levels of correlation will be possible for the beds exposed in the Calvert Cliffs that will greatly enhance the importance of the Calvert Cliffs record for global correlations and the Miocene climate record.

COMMERCIAL, RESIDENTIAL, MILITARY, AND INDUSTRIAL DEVELOPMENT ALONG CALVERT CLIFFS

Because of the steep cliffs and shallow, often rough nearshore waters, early settlement was very limited along the Calvert Cliffs because there are no natural harbors and few suitable landing sites. The first and only major lighthouse along the cliffs was installed on the Cove Point spit in 1828, and although unmanned and automated in 1986, it is still operational today. From the colonial period up to the late nineteenth century, landings were used to transport freight between the shore and commercial ships. With the advent of larger and more powerful steamboats, larger-scale wharves were needed to replace the earlier, smaller-scale landings in order to make loading and unloading of these larger ships possible. An additional consideration was that these newer wharves, built to accommodate the new steamboats, had to be long enough to reach navigable deep waters. An approximately 97.5 m (~320 ft) long L-shaped wharf was built in 1872 at Governor Run, where there was a prominent gap in the cliffs; it remained in use until about 1928. Lodging, somewhat

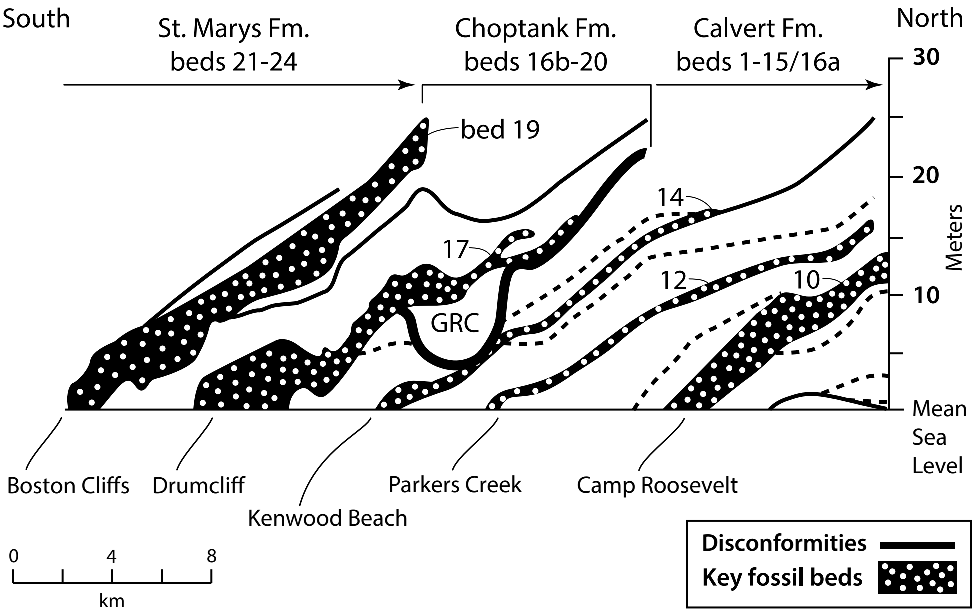


FIGURE 1.11. Simplified along-strike profile of the Calvert Cliffs, showing the Choptank and Calvert Formations at high vertical exaggeration and modified from Kidwell (1997). GRC refers to the filled Governor Run channel. Not shown here are the St. Marys Formation beds and the overlying nonmarine upland deposits exposed in the southern Calvert Cliffs.

like modern bed and breakfast lodging, was provided near the Governor Run wharf by 1896 or earlier, attracting tourists to fish and also probably to collect fossils along the nearby beaches. A second wharf was built at Cove Point as early as 1896 (Eshelman, 1996).

From the early nineteenth through the early twentieth centuries, almost all level land in Calvert County was farmed. Prior to cheap modern fertilizers, exhausted land was left to regrow forest for some years until its fertility recovered sufficiently to allow it to be recleared for further farming. Many fields extended to the very edge of the cliffs, and these, according to geologist J. T. Ducatel, afforded great bay views from nearby farms “commanding an extensive prospect of a magnificent sheet of water” (Ducatel and Alexander, 1837:8).

Tourist interest in the Calvert Cliffs began with steamboats from Baltimore bringing city people to rural waterfront inns. Bayside steamboat landings promoted fishing, swimming along sandy beaches, and good seafood. The opening of the Chesapeake Beach Railway from Washington, D.C., on 9 June 1900 brought thousands of visitors each year to the Chesapeake Beach Amusement Park just north of the northern end of Randall Cliffs, which are the northernmost cliff segment of the Calvert Cliffs. The land above the northern end of Randall Cliffs today is part of what is now known as Bayfront Park (formerly Brownie’s Beach). To judge from postcards and tourist brochures printed in the early 1900s, this northernmost part of the Calvert Cliffs was then known as the “Great Bluff,” and it apparently was a popular attraction. The railway era ended in 1935, a victim of the private automobile. The amusement park lingered on much longer, but it too finally closed in 1972. One of the authors (REE) found his first fossil shark tooth while swimming at Chesapeake Beach. In those days, it was not unusual for scores of children to be holding cherished shark teeth in their hands after a full day on the beach.

With the advent of cars and roads, opportunities expanded for people to see Ducatel’s great bay views, as well as to find recreational water and beach access for boating, swimming, fishing, and fossil collecting. From the 1920s through the 1960s, summer camps and vacation cabins sprang up all along the Calvert Cliffs. By far the largest was Chesapeake Ranch Estates, which had more than 6,000 lots plotted between 1957 and 1967, all of which were located along and near the southern end of the Calvert Cliffs. By the 1980s, nearly 20 other named towns and developments were clustered along the Calvert Cliffs from Chesapeake Beach in the north to Drum Point in the south.

The most famous of the summer camps was Camp Roosevelt, located on the northern cliffs. This was the first permanent Boy Scout Camp in Maryland and possibly the first in the United States. Camp Roosevelt, first leased by the Boy Scouts of America in 1914, was originally called Camp Archibald Butts, but it was renamed after President Theodore Roosevelt soon after his death in 1919. One of the authors (REE) attended this camp several times in his younger years and recalls that it was customary for each troop to make a plaque showing its troop number. These plaques were hung from the log rafters of the dining hall. Many of those plaques were decorated with glued-on fossil shark teeth collected from the beach. Since those days, the camp has largely disappeared. Attempts (involving author PV) were made to preserve the Camp Roosevelt tract as a county park, but these efforts failed largely because of opposition from neighboring landowners. In the late 1970s the camp became a large-lot subdivision. This and other new cliff-side developments appeared along the Calvert Cliffs. The developments expanded and spread during the later twentieth century; by the twenty-first century, the 305 m (1,000 ft) wide "Maryland Critical Area" along the Chesapeake shoreline was the most densely developed strip of land running the length of Calvert county. This was in sharp contrast to Smith's (1608) observation that the entire native population was clustered in tiny hamlets along the Patuxent River well to the west of the cliffs.

The Calvert Cliffs made military and industrial contributions during the middle and later twentieth century. During World War II (1941), the Naval Research Laboratory acquired approximately 1,220 m (4,000 ft) of cliff-front property at Randall Cliffs near the northern end of the Calvert Cliffs. The elevation of the cliff top overlooking the Chesapeake provided an excellent location for radar research, as it approximated the heights of naval shipborne radars above the water. Later, an amphibious training base was established at Solomons (1942–1944), just south of the southern end of the cliffs. This site was chosen because the beach at Cove Point and adjacent cliffs served as a training venue for troops preparing for similar amphibious landings at the bluffs of Normandy along the French coast in 1944.

In 1966, the Baltimore Gas and Electric Company purchased about 400 ha (986 acres) along the southern cliffs on which to build their Calvert Cliffs Nuclear Power Plant. A portion of the cliffs was removed in order to build the two reactors, which went on line in 1975–1976. The total size of the site has expanded since then to about 840 ha (2,076 acres), and the power plant is currently owned and operated by Exelon. The reactor site was placed on the southern cliffs in the 1960s because it was a safe distance from population centers in case of an accident; land was available at a relatively low cost, public opposition was low, and water for cooling was abundant. In 2000, the two reactors were recertified for operation through 2034 and 2036, with aboveground (dry cask) storage of radioactive waste to continue. In 2005, a 1,600 MW third reactor was proposed to be located inland from the cliff edge. Many hearings were held to try to assuage public opposition to this expansion, but the effort ultimately failed; several years later Exelon finally withdrew its application for a third reactor.

One positive outcome of the initial permitting negotiations for construction of the plant by Bechtel Corporation was a granting of permission to conduct a multidisciplinary paleoecological excavation on a portion of the cliff-edge area that had to be removed for construction of the reactor foundations. Principal funding was provided by the National Science Foundation, with additional financial support coming from the Ford Foundation and the National Geographic Society. The grant was administered by the Maryland Academy of Sciences, with participation from the National Museum of Natural History of the Smithsonian Institution. During a two-year excavation study in 1968 and 1969, scientists from around the world (including REE) completed what was at the time the most in-depth paleoecological and paleontological study of the cliffs ever undertaken, primarily in the Choptank Formation. Unfortunately, with a few exceptions (e.g., Whitmore, 1971a; Buzas and Gibson, 1990; Shideler, 1994) none of the results were ever published, although data from the project did influence subsequent work of others (e.g., Ward, 1992).

During 1970–1972 Columbia Gas System acquired about 412 ha (1,017 acres), including parts of the Cove Point marsh area, just to the south of the nuclear power plant; a liquefied natural gas (LNG) terminal (currently operated by Dominion Energy) was installed approximately 1.6 km (1 mi) offshore to accommodate deep-draft tankers. For financial reasons, the terminal was mothballed for many years, but it reopened in 2003. By 2012, new U.S. natural gas discoveries and improvements in hydraulic fracturing ("fracking") technologies had made it economical for the United States to become an exporter of LNG, so Dominion Energy filed for permits to expand its Cove Point facility for that purpose, with plans to be operational by 2018.

Both the nuclear power plant and the LNG facility took parts of the Calvert Cliffs shoreline that had been suggested for a bayside nature park as early as 1945. However, a legal challenge in 1972 by the Maryland Conservation Council and the Sierra Club resulted in preservation of much of the remaining Cove Point marsh region as well as some adjacent woodland containing a section of overgrown paleocliffs (i.e., a section of previously eroding cliffs now shielded from wave erosion by spit development). This preservation was possible because by then LNG could be delivered to the onshore liquefaction facility by pipeline under the Chesapeake Bay, so the new facility did not need to expand its industrial area into the adjoining (and now preserved) part of the property.

Three other major unrealized projects involving the area around the Calvert Cliffs have been proposed over the years. In 1963, Maryland state senator Louis Goldstein proposed a scenic "dream highway" from Annapolis to Drum Point (*Evening Star*, 1963), in part following the abandoned Drum Point rail right-of-way.[1] Along its length, this parkway would have offered motorists views of the Chesapeake Bay at various locations. Louis Goldstein also promoted construction of a third bridge across the Chesapeake Bay, from Cove Point to Dorchester County on the Eastern Shore. This site was reevaluated along with several others by a 2005–2006 task force, but no action was taken on a third Bay Bridge.[2] About 2008, the Potomac Electric Power Company (PEPCO) proposed constructing a high-voltage transmission line extending from Virginia through southern Maryland to the Delmarva Peninsula through a buried direct current cable that would pass under the Chesapeake Bay starting at a site at Western Shores on the Calvert Cliffs. This project was canceled in 2012, primarily for economic reasons.[3]

The Calvert Cliffs might have made a great national monument or even a national park, but even by 1940 the rapid development of vacation housing would have made that difficult. By 1950, when Klingel ([1951] 1984) described the scenic beauty of the Calvert Cliffs shoreline, he realized that it was already too late to preserve much of this shoreline (see also R. Mansueti, "Natural History Wonders of Calvert County in Southern Maryland, Md.," 1954, unpublished). A Calvert Cliffs State Park finally became a reality in 1966, eventually preserving about 530 ha (1,312 acres) and about 1.7 km (1 mi) of cliffs in their natural eroding (and fossil-producing) state. This was considerably smaller than the 850 ha (~2,100 acres) that was recommended by the State Planning Commission in 1945. The park cliffs expose the uppermost Choptank Formation and most of the St. Marys Formation. By the time that the northern part of the Cove Point spit and adjoining marsh and woods came to be preserved next to the LNG terminal, cliff erosion and outcrop exposure had already been arrested by spit development many centuries earlier. Similar cliff stabilization is found at Flag Ponds Nature Park, where a smaller prograding spit complex (called a cuspate foreland) has formed. This property was acquired by Calvert County in 1988, along with wooded paleocliffs and forestland behind the spit. The stabilized and forested cliffs at Cove Point (Beardslee, 1997) and Flag Ponds show what the Calvert Cliffs region looked like when, at the end of former interglacial times, sea levels began to drop and the cliffs slumped and grew over as world climate cooled and ice sheets expanded (Figures 1.5, 1.6).

No preservation progress was made along the middle Calvert Cliffs until 1995 and 1998, when The Nature Conservancy acquired—for subsequent resale to the state of Maryland—two large parcels that included cliff shoreline totaling about 2.5 km (1.5 mi) on both sides of Parkers Creek in addition to the beach at the mouth of the creek. This cliff segment is of special importance because the vertebrate-rich upper Plum Point and Calvert Beach Members (particularly beds 12 and 14) are exposed here just above sea level. Farther north, except for the tiny Bayfront Park (formerly Brownie's Beach; Figure 1.2), none of the cliffs in this region have been preserved, although a few privately owned segments, some including cliff sections up to about 1 km long, still remain undeveloped and could perhaps be preserved if funding and/or landowner generosity resulted in permanent preservation. Meanwhile, geoscientists have access to these sites only through the generosity of private landowners. Long sections of cliff face in this region have already been armored to protect property located immediately above and behind the cliffs, and the remaining segments not already preserved probably will be armored over during the next few decades in response to sea level rise and continuing wave and storm erosion along the base of the remaining unprotected cliffs.

Out of the approximately 40 km (25 mi) of Calvert Cliffs shoreline (including ravines and stream valleys such as Parkers Creek and Plum Point Creek), only about 7 km (4.3 mi) have been preserved in a natural state. If the preserved spit shorelines at Cove Point and Flag Ponds are subtracted, along with the salt marsh gap between cliff segments at Parkers Creek, then only 10% (~4 km or 2.5 mi) of actively eroding cliff faces (including ravines) are permanently protected. This leaves rather slim pickings for future paleontologists. It is especially ironic that none of the five type sections for various Chesapeake Group formations and members located within the Calvert Cliffs have been protected.

THE RELATIONSHIP BETWEEN ONGOING SEA LEVEL RISE AND CLIFF EROSION

Sea Level Rise

The Calvert Cliffs are maintained by several processes of erosion and, unlike a cliff made of granite or other very hard rock, would revert to more gentle forested slopes within several decades if erosion were to cease (e.g., Clark et al., 2004). The overall rate of cliff erosion is controlled by the rate of cliff toe erosion, which eventually causes oversteepening of the cliff face, so that its upper part collapses at intervals in a perpetual gravity-driven cycle. Cliff toe erosion thrives on continuing relative sea level (RSL) rise, which is regularly measured by tide gauges that show the rate of land subsidence plus the rate of global sea level rise. If RSL were to fall, cliff recession would erode back at ever lower rates until an angle of repose is reached, after which erosion would more or less cease. During the last century, RSL rise in the Chesapeake Bay region has reflected the net sum of ocean water warming (which produces thermal expansion), global glacier and ice sheet melting, isostatic effects resulting from an increasing ocean volume, and subsidence of remnants of a glacioisostatic forebulge (flexural arch; peripheral bulge) that persists from the last glaciation of North America when the weight of the massive Laurentide ice sheet caused the continental crust just south of the glacial front to warp upward. The contribution of forebulge subsidence (called glacial isostatic adjustment) adds about 1 mm/yr to the ongoing Chesapeake RSL rise because the region more or less occupies the crest of the residual forebulge just south of the maximum front of the last (Wisconsinan) North American glaciation (e.g., Engelhart et al., 2011; Raymo et al., 2011). Depending on the mantle viscosity structure, models predict that about 6–12 m of forebulge uplift left to subside remain before the crust in this region is again in equilibrium with the mantle below it (e.g., Raymo et al., 2011; J. Mitrovica, Harvard University, personal communication, 2013). Long-term tectonic and sediment-loading effects are comparatively minor and need not be considered (Pazzaglia et al., 2010). An additional recent and future factor adding to land surface subsidence is caused by extraction of groundwater, which creates land subsidence concentrated in cones of depression around major pumping areas. If the Gulf Stream weakens, as some models predict (Sallenger et al., 2012), additional sea level rise would occur along the U.S. East Coast.

Tide gauges record only RSL rise, which is the parameter to which the cliffs are responding. Boon et al. (2010) averaged tide-gauge-derived RSL rates that have been recorded since the gauges were installed. Largely because of short-period sea level noise (e.g., El Niño–Southern Oscillations and year-to-year variations), the formal errors for average RSL are higher for gauges with shorter observation histories. The Baltimore tide gauge, which has the longest record, has documented a 1903–2009 average sea level rise rate of 3.09 ± 0.1 mm/yr, and there is no strong evidence to suggest any recent acceleration in the rate of rise. Annapolis, closer to the cliffs, has documented an average of

3.37 ± 0.16 mm/yr from 1930 through 2009, whereas Solomons, just south of the Calvert Cliffs, has documented an average of 3.49 ± 0.19 mm/yr from 1940 through 2009. Directly across the bay from the cliffs at Cambridge the tidal gauges have documented sea level rise at a rate of 3.34 ± 0.46 mm/yr. Tide gauges located farther to the northwest at Washington, D.C., have documented a lower average rate of RSL rise of 2.96 ± 0.24 mm/yr, whereas gauges farther south and east in the Chesapeake region have documented higher RSL rise rates: 5.48 ± 1.67 mm/yr at Ocean City, Maryland; 4.12 ± 0.30 mm/yr at Gloucester Point, Virginia; and 5.82 ± 0.68 mm/yr at the south end of the Chesapeake Bay Bridge and Tunnel near Norfolk, Virginia. These figures suggest that the average RSL rise for the Calvert Cliffs has been about 3.4 mm/yr. This value is reasonably consistent with the results of Froomer (1980), who, on the basis of a study of sediment cores taken in the Parkers Creek marsh at a gap in the middle of the Calvert Cliffs (Figure 1.1), estimated that there has been an average RSL rise of 2.74 mm/yr from 1650 through 1975. This somewhat lower average RSL rise, based on a record more than 300 years long, may indicate that there has been an increase in the rate of sea level rise within the last century. Although not statistically significant, this conclusion is reinforced by comparing 1944–1975 tide gauge RSL data with 1976–2007 RSL data from the Chesapeake region (Boon et al., 2010). Although Boon et al. have concluded from tide gauge records that the eustatic sea level rise recorded in the Chesapeake region over recent decades to a century has been close to the 1.70–1.80 mm/yr global average for the twentieth century, radar altimetry has measured an apparent acceleration of global sea level rise to 3.0–3.1 mm/yr during the years 1993 through 2010, which is still a short interval of observation time. Using a different type of analysis, Ezer and Corlett (2012) inferred an even more dramatic acceleration, from a range of 1–3 mm/yr in the 1930s to 4–10 mm/yr in 2011.

Cliff Erosion Processes

A variety of processes are at work on the Calvert Cliffs, sculpting and eroding them constantly. For regional treatments of global coastal cliff erosion processes, see Emery and Kuhn, (1982) and Hampton and Griggs (2004). Various erosion processes specific to Calvert also are discussed by Leatherman (1986), Schweitzer (1993), Clark et al. (2004), and, especially, Miller (1995), who has by far the most comprehensive treatment, based largely on measurements taken from 1990 through 1994 at 22 boreholes created to monitor groundwater near the Naval Research Laboratory, Scientists Cliffs, Calvert Cliffs State Park, and Chesapeake Ranch Estates. It seems that the Calvert Cliffs may have become just as much of a laboratory for estuarine cliff erosion as they are for Miocene fossil studies.

Understanding erosion along the Calvert Cliffs comes in part from understanding the lithology and related geotechnical properties (especially permeability and cohesiveness) of the stack of Miocene sedimentary strata in the cliffs, which resembles a slightly tilted layer cake (Figures 1.10–1.12) that has its layers dipping gently toward the southeast (Shattuck, 1904; Kidwell, 1997). Physical properties vary far more from one bed to another than they do along any particular bed (Figures 1.10, 1.13, 1.14), but even so geotechnical properties do vary slightly even within any particular bed. The only major departure from this tilted layer cake pattern is the Governor Run channel, which was cut about 6 m into preexisting Calvert Formation strata at the beginning of Choptank time (Figures 1.10, 1.11; see Kidwell, 1997). The trend of this unique channel incised within the Calvert Cliffs remains unknown, but its cross section in outcrop extends from Governor Run to just south of Parkers Creek, which is a region that includes all of Scientists Cliffs, where the filled channel typically lies between 4 and 8 m above sea level. The fill primarily is fine to medium sand (hence the term Governor Run sand), with some clay present at its base and on its flanks. Because of its low cohesive strength and high permeability, Miller (1995:42) called the Governor Run sand “the single most important stratigraphic unit along Scientists Cliffs.”

Cliff profiles generally are more complex than simple slopes, and they vary both along the length of the cliffs and over time. Miller (1995; Figure 1.15A,B) proposed that there is a relationship between the shape of a cliff slope profile and the dominant erosional processes that act upon it (Figure 1.16) Many of the cliff erosion processes either cause or are caused by slope oversteepening, but slope oversteepening is ultimately controlled by the rate of toe erosion caused by wave action at the base of the cliffs (Wilcock et al., 1998; Figure 1.16A) or by wintertime cycles of freezing and thawing (Figure 1.16C,D), both of which keep the lower slopes steep except where and when they are covered by debris shed from above (Zwissler et al., 2014; Figure 1.16B). The uppermost part of the cliffs is also generally nearly vertical or even undercut, with soil bound by roots, forming the equivalent of a caprock at the top.

The middle slopes of the cliffs are commonly somewhat gentler and dominated by relatively frequent shallow translational slides. Miller (1995) measured the midslope angles at 12 sites along the Calvert Cliffs and found (from north to south) that their slope was 70° and 48° near Naval Research Laboratory and Randle Cliff (Leatherman, 1986, reported 40°–50°); 48°, 49°, and 49° where the Governor Run sand occupies the midslope from north of Scientists Cliffs to Governor Run; 41° (Rocky Point), 68°, 53°, and 49° around Calvert Cliffs State Park; and 53°, 47°, and 57° along the cliffs at the Chesapeake Ranch Estates. Much steeper slopes do occur locally, however, on the lower and upper middle to upper slopes (e.g., 70°–80° and nearly 90°, respectively) between Scientists Cliffs and Parkers Creek (Miller, 1995:45). Shell marl beds (beds 17 and 19) project slightly from the cliff face at many sites, even forming short vertical outcrops, except at beach level, where the shell beds are undercut by waves to form overhangs.

Loosening of the underlying, more cohesive clay-rich intact Miocene sediments can be caused by freeze–thaw cycles, desiccation, and vegetation root penetration, among other processes. Average slopes at 25 sites on the middle and southern cliffs (from

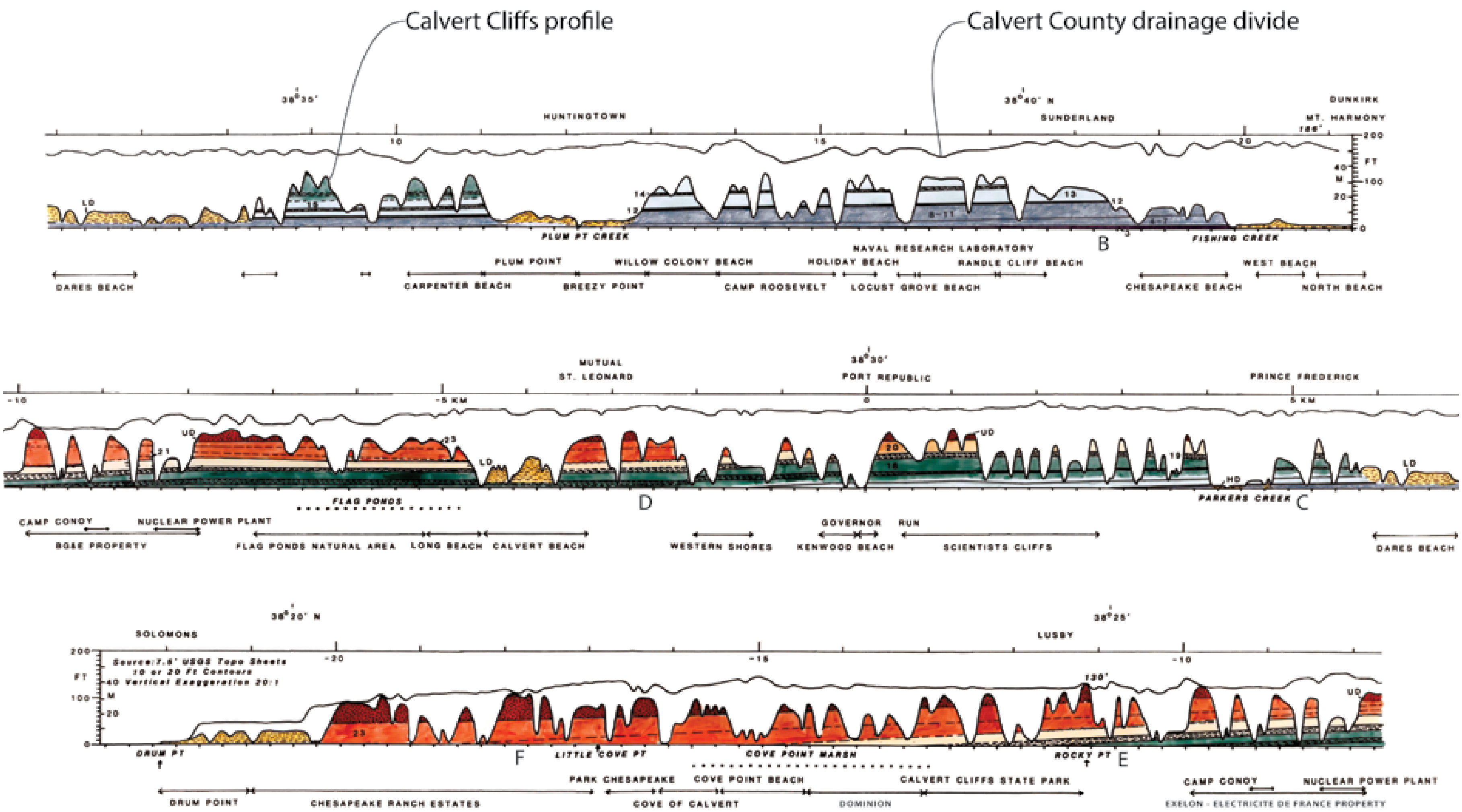


FIGURE 1.12. South (lower left) to north (upper right) profile, in three parts, of the Calvert Cliffs (adapted from fig. 2 of Vogt and Eshelman, 1987) constructed from Calvert County topographic map contours, with numbered biostratigraphic beds (zones of Shattuck, 1904) and modern place-names along the cliffs. Capital letters B to F show locations of photographs in Figure 1.2. Note that Governor Run channel (Figures 1.10, 1.11; Kidwell, 1997) and Moran Landing Fault are not identified on this generalized profile. The original (pre–late Quaternary) land surface along this cliff profile must have been above the level of the present highest Calvert County topography in this region (approximately along the watershed) west of the modern cliffs (upper profile, mostly along Maryland Route 4). The reason is because streams flowing west from a once higher upland, now eroded away from an area now occupied by the Chesapeake Bay, removed the upland gravel materials that once covered this region but are now gone (Vogt, 1991). Along other stretches of cliffs in the Chesapeake Bay region, for example, the Westmoreland Cliffs in Virginia and the cliffs around Popes Creek, Maryland, as well as along the southern Calvert Cliffs, overlying upland gravels are everywhere present along the tops of cliffs. The loss of the unconsolidated upland deposits (Schlee, 1957) is sufficient to account for most of the now missing, eroded material.

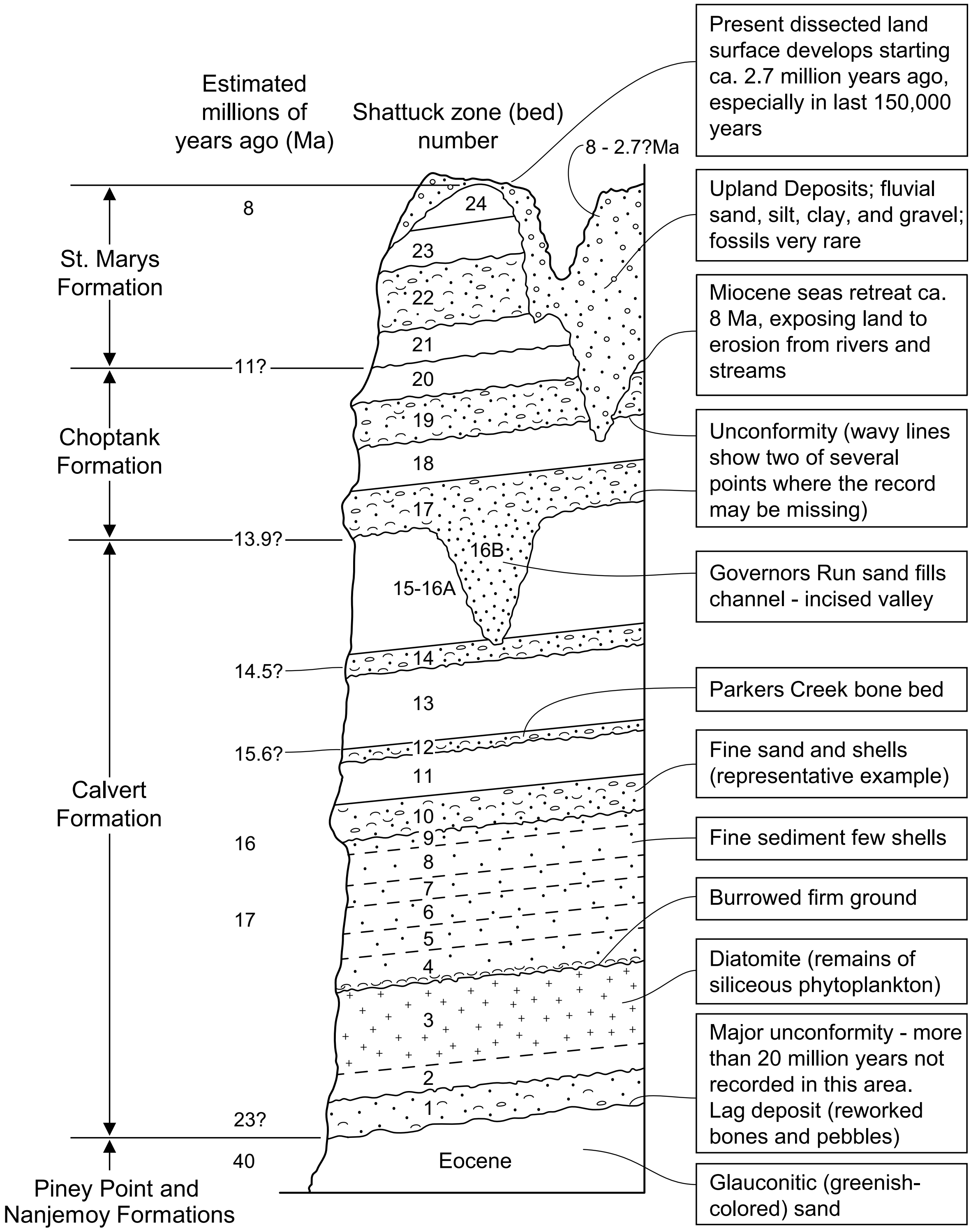


FIGURE 1.13. Composite section of the Miocene Chesapeake Group strata along the Calvert Cliffs that unconformably overlie the Eocene Piney Point and Nanjemoy Formations and underlie late Miocene(?) and Pliocene upland deposits. This section was originally constructed by Gernant et al. (1971), modified by Vogt and Eshelman (1987), and further modified here. Approximate depositional ages are generalized from Vogt and Parrish (2012).

Scientists Cliffs to Chesapeake Ranch Estates) were measured by Zwissler et al. (2014) starting in 2003 and later using lidar-based topographic contour maps (measurement uncertainties were not given). Only sites without toe erosion by waves were chosen. All but one of the slope angles were between 35° and 55°, with a median slope angle of around 44°. This is somewhat lower than the midslope values measured in the field by Miller (1995). Leatherman (1986) measured similar slopes near the northern end of the Calvert Cliffs in the vicinity of the Naval Research Laboratory. Some cliff slopes fall above this range. For example, Clark et al. (2004) reported slopes as high as 65° near Calvert Beach, whereas Zwissler et al. (2014) measured an 88° slope in that same vicinity. There appears to be no systematic difference between average slopes in the southern Calvert Cliffs and average slopes in the northern cliffs, even though there is a considerable difference between the lithology and physical properties of the Choptank and St. Marys Formations in the southern cliffs and the lithology and physical properties of the Calvert Formation in the northern cliffs. This conformity perhaps reflects the fact that the average slope angles are primarily controlled by noncohesive material on the middle slopes and (where debris covers the Miocene toes) also on the lower slopes.

Probably most of the Calvert Cliffs that have slopes greater than 35° to 40° are unstable. Clark et al. (2004) measured 47 slopes of stabilized and forested fossil cliffs that are naturally protected by foreland spit complexes at Flag Ponds and Cove Point. Forty-two of the stabilized slopes ranged between 26° and 36°, with a mean slope of about 31°; measurement errors were not estimated. Where the toe of the cliff face has been artificially protected for decades (for example, at the Naval Research Laboratory and at South Beach in Scientists Cliffs; see below), the lower slope of the cliffs, formed of debris, has a slope that is <35° and is covered with vegetation (e.g., Miller, 1995). In round numbers, we can predict that reducing an average Calvert Cliff slope by around 15° (from 45° to 30°) would turn most of the cliff into a forested escarpment with greatly diminished erosion rates but also with greatly diminished geological exposures and fossil yields. The slope at which a cliff slope becomes stabilized can differ from one locality to another because factors such as lithology and groundwater hydrology differ from one section of the cliffs to another.

The pace of cliff erosion varies with season and with weather and also from north to south along the cliffs and vertically within the cliffs from one stratum to another. Nearly all of the destructive processes are erosional because the clay, silt, and sand that compose the cliffs are chemically stable at the Earth's surface. Some chemical weathering occurs, but it is limited mostly to acidic rainwater dissolving fossil carbonate shells and to near-surface oxidation of ferrous iron to ferric iron, which turns the unweathered gray silty mudstones of the three formations to shades of red or yellow. Where there is groundwater penetration of the Miocene strata, it generally is limited to existing joints. Salt crystallization can occur where brackish bay water persistently wets the sediments, and heating of near-surface voids can promote sediment disintegration if there is thermal expansion of gases within the voids (Hampton and Griggs, 2004:21).

Precipitation of gypsum and calcium carbonate on the surface of a cliff can locally cover and thereby temporarily armor small patches or ledges of Miocene outcrop. Similarly, ferric iron oxide (hematite and limonite) may locally cement and protect patches of overlying upland deposits by forming reddish sandstone blocks that are usually about 10–20 cm thick but locally up to 1 m thick. These are locally collected and utilized for fireplaces, exterior building stonework, and yard decoration. They can be locally protective, but these chemical precipitates are generally too small and scattered in their occurrence to significantly affect the overall rate of erosion along the Calvert Cliffs. A notable exception occurs at Rocky Point in Calvert Cliffs State Park (Figure 1.2E), where bed 19 (the Boston Cliffs Member of the Choptank Formation), which forms the toe of the cliff there, has become indurated (cemented) by ferric iron oxide (Miller, 1995). Some iron cementation also occurs in the Plum Point Member just north of Parkers Creek. It has been proposed that the iron was first leached out of near-surface sediments (probably gravels of the upland deposits) by very acidic water associated with decaying vegetation. This iron later became redeposited when and where the acidic groundwater that contained it became exposed to oxygen, such as in the originally permeable bed 19 shell marl at Rocky Point. Similarly, at Cove Point there are abundant large iron-cemented blocks of post-Miocene(?) upland deposit material exposed in the upper part of the cliffs. Many of these have completely eroded out and litter the beach.

The erosional attack against cliff toes by waves is particularly efficient, although episodic (e.g., Wilcock et al., 1998), along the southern cliffs, where the sandier, less consolidated sediments of the Choptank Formation are exposed at or near the base of the cliffs. Erosion there is especially severe if winds and waves come from the southeast. Miller (1995) concluded that the rate of wave undercutting depends on tide level and the cohesive strength of the toe material. When tide levels are high and the cohesive strength of toe material is relatively low, wave erosion generates the highest rates of toe erosion observed along the cliffs. Among the sites examined by Miller, the highest rates of erosion were found along the cliffs just south of Parkers Creek (Figure 1.16A) and near Calvert Cliffs State Park. When high storm surges combine with easterly storm winds, significant wave erosion (tens of centimeters) can occur in a matter of just a few hours where less cohesive beds are exposed to the waves. The longest fetches, and thus the greatest damage, occur when winds are blowing from the NNE (70–105 km) or from the SSE (150–175 km). Annual maximum wave heights along the Calvert Cliffs regularly exceed about 1.2 m (4 ft; Zabawa, 1989: tbl. 1), and these can occur either during tropical storms (late summer and fall) or during late fall, winter, and spring storms called nor'easters. Some of the greatest historical storm surges along the Calvert Cliffs (~1.2–1.5 m or ~4–5 ft) occurred during the Chesapeake–Potomac hurricane of 23 August 1933 and Hurricane Isabel on 18 September 2003.

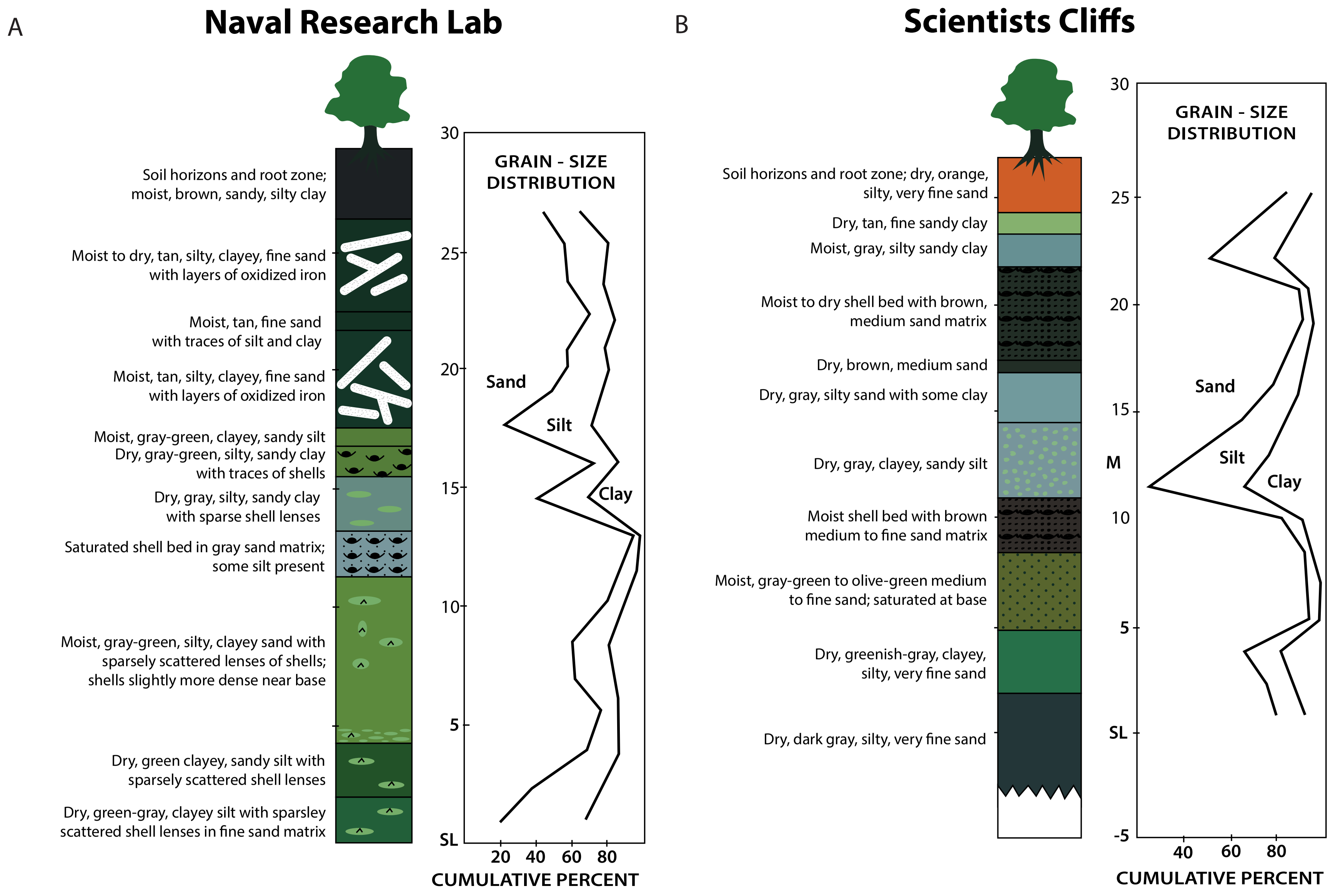


FIGURE 1.14A,B. Lithologic and grain size distributions within four shallow boreholes drilled just inland from the Calvert Cliffs. From north to south they are (A) the Naval Research Laboratory, (B) Scientists Cliffs, (C) Calvert Cliffs State Park, and (D) Chesapeake Ranch Estates. Adapted from Miller (1995), with Shattuck zone numbers and formation limits estimated by comparison of lithology with Figure 1.10. (Figure 1.14C,D on facing page.)

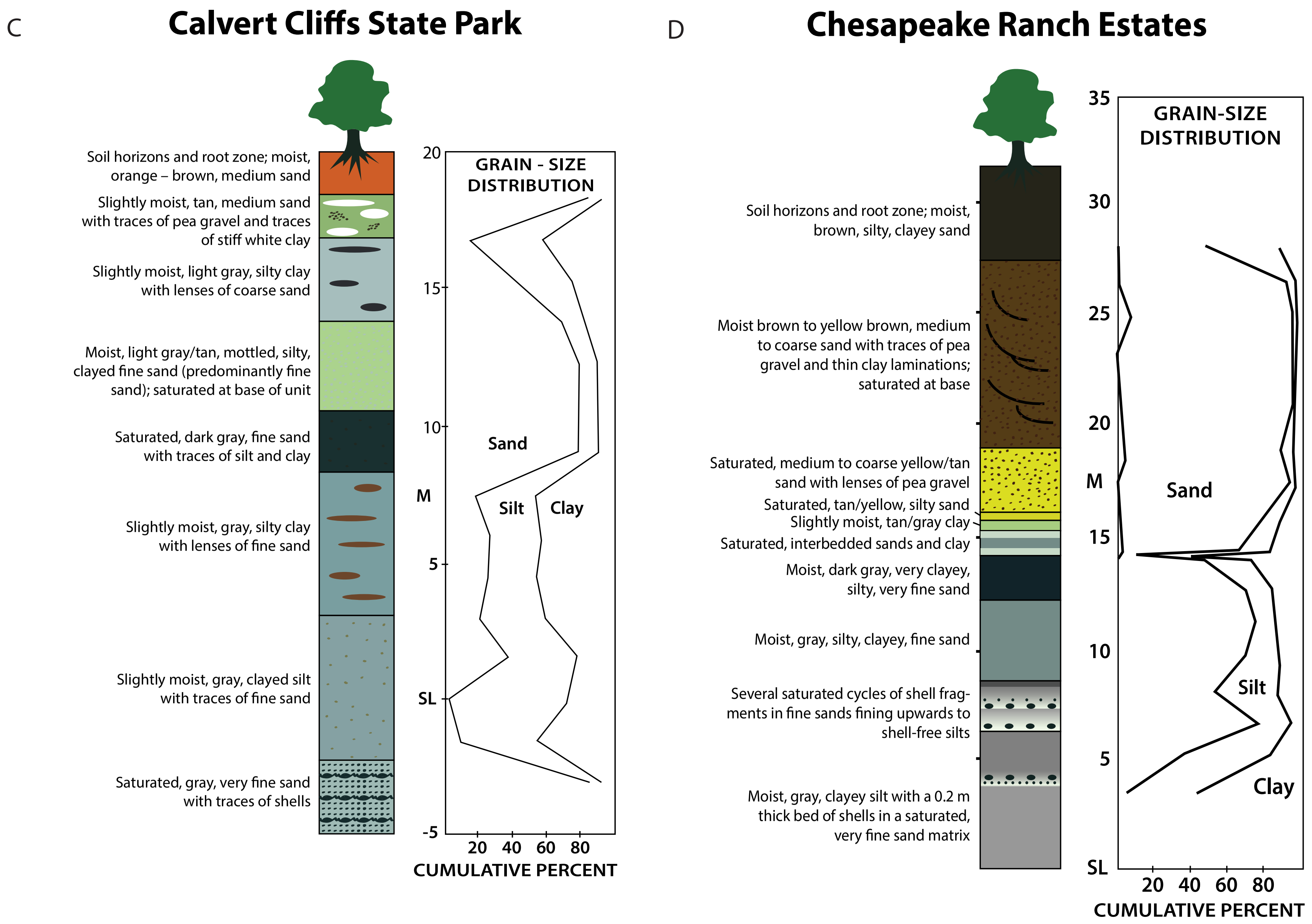


FIGURE 1.14C,D. Lithologic and grain size distributions within four shallow boreholes drilled just inland from the Calvert Cliffs. From north to south they are (A) the Naval Research Laboratory, (B) Scientists Cliffs, (C) Calvert Cliffs State Park, and (D) Chesapeake Ranch Estates. Adapted from Miller (1995), with Shattuck zone numbers and formation limits estimated by comparison of lithology with Figure 1.10. (Figure 1.14A,B on facing page.)

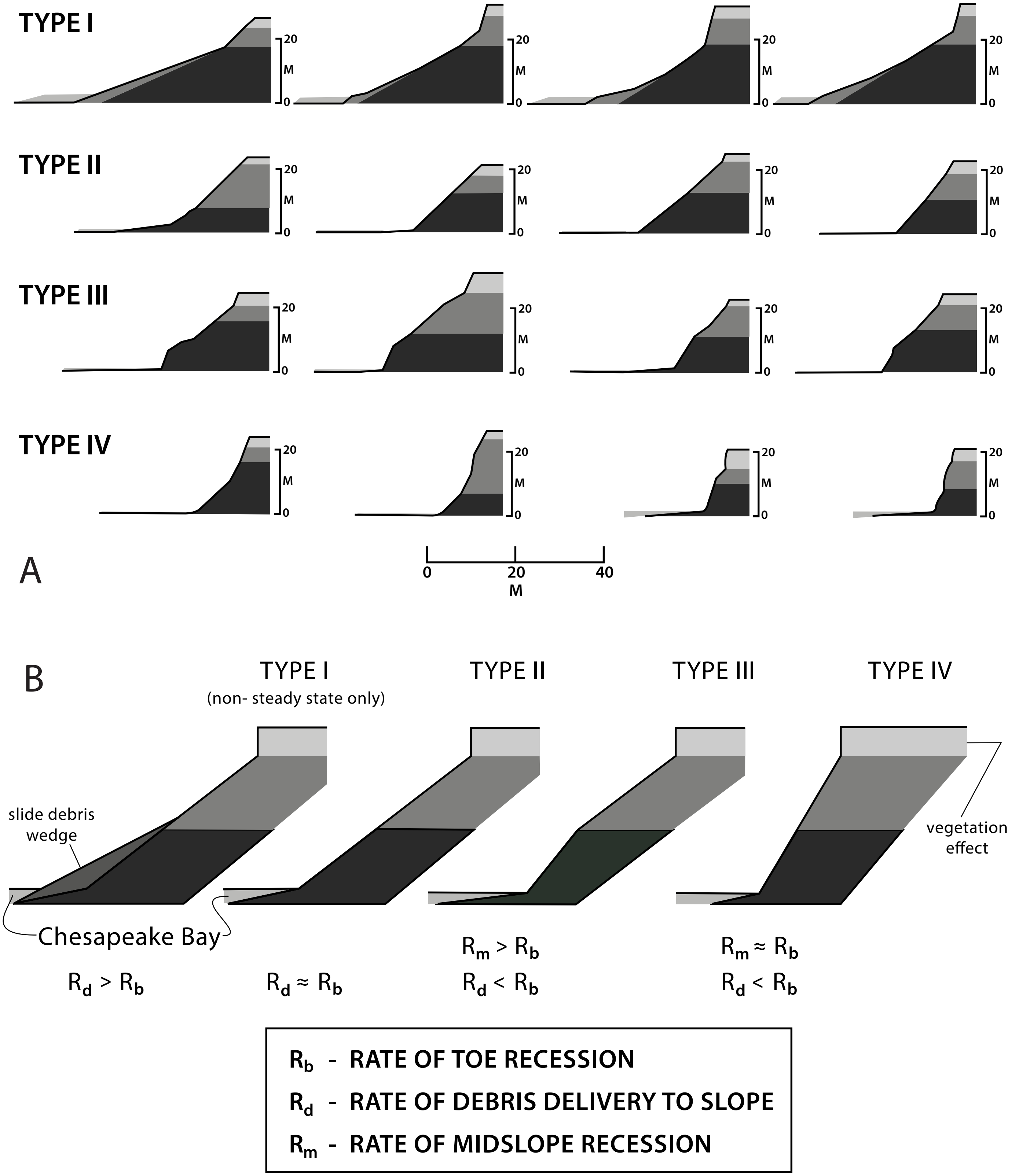


FIGURE 1.15. (A) The four types of Calvert Cliffs cliff-face slope profiles based on relative rates of toe recession, debris delivery to slope, and rate of midslope recession (Miller, 1995). (B) Four simplified examples of slope profile for each of the four slope types (Miller, 1995). See also Miller et al. (2006).

The more indurated (cohesive), massive, sparsely fossiliferous silt-clay beds (for example, beds 11 and 13 of the Plum Point Member) resist wave erosion where they are locally exposed near sea level along the middle and northern cliffs and can locally act as natural bulkheads, reflecting waves back out into the bay. This bulkhead effect can also serve to inhibit cliff base sand accumulation and beach formation, for example, north of Parkers Creek (Figure 1.2C). This particular environment essentially has a bimodal stability. There is a "beach state," which can occur because of a storm or persistent wind/wave pattern and can persist for some time, but most of the time there is a "no-beach" (natural bulkhead) state that is more normal. This bimodal stability is reflected both in anecdotal observations and in historical maps that show long intervals of time when a beach is present in these regions followed by long intervals of time when there is no beach at all. Man-made bulkheads (e.g., at the Naval Research Laboratory) create a permanent no-beach state that prevents erosion but also the formation of offshore sandbars (Miller, 1995).

Where they are at beach level, the interbedded, much sandier Plum Point Member shell marls (especially beds 12 and 14) are far more susceptible to wave erosion during high tides than beds 11 and 13. Waves quarry out mollusk shells contained in those beds, creating cavities that are then enlarged by hydraulic plucking (the toilet plunger effect). Where mollusk-rich bed 14 is exposed at sea level (from southern Scientists Cliffs to Kenwood Beach), such natural quarrying creates linear notches (undercuts) along the cliff face. When these notches are cut back 20–40 cm, slabs of the overlying bed 15 collapse (spall away). This usually happens along near-vertical, cliff-parallel fracture lines called exfoliation joints. The resultant collapsed blocks can be up to a meter thick and several meters tall and consist of parts of upper bed 14 and lower bed 15. These blocks, similar in appearance to the collapsed blocks shown in Figure 1.16A, are helpful for paleontologists because they create fresh exposures along cliff toes that are otherwise often hidden behind slide debris, moss, or vascular plants (Figure 1.16B).

A similar situation exists between the north end of Scientists Cliffs and the south end of Parkers Creek beach, where bed 12 (Parkers Creek Bone Bed) is exposed near sea level. This section of cliff is part of the Parkers Creek Preserve (Warrior's Rest Sanctuary) and is allowed to erode naturally. Wave erosion of bed 12, which is a sandy shell marl about 30–50 cm thick that contains broken small shells, locally produces linear undercut notches that create overhangs of bed 13 and, at the same time, forms benches on the top of bed 11. Large intact blocks of beds 13 and 14 often collapse onto the beach, providing access to strata derived from portions of the cliff face normally out of reach without ladders.

When slide debris accumulates along the toe of cliffs, it protects the Miocene strata at the base of the cliff from further erosion, sometimes for years. This debris (called colluvium) also can buttress the lower part of the cliff, reducing the likelihood of further sliding, although further sliding can and does occur on exposed surfaces in the upper part of the cliff above the slide debris. If the slide debris arrives on the beach with rooted vegetation (e.g., Figure 1.16B), particularly if there is time to grow new vegetation, the unconsolidated debris acquires some additional resistance to wave erosion and can develop miniature "undercliffs." Debris slides, which may be composed of one or more successive slides at the same site, can create a kind of cyclicity to the cliff erosion process in which the period of the cyclicity is determined by how long it takes the bay waves to remove the slide episode debris protecting the "Miocene toe." The longer it takes to erodes away the debris apron, the more time there is for deep-rooted vegetation to establish itself on the slopes above.

Groundwater moves through some strata in the Calvert Cliffs, flowing rather rapidly through the relatively permeable upland deposits, more slowly through the strata of the Choptank and St. Marys Formations, and only very slowly or not at all through the Calvert Formation, which is mostly impermeable layers (aquiclude or confining bed). Along parts of the Calvert Cliffs, the presence of alternating permeable and impermeable beds has created what are known as perched water tables (e.g., Leatherman, 1986; Miller, 1995). Groundwater seeping out at the base of these perched beds commonly creates horizons of darkened (wet) sediment, lines of vegetation, and, in winter, horizons of ice buildup (Figure 1.16C). Groundwater will exit from the cliff faces most often along the disconformity between the impermeable Calvert and more permeable Choptank Formations, perhaps most dramatically at the base of the Governor Run sand in the area of Scientists Cliffs. Locally, seepage erosion (called sapping) may occur (e.g., Leatherman, 1986; Miller, 1995), and water seeping along plant roots or joints also tends to weaken the sediments. A water-hose-like flow of water from about bed 17 levels of the cliff, observed on 6 August 2016 just after a massive sediment failure in Scientists Cliffs (discussed below), was likely caused by a sapping effect.

The more cohesive, wave-resistant beds (e.g., beds 11 and 13) are eroded in a different manner—primarily through intermittent cycles of freeze and thaw (Miller, 1995; Zwissler et al., 2014). The interstitial water freezes during winter cold snaps, prying apart the grains and shells in the sediment. When these icy shells thaw, the sediment turns to mud and falls off as flakes or is rinsed away by rains. The loose material initially accumulates next to the cliff toe but then is washed away during high tides and storms. When and where the gently seaward-sloping Miocene sediments are exposed near the cliff toe, the freeze–thaw cycle can also remove material from that surface, speeding up disintegration of intact sediment blocks on the beach. Typical winter cold spells will remove 1–2 cm from the cliff face, but during long, exceptionally cold periods up to 10 cm may be removed (Figure 1.16D). Repeated, separate cold spells degrade the cliff faces more rapidly than a single protracted cold spell. Miller (1995) concluded that the freeze–thaw cycle is the primary cliff retreat process at sites where the toes are not being undercut by waves, for example, at Calvert Cliffs State Park, where Zwissler et al. (2014) concluded that 65% of the toe recession at those six Calvert Cliffs study sites is due to the freeze–thaw cycle.

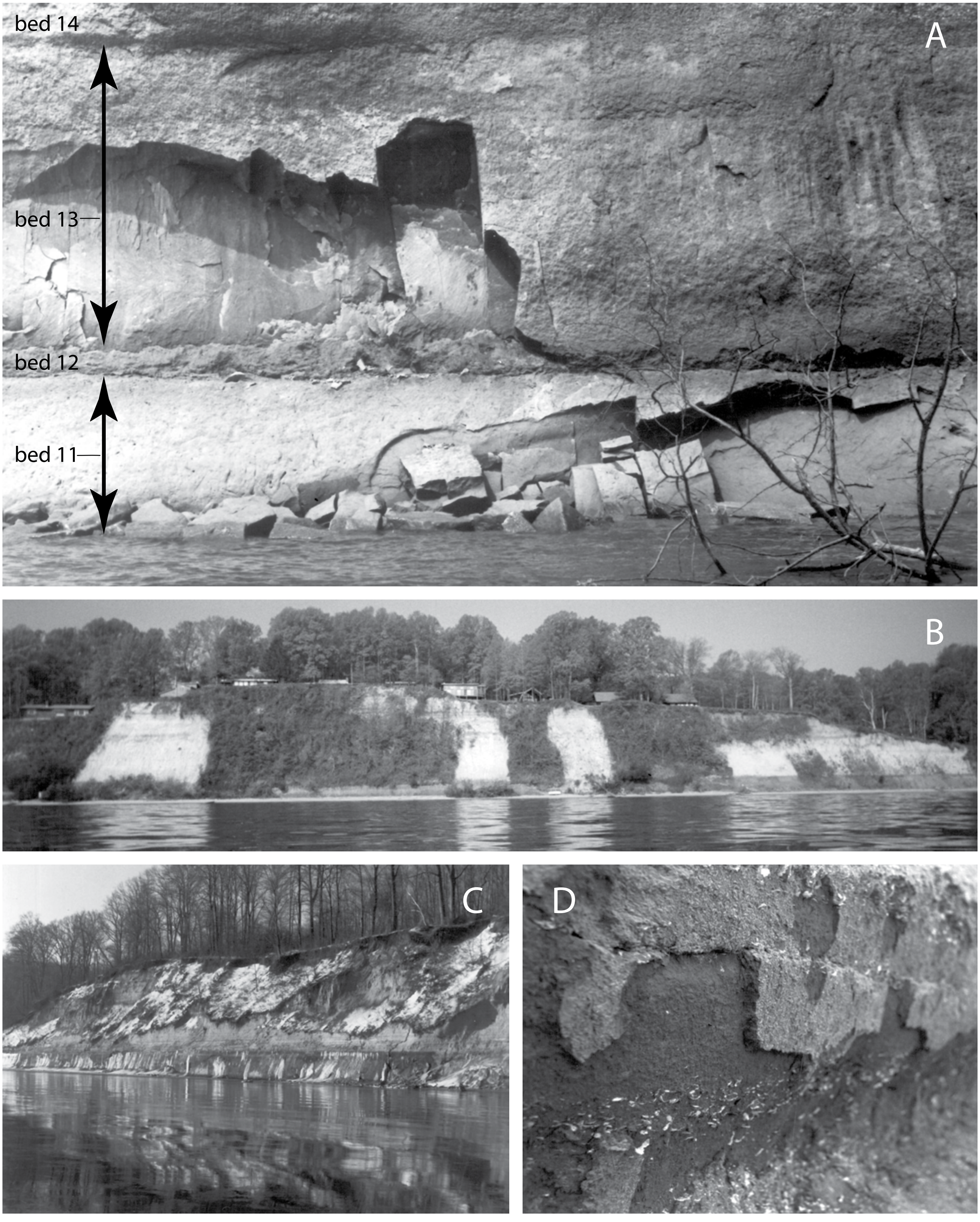

bed 14
A
bed 13
bed 12
bed 11
B
C
D

FIGURE 1.16. (*Facing page*) Examples (at Scientists Cliffs and at cliffs between there and Parkers Creek) of cliff erosion processes: (A) Undercut columnar blocks from bed 11 (lower) and bed 13 (upper) in the process of falling into the water. Note that storm waves are preferentially eroding the less resistant, ~50 cm thick bed 12 to create a ledge and undercutting of bed 13. (B) Section of cliffs in northern Scientists Cliffs, showing recent "wet rug" slide scars triggered by protracted heavy rains. (C) Winter view south of Parkers Creek, showing slide scars on middle cliff and icicle formation at the base of the Choptank Formation, where groundwater seeps out and freezes. (D) Calvert Formation (bed 14) just above the beach, showing an approximately 8 cm thick frozen surface that is still attached in some places (light gray) but already fallen off in other places (dark gray, with fresh exposure of bed 14 mollusks). Frozen sediment turns to mush as soon as the interstitial ice holding it together melts.

Desiccation, a diffusion-type process similar to but less important than the freeze–thaw cycle, can also loosen cohesive beds (for example, beds 11, 13, and 15) during long summer droughts, such as the one that occurred in 2002. As interstitial water evaporates from the surface of the exposed beds, the dried crust spalls off in thin flakes. Desiccation has been observed to remove several millimeters of sediment during droughts, but no systematic study has been conducted.

Erosion processes above the cliff toes continuously play catch-up in response to the oversteepened lower slopes. Freeze–thaw cycles, desiccation, and prolonged soaking rains are very effective at loosening sediment higher up on the cliffs, with gravity, wind, and flowing water doing the rest. Exposed Choptank and St. Marys Formation strata can be eroded into rills and small gullies in heavy rains, with their eroded clay, silt, and fine sand entrained in suspension flows and deposited as thin layers on adjacent sandy beaches.

Vegetation to some degree protects the Miocene strata from many erosional processes, but plant roots also tend to penetrate and loosen the strata to depths of 50 cm and sometimes more. It is notable that the rapidly receding, unvegetated cliffs between Parkers Creek and Scientists Cliffs stand at the same midslope angles (48°–50°) as the slowly receding, heavily vegetated cliffs of nearby northern Scientists Cliffs (47°–49°; Miller, 1995:187). This similarity suggests that vegetation has only a temporary effect on the long-term erosional cycle of the cliffs.

It seems likely that the typical 20–40 cm thickness (Miller, 1995) of shallow translational slides on the midslopes of vegetated cliffs (e.g., at Scientists Cliffs; Figure 1.16B) is determined largely by the thickness of Miocene sediment loosened by plant roots. These translational slides commonly begin near or slightly below the top of the cliff and tend to happen during and up to 24 h after protracted heavy rains (>5 cm/d; P. Vogt, personal observations; see also Miller, 1995; Miller et al., 2006). Brief but heavy summer thunderstorms produce water that comes down too fast to penetrate, whereas protracted rains saturate the sediment, thereby increasing the weight of the surface material and at the same time reducing its shear strength. Relatively more rain is needed to saturate soil on a sloping surface than on a more level surface. For example, a 5 cm rain falling vertically on a typical 45° will be equivalent to only 3.5 cm of rain falling on horizontal ground.

Typical translational slides are about 10–20 m in width (Figure 1.16B). The age of small trees carried down to the beach from slides on the cliff faces provides a measure of how long a cliff face has been stable. According to local conventional wisdom, large trees growing on the slopes or on top of the cliff actually promote cliff retreat because of the large root balls pulled out by these trees when they are uprooted in storms and because of the high "sail area" of tall trees, which makes them especially vulnerable to the power of strong winds. This idea is interesting, but there have been no studies undertaken on the long-term effect that large trees might have on cliff stability.

Among the less commonly observed processes that operate along the Calvert Cliffs, in the southern cliffs where they are occupied by Choptank, St. Marys, and younger fluvial strata, rotational slumps can locally occur that indent the cliff face by up to a few meters during single failures. Large-scale liquefaction is also a process not documented along the cliffs, except during a 1979 slide in southern Scientists Cliffs when the sediment above the Calvert–Choptank contact liquefied as a result of frozen and broken water pipes at an unoccupied cliff-edge house. All Miocene sediment back to the house foundation flowed down onto and across the beach, demonstrating that liquefaction is possible in at least some sediment of the Choptank, St. Marys, and upland gravels units but only under exceptional, probably man-made, circumstances. A similar, larger event occurred at Scientists Cliffs during August 2016 and is discussed in detail below.

Bioerosion includes scattered nesting holes slightly less than 10 cm in diameter created by rough-winged swallows and belted kingfishers, as well as minuscule holes a few millimeters in diameter that are excavated several decimeters into the cliff by insects, including Puritan tiger beetle larvae. Dens excavated by groundhogs occasionally can contribute to local sediment failure near cliff tops. Fossil quarrying by humans, usually for vertebrate remains near the cliff base, produces scattered small cavities that are typically 10–20 cm across. These cavities can be much larger, however, when remains of large vertebrates such as whales are removed. These larger cavities, which may be a cubic meter or more in volume, are too infrequent in space and time to accelerate the rate of cliff failure. In most cases, they are no longer visible within a year or two along the rapidly eroding southern cliffs, although farther north they may remain visible for some years in the more slowly eroding marls of the Plum Point Member. All these types of bioerosion have no significant impact on the rate of erosion along the Calvert Cliffs; however, industrial-scale cliff removal (e.g., during construction of the Calvert Cliffs Nuclear Power Plant) is another matter and will be discussed separately.

Man versus Cliff Erosion

Cliff erosion has long been observed (e.g., Shattuck, 1904; Schoonover, 1941), but apparently, it was not considered to be a problem worthy of mitigation until the expansion of housing and other high-value property developments near the cliff edges during and after World War II. In succeeding decades, more and more of the Calvert Cliffs shoreline has become variously modified from its natural state for the purpose of reducing erosion. It is the human perception of this problem, and not the natural erosion rate, that has changed, however. A study by Miller (1995:193) of early aerial photographs, mapping, and other observations led him to conclude "the slopes were eroding in much the same way nearly a century ago as they are today." However, land clearing for agriculture, beginning in the later seventeenth century, increased sediment delivery to the Chesapeake and helped nourish sand beaches along the Calvert Cliffs.

The Naval Research Laboratory Randall Cliffs facility, built atop the northern cliffs in 1941 for radar research purposes, was probably the first example of cliff erosion control: A 1.4 km long section of cliffs was armored by a steel bulkhead (seawall) in 1945, causing the beach below the cliff to disappear. In the early 1970s, a wooden bulkhead was constructed outside the deteriorating steel structure. Although toe retreat was arrested, the upper parts of the cliff have continued to erode (e.g., Leatherman, 1986). The Naval Research Laboratory bulkhead has significantly slowed the rate of cliff erosion there, but it has done so at the cost of destroying the underlying beach and also preventing the development of offshore sand bars (Miller, 1995). Similar bulkheads also have been constructed along the Dares Beach–Wind Cliffs shoreline and next to the Calvert Cliffs Nuclear Power Plant.

In 1993, the Calvert County Board of Commissioners appointed a Calvert County Cliff Policy Task Force to address the complex management issues involving the Calvert Cliffs. The task force (which included authors REE and PV) examined the cliffs from many perspectives: as a regional landmark and fossil repository; as the home of a species of federally listed endangered tiger beetle; and as a threat to cliff-edge developments due to the ongoing erosion that maintains the cliffs. The task force recommended a mandatory policy of setting new developments well back from the cliff tops (Calvert County Cliff Policy Task Force, 1993, unpublished report), and this policy was in part adopted by Calvert County in 1996. Under this policy, properties already built near the cliffs were grandfathered in and thus not directly subject to this new rule. A recommendation that was not adopted, however, was the requirement that prospective buyers of cliff-edge properties be warned of the erosion issue. It was not until 2008 that Calvert County printed a small brochure on this subject (Calvert County Department of Planning and Zoning, 2008). As a result, until 2008 cliff-edge homeowners could truthfully claim that they had never been told of the risk that was inherent to their properties (Property Owners Association Chesapeake Ranch Estates, 2010).

Through the years, various cliff-edge developments have tried different approaches to stopping cliff erosion, and some have simply let the cliffs erode. According to a 2010 tabulation by the Calvert County government, 234 houses were located within about 30 m (100 ft) of the cliff edge in 2003. Of these, 1 at that time was actually overhanging the cliff edge, 19 were within about 1.5 m (5 ft) of the cliff, 20 others were within about 3 m (10 ft), and 43 more were within about 6 m (20 ft) of the cliff. Lumping together all of these various houses along the cliffs is somewhat misleading because cliff retreat is slower along the middle and northern cliffs, where the Calvert Formation crops out at the base of the cliff, than it is along the southern cliffs, where the less cohesive Choptank and St. Marys Formations are exposed at beach level. For example, a house about 8 m (25 ft) from the cliff edge in the Scientists Cliffs community might have 50 years of remaining life before it succumbs to cliff erosion, whereas a similar house at the same distance in parts of Chesapeake Ranch Estates might succumb to cliff erosion in just a decade or two.

The grandfathered cabin development of Scientists Cliffs, which had been laid out beginning in 1936 south of Parkers Creek, by 2003 had come to include 79 cliff-edge houses, of which 40 were wholly or partly within about 6 m (20 ft) of the cliff edge. In an attempt to protect these properties, the Scientists Cliffs Association constructed a groin jetty perpendicular to the approximate 1.9 km (1.2 mi) of shoreline in 1946 and a second one in 1948. Many more were built in the 1950s and later. Such structures (Schultz and Ashby, 1967) were less effective than bulkheads at slowing cliff toe retreat, but they did maintain and widen the beach by trapping sand moving southward under longshore drift (Downs, 1993). The beaches at the Scientists Cliffs community and elsewhere along the cliffs have long been a major recreational asset for boaters, swimmers, sunbathers, fishermen, fossil collectors, hikers, and others. By the 1970s, the early Scientists Cliffs groins (variously built of wood, old tires impaled on steel rods, and well casings) began to be replaced by gabions (wire cages filled with rocks about 20 cm in size, which individually are too small to stay in place under Chesapeake wave climates without the cages). The longest groin, progressively lengthened over the years, comprises boulders ("rip-rap") too large to be moved by Chesapeake storm waves. This groin eventually built up an approximately 300-m-long northward-narrowing permanent beach on its north (up-drift) side. On its southern down-drift side, however, cliff toe erosion actually was facilitated because the beach there was starved of sand.

Similar efforts were made at other places along the Calvert Cliffs, in which groins or jetties were constructed to control shoreline processes. The Flag Harbor marina, created by dredging out the lower part of Calvert Beach Run, eventually required regular effort to keep its boating channel open to the waters of the Chesapeake. Shoreline modifications were added between 1950 and 1980, including several groins, to protect nearby housing developments (Clark et al., 2004), and a jetty was built at the mouth of Kings Creek (Calvert Beach development) in 1975. All these shoreline modifications have impeded southward transport of beach sand, causing starvation and beach erosion along the northern part of the popular Flag Ponds Nature Park.

On the basis of questionnaire responses from cliff-edge cabin owners, Vogt in 1979 estimated the average long-term recession rate of the cliff face at Scientists Cliffs to be about 5–10 cm/yr. Although newer estimates suggest the long-term rate is closer to 5 cm/yr, by the 1990s, some owners began to construct toe revetments in the form of gabions to slow erosion. At the same time, however, the gabion construction reduced the already narrow beach width, required repair when the wires broke, and obviously had an unnatural and unsightly appearance. Also they were hazardous once gabions began to break: the insulation is damaged during storms, giving the saline bay water the opportunity to corrode and break the metal wire core.

Concerns about a possible acceleration of cliff erosion rates, exacerbated by the exceptional storm surge associated with Hurricane Isabel in 2003 and by several anomalously heavy, protracted rains that occurred during 2009–2010 (discussed by Property Owners Association Chesapeake Ranch Estates, 2010), led to the formation of an ad hoc Calvert Cliffs Stabilization Committee (Steering Committee, 2010), which included representatives from a number of the developments bordering the Calvert Cliffs. Only one geologist was appointed to this committee. A central goal of this committee was to help cliff-edge owners and their associations obtain the various county, state, and federal permits needed to construct additional cliff erosion control measures. In the community of Scientists Cliffs, new permits issued in 2013 cleared the way to construct an additional 500 m (~1,650 ft) of gabions that year as toe revetments that were located at various places where the toe of the Miocene cliff was exposed and thus eroding. More robust and expensive toe revetments composed of boulders (riprap), similar to one constructed by Western Shores in 1996, were proposed for about 490 m (~1,600 ft) of cliff base at Chesapeake Ranch Estates, where an earlier experiment in 2005 had deployed concrete “reef balls” along about 175 m (~580 ft) of shoreline to absorb wave energy but without notable effect. Similarly, a shoreline stone revetment was constructed in Calvert Beach during 2014–2015, and others have just been completed at Western Shores and at Chesapeake Ranch Estates.

Critics of the more aggressive erosion control measures (termed “hard armoring”) decry the resultant loss of a scenic landmark, beaches, tiger beetle habitat, and fossil-producing exposures. Skeptics of these efforts further point out that cliff erosion will continue above the revetments at least for a few decades (e.g., Leatherman, 1986; Clark et al., 2004) as the cliff top continues to erode back until the entire slope reaches a relatively stable angle of repose. This angle is different for different sections of the cliff because it depends on the type of sediment that is present at each site. Curiously, the cliff edge above Rocky Point, which is the only site along the Calvert Cliffs that has not significantly receded in 150 years, exhibits a relatively low 41° midslope angle. This suggests that although shore retreat is not significant there, slope erosion is continuing nonetheless (Miller, 1995).

Skeptics also point out that revetment, especially the riprap type proposed for Chesapeake Ranch Estates that extends up to about 9 m (30 ft) from the cliff toe, would reduce or even eliminate the already relatively narrow beaches, which are enjoyed by those who live inland from the cliffs in the same communities. Cliff stabilization supporters argue that continuing cliff erosion increases bay siltation and turbidity, but revetment critics counter by pointing out that cliff erosion is a perfectly natural process that contributes at least some sand to the beaches.

In 2012, the ad hoc Calvert Cliffs Stabilization Committee succeeded in obtaining Maryland Emergency Management Agency and Federal Emergency Management Agency funding for the 2013 purchase and 2014 demolition of the 10 most threatened cliff-top houses: two in the Scientists Cliffs community, two in the Kenwood Beach community, one in the Calvert Beach community, and five in Chesapeake Ranch Estates. Once the houses had been demolished, their sites were returned to their natural condition. Thus, the years 2013–2014 marked a turning point for grandfathered cliff-top developments, which undoubtedly will have to sacrifice additional houses in the future, even in some places where recession of the Miocene cliff toes is already blocked by revetments.

Occasionally, broken water pipes in cliff-edge structures have triggered landslides on a scale not previously observed even after heavy rains and high tides. One such slide occurred in southern Scientists Cliffs in about 1979, when the plumbing in an unoccupied cliff-edge home froze and cracked during a cold spell. Water from the cracked pipes flooded the basement of the house and then ran outside and saturated the surrounding soil and much of the underlying Miocene Choptank Formation sediment between the house and the cliff edge. The saturated sediment liquefied and failed, creating a slide headwall that lay directly below the outer part of the foundation. The liquefied toe of the slide, about 2 cm thick, spread out across the beach into the bay. The house was saved by constructing concrete beams across the slide scar, which also were used to support a new deck that projected out across the subsequently vegetated slide scar. Since then, only some relatively minor failures have occurred on the edges (shoulders) of the slide scar. An even more dramatic failure—possibly the largest historic landslide along the middle and northern portion of the Calvert Cliffs—began on 6 August 2016 in front of an unoccupied cliff-edge home atop an approximately 25-m-high (80–85 ft) cliff in the middle part of the Scientists Cliffs community. The owners had been there over the Fourth of July holidays, but a week or two later, the connection between the incoming water line and the house plumbing failed. Water flowed continuously into and just outside the basement and from there soaked into the ground below and next to the foundation. According to a neighbor (E. Dodsworth, personal communication, 2016), seven slides occurred over a three-week period, even long after the water had been shut off. Several other slides occurred in the following weeks. According to the neighbor, until the water was turned off, it actually flowed as if from a hose out of the cliff about 10–12 m below the cliff top (probably out of the sandy shell marl of bed 17 of the Choptank Formation). The final headwall of the slide, its outer cliff-edge corners forming a reentrant 21 m (70 ft) wide, did not stabilize until it lay under the foundation of a house that, before the slide occurred, had been located about 9 m (30 ft) from the original cliff edge. There was no choice except to have the house condemned and demolished. In this remarkable event, the cliff edge had retreated in three weeks by an amount that under natural conditions would have taken one or two centuries. The sole of this slide appears to follow the base of bed 17, a shell marl. The community manager (S. Dean, Scientists Cliffs Association, personal communication, 2016) compared daily water use by the community on the same dates in 2015 and 2016 and, from this comparison, concluded that the water leak averaged approximately 106 m^3/d (28,000 gal/d) beginning about 21 July, and totaled approximately 1,800 m^3 (~475,000 gal) of water during the 17 days preceding failure. If we assume that the Choptank Formation at this site had an available porosity of about 40%, then the leaked water would likely have been stored within a volume of sediment about 10 m wide × 15 m deep × 22 m long. This is roughly the same magnitude of sediment volume present in the slide at the time of failure.

Measuring the Rates of Erosion and Recession along the Calvert Cliffs

Using a representative 30 km section of eroding Miocene cliffs and assuming an average shoreline retreat rate of 30 cm/yr (~1 ft/yr) and an average cliff height (allowing for sediment "missing" in ravines) of about 15 m, we can estimate that an average of about 135,000 m^3 of sediment is removed from the cliffs annually and deposited on the beaches and in the adjacent Chesapeake Bay. This provides a reasonable estimate of the overall rate of erosion along the cliffs, but it tells us nothing specific about particular areas along the cliffs. Quantitative estimates of average shoreline erosion rates along particular portions of the Calvert Cliffs apparently were not attempted until after World War II (Singewald and Slaughter, 1949), when such estimates came to be of vital importance for long-term planning purposes such as imposing setback restrictions for new construction, for possible mitigation measures, and for the assessment of risk (and life expectancy) for structures near the cliff tops.

The position of the top edge (lip) of a cliff and the position of its toe are the two most obvious and consistently measurable points that can be made on the Calvert Cliffs. However, even after compiling a table of these measurements, deriving a meaningful numerical rate of cliff recession is still difficult because cliff erosion is highly variable over both short periods of time and small scales of distance. A particular cliff top may remain nearly stable for many years, then recede 1 m or more because of a single failure. Periods of fast erosion during unusual episodes of heavy rains (e.g., in 2009–2010), hurricanes (e.g., Isabel in 2003), or severe winters (e.g., 1976–1977, 2013–2014, and 2014–2015) can have a much larger impact on cliff erosion than the long-term average. Further complicating estimation efforts is the fact that although a numerical average of 0.3–0.6 m/yr (1–2 ft/yr) is numerically accurate for the Calvert Cliffs as a whole (Zabawa, 1989), the erosion rate along the northern and central Calvert Cliffs is consistently less than along the southern cliffs. Even within each of these regions, differences in local shoreline conditions create further differences in the local rates of erosion.

Along much of the Calvert Cliffs, sedimentary debris shed from the cliffs accumulates to form an apron along the foot of the cliffs, covering the toe of the cliffs and protecting their Miocene sediments from erosion for lengthy intervals of months or even years. This means that the average long-term retreat of the Miocene toe is significantly less in these areas than what is seen at times when the toe of the same cliff is exposed to cycles of freezing and thawing or to hydraulic plucking. Debris aprons are composed mostly of very loose materials, so when they are occasionally subjected to storm wave damage, they can be removed quickly in very large volume. Such storm losses create an appearance of very rapid cliff retreat that does not reflect the long-term trends important to planning policies.

A third obvious but ephemeral measurement that can be taken along the base of the cliffs is the landward edge of the water of Chesapeake Bay. The edge of the bay is constantly moving in and out beneath the cliffs with tides and weather, which over time can create and destroy sand beaches. This measurement provides valuable information about the health of the beaches along the Calvert Cliffs, but it does not tell much about the cliffs themselves.

Shoreline retreat rates can be measured on the ground or, much more practically, by remote sensing or surface mapping. Measuring cliff retreat on the ground has been done by use of a fixed reference marker (e.g., Leatherman, 1986) or by driving rows of rebar stakes (pins) into the lowermost cliff face and measuring the increasing length of the protruding part of the stakes over time (Miller, 1995) as erosion progresses. Leatherman (1986) reported an average cliff retreat rate of 15 cm/yr at Randle Cliff Beach Benchmark #7 from December 1951 to April 1978 near the northern end of the cliffs. During the period 1992–1994, pin fields were installed and measured at three cliff toe sites along Scientists Cliffs in the central part of the cliffs and one site at Calvert Cliffs State Park at localities where wave undercutting was not taking place (Schweitzer, 1993; Miller, 1995). Although the observation time was short, the results (Miller, 1995) are generally consistent with what is known about processes where freeze–thaw cycles are a major factor in the erosion rate and no undercutting takes place. The results of this study indicate long-term average rates of cliff retreat are slow at Scientists Cliffs, where they average about 5 cm/yr, and much faster at Calvert Cliffs State Park, where erosion rates were 31 cm/yr during a mild winter with little or no erosion except in winter. During cold winters, the erosion rates are even higher.

The Maryland Geological Survey initiated a long-term and ongoing investigation of the state's tidewater shoreline erosion rates. The first study (Singewald and Slaughter, 1949) compared the 1847–1848 U.S. Coast Survey maps with 1938 aerial photographs. Man-made structures identified on both images were used as reference points for cliff shoreline locations, a technique basically still used today (e.g., Zwissler et al., 2014). The accuracy of the 1949 study was limited, partly because of difficulties in consistently identifying the cliff edge and the Miocene cliff toe and also partly because of inaccuracies inherent in the 1847–1848 maps, which were based on plane table surveying at scattered locations. The Maryland Department of Natural Resources (DNR) updated and continued this work, eventually publishing a four-volume atlas of Maryland tidal shorelines and erosion rates that was based on comparison of temporally successive aerial photographs (Maryland Coastal Zone Management Program, 1975). By the 1990s, geographic information system (GIS) mapping software and inexpensive GPS navigation tools were greatly improving shoreline and cliff mapping accuracy, so that the latest Maryland coastal erosion rates and background data now are available online (Maryland Geological Survey, 2018a, 2018b).

According to the Maryland coastal zone website (Maryland DNR, 2013), the state has 12,330 km (7,660 mi) of tidal shoreline. Of this, 65% (including Calvert Cliffs) has eroded, on average, 0–0.6 m/yr (0–2 ft/yr) from around 1940 to around 1998. Accurate measurements of erosion rates less than 0.3–0.6 m/yr (1–2 ft/yr) were not possible. "Shorelines" were defined as the water's edge seen in the photographs. Some parts of Maryland's eroding tidal shoreline are eroding even faster, with 11% of the state's tidal shoreline eroding at 0.6–1.2 m/yr (2–4 ft/yr), 3% at 1.2–2.4 m/yr (4–8 ft/yr), and 1% eroding at a rate of 2.4 m (8 ft) or more per year. Overall, 69% of Maryland's coastlines have been retreating due to erosion. The most rapidly eroding parts of the Chesapeake Bay shoreline are along the edges of low Pleistocene terraces that are composed of poorly compacted sediment and exposed to the open bay on the Eastern Shore. The slowly or noneroding shorelines are mostly along narrow estuaries and sheltered coves. The Calvert Cliffs, accounting for only 0.35% of Maryland's total tidal shoreline, are exceptional in that they combine relatively slow rates of erosion with full exposure to the open Chesapeake. The difference in erosion rate under very similar circumstances between poorly compacted Pleistocene sediment and well-compacted Miocene sediment shows the importance of the relatively indurated (cohesive) nature of the Miocene sediments at the base of the cliffs in resisting erosion, particularly the nature of the Plum Point Member of the Calvert Formation, which is the unit directly exposed to wave erosion along the middle and northern cliffs.

Erosion (cliff retreat or recession) rates provided on the Maryland coastal zone website (Maryland DNR, 2013) vary substantially along the Calvert Cliffs. Some of the rates and their variations are artifacts, depending on various uncertainties and on the interval of time considered, that is, between successive aerial photographs. For example, for the northern half of the cliffs, included in the U.S. Geological Survey Prince Frederick and North Beach quadrangles, the most recent rates are based on the interval 1960 to 1993. For the southern half of the cliffs (Cove Point and Solomons quadrangles), the most recent rates are based on the interval 1942 to 1993. In general, the erosion rates along the middle and northern cliffs located north of Flag Ponds Nature Park, where the Plum Point Member of the Calvert Formation is exposed at beach level, are mostly in the 10–30 cm/yr range, consistent with the local 15 cm/yr (1951–1978) measurement at Randle Cliff reported by Leatherman (1986). The unprotected cliffs immediately north and south of Parkers Creek have been eroding somewhat faster than this average rate (about 40 cm/yr). To the south of Flag Ponds, eroding cliffs have been retreating at about 50–150 cm/yr, with more spatial variability than seen to the north. Exceptionally, the formerly eroding cliffs behind the Flag Ponds and Cove Point sand spits (cuspate forelands) have become stabilized wooded slopes (e.g., Clark et al., 2004) and so are not eroding at all at present, although the nearby shoreline sands are being eroded north of the spit tips and deposited just south of the tips, accreting new land (Beardslee, 1997).

By comparing aerial photographs, Miller (1995:194) independently estimated historic cliff recession rates at sites he studied. He determined a cliff recession rate of 10 cm/yr for the Scientists Cliffs segment, 80 cm/yr for the cliffs just north of Scientists Cliffs, 40–120 cm/yr for sites near Calvert Cliffs State Park (except for the very anomalous rate of <10 cm/yr at Rocky Point), 30–35 cm/yr around the Naval Research Laboratory and Randle Cliff, and <10–60 cm/yr for the Chesapeake Ranch Estates cliffs.

To estimate what fraction of Calvert Cliff recession is due to freeze–thaw cycles, Zwissler et al. (2014) analyzed accurate aerial photographs of the Calvert Cliffs from 2003, 2006, 2007, and 2011, which were taken more than a decade after the 1993 baseline photographs used by the Maryland DNR. They measured the distances from cliff-adjacent houses to the nearest cliff edge at nine sites in Scientists Cliffs and four sites each in Calvert Beach, Calvert Cliffs State Park, Park Chesapeake, and Chesapeake Ranch Estates. The specific measurement sites were not chosen at random, but rather were selected to avoid cliffs where wave erosion was occurring. From data at 25 sites, Zwissler et al. (2014) calculated average recession rates for 75 different individual locations, which ranged from nearly 0 to 158 cm/yr. Almost half of these values were between 25 and 75 cm/yr. On the basis of the average rates for each locality, Chesapeake Ranch Estates (71 cm/yr) and Calvert Cliffs State Park (65 cm/yr) in the south had the highest rates of land loss, four sites in northern Scientists Cliffs had little or no loss over this period, and the remaining sites had rates of land loss clustered in the middle (26–35 cm/yr). These data are also consistent with the observation that there was relatively higher short-term erosion loss during the extreme rain events that occurred in 2009 and 2010. The dramatic difference between recession rates in northern versus southern Scientists Cliffs (<5 versus 35 cm/yr) probably reflects the physical properties of the strata exposed to Chesapeake wave erosion. The cohesive clay-rich bed 13 stratum along the base of the northern cliffs at Scientists Cliffs is much less susceptible to erosion than the easily wave erodible shell marls of bed 14 that form the base of the southern cliffs at Scientists Cliffs. Zwissler et al.'s 2003–2011 cliff recession rates, which were determined at specific localities chosen deliberately, are roughly consistent with the more regionally estimated rates for the period 1960–1993 that are reported on the Maryland DNR (2013) coastal erosion website.

Offshore Sand Bars

Sand beaches and offshore sand bars (see, e.g., Shea, 1994) play a significant role in slowing Calvert Cliff erosion, but their multiyear and multidecadal trends are poorly known. Beach sand is typically of medium-grained particle size, with finer sand concentrated offshore (Figure 1.17). The 1847 Coast Survey map and the 1938 aerial photographs (see Singewald and Slaughter, 1949) are the earliest depictions of beach locations in this area, and their distribution is rather different from where we see beaches today. For example, the cliff between Governor Run and Scientists Cliffs was bordered by a narrow sand beach for a number of years until 1991, when the beach completely disappeared and left the toe of the cliff prey to continuous wave erosion (Miller, 1995). After Hurricane Isabel struck in 2003, however, a new beach formed and remained until 2016, when the Miocene toe of the cliff was reexposed in some areas.

Four or more sand bars, arranged nearly parallel to the shoreline, may be present along parts of the cliffs provided enough sand is available to sustain them. Multiple sand bars are not unusual in places where littoral depth gradients are very gentle, which is often the case along the Calvert Cliffs. The gentle gradients and shallow offshore water depths have resulted from the presence of underlying, relatively consolidated Miocene strata, which Chesapeake Bay surf is unable to excavate to a depth of more than about 0.5–1 m below sea level in the littoral zone. The resultant multiple sand bars (Shea, 1994) absorb wave energy, and sometimes waves even break on the nearshore bars before they reach the beach if winds and tides are favorable. Sand bars thus help to decrease the rates of cliff erosion when tides and water levels are in the normal range, although during high water levels and storm surges, wave energy can still become concentrated on the cliff toe.

Conventional wisdom attributes beach nourishment to cliff erosion, but in fact the Miocene strata exposed in the cliffs are primarily composed of fine sand (the primary constituent in most beds; Downs, 1993; Miller, 1995), silt, and clay, none of which remain on the beach under the Chesapeake's extant wave climate. The fine sand that washes out can help to nourish the offshore bars (Figure 1.17), but suspended finer material ends up farther offshore or, in the case of clay, probably is deposited in the deep central offshore channel. Sand sufficiently coarse to be stable along the beaches of the northern and central Calvert Cliffs beaches probably originates largely from the fluvial upland deposits that are being carried to the beaches from more inland areas via ravines and streams. Along the southern cliffs, however, the upland deposits that cap the cliffs do contain large quantities of medium to coarse sand that help to replenish the beaches there. This abundance of sand helps explain why the exceptionally large sand accumulations at Flag Ponds and Cove Point are there and nowhere else along the cliffs. A 2015–2016 study of zircon age distributions (McCormick et al., 2017) also supports the conclusion that most of the sand along modern Calvert Cliffs beaches originated by erosion of fluvial late Miocene to Pliocene upland deposits and not primarily by erosion of the Miocene marine sediments exposed in the Calvert Cliffs.

TECTONIC INFLUENCES ON THE CALVERT CLIFFS

The Calvert Cliffs and the Miocene strata they expose can be explained by depositional and erosional processes ultimately driven by eustatic sea level variations caused by climate change and attendant fluctuations in global ice sheet volume (Ruddiman, 2008). There are, however, some joints of possible tectonic origin in the Plum Point Member, and one reverse fault penetrating the entire Choptank Formation. The nearly vertical, east-striking joints, spaced about 20 cm apart, are prominent in beds 11 and 13 south of Parkers Creek. These joints may reflect thermal contraction and expansion of cohesive sediments within several decimeters of the cliff face. However, studies in the coastal plain of northern Virginia have attributed similar features to a subtle but pervasive tectonic stress field in the early part of the late Miocene that was related to the forces that uplifted the modern Appalachian Mountains (Newell, 1985; Weems et al., 1996, 2017). The preferred joint trends in the Northern Neck region in Virginia closely match the trends of the creeks there, suggesting that the creeks became preferentially incised along the joint trends. This may also be the case for ravines and stream valleys interrupting the Calvert Cliffs. However, vertical cliff-parallel joints 25–50 cm inside the cliff face are almost certainly caused by the cliffs themselves changing the stress field after removal of once-continuous layers located where the Chesapeake Bay is today.

The only other tectonic feature so far recognized along the Calvert Cliffs is a fault that, although noted as an offset in earlier biostratigraphic research, is most evident in the along-strike cliff profile of Kidwell (1997) and reproduced here as Figure 1.10 (also see Powars, 2013). At Moran Landing, between the Calvert Cliffs State Park and the Calvert Cliffs Nuclear Power Plant, the Miocene strata do not project directly across a small, semicircular gap in the cliffs but instead show an offset of about 3 m, indicating the presence of a high-angle reverse fault (here called the Moran Landing Fault) with its south side upthrown relative to its north side. The offset of these beds is not likely to

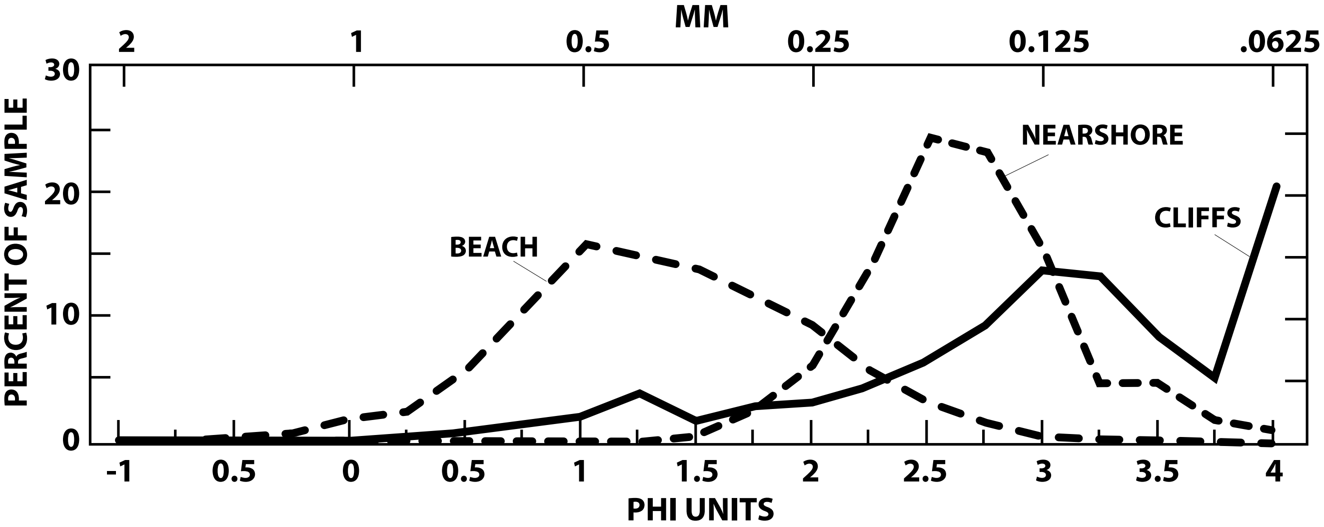


FIGURE 1.17. The size distribution of sand particles in beach sand, nearshore bar sand, and cliff sediment at Scientists Cliffs (Downs, 1993). Coarser sand is to the left, and finer sand is to right. Note that most sand from the Calvert Cliffs at this locality is too fine to remain in the beach sands, so erosion from the cliffs can serve only to replenish sand in the sand bars. Along the southern Calvert Cliffs, the overlying sandy and gravelly upland deposits do yield medium and coarse sand fractions that are heavy enough to remain on the adjacent beaches.

be due to a mapping error and likely is related to a contortion of the bed 15–17 interval into a tight anticline at Conoy Landing, just to the north of Moran Landing. Both the fault and the presence of the anticline indicate that these strata were disrupted after deposition of the Choptank Formation. Whether the fault continues into the overlying nonmarine sediments has not been determined because the overlying upland deposits are very variable in their lithology and have very discontinuous layers (Figure 1.10; see also Schlee, 1957). The strike of this fault is poorly constrained, and no younger limit has been established for its activity, but the structure may have been formed by the same regional tectonic event documented in Virginia that occurred in the early part of the late Miocene. The unusual, semicircular valley at Moran Landing is probably related to the fault and its effect on the strength of sediments in its immediately surrounding area. Hansen and Edwards (1986) identified a structure that they believe to be a NE-trending reverse fault with the south side upthrown, in the same sense as the Moran Landing Fault but crossing the Calvert Cliffs about 10 km north of it. It is quite possible that the Moran Landing Fault is related to a similar deep structure and is rooted at great depth in the basement rocks below the Coastal Plain. Numerous faults and other structures of many ages lace this Pre-Jurassic basement (Hansen and Wilson, 1984) underlying the area of the Calvert Cliffs. Some of these ancient structures may have become reactivated and have penetrated the sediment wedge deposited since formation and growth of the modern Atlantic Ocean (e.g., Mixon and Newell, 1977; Hansen, 1978, 1988; Powars and Horton, 2010).

THE CALVERT CLIFFS AS A REGIONALLY SIGNIFICANT COASTAL PLAIN LANDMARK

Most famous scenic landmarks (for example, the Grand Canyon and Yosemite Valley) have been created by erosion. The Calvert Cliffs are a lesser example of that process, but lesser is a relative term. Although 50 or 100 Calvert Cliffs would have to be stacked together to equal the relief of many U.S. western landmarks, the 42 km length of the cliffs is a respectable dimension. Moreover, on the otherwise flat and even monotonous Atlantic Coastal Plain that runs from Long Island, New York, south through Florida and then wraps around the north shore of the Gulf of Mexico as the Gulf Coastal Plain, the Calvert Cliffs stand out as a major natural landmark (Mansueti, unpublished), most easily appreciated from a small boat (such as the view seen in Figure 1.2). The Calvert Cliffs are featured in paintings, photographs, and fiction (e.g., Vogt, 2009). In the early seventeenth century John Smith, a man raised in the lowlands of southeastern England, could rightly call them “great high cliffs.” Old-growth forest capped the cliffs until the end of the seventeenth century, and its presence made the cliffs look about twice their actual height until they were later deforested for agriculture. Had the cliffs been owned by the U.S. government, as much of the land west of the Mississippi River was, it is almost certain that given their prominence as a regional landmark and because of their unexcelled fossil wealth, there would now be a “Calvert Cliffs National Monument” or perhaps even a “Chesapeake National Park,” with the Calvert Cliffs as a prime attraction, competing in fossil wealth with Dinosaur National Monument and the Florissant Fossil Beds in Colorado. Even today, the largest remaining natural segment of the Calvert Cliffs on either side of Parkers Creek deserves recognition as a national natural landmark.

Unlike most well-known landmarks, the Calvert Cliffs are best appreciated from the perspective of a boat located some hundreds of meters to several kilometers to their east, out in the Chesapeake Bay. Standing on the naturally forested cliff edge, one can see only a small part of the cliffs. If one tries to access them along the shore, they still can be difficult to fully appreciate because of landslide debris and trees shed from the cliffs and because the beach is narrow or, in many places, nonexistent. From either their top or their base, there is a very real and ever-present danger of landslides, as can be seen in Figure 1.16A,B, particularly after protracted heavy rains. Two fatalities occurred during the second half of the twentieth century, both along the southern Calvert Cliffs. In both cases, beach walkers simply were at the wrong place at the wrong time. The southern Calvert Cliffs truly are the most dangerous section because that is where the rapidly eroding Choptank and St. Marys Formations are present at beach level, and the only modestly compacted upland gravels overlie them (Figure 1.10). Indeed, the threat of cliff collapse is so great in this area that the beach south of the cliffs at Calvert Cliffs State Park is off limits to visitors.

Some segments of the Calvert Cliffs remain in a precarious legal state, developed neither for housing nor for industry yet at the same time not preserved. A striking example is the cliff just north of Governor Run, which is the second highest cliff along the Calvert Cliffs. This cliff was described by Ducatel and Alexander (1837:12) as "perhaps the most interesting spot at which to determine the geological features," one which "affords a luminous view of all the strata containing fossils." Ironically, the senior author of this chapter has since 1981 been a 1/15 shareholder in a corporation that owns the roughly 28 ha (70 acre) forested tract that lies above this cliff and extends back from it about 1,200 m from the 243-m (800-ft)-long segment of cliff and beach. Despite several efforts led by this author and the availability of a market value payment for it, this famous cliff remains unpreserved. Until 1981, it was one of the few spots along the cliffs where the public could collect fossils for a small fee (Glaser, 1979:54–66). Road access to this site is now closed to all but local cottage owners, who want to prevent trespassing on their long pier. This change illustrates the continuing challenges to preservation efforts along the Calvert Cliffs.

BEACHES AND BLUFFS ALONG THE CALVERT CLIFFS: A DYNAMIC AND EVER-CHANGING ENVIRONMENT

Quite apart from, and in some ways at odds with, their value as a rich repository of fossils, the Calvert Cliffs and adjacent shoreline area also constitute a narrow, unusual, complex, and constantly changing ecological niche. Although this chapter naturally emphasizes the cliffs themselves and their relationship to their adjacent shoreline, it also needs to be noted that the Calvert Cliffs are part of a narrow belt of steep dissected land and an adjacent shallow littoral zone. Landward of the cliffs, Holocene and earlier interglacial shoreline erosion of semi-indurated Miocene sediments has steepened eastward topographic gradients, causing the cliffs to be incised with numerous steep-sided ravines that are steadily extending westward by headward erosion. The resultant steep topography, formed just inland from the actual faces of the cliffs, has created many ecological niches that would not be present without erosion driven by the adjacent Calvert Cliffs and Chesapeake Bay. Seaward of the cliffs the bay remains shallow for 100 m or more offshore, and in many areas this shallow shelf locally hosts four or more nearly shore-parallel sand bars. Such bar systems require a low seafloor gradient to form, which has been possible because of the resistance of the Miocene strata to downward erosion in the littoral zone under present wave climates. In contrast, unconsolidated Quaternary sediments on the Eastern Shore are rapidly eroded down to 1.5–2 m below sea level, even near the water's edge.

Until Europeans arrived, there were only a few eroding outcrops other than the Calvert Cliffs, and these were located only along some of the larger tributaries of the bay such as the Choptank, Patuxent, and Potomac. All of these eroding outcrops supported, and still support, an ever-changing mix of microhabitats. For example, when a new slide occurs, even across an area with dimensions of just a few square meters, it exposes fresh Miocene strata on the cliff face. The resultant scar on the cliff face is then rapidly colonized by seeds or by regrowth of plants surviving in the slide mass or from the roots whose tops were sheared off. Concurrently, at the base of the cliff where slide debris piles up, the debris is itself rapidly recolonized. The beach surrounding the slide debris, where present, is also constantly changing and supports its own array of narrow ecological niches. To date, no scientific study has been done on the natural revegetation of slide scars and slide debris along the Calvert Cliffs. The wealth and diversity of wildlife made possible by the ever-changing face of the Calvert Cliffs is commonly overlooked. One documented example is the case of certain tiger beetles that lay their eggs in small holes made in bare cliff exposures (Figure 1.4E; discussed below).

The cliffs and their adjacent beach form a natural transition zone, called an ecotone, between what was once continuous forest to the west of the cliffs and the open water of the Chesapeake Bay to their east. This border region creates a sunlit "edge habitat" similar to what modern man creates when roads are built or fields are cleared but which in nature was very rare until European settlement. The sunlit aspect of this edge habitat must have supported thick vegetation, accounting for John Smith's 1608 (1986, vol.2:165) observation that the woods he saw from the water were "extreame thicke." At that time and for the next half century, when large trees collapsed onto the beach because of slides, their presence made the shoreline remain wild and impassable. Even two centuries later, access to the beach below the cliffs must have been arduous without a small boat except where plantation owners had built farm roads down to landings or piers.

In the modern world, most subdivisions along the Calvert Cliffs remove or trim fallen trees to make their beaches passable. There are no professional botanists among the authors of this paper, but the senior author notes that flora growing on the cliffs near Scientists Cliffs and on the debris cones sloughed off the cliffs commonly include many native species that are mostly fast growing and shade intolerant, such as black locust (the most common), bayberry, sycamore, black willow, slippery elm, tulip poplar, black cherry, and others. Oaks, hickories, and conifers, all characteristic of the forest habitats above and behind the cliffs, are rare in this environment.

Many alien species (mostly invasive) also easily establish themselves on the cliffs or, in some cases, were deliberately planted to try to help slow cliff erosion. These species, mostly of East Asian origin, include kudzu, Oriental bittersweet, ailanthus (tree of heaven), weeping willow, autumn olive, Japanese honeysuckle, mimosa, multiflora rose, English ivy, and various grasses. A native species of equisetum (horsetail rush), cattail (*Typha* spp.), and *Phragmites* (possibly including the native American variety), as well as various types of moss, successfully colonize the very moist environments—even tiny microswamps—perched on slide debris or on ledges formed on the top surface of impervious Plum Point Member strata. European coltsfoot, generally absent from the acidic soils of the Coastal Plain, exploits the Miocene shell beds and shelly slide debris because they offer a geologically limed neutral or even alkaline pH.

A different and less diverse flora inhabits the sandy beaches above normal high tide. The most common natives of this environment are the brackish-tolerant orach (also called orache) and sea rocket, although invasive Japanese knotgrass has also become established locally on the back beaches. Older and higher beaches, inundated only during rare storm surges, occur at only a few places along the Calvert Cliffs shoreline. Examples include the older spit beaches at Flag Ponds and Cove Point and the barrier beach that separates the Chesapeake Bay from the salt marsh of Parkers Creek. Common floral inhabitants of this habitat, mostly native, include loblolly and Virginia pine (especially at Flag Ponds), persimmon, eastern "red cedar" (actually a juniper), greenbrier, bayberry, prickly pear cactus (*Opuntia* spp.), and, of course, poison ivy.

Chesapeake waves periodically wash ashore abundant dead or dying fishes, crabs, driftwood, subaquatic vegetation, and other organic debris that quickly attracts a food chain of consumers. Before European settlement, black bears and wolves such as those seen by John Smith in 1608 were surely common diners on this bountiful food supply. Today, the bears and wolves are gone, and the largest remaining consumers are primarily birds and raccoons. Bald eagles and ospreys scout for fish by routinely riding along updrafts created by air moving over the Calvert Cliffs, whereas great blue herons stand patiently below in shallow waters, waiting for unwary prey. Turkey vultures and black vultures help to clean up what the more active predators leave behind. The cliffs are also important to wildlife in other ways. Here and there, rough-winged swallows and belted kingfishers peck nesting cavities into the cliffs. In spring, cow-nosed rays mate close to shore and scour the shallow sandy bay floor for mollusks, and horseshoe crabs come ashore below the cliffs to spawn. In summer and early fall, vast schools of menhaden hug the shoreline to evade their finny predators. Some of the human efforts to reduce shoreline and cliff erosion, notably the emplacement of groins, have provided otherwise rare hard substrates for sessile biota such as algae, barnacles, and blue mussels, whereas crabs find safe hideouts among the nonnative rocks. Natural hard substrates along the beaches bordering the Calvert Cliffs are relatively rare but include driftwood, large fossil pecten shells and vertebrate bones, and blocks of iron oxide–cemented sandstone, derived largely from post-Miocene fluvial deposits topping the cliffs. It is a fascinating fact that beachcombers can find 13 million-year-old pecten shells from the Choptank Formation that are encrusted with both Miocene and modern barnacles!

The waters immediately offshore of the Calvert Cliffs have been (and often still are) an important food source for humans. Commercial fishing, formerly important, has mostly passed into history, although a pound net fishery still survives locally off parts of the southern Calvert Cliffs. Until modern times, oyster beds existed along much of the Calvert Cliffs shoreline. They and the oyster boats (called bugeyes) that dredged for them are gone now, victims of overfishing and two oyster diseases. Crabs are still present, however, and crab pots are still emplaced every summer and fall in long, parallel lines offshore from the Calvert Cliffs.

Two tiny beetles—species of the carnivorous genus *Cicindela*—have in recent years emerged, by their rarity, as the best-known biota inhabiting the cliff environment (e.g., Vogler et al., 1993; C. Barry Knisley, Randolph-Macon College, "Studies of Two Rare Tiger Beetles (*Cicindela puritana and C.d. dorsalis*) in Maryland, 2010," unpublished). *Cicindela puritana*, the Puritan tiger beetle (Figure 1.4E), requires eroding sandy cliffs for its reproduction. This beetle was first scientifically collected in Maryland near Chesapeake Beach in 1911. The other species, *Cicindela dorsalis dorsalis*, the Northeastern Beach tiger beetle, requires an undisturbed sandy beach for reproduction. Along the Calvert Cliffs, this beetle was first collected at Flag Ponds and Kenwood Beach in the 1950s (Knisley, personal communication, 2012). In the mid-1980s, Knisley began to study these beetles along the cliffs and at a few other sites where they exist. Sampling along transects, he began to monitor population densities along the cliffs, first in 1986 and then annually starting in 1988. Having established their rarity, Knisley had them successfully added to the federal list of threatened species in 1990. This designation has put legal constraints on human cliff-edge and beach modifications, particularly those reducing cliff erosion. This restriction has become a problem for about half of the 234 houses located within 30.5 m (100 ft) of the cliff edge that were discussed above because as of 2007 Puritan tiger beetle populations had been discovered at the base of the cliff below those houses. This situation has not served to make cliff-edge property owners friends of Puritan tiger beetles, but paleontologists are happy that these beetles help to keep at least portions of the cliffs in their natural eroding state. Efforts at the preservation of these beetles do not seem to be going well, however, because Knisley's annual beetle counts show a long-term decline in both species, especially in *C. d. dorsalis*. Some of the sites along the cliffs that supported beetle populations during the late 1980s and early 1990s no longer do.

THE FUTURE OF THE CALVERT CLIFFS

The history of previous predictions about the future of the Calvert Cliffs shows that most of these predictions have been far from what has actually happened. However, because the future of the Calvert Cliffs is tied to the future of RSL rise, to ongoing efforts to restore the water quality and ecosystems of the Chesapeake Bay, and most particularly to the efforts of cliff-top landowners to armor the cliff shoreline against erosion, we can hazard some fairly conservative and well-justified predictions. First, residential and other development along the Calvert Cliffs has slowed drastically since the 1980s, in large part due to environmental concerns that shoreline housing and other development on land near the Chesapeake Bay have a disproportionately negative effect on Chesapeake water quality due to resultant sediment, nutrient, and other runoff.

Nowhere is the conflict between Calvert Cliffs shoreline development and protecting the Bay better illustrated than in Scientists Cliffs in the Maryland Critical Area about midway along the cliffs. As of this publication, 287 houses plus buildable lots currently exist on about 113 ha (280 acre)—three fewer, due to imminent or actual loss of houses to cliff erosion, than cited in Scientists' Cliffs History Book Committee (2010). If today these 113 ha were still farmland or forestland, only 14 buildable lots would be allowed because of the Critical Areas legislation enacted by Maryland in 1984 and adopted by Calvert County in 1989. The legislation reduced building density, absent wastewater treatment plants, for land within 305 m (1,000 ft) of tidewater to improve water quality in the Chesapeake and its connected estuaries. In addition, Calvert County now requires setbacks of three times the cliff height for new cliff-side houses other than those in grandfathered subdivisions like Scientists Cliffs.

According to Boon et al. (2010), the U.S. Army Corps of Engineers and National Research Council estimate that RSL in the Chesapeake Bay region will be about 50 to 150 cm higher than today by the early twenty-second century. This value is based on an estimated RSL rise of 5 to 15 mm/yr, which will be considerably higher than the 3.4 mm/yr rate that prevailed during the last century. This much higher RSL rise will mean increased shoreline erosion rates, particularly along unprotected segments of the Calvert Cliffs, which lie across the Chesapeake Bay from the low-lying salt marshes of Dorchester County. These marshes, already rapidly eroding today, will almost certainly be lost to future sea level rise. The loss of these marshlands will increase the fetch of easterly storm winds, and these will create wave energies that are higher on average than today and will attack the cliffs more strongly than today. The only countervailing factor that can be expected is that a warming climate and warmer winters probably will reduce the effects of freeze–thaw cycles on cliff erosion during the winter months.

Because the formations, members, and beds differ in their resistance to wave erosion, future sea level rise will change the rate and character of erosion at any place over decades and centuries. For example, at RSL rise of 3–6 mm/yr, the 25-cm-thick Parkers Creek Bone Bed (bed 12) will take only 83–42 years, respectively, to pass through sea level. Active wave erosion of this sandy layer is the primary reason for the rapid cliff retreat and fossil release between Scientists Cliffs and Parkers Creek, where the cliffs are allowed to erode naturally. In the adjacent northern Scientists Cliffs, cohesive bed 13 retards cliff erosion, while the cliffs just north of Parkers Creek are protected at sea level by cohesive bed 11. The gentle, apparent southward dip (around 1:1000) of Miocene strata exposed along the middle and northern cliffs (Kidwell, 1997) indicates that an intersection between the stratigraphy and sea level migrates north at 3–6 m/yr. We can thus predict that by the twenty-second century, rapid cliff erosion and fossil release will be shifting north of Parkers Creek as rising sea levels bring bed 12 within reach of Chesapeake waves, while the cliff south of this creek will then be naturally armored by bed 13. In the same way, the Choptank–Calvert boundary will migrate north along the cliffs, increasing wave erosion where the Choptank Formation will also likely be exposed.

An increase in future rates of cliff erosion along unprotected parts of the Calvert Cliffs probably will mean increased rates of fossil exposure and continuing favorable habitats for the Puritan tiger beetle *Cicindela puritana*. At the same time, however, the increasing value of shoreline real estate will probably motivate ever more aggressive and expensive engineering efforts on the part of landowners to arrest or slow shoreline erosion, using methods such as boulder or gabion-type revetments, reef balls, offshore T-shaped groins, bulkheads, and even cliff face armoring. Over long periods of time, this alternation of armored and naturally eroding cliffs will turn today's relatively straight coastline of the Calvert Cliffs into a strongly crenulated pattern of projecting armored segments and indented unprotected segments. Cliff erosion along the unprotected segments will eventually produce arcuate coves that will have wider beaches and reduced cliff erosion. At the same time, abandonment and demolition of threatened cliff-edge structures (which began in 2014) might eventually return some strips of cliff-front terrane back into their predevelopment natural state.

The Calvert Cliffs constitute one of the greatest natural assets of Calvert County and southern Maryland. The fossils and sediments exposed in the eroding Calvert Cliffs are silent witnesses to how the environment and its ecological response have changed during the course of approximately ten million years (ca. 18–8 Ma). This ten-million-year-long history "book" likely has pages or even a chapter or two missing (as recorded by disconformities—e.g., Kidwell, 1997) and lacks death-assemblage "snapshots" (e.g., Tucker et al., 2014). The knowledge gained from more than a century of studies of the paleoenvironmental information recorded in the Miocene strata of the Calvert Cliffs adds to knowledge obtained from geological deposits of other places and times. Taken together, these studies will lead humankind to a better understanding of how and why the Earth's surface environment and the life it supports have changed over "deep time."

Apart from its Middle Miocene paleoenvironmental archive, the Calvert Cliffs and adjacent beaches as they exist now present a natural laboratory for study of littoral and mass-wasting processes associated with dynamic shoreline changes forced by rising sea levels. Although the Calvert Cliffs will no doubt continue to inform future generations of earth scientists, so too will they generate controversy as society wrestles with whether and how much the cliffs should be fortified against the natural processes of erosion. The result of this struggle will greatly affect the fate of the Calvert Cliffs in coming years.

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NOTES

1. The *Evening Star* newspaper published "Dream Road Realized for Maryland's Western Shore" on 26 September 1963.
2. A new bridge across the Chesapeake Bay running from Lusby (Cove Point) to Taylor's Island (6.3 miles) as proposed by Louis Goldstein (actual proposal not seen) was formerly studied by contract from State Roads Commission in 1964. During 1985–1986 local papers report Goldstein again promotes such a bridge, but Calvert Board of County Commissioners and other politicians including Thomas Rymer oppose the plan, and the State Highway Commission decided that the bridge was not feasible at that time. In 2003, then Governor Robert Ehrlich appointed a local task force that included Maryland state delegates Sue Kullen and Tony O'Donnell, who both opposed the bridge, as reported in *Calvert Recorder*, 27 May 2005.
3. The Mid-Atlantic Power Pathway (MAPP) proposal was formally presented to the Calvert Board of County Commissioners (BOCC) on 16 October 2010. It was opposed by the BOCC majority and others. On 27 August 2012, PEPCO Holdings International was notified that Pennsylvania–New Jersey–Maryland Interconnections cancelled the MAPP project.

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2

The Cartilaginous Fishes (Chimaeras, Sharks, and Rays) of Calvert Cliffs, Maryland, USA

Bretton W. Kent

ABSTRACT. The Miocene sediments of Calvert Cliffs contain a remarkable fauna of cartilaginous fishes, with a total of 54 species. Of these, there are 3 species of chimaeras (ratfishes), and the remaining 50 are elasmobranchs (39 species of sharks and 12 species of rays). This number of species is slightly larger than the Holocene chondrichthyan fauna of the Middle Atlantic states of 46 species (28 sharks and 18 rays). The sharks of Calvert Cliffs are particularly diverse and contain two complex assemblages, both of which had their evolutionary roots in the Paleogene. One assemblage consists of the newly emerged, largely mesotrophic carcharhiniforms spreading from the tropics into more temperate, middle-latitude habitats of the northwestern Atlantic. The other assemblage represents an essentially simultaneous diversification of gigantic, macrotrophic species, principally among the lamniforms. Included within this assemblage is a previously unnamed giant thresher shark (Lamniformes, Alopiidae) with serrated teeth. Taken as a whole, the Calvert Cliffs chondrichthyan fauna is richer in large, free-ranging macrophagous sharks and large, neritic rays than the Holocene fauna of the Middle Atlantic states.

INTRODUCTION

Shark and ray teeth are perhaps the signature fossils collected along Calvert Cliffs, drawing thousands of collectors to the fossil-strewn beaches of the western shore of the Chesapeake Bay each year. Isolated teeth are extremely abundant and can range in size from not much larger than a grain of sand to that of a man's hand. Color is likewise varied, from light ruddy or grayish browns to nearly black. Their popularity has led to a number of publications documenting the diversity of Calvert Cliff chondrichthyans. The oldest was published by the Maryland Geological Survey on the fossils of the Maryland

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Miocene (Eastman, 1904). Later works included Leriche (1942), McLennan (1971), Ashby (1986), Kent (1994), Müller (1999), Vokes et al. (2000), and Visaggi and Godfrey (2010).

Historical Context

Elasmobranchs have a long, complex evolutionary history (Compagno, 1990b; Maisey et al., 2004; Wilga et al., 2007). Following the loss of a number of elasmobranch genera at the end of the Cretaceous, elasmobranchs reradiated during the early Paleocene (Danian) and attained a high diversity by the Eocene, which was correlated with elevated global temperatures. Elasmobranch diversity then declined during the late Paleocene (Guinot et al., 2012), coinciding with a prolonged period of severely depressed global temperatures in the middle Oligocene. During the late Oligocene and early Miocene changes in oxygen isotope readings are consistent with rapidly increasing global temperatures. Simultaneously, global CO_2 levels increase until they are comparable to those of the Holocene (Zachos et al., 2001; Thomas, 2008; McGowran et al., 2009; Potter and Szatmari, 2009). The sediments of Calvert Cliffs were deposited during this period of increasing temperature and represent the most recent period of evolution in elasmobranch communities (Guinot et al., 2012). The end of the Neogene began with an episode of global cooling 3.6–2.0 MYA in the Pliocene (McGowran et al., 2009) and ended with a major turnover in marine biotas 2–1 MYA (Chapman, 2000; Jackson and Johnson, 2000).

During the Neogene chondrichthyan faunas underwent two fundamental changes, driven by morphological diversification in the elasmobranchs. The first of these is a modernization of neritic and pelagic elasmobranch faunas. Prior to the Neogene diversification of sharks, these faunas are dominated by

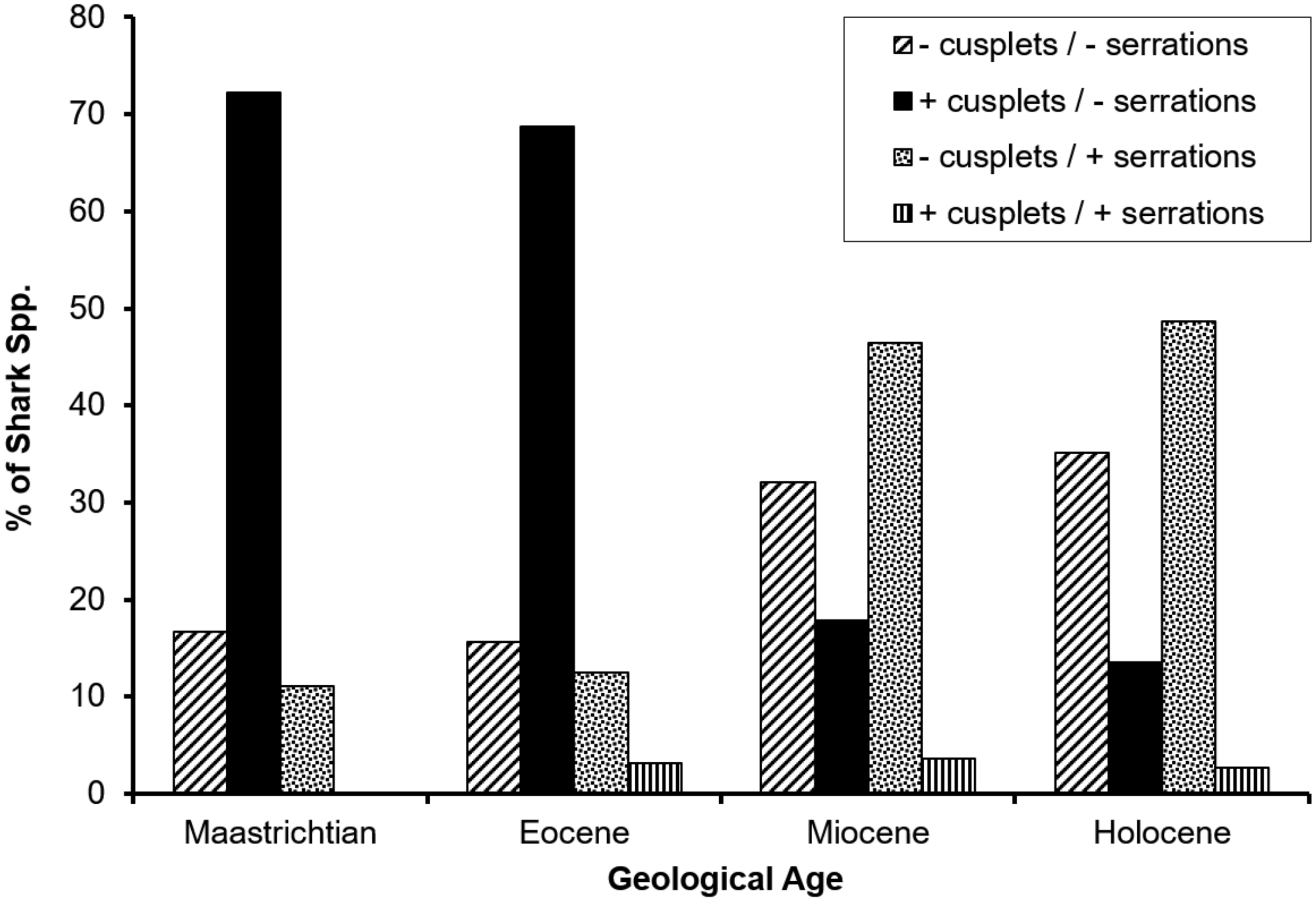


FIGURE 2.1. Temporal changes in tooth morphology from the Late Cretaceous through the Holocene of the Mid-Atlantic states of the eastern United States based on the presence or absence of cusplets and serrations. Data were compiled from Cappetta (1987), Kruckow and Thies (1990), Kent (1994), Müller (1999) and from unpublished data collected by Meredith Phillips (Master of Chemical and Life Sciences Program, University of Maryland, College Park).

sharks with tearing-type dentitions consisting of teeth with tall, slender crowns and accessory cusplets. Teeth of this morphology are adapted for grasping and restraining small, active prey (Cappetta, 1987; Kent, 1994; Williams, 2001). By the late Oligocene and early Miocene shark faunas have a more complex mixture of tooth morphologies comparable to that of the Holocene (Figure 2.1). This change is partially correlated with a fundamental shift from faunas dominated by lamniforms to one dominated by carcharhiniforms (Leriche, 1942; Maisey, 1984; Purdy, 1998b; Visaggi and Godfrey, 2010). Diversification in the carcharhiniforms was particularly pronounced in the carcharhinids, a family with a number of medium to large sharks that rose to prominence in tropical littoral habitats. The carcharhinids first appeared in the early Eocene and diversified during the explosive adaptive radiation of marine invertebrates and teleosts during the Paleogene (Musick et al., 2004; Alroy et al., 2008; Santini et al., 2009; Friedman, 2010; Vermeij, 2011; Sorenson et al., 2014). Many carcharhinids have a cutting-clutching-type dentition, with serrated, bladelike teeth in the upper jaw and slender, erect teeth in the lower jaw. Such dentitions are better at gouging chunks of flesh from prey and are more versatile, allowing sharks to handle a broader range of prey types and sizes (Cappetta, 1987; Kent, 1994; Williams, 2001). Others, such as the tiger sharks (*Galeocerdo*) evolved specialized cutting dentitions with acutely notched distal margins of the crowns that are capable of efficiently handling many different prey types (Motta, 2004). Carcharhinid teeth also represent a shift in the biomechanical properties of the teeth from the taller, narrower teeth of lamniforms that functioned like cantilevered beams in both puncture and draw movements to lower, wider teeth of many carcharhiniforms with notches in the cutting edges that concentrated forces on prey tissues during lateral head shaking (Whitenack et al., 2011).

By the early Neogene the carcharhinids had become increasingly diverse and numerically abundant, although the lamniforms maintained a substantial presence, particularly among the largest species (Purdy et al., 2001; Musick et al., 2004; Visaggi and Godfrey, 2010). The shift toward a carcharhiniform-dominated fauna continued well after the Neogene, with the blue shark, *Prionace glauca* (carcharhiniform), eventually replacing the shortfin mako, *Isurus oxyrinchus* (lamniform), as the most abundant open-ocean shark within only the last few thousand years (Litvinov, 2007).

The second revolution in Neogene shark faunas was a burst of gigantism among large, macrophagous sharks. In this context, gigantism and giant species refer to the evolution of the largest species in a clade (McClain et al., 2015; Vermeij, 2016; Ferrón et al., 2017) and are not without precedent in chondrichthyan faunas. Similar bouts of gigantism have previously occurred among the eugeneodontid "sharks" (*Edestus, Helicoprion, Parahelicoprion*) in the Permian (Merino-Rodo and Janvier, 1986; Grogan and Lund, 2004; Mutter and Neuman, 2008; Lebedev, 2009; Tapanila et al., 2013) and the lamniform sharks in the Cretaceous (*Cardabiodon, Cretolamna, Cretoxyrhina, Leptostyrax, Squalicorax*; Shimada, 1997, 2007; Siverson, 1999; Rothschild et al., 2005; Siverson and Lindgren, 2005; Cappetta, 2012; Frederickson et al., 2015) and the Paleogene (*Carcharocles, Jaekelotodus, Macrorhizodus, Otodus, Palaeocarcharodon*; Renz, 2002; Cappetta, 2012; Shimada et al., 2016). Gigantism in Neogene macrophagous sharks differs from the previous ones by the independent evolution of large body size in a number of genera belonging to distantly related orders, including the hexanchiforms (*Hexanchus*), lamniforms (*Alopias, Carcharocles, Carcharodon, Isurus, Megalolamna, Parotodus*), and carcharhiniforms (*Galeocerdo, Hemipristis*; Renz, 2002; Gallagher, 2006; Mutter and Neuman, 2008; Lebedev, 2009; Cappetta, 2012; Shimada et al., 2016). Neogene elasmobranch gigantism was also characterized by the evolution of the largest known macrophagous shark, *Carcharocles megalodon*. As with the diversification of the carcharhiniforms, gigantism in Neogene sharks had its origins within the Paleogene, when all of these genera of large sharks first appeared.

Gigantism is typically correlated with elevated levels of benthic and planktonic diversity (Pyenson and Vermeij, 2016; Vermeij, 2016; Slater et al., 2017). This pattern appears to be the driving force for the Neogene giant sharks as well, where gigantism is correlated with a corresponding diversification of large prey (i.e., cetaceans; pinnipeds; sirenians; scombrid, xiphiid, and istiophorid teleosts; and lamniform, carcharhinid, and myliobatiform elasmobranchs; Domning, 1978; A. P. Martin, 1995; Fierstine, 1998; Purdy et al., 2001; Walsh and Naish, 2002; Musick et al., 2004; Ehret, 2010; Boessenecker, 2011, 2013; Cappetta, 2012; Gottfried et al., 2012; Maisey, 2012; Santini and Soreson, 2013; Sorenson et al., 2014; Aguirre-Fernández et al., 2016; Valenzuela-Toro et al., 2016). However, much of this proliferation of giant sharks appears to be due to two specific groups of large prey, the advanced cetaceans and pinnipeds. Both of these groups radiated and diversified from the Oligocene through the early Pliocene in middle latitudes. Beginning in the late Pliocene, diversity in both of these groups shifted to higher latitudes (Deméré et al., 2003; Arnason et al., 2006; Adnet and Martin, 2007; Marx and Uhen, 2010; Klimley, 2013:38; Kelley and Pyenson, 2015; Collareta et al., 2017a). The giant sharks of the Neogene were principally inhabitants of temperate oceans and of pelagic, rather than benthic, ecomorphotypes. Fast, pelagic sharks must swim continuously to ventilate the gills and, to accommodate these demands, have metabolic rates 5 to 10 times higher than those of comparable benthic sharks. The colder, largely oligotrophic polar waters would make the fast, pelagic lifestyle energetically unsustainable and prevent these sharks from expanding their ranges into higher latitudes (Priede et al., 2006; Seibel and Drazen, 2007; Aronson et al., 2007). Cold temperatures certainly do not preclude the presence of all large sharks since the sleeper sharks (*Somniosus*) are quite successful in polar seas. Sleeper sharks are at least as large as extant great white sharks (*Carcharodon carcharias*, maximum length of about 6 m; Castro, 2010), with the largest of the species, the Greenland shark (*S. microcephalus*), reaching at least 6.4 m and perhaps as much as 7.3 m (Compagno et al., 2005). But unlike *C. carcharias* and other fast, pelagic sharks, sleeper sharks are epibenthic and exceptionally sluggish, with maximum swimming speeds of about 0.7 m/s (Watanabe et al., 2012).

The inability of the fast, pelagic Neogene giant sharks to follow the geographic shift of cetaceans and pinnipeds toward the poles reduced the availability of suitable prey and was likely associated with their eventual decline and extinction (Adnet and Martin, 2007; Pimiento et al., 2016; Collareta et al., 2017a). This scenario is supported by research on extant *C. carcharias* along the coast of Argentina. White sharks were abundant during the Pleistocene and Holocene in the temperate marine waters of the southwestern Atlantic but are rare today, a change attributed to extensive harvesting of pinnipeds by humans in these waters in the nineteenth and twentieth centuries. Pinnipeds are still abundant farther south in Patagonia, but these waters are too cold to support *C. carcharias*, which is limited to temperatures of 15°C–23°C (Cione and Barla, 2008). This thermal limit is consistent with the known contractile properties of mesothermic shark aerobic muscles (e.g., the shortfin mako, *Isurus oxyrinchus*), which become less efficient below 15°C–16°C than the muscles of ectothermic sharks (Donley et al., 2007). But this reduced efficiency of muscles in mesothermic sharks does not prevent them from brief excursions into colder water (Bonfil et al., 2005; Nasby-Lucas et al., 2007; Weng et al., 2007; Domeier and Nasby-Lucas, 2008; Johnson et al., 2009; Block et al., 2011; Jewell et al., 2013; Hoyos-Padilla et al., 2016; McAuley et al., 2017). These studies have helped distinguish between resident and transient sharks that exhibit very different behaviors. Resident sharks engage in behaviors that are associated with active foraging, including relatively slow, area-restricted swimming and repeated, brief vertical dives. Conversely, transient sharks exhibit relatively rapid, directed swimming and make only infrequent changes in depth. The differences between these behaviors are important because resident sharks will have a significant impact on local prey communities, whereas transients will not. For example, detailed analysis of telemetry data on *C. carcharias* in the northwest Pacific (Block et al., 2011, figs. 3a, 4c) found that resident white sharks occur between 25°N and 35°N latitude. Records at higher latitudes were due to the occasional transient individual. Later studies (Jewell et al., 2013; Hoyos-Padilla et al., 2016; McAuley et al., 2017) have reached similar conclusions in other geographic regions, including Australia, Mexico, and South Africa.

Giant sharks also may have been precluded from higher latitudes by the evolution of the killer whales (Delphinidae; *Orcinus*) during the early Pliocene. The distribution of *Orcinus* extends farther into the colder waters near both poles than that of fast, macropelagic sharks. Further, they feed opportunistically on a variety of large prey, including cetaceans and pinnipeds, and can hunt cooperatively in social groups (Heyning and Dahlheim, 1988; Lindberg and Pyenson, 2006; Pimiento and Balk, 2015; Vermeij, 2016).

Unlike earlier, Mesozoic elasmobranch diversifications, the complex selachian faunas of the Neogene arose during a period of comparative stasis in higher elasmobranch taxa (Guinot et al., 2012). Instead, during the Neogene speciation and adaptive radiation occurred within genera that had already become established by the late Paleogene taxa (Guinot et al., 2012: fig. 3). Conversely, the end of the Neogene is characterized by the loss of relatively few, species-poor lamniform genera and the retention of species-rich carcharhiniform genera (A. P. Martin, 1995; Cappetta, 2012).

Relevance of Calvert Cliffs Chondrichthyans

The Calvert Cliffs fossil beds were deposited during the transition from the early, expansive phase of the Neogene diversification in the early Miocene (early Burdigalian) to the more established chondrichthyan faunas of the middle and late Miocene (Langhian–early Tortonian). During this period, the combination of gigantism and modernization produced a complex chondrichthyan fauna that clearly foreshadowed the modern fauna while simultaneously containing a number of unique elements. The roughly 10-million-year (MY) interval encompassed by the Calvert Cliffs fossil beds is eminently suited to examining a number of unresolved issues related to the Neogene chondrichthyans, including the mechanisms for the evolution of large size in sharks, trophic interactions in complex faunas, and speciation and adaptive radiations in different taxa.

Evolution of Elasmobranch Gigantism

The evolution of gigantism in a diverse range of elasmobranchs in the Neogene is remarkable for both the size of the largest species and the diversity of genera involved but also raises a number of essential issues. The most obvious is that the evolution of large body size requires fundamental changes in scaling relationships and developmental pathways. Exactly how these changes came about has never been fully documented.

In organisms, the relationship between size and functionality is nonlinear, producing a fundamental trade-off between shape and function. So to maintain function as size increases, shape must change, whereas to maintain shape, function must change (Schmidt-Nielsen, 1984; Koehl, 2000). This scaling of shape in most biological systems is fundamentally limited by the ability to deliver nutrients to, and remove wastes from, metabolically active tissues (Banavar et al., 2002) using fractal circulatory systems in large organisms (West et al., 1997, 2003; Brown et al., 2005). These vascularization networks arise by iterative branching, with the number of capillaries in the circulatory system increasing as the three-quarter power of mass. With extinct sharks we are limited almost exclusively to teeth, so the evolution of tooth vascularization at very large sizes is an important consideration. Following this circulatory scaling relationship with body mass, the tooth of a hypothetical descendant species that was 4 times taller than those of its ancestral species will require almost 23 times as many capillaries as those of a smaller-toothed ancestor. Such a dramatic increase in the complexity of the capillary beds will require a substantial elaboration of tooth vascularization beyond the comparative simplicity of the ancestral species. Further, different lineages of sharks would be expected to independently solve the problem of large tooth size by evolving unique patterns of vascularization, which are most readily apparent as the distribution of nutrient foramina on the root surface of a tooth. At present, the complex interplay of scaling issues related to gigantism in the various taxa of giant Neogene sharks is little studied and poorly understood. The one study that has examined at least some aspects of these scaling issues found that *Carcharodon* and *Carcharocles* evolved fundamentally distinct ontogenetic solutions to the problems of larger tooth sizes (Nyberg et al., 2006: figs. 6,7).

Trophic Interactions

Holocene shark communities lack the diversity of giant species present in Neogene paleocommunities and provide few insights into the question of how so many large shark species could be accommodated in the same area. Understanding the trophic interrelationships of Neogene giant sharks with each other and with the rapidly diversifying carcharhiniform sharks requires a fundamentally different approach. Several sources of information can be used to reconstruct feeding relationships, including (1) analogies with living species, (2) bite marks on prey species, and (3) associations of teeth with prey remains. All of these provide useful information, although each must be interpreted somewhat differently.

Tooth morphology analogies provide a means of directly comparing an extinct species with a living one (Siverson, 1992; Welton and Farish, 1993; Purdy et al., 2001), although there are two specific problems with such interpretations. First, the teeth will be similar, but not identical, in morphology, and even subtle differences can be important. The extant tiger shark (*Galeocerdo cuvier*) is a large, eurytrophic shark capable of eating an exceptional range of prey types (Compagno, 1984, 2002; Compagno and Niem, 1998). The tiger shark from Calvert Cliffs (*G. aduncus*) is so similar in morphology that Purdy et al. (2001) listed it as a junior synonym of *G. cuvier*. But it differs in two important respects; the teeth of *G. aduncus* are roughly half the size of those of *G. cuvier* and exhibit a higher degree of heterodonty than those of the living species. The difference is size would seem to be relatively inconsequential, except that the deflection force at the tip of the crown is proportional to the length of the crown raised to the fourth power (Koehl, 2000). Consequently, assuming geometric similarity, the teeth of the extant *G. cuvier* would have a deflection force 16 times greater than that of the extinct *G. aduncus*. This difference would have considerable consequences for diet choice in these two species. The more extensive heterodonty in *G. aduncus* further complicates any dietary reconstructions. Although many teeth in *G. aduncus* have broad crowns and resemble small versions of those of *G. cuvier*, other teeth are somewhat more delicate, with narrower crowns. Apical stress applied to food is inversely proportional to the radius of curvature of the coronal tip, so that narrow-crowned teeth will concentrate stress in a smaller area and more readily pierce compliant tissues than teeth with broader tips (Lucas, 1982; Evans and Sanson, 2003; Freeman and Lemen, 2007). Obvious differences exist in functional morphology between the broad and narrow tooth forms of *G. aduncus*, but how these ultimately affected prey selection remains unknown since the disposition of these teeth within the dentition (i.e., gradient monognathic heterodonty, dignathic heterodonty, or gynandric heterodonty) is unresolved.

Bite marks are reasonably common on fossil bones, usually taking the form of deep incisions or gouges on prey hard tissues (Deméré and Cerutti, 1982; Mapes and Hansen, 1984; Cigala-Fulgosi, 1990; Schwimmer et al., 1997; Bianucci et al., 2000, 2010; Neumann, 2000; Noriega et al., 2007; Cicimurri and Knight, 2009a; Kallal et al., 2010). Such marks can be difficult to assign to a specific species, although there are exceptions. Deméré and Cerutti (1982) were able to match the spacing of parallel grooves in the bite marks on a cetotheriid whale fossil with the serrations on the teeth of co-occurring *Carcharodon sulcidens* (junior synonym of *C. carcharias*). Bite marks produced by unserrated teeth are more difficult to assign to species, although with detailed analysis, plausible inferences are possible. Bianucci et al. (2010) examined smooth bite makes on a Pliocene cetacean. They artificially produced bite marks of *Carcharodon hastalis* (or *C. plicatilis*?) and *Isurus oxyrinchus* teeth but were unable to consistently distinguish between these two species. The size of the skeletal bite marks and their disposition in a dental arcade were more informative and were consistent with the larger *Carcharodon* species. In some rare cases, bite marks on softer materials can be definitively assigned to a shark species; Godfrey and Smith (2010) were able to match tooth marks on a crocodilian coprolite with the extinct tiger shark *Galeocerdo aduncus*. Govender (2015) examined bite marks on cetacean bone fragments and was able to distinguish bite marks produced by serrated teeth (*C. carcharias and Carcharocles megalodon*) and unserrated teeth (*Isurus* spp. and *C. hastalis*).

Teeth embedded within prey skeletal elements (usually bones) are more informative since the teeth can be more easily identified to species (Rothschild and Martin, 1993; Everhart et al., 1995; Schwimmer et al., 1997; Shimada, 1997; Shimada and Everhart, 2004; Shimada and Hooks, 2004; Rothschild et al., 2005; Cicimurri and Knight, 2009a; Ehret et al., 2009b). If the entire tooth is present, identification is comparatively simple. Unfortunately, during feeding and fossilization the tooth may fracture, leaving only the tip of the crown embedded within the bone. This fracturing complicates tooth identification but still is more definitive than identifications based on bite marks alone. In some rare cases, prey parts may be preserved in shark teeth. A particularly intriguing example (Figure 2.2A,B) is a *C. hastalis* tooth (CMM-V-3990) from Calvert Cliffs completely penetrated by a myliobatiform caudal spine. What is unusual about

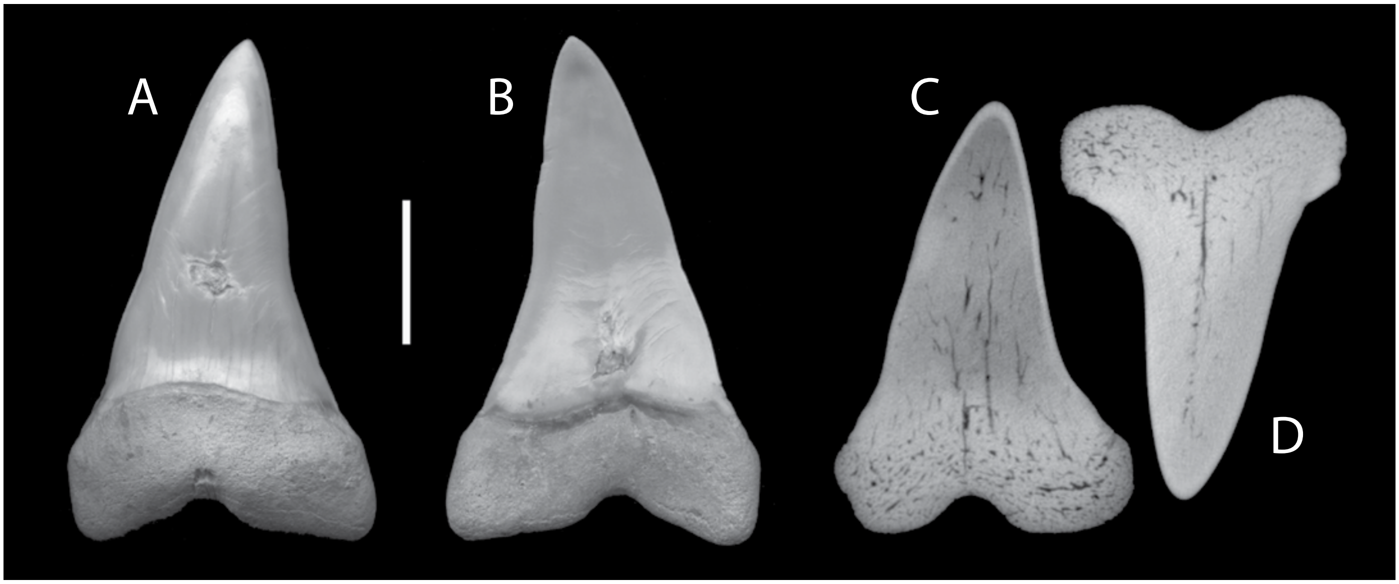


FIGURE 2.2. (A–C) *Carcharodon hastalis* left upper anterior tooth penetrated by a myliobatiform spine (CMM-V-3990; beds 3/4, Pamunkey River, Virginia; images provided by Stephen Godfrey; 1 cm scale bar). (A) Labial view. (B) Lingual view. (C) Single-image micro-CT scan of CMM-V-3990 tooth interior. (D) Single-image micro-CT scan of undamaged *C. hastalis* tooth. CT images courtesy of the University of Texas High-Resolution X-ray Computed Tomography facility.

this tooth is that the spine must have penetrated very early in the formation of this tooth, as the enameloid on both faces is thrown into folds around the spine. Further, a micro-computed tomography (micro-CT) scan (Figure 2.2C) shows no internal evidence of the spine within the osteodentin of the crown, although the medial vascular tubule normally present in this species (Figure 2.2D) has bifurcated around the original position of the spine. Presumably, prior to the final mineralization of the tooth, the material from the spine was resorbed and remodeled within the osteodentin, leaving only the remnants embedded in the enameloid of the labial and lingual faces and the modified vascularization pattern.

Associations of shark teeth with prey skeletons are also well documented in the paleontological literature (Cione and Medina, 1987; Repenning and Packard, 1990; Druckenmiller et al., 1993; Bigelow, 1994; Schwimmer et al., 1997; Shimada, 1997; Bianucci et al., 2000; Cicimurri and Knight, 2009a). The presumption is that these are teeth shed during feeding. In situations where the associated teeth are consistent with the species inferred from bite marks or embedded teeth (e.g., Cicimurri and Knight, 2009a) this interpretation is plausible. But in the absence of such corroborating evidence it is difficult to know whether the teeth were functionally associated with the skeleton or present by coincidence. Background data on the abundance and diversity of shark teeth in the same stratum as the skeleton could help such difficulties but are rarely available. A notable exception is a study on the Cretaceous lamniform *Squalicorax* (Schwimmer et al., 1997); *Squalicorax* teeth were uncommon components of the local shark fauna but became numerically dominant adjacent to vertebrate skeletal remains. Unfortunately, other factors, such as predators attracted to the swarm of scavengers around the carcass or the postmortem deposition of teeth by hydraulic sorting, could also produce a concentration of teeth near a skeleton.

The problem with all of these sources of biological evidence is that it is frequently difficult to distinguish between active predation and the scavenging of carcasses. Certainly, the presence of small shark teeth or bite marks with a large prey would preclude predation and be more consistent with scavenging. Large teeth and bite marks associated with a skeleton are more difficult to interpret but can be deduced with careful observations. Ehret et al. (2009b) interpreted a *Carcharodon* tooth embedded in a mysticete mandible as the result of scavenging, as this body region is normally avoided by extant white sharks during attacks on living cetaceans. More direct evidence is sometimes present where the bite is not immediately fatal and the prey survives long enough to physiologically respond to skeletal damage. Rothschild et al. (2005) were able to attribute shark bites in mosasaur caudal vertebrae to a failed attack by *Cretoxyrhina* because the bite marks and an embedded tooth tip are spatially associated with abscesses in the bone produced by an inflammatory response. Likewise, Kallal et al. (2010) attributed similar bone damage in a Pliocene cetacean to an attack by a lamniform shark.

Species Recognition and Identification

The diversification of the elasmobranchs, especially the carcharhiniforms, during the Neogene creates numerous difficulties in understanding speciation events and in identifying individual species. Biologists have an enormous advantage in this regard when studying extant species. Not only can they examine whole-body morphology, they can directly observe reproduction and feeding and more easily document geographic ranges. These observations produce species descriptions that are both comprehensive and detailed. Further, when there are doubts about species identity, molecular techniques can be used to separate closely related species. These techniques are particularly useful, as they allow researchers to define biological species on the basis of the degree of interbreeding that has occurred. Paleontologists must work with far less information, typically limited to morphological features. As a result, paleontologists work with morphologically defined species (i.e., morphospecies), rather than true biological ones.

The most rigorous interpretations of fossil chondrichthyans are based on articulated skeletons and dentitions (e.g., Shimada, 2007; Ehret et al., 2009a), as these provide evidence of the whole-body morphology. These specimens are exceptionally rare, as the tesserate cartilage that makes up the chondrichthyan skeleton is easily crushed and dissociated during fossilization (Maisey, 2012). Even under ideal conditions, these specimens are usually incomplete but can still provide useful information about hard tissues and allow more rigorous reconstructions of the missing soft tissues. They can also help correct misconceptions about higher taxonomic assignments of extinct species (Shimada, 2005; Shimada et al., 2009).

In the absence of intact skeletons and dentitions, whole-body reconstructions of fossil sharks and rays (Gottfried et al., 1996; Kent, 1999c; Shimada et al., 2010) are fraught with difficulties. Unfortunately, since the majority of extinct species are known only from isolated teeth, reconstructions must rely on analogies with extant species. Measurements on extant species can provide more rigorous evaluations of morphology that can, in turn, be used to predict the most likely morphology of extinct species. But relying too heavily on extant forms produces an intellectual "keyhole" through which we obtain a severely restricted view of the possible morphologies and lifestyles available to extinct forms (Bengtson, 1987, 2001) and constrains extinct animals to be generic versions of extant ones (Pagel, 1991). Further, this approach overlooks critical evolutionary innovations not evident in the extant analogs. As discussed above, this modern bias is particularly troublesome where extinct species are substantially larger than extant ones. Research on the Late Cretaceous shark *Cretoxyrhina mantelli* (Shimada, 1997) demonstrates the dangers of ignoring the admonition against relying too heavily on extant analogs. Earlier dentition reconstructions of this shark were based on analogies with the extant lamniform, *Lamna nasus* (Eastman, 1895; Welton and Farish, 1993). The teeth of *C. mantelli* are also substantially larger than those of *L. nasus* (2 versus 6 cm; Cappetta, 1987). The developmental problems of producing both these larger teeth and the sharks with larger bodies cannot be simply ignored and may require evolutionary innovations not present in the extant species.

The abundance of isolated teeth present in the unconsolidated sediments of Calvert Cliffs greatly simplifies collecting, so that huge samples can be obtained surprisingly quickly. The ease of collection means that the range of morphological variability within a species is easily documented, even for relatively rare species. But because the teeth are almost entirely collected as isolated specimens, this variability in form can be difficult to interpret in an unambiguous way.

Smith (1994:20–22) proposed a two-step process for critically evaluating and documenting fossils where sample sizes large enough for statistical analysis are available. The first step is to use a range of bivariate plots of morphological features to assess variability. By testing various morphological features against each other informative characters can be identified. When performed over a sufficiently large size range, these plots can also detect ontogenetic changes and sexual dimorphism. Smith's second step was to compare the values for this sample with other samples to assess the number of species present. This comparison establishes the degree of morphological overlap and provides objective criteria for documenting and interpreting morphospecies in the fossil record.

Figure 2.3 is a bivariate plot of data for teeth from three alopiids, the small-toothed *Alopias* cf. *A. vulpinus* and two giant species, *A. grandis* and an unnamed species with serrated cutting edges (see this chapter's Addendum) based on teeth housed in the Smithsonian Institution's National Museum of Natural History, the Calvert Marine Museum, and the author's reference collection at the University of Maryland at College Park. Figure 2.3A compares teeth of these three species with respect to tooth height and root width. Not unexpectedly, the teeth of the two giant species are noticeably larger than those of the small-toothed *A.* cf. *A. vulpinus*. There is no overlap between *A.* cf. *A. vulpinus* and the two giant species but extensive overlap between the two giant species. The height-width regression line for *A.* cf. *A. vulpinus* (dashed line), when extended to larger tooth sizes, demonstrates that the teeth of the giant *Alopias* species are consistently taller for a given tooth width than would be expected by simple allometric scaling. But extensively extrapolated data should always be viewed with some suspicion since even slight changes in the data for *A.* cf. *A. vulpinus* could produce a marked change in the regression line and interpretations about the tooth morphology in the giant species.

A more direct approach to compare the three species is to use derived metrics that have higher information content. Figure 2.3B compares teeth of these three species on the basis of relative elevation (i.e., the ratio of the tooth height to the root width) and relative coronal width (the ratio of the mid-crown width measured at the height of the inflection point on the distal cutting edge to the root width of the tooth). Both metrics are based on ratios, and size has been suppressed as a confounding

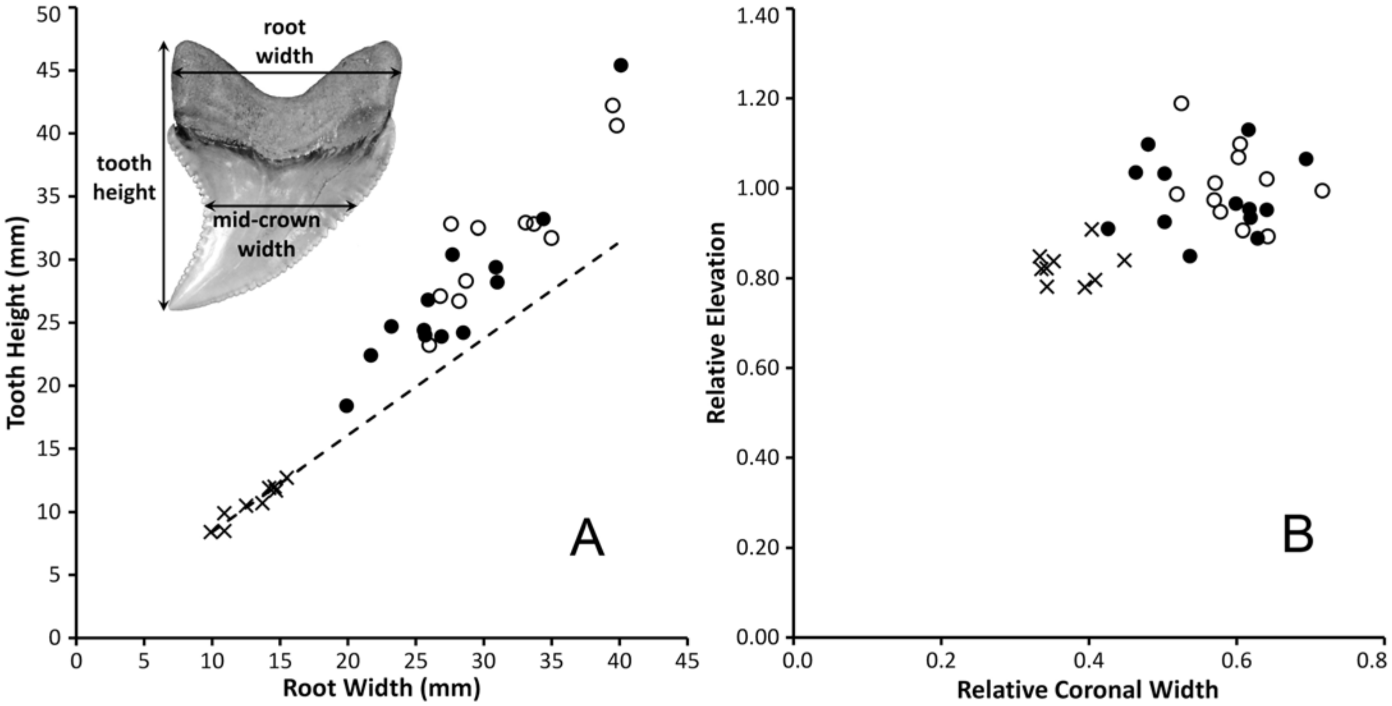


FIGURE 2.3. Bivariate plots of tooth morphology in Calvert Cliffs alopiids. A cross (×) = *Alopias* cf. *vulpinus*; solid circle (●) = *A. grandis*; open circle (○) = serrated *Alopias* (see this chapter's Addendum). (A) Tooth height versus root width. Reduced major axis regression (dashed line) extrapolated from *A.* cf. *vulpinus*; tooth height = 0.77(root width) + 0.76, $R^2 = 0.922$, $N = 9$. (B) Relative elevation versus relative coronal width; see text for details.

variable. Teeth of *A.* cf. *A. vulpinus* are morphologically very distinct from each of the giant species in both elevation (one-way analysis of variance [ANOVA] with pairwise Tukey honestly significant difference [HSD] tests; $F_{2,29} = 17.2$, $P < 0.0001$; HSD $P < 0.01$) and relative coronal width ($F_{2,29} = 33.3$, $P < 0.0001$; HSD $P < 0.01$), although differences are less pronounced than in Figure 2.3A. The teeth of the serrated species tend to be somewhat taller and more bladelike than those of *A. grandis*, although variability clouds for these two species broadly overlap, and neither relative elevation nor relative coronal width is statistically different between the two giant species (HSD $P > 0.05$).

This discussion of tooth morphology in *Alopias* is overly simplistic in several respects. The most obvious is that the teeth for the two giant species represent a substantial, but incomplete, subset of their size range, as no teeth from smaller individuals are included. Of particular importance are morphological comparisons between similarly sized teeth of *A.* cf. *A. vulpinus* and juveniles of the two giant species. A second complication is that alopiids have relatively mild heterodonty, and teeth from different positions in the jaws can be compared with little difficulty. Sharks with more extensive heterodonty have teeth with several different morphologies that must be analyzed separately. Finally, the alopiids are not particularly speciose compared to other families, such as the carcharhinids. So although bivariate plots can provide considerable clarity when only a few species are involved, the presence of numerous species with high morphological overlap is more troublesome.

Part of the difficulty in more diverse species complexes is that not all morphometric measurements are equally informative and it is not always obvious by visual inspection of teeth which metrics will be the most useful. To be practical, the bivariate plot technique relies on using a large number of morphometric measurements in order to determine which are most informative. Reinecke et al. (2005, 2011) have successfully employed this technique to rigorously test differences between closely related species of Oligocene and Miocene sharks. Unfortunately, simple measurements on teeth may not provide clear resolution in some cases, and more sophisticated metrics must be used to generate the bivariate plots (e.g., Naylor and Marcus, 1994; Adnet, 2006; Chandler et al., 2006; Nyberg et al., 2006; Shin, 2010; Whitenack and Gottfried, 2010).

Two closely related species are likely to share some similarities in morphology, so simply finding some specimens from different samples that appear to be nearly identical in form is not unexpected. The real problem is in determining the extent of morphological overlap. Extensive overlap would be indicative of a single species and would justify placing a fossil species and an extant species in synonymy. A reduced level of overlap would increase the likelihood that two species were present, and the application of the extant species name to the fossil species would be inappropriate. This distinction is essentially a statistical one (Hammer and Harper, 2006:8–19); what is the probability that a sample of fossil teeth and a sample of extant teeth are from the same species? Unfortunately, the application of extant names to fossil specimens typically has been based on a visual inspection of specimens to assess the degree of morphological overlap. This procedure is adequate only where the relevant characters are based on the presence or absence of a specific structure (e.g., the serrations of the previously unnamed giant *Alopias*). Where differences are based on magnitude, delineating species is far more difficult. In these cases, the most reliable method is to utilize morphometric procedures.

For much of the history of research on fossil elasmobranchs, species names have been erected on relatively meager evidence. The complex interactions of ontogenetic, sexual, and positional differences in morphology produced numerous situations where a single species was identified by multiple names. The problem is compounded by species being erected with a limited number of specimens, so that multiple names may have been erected for the same species; for example, Marsili et al. (2007) list seven junior synonyms for the specific name of *Parotodus benedenii*, a species with relatively mild heterodonty. This synonymy produced a confusing proliferation of species names and undoubtedly produced numerous examples of having too many species names for the number of species actually present. In reaction to this taxonomic nightmare, a recent trend in the taxonomy of Neogene fossil sharks has been to suppress most fossil specific names in favor of placing these in synonymy with extant species (e.g., Purdy et al., 2001; Ward and Bonavia, 2001; Marsili, 2007a,b). This practice is conservative and minimizes the perpetuation of unnecessary names. It also reduces a number of species names to junior synonyms and helps clarify the broad evolutionary framework for the extant sharks. This practice also produces a new set of problems since it implicitly assumes that Neogene sharks have exhibited evolutionary stasis. A rapidly growing body of evidence suggests that such stasis is unlikely and that numerous taxa have diversified during the Neogene and Quaternary: *Squatina* (two bursts of speciation 18–15 MYA and 3.5–2.9 MYA; Stelbrink et al., 2010), orectolobids (three bursts in the early late Miocene, late Miocene to early Pliocene, and late Pliocene to early Pleistocene; Corrigan and Beheregaray, 2009), *Mustelus* (Miocene; Boomer et al., 2012), *Carcharhinus* (23–9 MYA; A. P. Martin 1995), *Negaprion* (about 14 MYA; Schultz et al., 2008), sphyrnids (late Miocene to middle Pliocene; Lim et al., 2010), rajids (late Miocene to Pleistocene; Valsecchi et al., 2005; Pasolini et al., 2011), and *Potamotrygon* (relatively recent and ongoing; Toffoli et al., 2008).

When the last major reviews of Calvert Cliffs chondrichthyans (Kent, 1994; Müller, 1999) were published, the available research on fossil chondrichthyans was largely descriptive and qualitative. This information provided extensive and detailed documentation of stratigraphic and geographic ranges, as well as relevant diagnostic characters for distinguishing different taxa. But such research was inherently limited by problems of sorting through the immense clouds of variability to determine which tooth attributes are informative and which are not. Over the past two decades, newer technologies and methodologies have produced data that are more quantitative and rigorous on a broad range of fossil vertebrates, including chondrichthyans. When coupled with the large body of earlier descriptive work, these analytical tools have triggered an almost explosive growth in our understanding of the remarkable fossil record of chondrichthyans, including those of Calvert Cliffs.

The following represents the current state of our knowledge of the fossil cartilaginous fishes of Calvert Cliffs. This record is extensive, detailed, and part of an ongoing, wide-ranging effort by numerous individuals to more fully understand this dramatic period in chondrichthyan evolution.

Museum Abbreviations

CMM	Calvert Marine Museum, Solomons, Maryland, USA
NHMUK	Natural History Museum, London, UK
UMCP	author's reference collection at the University of Maryland, College Park, Maryland, USA
USNM	National Museum of Natural History (formerly U.S. National Museum), Smithsonian Institution, Washington, D.C., USA

Statistical Analysis

Statistical analyses were based on the recommendations in Sokal and Rohlf (1995) and Hammer and Harper (2006). Basic statistical calculations (*t*-test, analysis of variance, reduced major axis regression) were performed using the PAST (Palaeontological Statistics, version 3.01) statistical computation software (http://folk.uio.no/ohammer/past/). The Crawford-Howell modified t-test, an adaptation of that proposed by Sokal and Rohlf (1995:227–229) for comparing a single specimen with a sample, was computed using the downloadable Singlims_ES.exe calculator (http://homepages.abdn.ac.uk/j.crawford/pages/dept/psychom.htm; Crawford et al., 2010). Statistical results are expressed as exact, two-tailed probabilities, except as noted in the text.

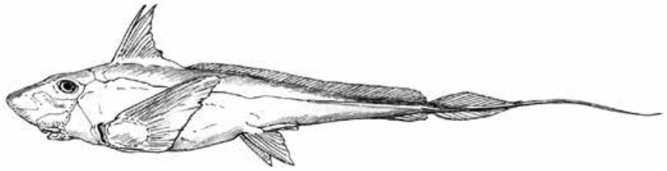
Taxonomy

Taxonomy follows that of Stahl (1999) for holocephalans and Cappetta (2012) for elasmobranchs, except where noted in the text.

SYSTEMATIC PALEONTOLOGY

SUBCLASS HOLOCEPHALI BONAPARTE, 1832

ORDER CHIMAERIFORMES OBRUCHEV, 1953



Ratfishes – Chimaeriformes

The chimaeroid fishes are an ancient group of cartilaginous fishes. Extant chimaeroids, or ratfishes, are found worldwide in deepwater marine habitats, although the group was more widespread on continental shelves during the Mesozoic and early Cenozoic (Averionov and Popov, 1995). The fossil record consists primarily of isolated dental plates, which occur in three pairs, with two pairs (vomerine and palatine) in the upper jaw and one pair (mandibular) in the lower jaw. Each plate is composed of acellular bone with pleromin-reinforced areas, referred to as tritors. Pleromin is a unique hard tissue found only in chimaeroids that strengthens the tritors, which are the functional surfaces for processing food (Lund et al., 1992). The pleromin in tritors can be either laminated (=tightly packed sheets of pleromin) or vascular (=less compact masses of pleromin). The number and distribution of tritors, along with their pleromin structure (laminated versus vascular) on different dental plates, are diagnostic for chimaeroid taxa. Terminology for identifying and describing tritors is based on Ward and Grande (1991), Patterson (1992), and Stahl (1999).

Unfortunately, isolated chimaeroid tooth plates can be difficult to correctly identify, as they can be quite variable. Extant species that have been examined in detail have been found to have a high level of intraspecific variation, including that between individuals and ontogenetic changes resulting from feeding-related wear (Stahl, 1999:15–16).

Dorsal spines and egg cases of chimaeroids are also occasionally collected but are difficult to assign to a specific species unless found in association with dental plates.

FAMILY CALLORHYNCHIDAE PATTERSON, 1965

Chimaeroids in the family Callorhynchidae from Calvert Cliffs are known only from isolated dental plates of two genera, *Edaphodon* and *Ischyodus*. The two genera can be separated by several characters, including the number and disposition of tritors and the presence or absence of a descending lamina. Unfortunately, these characters are somewhat variable, and additional variation during ontogeny, evolutionary changes over the history of these genera, and due to tritoral wear can complicate identifications of these two genera (Stahl, 1999:127).

Genus *Edaphodon* Buckland, 1838

Edaphodon cf. *E. sweeti* Chapman and Pritchard, 1907

FIGURE 2.4A,B

Synonymy follows Kemp (1991) and Stahl (1999).

DESCRIPTION. The description of *Edaphodon* in Calvert Cliffs is based on two well-preserved mandibular plates (CMM-V-1386 and USNM 546145). The plates are thick, robust, and anteroposteriorly elongated into a beak. The symphyseal surface is narrower adjacent to the beak and broadens distally. A laminated tritor is typically present on the beak of *Edaphodon* mandibular plates but is not present in either of the specimens examined. Three principle tritors are present, anterior and posterior outer tritors and a middle tritor. The middle tritor is divided longitudinally, a condition known to occur in this genus (Stahl, 1999:138). The sizes and shapes of the tritors of the two illustrated specimens are quite varied and likely result from differences in premortem wear; Figure 2.4A is largely intact and has little wear, whereas wear is much more extensive in Figure 2.4B.

DISCUSSION. *Edaphodon* fossils occur from the Cretaceous through Pliocene of Africa, Australia, Europe, and North America. They are particularly abundant during the Cretaceous and Paleogene, but by the Neogene only a few *Edaphodon* species have been described, including *E. antwerpiensis* Leriche, *E. mirabilis* Chapman and Cudmore, *E. pliocenicus* Carraroli, and *E. sweeti* Chapman and Pritchard (Stahl, 1999). On the basis of only a few specimens, any identification of Calvert Cliffs *Edaphodon* is tentative, but they appear to be closest to *E. sweeti* (Kemp, 1991: pl. 40C; Stahl, 1999: fig. 144B).

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Edaphodon* tooth plates are very rarely collected from Calvert Cliffs and are known only from the two specimens shown in Figure 2.4A,B. The only other records of *E. sweeti* are from the late Miocene to the early Pliocene of Australia (Kemp, 1994; Stahl, 1999).

Genus *Ischyodus* Egerton, 1843

Ischyodus sp.

FIGURE 2.4C

DESCRIPTION. The illustrated specimen is a robust plate with two oblong, closely spaced tritors. The plate, although fragmentary and worn, is consistent with the triangular palatine plate of the genus *Ischyodus*, with both the outer tritor and middle tritor present.

DISCUSSION. Many chimaeroid tooth fragments from Calvert Cliffs are much less complete than the mandibular plates in Figure 2.4A,B. The specimen in Figure 2.4C is more typical

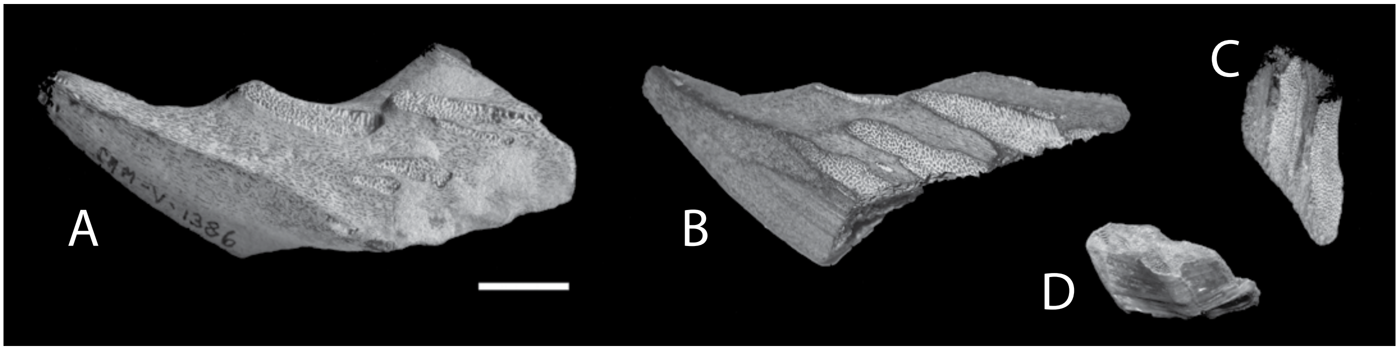


FIGURE 2.4. Chimaeroid tooth plates (1 cm scale bar). (A) *Edaphodon* cf. *sweeti* right mandibular plate; oral view (CMM-V-1386; Parkers Creek, Maryland). (B) *Edaphodon* cf. *sweeti* right mandibular plate; oral view (USNM 546145; Scientists Cliffs, Md.). (C) *Ischyodus* sp. right(?) palatine plate; oral view (CMM-V-1588; Scientists Cliffs, Md.). (D) *Chimaera* sp. indeterminate position; oral view (CMM-V-1385; Parkers Creek, Md.).

and can be difficult to identify to genus. This thick specimen is comparable with those of *Ischyodus* (e.g., Stahl, 1999: fig. 138, E2 and E3; Otero et al., 2012: fig. 3 V1). *Ischyodus* fossils are known from the Middle Jurassic through the Pliocene. Like *Edaphodon, Ischyodus* has reduced diversity by the Neogene, and only two species (*I. dolloi* Leriche and *I. mortoni* Chapman and Pritchard) are known (Stahl, 1999).

Stratigraphic and Geographic Ranges. Plates such as the one shown are only very rarely collected from Calvert Cliffs, and only the illustrated specimen was available for detailed study. Too few specimens are known to determine any distributional patterns.

FAMILY CHIMAERIDAE BONAPARTE, 1831

Genus *Chimaera* Linnaeus, 1758

Chimaera sp.

FIGURE 2.4D

Description. Plate fragments are thin and fragile. The occlusal surface is undulating with comparatively thick tritoral ridges alternating with thin intertritoral dentine. There is little wear on either the tritors or the intertritoral dentine. The latter has obvious incremental growth lines.

Discussion. The two tooth plate fragments tentatively assigned to the genus *Chimaera* are quite thin and fragile, compared to the very robust tooth plates of *Edaphodon* and *Ischyodus*. The growth lines, which are quite obvious on these fragments, have not been observed on either *Edaphodon* or *Ischyodus* from Calvert Cliffs. Their assignment to *Chimaera* is based on their general resemblance to this genus (e.g., Stahl, 1999: fig. 161B; Laurito Mora, 2008: fig. 1). The fragmentary nature of the available specimens precludes assigning them to a specific jaw position.

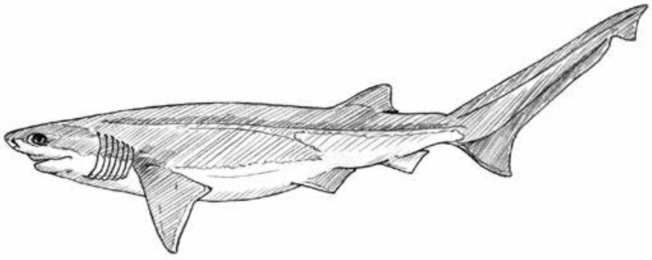
Stratigraphic and Geographic Ranges. Only two specimens are known for this species, although the illustrated fragment (Figure 2.4D) was found in situ (bed 14). The genus *Chimaera* is extant with seven species but does not presently occur in the Mid-Atlantic region. The diet consists of crustaceans, mollusks, and small teleosts and in at least one species changes with larger body sizes (Didier, 2002, 2004; Moura et al., 2005).

SUBCLASS ELASMOBRANCHII BONAPARTE, 1838

SUPERORDER SELACHIMORPHA NELSON, 1984

ORDER HEXANCHIFORMES DE BUEN, 1926

FAMILY HEXANCHIDAE GRAY, 1951



Cow Sharks – Hexanchidae

The hexanchids, or cow sharks, are generally considered to be relatively primitive sharks that have only a single, posteriorly positioned dorsal fin, an anal fin, six or seven pairs of gill slits, and weakly calcified vertebral centra. The dentition has very distinctive teeth and pronounced dignathic heterodonty. The subterminal mouth has large, comblike lower teeth with an acrocone and numerous accessory conules that become progressively reduced distally. The teeth of the upper jaw are smaller and exhibit monognathic heterodonty with substantial changes in morphology along the jaw (Cappetta, 1987, 2012). The distinctive teeth of hexanchids have relatively poor cutting ability compared to other sharks, such as carcharhinids, but have greater durability (Corn et al., 2016).

The identification of fossil hexanchids is complicated by extensive ontogenetic and individual variability (Kemp, 1978; Cione and Reguero, 1994; Herman et al., 1994a). A detailed morphometric analysis of fossil and Holocene *Hexanchus* anterolateral teeth (Adnet, 2006) has helped clarify ontogenetic and phylogenetic variation in this genus and provides a practical means of evaluating other hexanchids.

There are two hexanchid genera known from Calvert Cliffs, a seven-gilled cow shark (*Notorynchus*) and a six-gilled cow shark (*Hexanchus*).

Genus *Notorynchus* Ayres, 1855

Notorynchus primigenius (Agassiz, 1843)

FIGURE 2.5A–E

Synonymy follows Reinecke et al. (2011).

Description. The distinctive saw- or comblike lower anterolateral teeth (Figure 2.5A) are broader than high, with an acrocone and five or six distal conules of progressively smaller size. The acrocone is only slightly larger than the adjacent first distal conule and has recurved serrations basally on the mesial cutting edge. The root is rectilinear and compressed, with a weakly concave mesial margin. In profile, the root is wedge shaped, thickest at the coronal base, and tapering to a thin basal margin. Both the labial and lingual root faces are flat, but although the labial face is smooth, the lingual face typically has numerous, fine vertical grooves. Pathological lower anterolateral teeth are occasionally collected, and these teeth frequently have larger, more pronounced mesial serrations (Figure 2.5B).

Lower, medial teeth also have multiple conules but are nearly symmetrical (Figure 2.5C). The central conule is the largest on the tooth but is inclined laterally. Lateral to the largest conule there are three to five additional conules of decreasing size on each shoulder. The root is compressed, with a beveled profile and fine vertical grooves on the lingual face.

Upper teeth are more variable in morphology. Upper anterior teeth (Figure 2.5D) have a crown consisting of a single conule that is erect to weakly distally inclined. The root is robust and quadrate. In profile, the crown is lingually arched, and the lingual face of the root is steeply beveled. Upper anterolateral teeth (Figure 2.5E) retain the enlarged principal conule. Anterolateral row groups close to the anterior teeth have only a single distal conule, whereas more posteriorly positioned teeth become progressively broader with two to five distal conules. The mesial cutting edge is somewhat variable but usually has a series of basal serrations or, on some teeth, a single small conule. The root is similar to that of the lower anterolaterals, although the mesial margin is weakly convex, rather than concave.

Discussion. Purdy et al. (2001) regarded *N. primigenius* as a junior synonym of the extant *N. cepedianus* on the basis of the overall similarity in tooth morphology, although, as yet, no detailed morphometric analysis has been performed to test this assertion. However, the geographic distribution of *N. cepedianus* is quite unlike the Neogene *N. primigenius*, with the former species generally restricted to cool temperate waters, whereas the latter is also widely distributed in warm temperate and tropical waters (Reinecke et al., 2011). On the basis of these geographic differences, Miocene *Notorynchus* from Calvert Cliffs are, for the present, retained in *N. primigenius*.

The largest lower anterolateral teeth of *N. primigenius* are about 30 mm wide. On the basis of comparisons with the extant species *N. cepedianus* Purdy et al. (2001:84) estimated the body length for teeth of this size to be 3–4 m. This size compares to a maximum length of 2.9 m for *N. cepedianus* (Van Dykhuizen and Mollet, 1992; Ebert, 2002; Compagno et al., 2005).

Stratigraphic and Geographic Ranges. This is the more common of the two cow sharks in the Chesapeake Group with more than 40 specimens examined for this study. Like most fossil hexanchids, it is represented primarily by the large lower anterolateral teeth. *Notorynchus primigenius* is most common along the northern end of Calvert Cliffs and has been collected in situ for beds 3–5, 8, and 10–14. This species is also known from Mid-Atlantic exposures of the slightly older bed 1 of the Calvert Formation. This species (sometimes listed as *N. cepedianus*) has been reported from the late Oligocene (Chattian) through late Miocene (Messinian) of Florida(?), Maryland, North Carolina, and Virginia, as well as Australia, Austria, Azores, Belgium, Denmark, France, Germany, Japan, the Netherlands, Poland, Portugal, Slovakia, Spain, and Switzerland (Radwański, 1965; Antunes and Jonet, 1970; van den Bosch et al., 1975; Cappetta, 1987, 2012; Kemp, 1991; Kent, 1994; Yabumoto and Uyeno, 1994; Müller, 1999; Hulbert, 2001; Purdy et al., 2001; Reinecke et al., 2008, 2011; Visaggi and Godfrey, 2010; Ávila et al., 2012; Bor et al., 2012).

The extant *N. cepedianus* is a wide-ranging, littoral eurytrophic shark of cool temperate, coastal waters worldwide, with the exception of the North Atlantic and Mediterranean. These robust, strong-swimming sharks are known to feed on a diverse range of prey (elasmobranchs, teleosts, pinnipeds, and carrion), with an ontogenetic shift in dietary preferences from teleosts to elasmobranchs to pinnipeds with increasing body size. The maximum body length of *N. cepedianus* is at least 2.9 m (Compagno, 1984, 1990b, 2002; Last and Stevens, 1994; Ebert, 2002; Compagno et al., 2005).

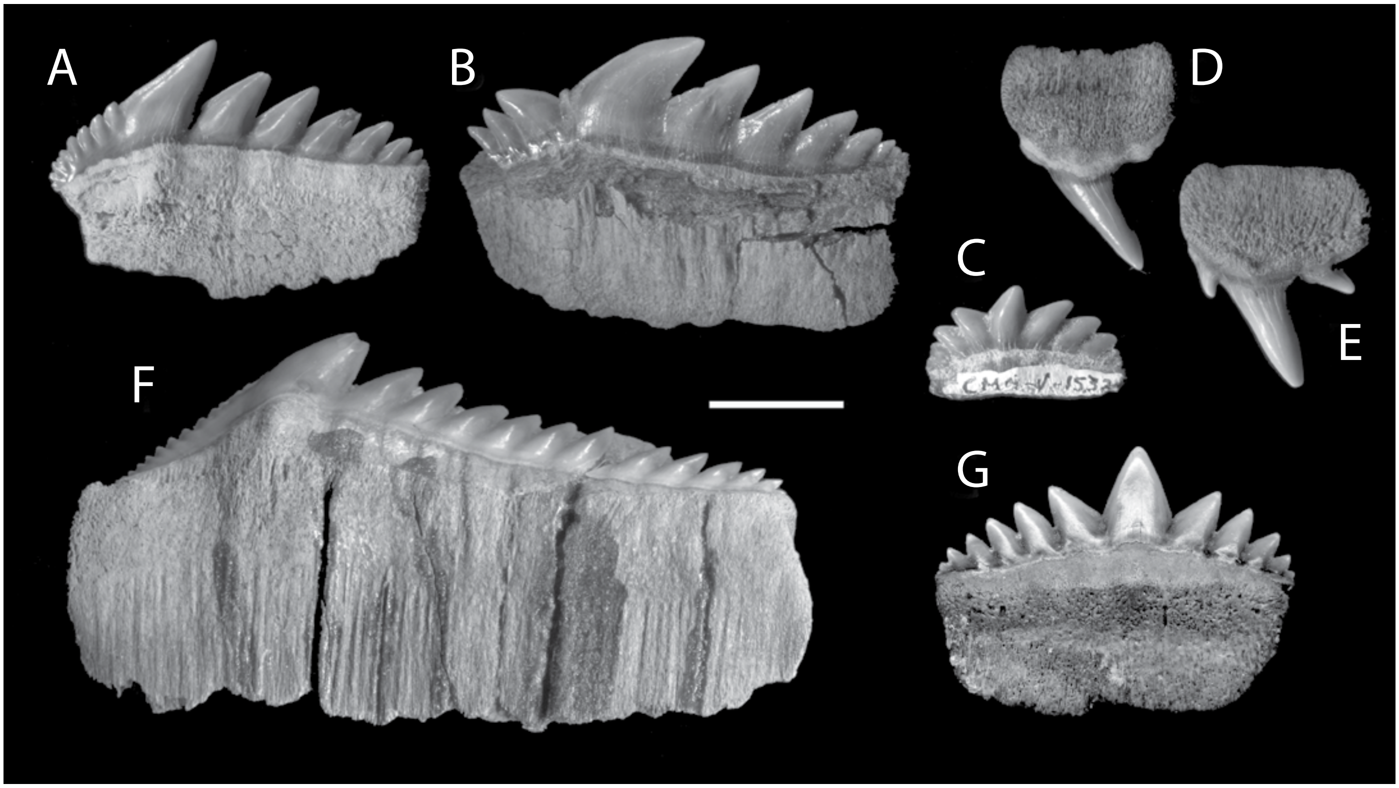


FIGURE 2.5. *Notorynchus* and *Hexanchus* teeth (1 cm scale bar). (A) *Notorynchus primigenius* right lower anterolateral tooth; lingual view (CMM-V-773; bed 14, Governor Run, Maryland). (B) *N. primigenius* pathological right lower anterolateral tooth; lingual view (CMM-V-422; Parkers Creek, Md.). (C) *N. primigenius* lower medial tooth; lingual view (CMM-V-2270; Parkers Creek, Md.). (D) *N. primigenius* right upper anterior tooth; lingual view (CMM-V-416; bed 12, Parkers Creek, Md.). (E) *N. primigenius* right upper anterolateral tooth; lingual view (CMM-V-1629; Scientists Cliffs, Md.). (F) *Hexanchus gigas* right lower anterolateral tooth; lingual view (CMM-V-3776; Windmill Point, Md.). (G) *H. gigas* lower medial tooth; lingual view (USNM 609547; Willows Beach, Md.).

Genus *Hexanchus* Rafinesque, 1810

Hexanchus gigas (Sismonda, 1857)

FIGURE 2.5F,G

Description. The lower anterolateral teeth superficially resemble those of *N. primigenius* but can be larger, are considerably broader, have seven or more distal conules, and have basal serrations on the mesial cutting edge. The root, like that of *N. primigenius*, is compressed, with a wedged-shaped profile, fine vertical grooves on the lingual face, and a concave mesial margin.

Medial teeth (Figure 2.5G) are again comparable to those of *N. primigenius* but are larger (width of at least 25 mm) and have five or more conules on each shoulder.

Several worn and fragmented teeth possibly representing other *H. gigas* tooth positions were examined, but none could be unambiguously assigned to this species, and they may fall within the variation inherent within *N. primigenius*.

Discussion. *Hexanchus* lower anterolateral teeth occur in two different morphologies (Ward, 1979): (1) grisiform teeth with mesial serrations that are either small or completely lacking and a low acrocone only slightly larger than the first distal conule and (2) vituliform teeth with large serrations and a tall acrocone of noticeably larger size than the remaining conules. These differences were later attributed to gynandric heterodonty, with the grisiform teeth representing females and the vituliform teeth representing males (Kent, 1994; Purdy et al., 2001). A detailed morphometric analysis found that this difference is ontogenetic, rather than genderal. Vituliform teeth are associated with sexual maturity, and their prevalence in males may simply reflect the maturation of males at smaller body sizes (Adnet, 2006).

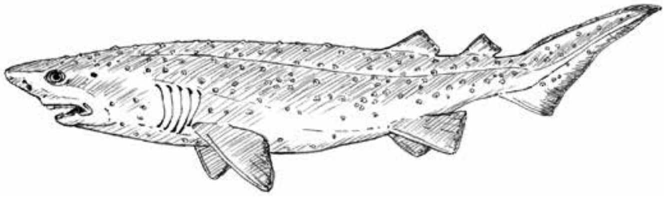
The teeth of *H. gigas* are similar to, but larger than, those of the extant bluntnose sixgill shark, *H. griseus* (Adnet and Martin, 2007), and as yet it is unclear whether they represent separate species or are conspecific. The extant *H. griseus* is a large benthic shark with a maximum length of at least 4.8 m and possibly 5.5 m. *Hexanchus griseus* is a versatile, eurytrophic shark of tropical and temperate marine shelf and upper slope habitats, occurring to depths of at least 1,875 m. The diet is very broad and includes a variety of teleosts, elasmobranchs, cephalopods, crustaceans, pinnipeds, and carrion. Adnet and Martin (2007) correlate the evolution of large body size in *Hexanchus* species, such as *H. gigas* and *H. griseus*, with the inclusion of cetaceans and pinnipeds in the diet; large fossil *Hexanchus* teeth of these species are particularly abundant in formations with large concentrations of marine mammals (Fordyce, 2009). The large *H. gigas* tooth (Figure 2.5F) was associated with a cetacean skeleton (*Cephalotropis coronatus* Cope, CMM-V-3277) from the St. Marys Formation, although it is unclear whether this represented active predation or scavenging.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. The teeth of *H. gigas* are far less commonly collected from Calvert Cliffs than those of *N. primigenius*, and only four specimens were available for study. The rarity of *H. gigas* teeth from Calvert Cliffs precludes a detailed assessment of the distribution of this species in different horizons. Beach specimens are from the northern end of Calvert Cliffs, suggesting derivation from the Calvert Formation. The tooth shown in Figure 2.5F was collected from bed 24 of the St. Marys Formation. Fossils of very large *Hexanchus* teeth comparable with those of *H. gigas* have been widely, if rarely, collected from the Miocene and Pliocene of Belgium, Chile, Italy, Japan, Malta, Peru, Portugal, Spain, and California and North Carolina in the United States (Antunes and Jonet, 1970; Itoigawa and Nishimoto, 1974; Muizon and DeVries, 1985; Cappetta, 1987; Nolf, 1988; Yabumoto and Uyeno, 1994; Müller, 1999; Purdy et al., 2001; Ward and Bonavia, 2001; Adnet and Martin, 2007; Reinecke et al., 2011).

ORDER ECHINORHINIFORMES SHIRAI, 1996

FAMILY ECHINORHINIDAE GILL, 1862

Genus *Echinorhinus* Blainville, 1816



Bramble Sharks – Echinorhinidae

The bramble sharks (*Echinorhinus*) are large, distinctive squaliform sharks that attain a maximum length of about 4 m. Their most conspicuous diagnostic character is the presence of numerous enlarged, thornlike dermal denticles embedded within the skin. The denticles are scattered over the body surface, although adjacent denticles may become fused into irregular plates. Bramble sharks are epibenthic in deeper (400–900 m), temperate and tropical marine environments. They occasionally venture into water as shallow as 11 m, and much of what is known about their biology is derived from sharks in these more accessible habitats. They have a relatively generalized diet of small sharks and bony fishes, as well as benthic invertebrates, such as cephalopods and crustaceans (Silas and Selvaraj, 1972; Taniuchi and Yanagisawa, 1983; Compagno, 1984:25–27; Aguirre et al., 2002; Dawson and Starr, 2009). *Echinorhinus* are present but exceptionally rare in the Holocene fauna of the Mid-Atlantic states. The only known specimen is an *E. brucus* captured off the coast of Virginia in 187 m of water (Musick and McEachran, 1969).

The *Echinorhinus* dentition is homodont with uniquely shaped teeth. Each tooth is highly compressed, with a crown strongly inclined distally. One or more cusplets are also present on each shoulder in teeth from Neogene species, although they are typically absent on posterior and juvenile teeth. The root is compressed and rectangular in outline.

Echinorhinus blakei Agassiz, 1856

FIGURE 2.6A–6C

Synonymy follows Pfeil (1983:205) and Reinecke et al. (2011).

DESCRIPTION. As is typical of *Echinorhinus* teeth, the low crown is compressed, smooth edged, and distally inclined. Only a single well-developed cusplet is typically present on each shoulder and is so strongly divergent as to be nearly horizontal. On some specimens (Figure 2.6A) a weak secondary cusplet may also be present. Posterior teeth (Figure 2.6B) may have low, rounded mesial and distal heels, rather than cusplets. The root is highly compressed and rectilinear. The lingual face of the root has two or three medial nutrient grooves, and a large number of small nutrient pores are scattered along the root immediately adjacent to the basal margin of the enameloid.

Presumed dermal thorns of *Echinorhinus* have been collected from Calvert Cliffs (Figure 2.6C). The base is ovoid with radial grooves extending from an enameloid-capped apex to the margins.

DISCUSSION. Purdy et al. (2001) suggested that *E. blakei* is conspecific with the extant prickly shark, *E. cookei* Pietschmann, although there are some differences. Most large teeth of *E. cookei* have two distinct cusplets on each shoulder, whereas similarly sized teeth of *E. blakei* normally have only one. The crown of *E. blakei* is also lower than that of the extant species but appears to be more conspicuous because of the less prominent cusplets (Pfeil, 1983:205–211). In his exhaustive review of the echinorhiniforms Pfeil (1983:180–212) lists these two forms as separate species, although noting that there are obvious similarities between them.

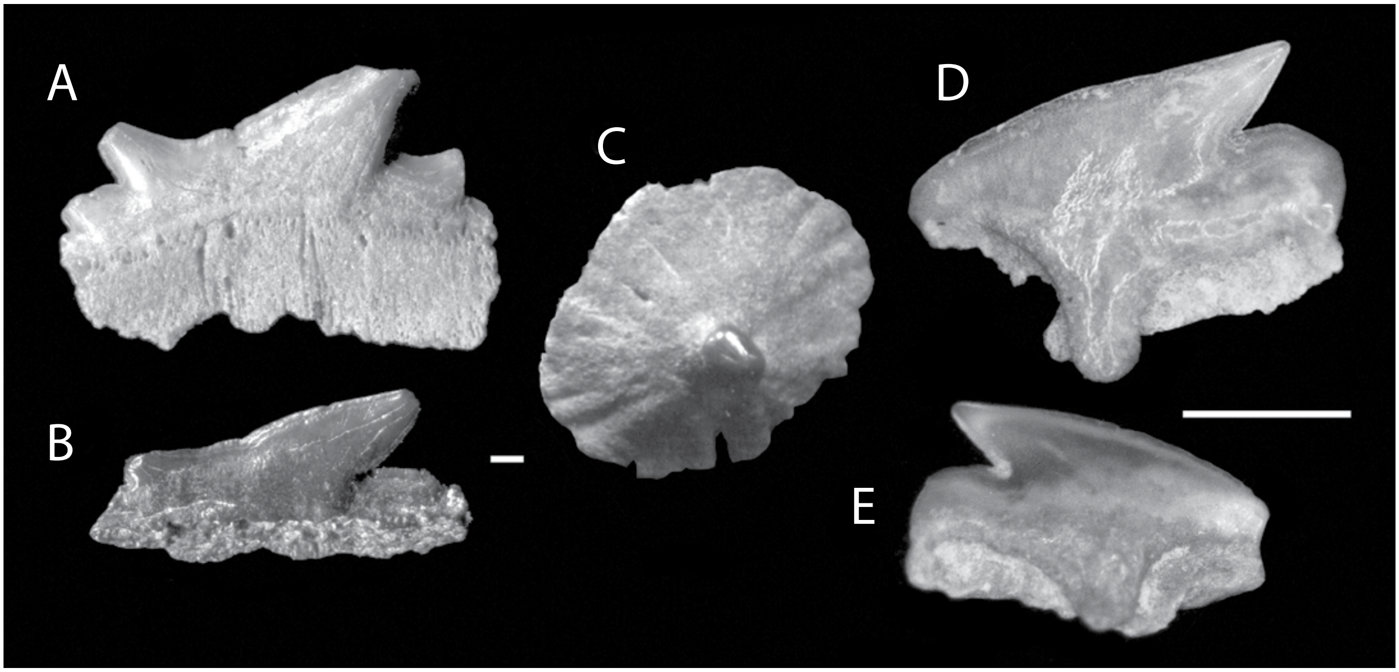


FIGURE 2.6. *Echinorhinus* and *Squalus* fossils (separate 1 mm scale bars for A–C and D+E). (A) *Echinorhinus blakei* right anterolateral tooth; lingual view (CMM-V-7691; bed 3, Pamunkey River, Virginia). (B) *E. blakei* right lateral tooth; lingual view (CMM-V-7743; Chesapeake Beach, Maryland). (C) *Echinorhinus*? dermal thorn; apical view (CMM-V-2775; Bayfront Park, Md.). (D) *Squalus* sp. 1; labial view (CMM-V-7724; bed 3B, New Kent County, Va.). (E) *Squalus* sp. 2; labial view (CMM-V-7725; bed 3B, New Kent County, Va.).

The Calvert Cliffs dermal thorns attributed to *E. blakei* resemble those of the extant bramble shark, *E. brucus* (Bonneterre), in having radial grooves. But the composite thorns arising from the fusion of two or more individual thorns that occur in *E. brucus* (Pfeil, 1983: pl. 65, fig. 4) have not been observed in Calvert Cliffs specimens. In this respect, the Calvert Cliffs dermal thorns resemble those of *E. richiardii* Lawley from the early Pliocene of Italy (Pfeil, 1983: pl. 66, figs. 4 and 6), although Cappetta (2006) considers this a junior synonym of *E. brucus*.

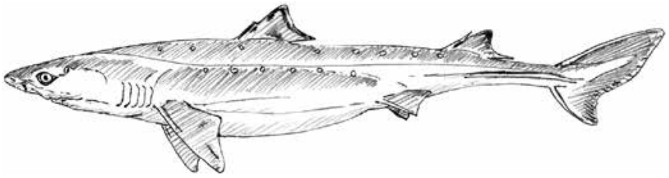
Stratigraphic and Geographic Ranges. *Echinorhinus blakei* is one of the rarest sharks from Calvert Cliffs and is reliably known only on the basis of a single intact tooth, a few tooth fragments, and two presumed dermal thorns from the northern end of the cliffs. This scarcity of specimens is understandable, given the preference of bramble sharks for waters deeper than those represented by the Calvert Cliff strata. This scarcity is exacerbated by the delicacy of the thin, compressed teeth, which are easily damaged by wave action.

This species has been previously reported from California, Oregon, Maryland, and North Carolina (Case, 1973; Pfeil, 1983; Cappetta, 1987, 2012; Kent, 1994; Purdy et al., 2001).

Order Squaliformes Goodrich, 1906

Family Squalidae Blainville, 1816

Genus *Squalus* Linnaeus, 1758



Spiny Dogfish Sharks – Squalidae

The spiny dogfish sharks, or spurdogs, are mesotrophic littoral species that are known to move into deeper shelf habitats. They have an elongated body and two widely spaced dorsal fins, each with a stout spine on the leading edge. Dogfish are active sharks feeding on a variety of prey, including teleosts, elasmobranchs, crustaceans, and cephalopods. The maximum size for most species is about 1 m (Bigelow and Schroeder, 1948; Compagno, 1984, 1990b; Castro, 2011).

The cutting teeth of *Squalus* have a simple, distally angled crown and a well-defined apron. They are similar in both jaws, except that lower teeth are somewhat larger than the uppers. The cutting edges are usually smooth, although some species have weakly crenulate or serrate cutting edges. There is a prominent distal heel, separated from the distal cutting edge of the crown by a distinct notch. The enameloid forming the crown protrudes lingually into a short uvula, and an obvious apron in the labial face extends below the basal margin of the root. There is mild gynandric heterodonty, with male teeth having crowns that are somewhat more erect than those of females (Bass et al., 1976; Cappetta, 1987; Herman et al., 1989).

There are two tooth forms of *Squalus* from Calvert Cliffs, which are both very small and easily overlooked. In situ specimens collected by washing and screening are necessary for definitive identification, as beach specimens are almost always too badly worn and broken. The roots in particular are highly susceptible to damage and are missing even on many screened specimens. Fragmentary *Squalus* have been rarely collected in screened material from the northern end of the Calvert Formation but are too worn and incomplete to be easily identifiable. The more complete teeth shown in Figure 2.6 were obtained from screened samples from bed 3 of the Calvert Formation in Virginia and are consistent with those from Calvert Cliffs.

Purdy et al. (2001), Ward and Bonavia (2001), and Reinecke et al. (2011) have all commented on the difficulty of assigning isolated *Squalus* teeth to individual species. The two *Squalus* tooth morphologies from the Calvert Formation are listed without specific attribution since it is unclear whether they represent two species or positional variants of a single species.

Squalus sp. 1

FIGURE 2.6D

Description. These small teeth (≤3 mm) are as high as they are wide. The mesial cutting edge is weakly sigmoidal, convex basally and becoming weakly concave near the apex. The strongly arcuate distal heel is separated from the convex distal edge of the crown by a deeply incised notch. The uvula is slender and bent mesially. The apron is broad based but tapers quickly to a long, narrow basal end with parallel sides that extend below the basal root margin.

Discussion. These teeth are similar to the late Oligocene (Chattian) *Squalus* aff. *cubensis* specimens illustrated by Reinecke et al. (2005), the early Miocene (Burdigalian) *Squalus* sp. of Reinecke et al. (2011), and the middle Miocene (Langhian) *S. alsaticus* of Bor et al. (2012).

Squalus sp. 2

FIGURE 2.6E

Description. The teeth are small (≤3 mm wide) and are generally wider than they are high. The crown is compressed and oblique, with smooth cutting edges. The mesial cutting edge is broadly convex. The distal cutting edge is weakly convex and meets the moderately convex distal heel at an acute angle in a moderately deep notch. A short, robust uvula is present, positioned roughly perpendicular to the lingual face of the crown. The apron is broad based, tapering to a short, relatively wide basal end extending below the basal root margin.

Discussion. Müller (1999:32; pl. 1, fig.7) reports *S.* aff. *acanthias* from the Calvert Formation and the St. Marys Formation (Little Cove Point Member). The illustrated specimen in Müller (1999) is close to the tooth morphology of *Squalus* sp. 2 described here, although details of this specimen are not easily observed. These teeth also are generally comparable with the late Oligocene (Chattian) *S. acanthias* (Müller, 1999: pl. 1, figs. 4–6; Reinecke et al., 2005: pl. 5), and the late Miocene (Tortonian) *S. almeidae* (Antunes and Jonet, 1970: fig. 7).

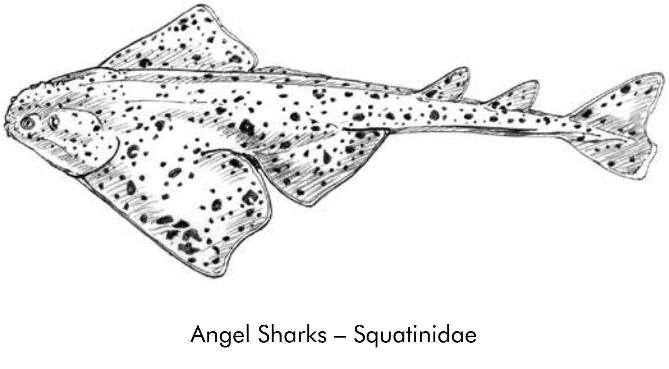
Squalus teeth are exceptionally rare from Calvert Cliffs, at present known for eight teeth. Some damaged teeth from the Calvert Formation may represent additional species. Unfortunately, the range of variability is so poorly known for both extinct and extant *Squalus* that at present it is unclear whether these represent additional species or simply variants of the two morphospecies already identified.

The fin spines of *Squalus* are known as fossils (Cappetta, 1987, 2012) but, as yet, have not been collected from Calvert Cliffs.

ORDER SQUATINIFORMES BUEN, 1926

FAMILY SQUATINIDAE BONAPARTE, 1838

Genus *Squatina* Dumeril, 1806



Angel Sharks – Squatinidae

Angel sharks (*Squatina*) are demersal sharks occurring from the littoral zone to the upper continental slope. They are unusual sharks in that they have a depressed body and greatly enlarged pectoral fins. In many respects they closely resemble batoids, although the leading edge of *Squatina* pectoral fins is free, rather than fused to the head, as in skates and rays. Angel sharks are ambush predators, lying buried in soft sediments to await prey, primarily small bony fishes, crustaceans, and mollusks. The

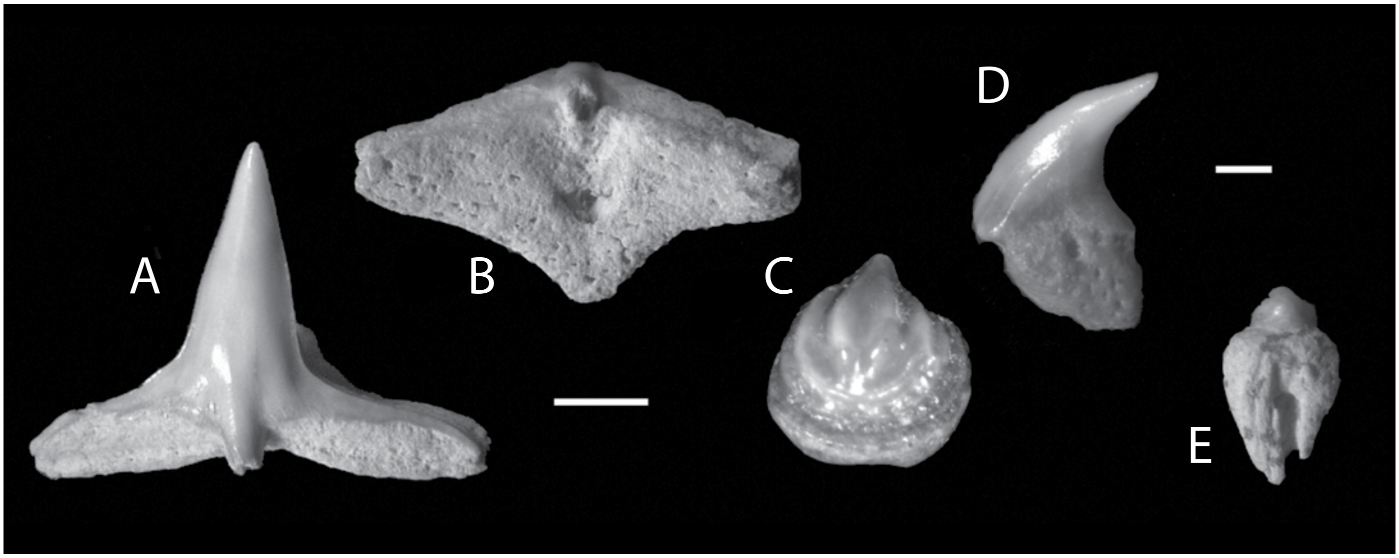


FIGURE 2.7. *Squatina* and *Rhincodon* fossils (separate 1 mm scale bars for A–C and D+E). (A) *Squatina* sp. lateral tooth; labial view (CMM-V-7732; bed 3B, New Kent County, Virginia). (B) *Squatina* sp. lateral tooth; basal view (CMM-V-7732; bed 3B, New Kent County, Va.). (C) *Squatina* sp. dermal thorn; apical view (CMM-V-7731; bed 3B, New Kent County, Va.). (D) *R. typus* tooth; profile view (CMM-V-7692; bed 3, Pamunkey River, Va.). (E) *R. typus* tooth; basal view (CMM-V-7693; bed 3, Pamunkey River, Va.).

maximum size for most species is about 1.6 m, although at least one species reaches 2 m (Bigelow and Schroeder, 1948; Castro, 1983; Compagno, 1984, 1990b, 2002; Compagno et al., 2005; Castro, 2011).

The clutching teeth of *Squatina* have a simple, erect crown, smooth cutting edges extending onto the shoulders, and a conspicuous apron on the labial face of the root. This tooth morphology is evolutionarily conservative and has been largely unchanged since the Late Jurassic. The virtually homodont dentition exhibits only a slight decrease in coronal height toward the corners of the jaws (Cappetta, 1987).

Squatina sp.

FIGURE 2.7A–C

Description. The teeth are small (≤10 mm), with a slender crown and a reduced, platform-like root (Figure 2.7A,B). The cutting edges of the crown are smooth and extend out onto conspicuous enameloid shoulders. The root is very short and protrudes lingually (i.e., perpendicular to the plane of the crown and enameloid shoulders) to form a conspicuous shelf. This shelf is roughly triangular in basal view and has a weakly concave basal surface. The labial face of the crown is convex and medially extends below the basal margin of the root to form a prominent apron.

Anterior teeth have a relatively tall, erect crown and are roughly equal in height and width. Lateral teeth are similar in shape, although the crown becomes lower and distally inclined and the tooth height becomes smaller than the width.

Discussion. Eastman (1904) applied the name *S. occidentalis* to *Squatina* teeth from Maryland. Kent (1994) listed this species as *S. subserrata*, a species known from the Miocene of Europe (Cappetta, 1987; Nolf, 1988), because Maryland teeth could not be reliably separated from the European teeth. The approximately 16 species of extant angel sharks all have relatively restricted geographic ranges, and none occur on both sides of a major ocean basin. These restricted ranges are unsurprising, given the demersal lifestyle of angel sharks on continental shelves, so it seems unlikely that *S. subserrata* would be found along both the eastern and western coasts of the North Atlantic. Further, David Ward (in Ward and Bonavia, 2001) notes that the Mediterranean Sea has three extant *Squatina* species that are readily identifiable on the basis of whole-body morphology but are, for practical purposes, indistinguishable on the basis of tooth morphology. For these reasons, identifying the Calvert Cliffs teeth as *Squatina* sp., rather than *S. occidentalis* or *S. subserrata*, is the most prudent designation.

Stratigraphic and Geographic Ranges. *Squatina* sp. teeth are found along the length of Calvert Cliffs, although they are never abundant (Visaggi and Godfrey, 2010), and only 15 teeth were examined for this study. These teeth are primarily beach specimens, although teeth have been collected in situ from beds 3, 4, 8, and 10. The scarcity of these teeth and their conservative tooth morphology preclude any determination of whether these teeth represent one or more species.

Neogene *Squatina* fossils are very widely distributed, including Belgium, the Czech Republic, France, Hungary, Germany, Malta, the Netherlands, Peru, Portugal, Venezuela, and the Mid-Atlantic coast of the eastern United States (Antunes and Jonet, 1970; Cappetta, 1970, 1987; Itiogawa and Nishimoto, 1974; Nolf, 1988; Kent, 1994; Antunes et al., 1999a; Müller, 1999; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Kocsis, 2007; Schultz et al., 2010; Reinecke et al., 2011; Vialle et al., 2011; Cappetta, 2012; Bor et al., 2012; Landini et al., 2017).

DERMAL THORNS. Extant *Squatina* have enlarged dermal thorns scattered among the smaller dermal denticles on the body surface (Bigelow and Schroeder, 1948). Cappetta (1970: fig. 10, type E) illustrated similar dermal thorns from the Miocene of France but did not assign them to a taxon. Case (1980) attributed similar thorns from the early Miocene Trent Formation to *Squatina subserrata*. Van den Bosch (1984: fig. 62a-c, type D) tentatively assigned thorns to the cetorhinids on the basis of similarities in morphology. Reinecke et al. (2005) and Cicimurri and Knight (2009b) concurred and attributed these thorns to *Cetorhinus*. Reinecke et al. (2011) disagreed and assigned them to *Squatina*. Bor et al. (2012) concurred with this interpretation and assigned these dermal thorns to *Squatina*.

Bigelow and Schroeder (1948: figs. 23, 104) provided anatomical line drawings of the thorns of both *Cetorhinus maximus* (fig. 23) and *Squatina dumeril* (fig. 104). *Cetorhinus maximus* dermal thorns have relatively erect, recurved cusps, a medial ridge on the face, and a base consisting of numerous radiating ridges. The *S. dumeril* thorns have more recumbent cusps with four or more ridges and a rounded base.

The dermal thorns from Calvert Cliffs have a low, reclined cusp (Figure 2.7C). The surface of the cusp has a medial ridge flanked on either side by irregular wrinkles and pits. The base is flattened, circular, or ovoid in outline and has a weakly convex basal surface. In form, these thorns are very similar, but not identical, to those of *S. dumeril* and are allied here with the *Squatina* sp. from Calvert Cliffs.

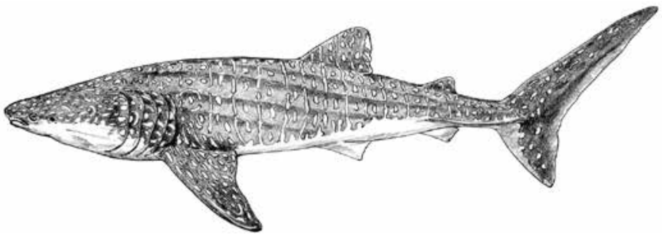
These dermal thorns are small and easily overlooked. The six specimens examined for this study were all obtained by screening Calvert Formation sediments.

SUPERORDER GALEOMORPHII COMPAGNO, 1973

ORDER ORECTOLOBIFORMES APPLEGATE, 1972

FAMILY RHINCODONTIDAE MÜLLER AND HENLE, 1838

Genus *Rhincodon* Smith, 1829



Whale Sharks – Rhincodontidae

The whale sharks are represented by a single extant species found worldwide in tropical and warm temperate oceans, except for the Mediterranean. They are open-ocean, pelagic sharks, although they are known to also occur in nearshore waters. Whale sharks are the largest living elasmobranchs, reaching lengths of at least 8 m and perhaps as much as 21 m. They are derived littoral-tachypelagic sharks that are exclusively microphagous. Unlike the ram-feeding basking sharks, whale sharks are suction feeders and are capable of feeding on a somewhat larger size range of planktonic and small nektonic prey, including teleosts, cephalopods, and crustaceans. Consistent with their planktivorous lifestyle, the *Rhincodon* dentition consists of numerous rows of simple, minute teeth (Compagno, 1984, 1990b, 2002; Colman, 1997; Compagno et al., 2005; Hazin et al., 2008; Castro, 2011).

Rhincodon typus Smith, 1829

FIGURE 2.7D,E

1970	*Rhincodon typus* Smith – Cappetta, p. 40, text-fig. 8, pl. 7:7.
2001	*Rhincodon* sp. – Purdy et al., p. 100, fig. 15o.
2009b	*Rhincodon* cf. *typus* Smith – Cicimurri and Knight, p. 630, fig. 3C.

DESCRIPTION. These teeth are small (maximum dimension of about 6 mm) and easily overlooked. In profile (Figure 2.7D), the acutely pointed crown is short and arched lingually, whereas the root is laterally compressed and has a convex basal margin. Both the labial and lingual surfaces of the crown are smooth and convex. The labial surface of the root is covered by an obvious enameloid apron. The cutting edges are smooth but inconspicuous and may not reach the basal margin of the enameloid. The root has a pronounced lingual protuberance but lacks conspicuous lobes. Basally, the root is bisected by a strong nutrient groove with a single nutrient foramen (Figure 2.7E). There is an obvious margin-lingual foramen on each lateral face of the root in a shallow depression basal to the crown.

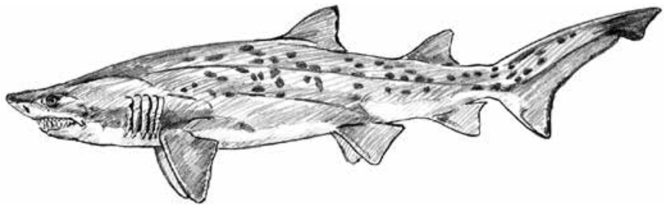
DISCUSSION. In both size and morphology Miocene *Rhincodon* teeth appear to be indistinguishable from those shown by Herman et al. (1992) for the extant *R. typus*.

Stratigraphic and Geographic Ranges. Visaggi and Godfrey (2010) report a beach specimen of *Rhincodon* from the northern ends of Calvert Cliffs, but this attribution appears unlikely, and this tooth is likely a worn symphyseal carcharhinid tooth (see Figure 2.28F,G). In situ specimens of *R. typus* teeth are known from the Fairhaven/Plum Point Members (beds 3–4) of the Calvert Formation (Mark Bennett, Marks' Fossils, Halethorpe, Maryland, personal communication, 2014). Seven teeth were examined for this study.

Rhincodon teeth have been reported from the Miocene of Delaware, Maryland, North Carolina, Virginia, and southern France (Cappetta, 1970, 1987; Kimmel and Purdy, 1984; Kent, 1994; Purdy, 1998a; Purdy et al., 2001), as well as the late Miocene/early Pliocene of Costa Rica (Laurito Mora, 1999). Similar teeth have also been reported from the late Oligocene of South Carolina (Cicimurri and Knight, 2009b).

Order Lamniformes Berg, 1958

Family Odontaspididae Müller and Henle, 1839



Sand Tiger Sharks – Odontaspididae

The sand tiger sharks of the family Odontaspididae are represented by two extant genera, *Carcharias* and *Odontaspis*. Despite a number of similarities, these two genera have very different lifestyles and long, separate evolutionary histories. Recent morphological and molecular research does not support odontaspidid monophyly and raises the possibility of splitting the Odontaspididae into two families (Shimada, 2005; Vélez-Zuaro and Agnarsson, 2011; Maisey, 2012).

Carcharias sand tigers are littoral species of tropical and temperate coastlines and continental shelves. They have a stocky, fusiform body and a tearing-type dentition and reach lengths in excess of 3 m. The diet consists of a diverse range of small teleosts and elasmobranchs, as well as cephalopods and crustaceans (Compagno, 1984, 1990b, 2002; Compagno et al., 2005; Castro, 2011).

The *Odontaspis* sand tigers are morphologically similar in overall morphology and reach even larger sizes (to 3.6 m). But they are also bathic sharks with smaller, more delicate teeth, relatively soft muscles, and poor skeletal mineralization, which are associated with the deeper waters of outer continental shelves and continental slopes in tropical and warm temperate climates. The diet is similar to that of *Carcharias* but, because of their less substantial dentitions, is believed to consist of somewhat smaller, less heavily armored prey (Compagno, 1984, 1990b, 2002; Compagno et al., 2005; Castro, 2011).

The Calvert Cliffs odontaspidids are represented by three species in the genus *Carcharias* and one species in the extinct genus *Carcharoides*. The latter genus is usually allied with the family Lamnidae, but recent research (Reinecke et al., 2011) makes a placement in the odontaspidids more plausible. Although sharks in the genus *Odontaspis* are known from older Paleogene formations in Maryland (Kent, 1994), none have been found in Calvert Cliffs.

Genus *Carcharias* Rafinesque, 1810

Carcharias cuspidatus (Agassiz, 1843)

FIGURE 2.8A–F

1843	*Lamna cuspidatus* Agassiz – Agassiz, p. 290, pl. 37a, figs. 45–49.
1994	*Carcharias cuspidata* (Agassiz) – Kent, p. 42, fig. 9.3G.
1999	*Carcharias cuspidatus* (Agassiz) – Müller, p. 36, tafel [fig.] 2, fig. 20–27.
2001	*Carcharias cuspidata* (Agassiz) – Purdy et al., pp. 102–103, figs. 17a,b, 18.
2005	*Carcharias cuspidatus* (Agassiz) – Reinecke et al., pl. 9, figs. 1–7.
2009b	*Carcharias cuspidatus* (Agassiz) – Cicimurri and Knight, p. 631, fig. 4D.

Description. The teeth of this common species differ from those of the other *Carcharias* species from Calvert Cliffs by the complete absence of striations on the lingual face of the crown. They reach large sizes, with anteriors reaching heights of nearly 30 mm.

Upper anterior teeth have tall, erect, broad upper cusps that are erect to slightly inclined distally. The labial coronal face is flat, whereas the lingual face is convex. The cutting edges are smooth and incomplete, restricted to the apical two-thirds of the crown in first and second anteriors and nearly complete in third anteriors. The crown is weakly to moderately recurved when viewed in profile. Each shoulder has one or two short, curved mediolingually directed cusplets. On many teeth, the secondary cusplets are very small and inconspicuous; these secondary cusplets are missing on many beach specimens. The lingual protuberance is moderately strong. The nutrient foramen is basal to the most elevated portion of the lingual protuberance in a short medial groove. The root lobes are thick and moderately long and meet at a weakly obtuse angle. Lower anterior teeth have less compressed, more recurved crowns, a more elevated lingual protuberance, and longer root lobes that form a more acute angle. In basal (Figure 2.8F) and profile perspectives, the lobes of both upper and lower anteriors taper smoothly from the lingual protuberance to the tips.

Lateral teeth (Figure 2.8B–D) have lower, relatively broad crowns that are distally inclined in uppers and erect in lowers. The

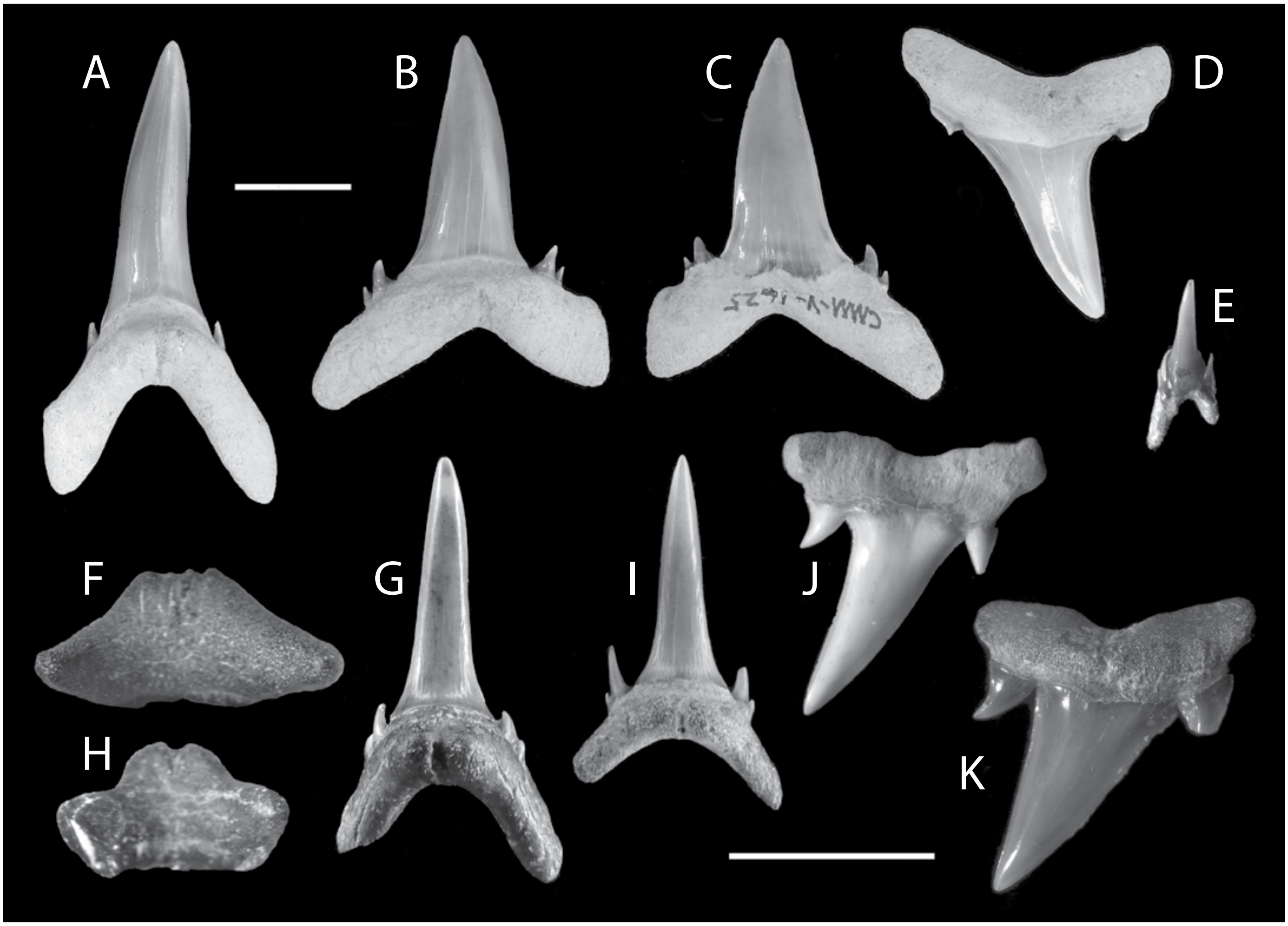


FIGURE 2.8. *Carcharias* and *Carcharoides* teeth (separate 1 cm scale bars for A–D and E–K). (A) *Carcharias cuspidatus* right lower anterior tooth; lingual view (CMM-V-1625; Scientists Cliffs, Maryland). (B) *C. cuspidatus* lower lateral tooth; lingual view (CMM-V-1625; Scientists Cliffs, Md.). (C) *C. cuspidatus* lower lateral tooth; labial view (CMM-V-1625; Scientists Cliffs, Md.). (D) *C. cuspidatus* upper lateral tooth; lingual view (CMM-V-794; Popes Creek, Md.). (E) *C. cuspidatus* symphyseal tooth; lingual view (CMM-V-7728; Bayfront Park, Md.). (F) *C. cuspidatus* lower anterior tooth; basal view (UMCP 1041; Clifton, Md.). (G) *Carcharias taurus* lower anterior tooth; lingual view (UMCP 1130; Pamunkey River, Virginia). (H) *C. taurus* lower anterior tooth; basal view (UMCP 1130; Pamunkey River, Va.). (I) *Carcharias reticulatus* lower anterior tooth; lingual view (CMM-V-2736; Randle Cliff, Md.). (J) *Carcharoides catticus* upper lateral tooth; lingual view (CMM-C-203 [voucher cast]; bed 3, Pamunkey River, Va.). (K) *C. catticus* upper lateral tooth; labial view (CMM-C-204 [voucher cast]; bed 3, Pamunkey River, Va.).

cutting edges are complete or nearly so and smooth, although on some lateral teeth the cutting edges are weakly crenulate adjacent to cusplets. The cusplets are short and sharp, with two or, rarely, three present on each shoulder. The taller, medial cusplet on each shoulder is curved mediolingually, whereas more lateral cusplets are more erect. On some laterals the cusplets partially fuse basally, forming jagged heels (Figure 2.8D). The root lobes are robust and meet at a very broad angle.

Lower first anterior (=symphyseal) teeth (Figure 2.8E) are small, with heights typically less than 10 mm. They resemble the larger anterior teeth but are narrower, with asymmetrical root lobes meeting at a very acute angle.

DISCUSSION. Upper and lower anteriors of *C. cuspidatus* have crowns that are somewhat broader than those of *C. reticulatus* and short, curved cusplets (like those of *C. taurus*), although two pairs of cusplets are usually present. Upper and lower laterals have wider crowns, more robust roots, and shorter, more lingually curved cusplets than *C. reticulatus*.

Carcharias cuspidatus is an Oligocene species that is closely allied with, and likely ancestral to, the Miocene species *C. vorax* (De Schutter, 2011), although there is disagreement on whether this name should also be applied to early Miocene teeth from the northwestern Atlantic. On the basis of the presence of multiple low cusplets on lateral teeth, Reinecke et al. (2011) consider the Miocene form of *C. cuspidatus* to be a junior synonym of *C. vorax*, although they note that there are differences between Miocene teeth from the northwestern and northeastern Atlantic. On the other hand, De Schutter (2011) considers *C. vorax* to be endemic to the northeastern Atlantic and the more robust teeth from the early Miocene of the northwestern Atlantic to be closer to the Oligocene *C. cuspidatus*. He also argues that the multiple cusplets on lateral teeth that were used by Reinecke et al. (2011:21) to place these teeth in *C. vorax* are inappropriate since this character also occurs in Oligocene *C. cuspidatus*. Overall, teeth from Calvert Cliffs (and the Pungo River Formation of North Carolina; Purdy et al., 2001) are relatively stout, with broader crowns and smaller cusplets than *C. vorax* from Europe and appear to represent relict populations of the Oligocene *C. cuspidatus* (De Schutter, 2011). The teeth of *C. cuspidatus* from both Calvert Cliffs and the Pungo River Formation are quite large, with a maximum height of more than 40 mm.

Cappetta (2012:191–192) assigns these teeth to the genus *Araloselachus* Glikman, as *A. cuspidata*. As such, it represents the terminal species of a lineage originating in the late Eocene. His arguments are based on several distinctive characters (the lack of a sigmoidal coronal profile, simple cusplets on anterior teeth, low cusplets on lateral teeth, and a completely smooth lingual coronal face). This generic assignment is plausible, but in the absence of a detailed phylogenetic analysis of fossil *Carcharias*-like odontaspidid teeth the lability of these characters is unknown. For the present, these teeth are retained within *Carcharias*, with the understanding that future research could produce justification for a separate genus.

Stratigraphic and Geographic Ranges. This species is by far the most abundant *Carcharias* shark collected from Calvert Cliffs and has previously been reported from this area by Kent (1994) and Müller (1999). Teeth of *C. cuspidatus* are most abundant along the northern half of the cliffs, and more than 100 were examined for this study. This species has been collected in situ in beds 3–4, 8, 10, 12, and 17 or 19. *Carcharias cuspidatus* teeth have also been collected from river exposures of older beds 1 and 2 of the Calvert Formation in Maryland and Virginia.

Many paleontological records of *C. cuspidatus* are more likely attributable to *C. vorax* (De Schutter, 2011; Reinecke et al., 2011). There are numerous records for *C. cuspidatus* from the late Oligocene (Chattian) through middle Miocene (Serravallian) of the eastern United States (Maryland, North Carolina, South Carolina, and Virginia; Leriche, 1942; Kent, 1994; Müller, 1999; Purdy et al., 2001; Cicimurri and Knight, 2009b), as well as the Oligocene (Rupelian-Chattian) of Europe, northern Africa, Chile, Peru, and Japan (Leriche, 1942; Radwański, 1965; Nolf, 1988; Kent, 1994; Yabumoto and Uyeno, 1994; Antunes et al., 1999a; Müller, 1999; Purdy et al., 2001; Reinecke et al., 2005, 2011; Suarez et al., 2006; Kocsis, 2007; Marsili et al., 2007; Cicimurri and Knight, 2009b; Cook et al., 2010; Landini et al., 2017).

Carcharias taurus **Rafinesque, 1810**

FIGURE 2.8G,H

Synonymy follows Marsili et al. (2007; as *C. acutissima*) and Reinecke et al. (2011).

Description. Upper anterior teeth have tall, broad upper cusps that are erect to slightly inclined distally. The labial coronal face is flat, whereas the lingual face is convex. The cutting edges are smooth and incomplete basally to complete. In profile, the crown is lingually inclined with an apex that is straight or only weakly recurved. A single short, triangular, mediolingually hooked cusplet is present on each shoulder. On some well-preserved teeth a low, rounded bump is present in areas where secondary cusplets would occur. The lingual protuberance is pronounced and forms a distinct mound clearly separated from the root lobes. The root lobes are narrow and meet at an acute angle. There is a short medial groove with a nutrient foramen that is basal to the most elevated portion of the lingual protuberance. Lower anterior teeth have less compressed, more recurved crowns, a more elevated lingual protuberance, and longer root lobes that form a more acute angle. In both upper and lower anteriors the lingual protuberance forms a distinct mound clearly separated from the root lobes in both basal (Figure 2.8H) and profile views.

The lateral teeth of *C. taurus* have narrow crowns that are distally inclined in upper teeth and erect in lower teeth. The cutting edges are smooth and complete or nearly so. A single mediolingually curved cusplet is present on each shoulder but is generally shorter than on anterior teeth. Rarely, a secondary, more laterally placed cusplet is present. The root lobes are robust and meet at an obtuse angle.

Discussion. Research on extant *C. taurus* has shown that tooth morphology can be quite variable between individuals (Lucifora et al., 2001, 2003), and this variation can complicate the assignment of individual fossil teeth to specific jaw positions. Jaw regions (upper anterior, lower lateral, etc.) can be determined with more confidence, and with care more definitive positional placements are possible for most teeth (Cunningham, 2000, 2004).

The teeth of *C. taurus* can easily be confused with those of *C. cuspidatus* because of similar morphologies and large size (exceeding 25 mm in height). The presence of lingual coronal striations on *C. taurus* teeth is sufficient to separate the two species, although they can be inconspicuous, especially on larger, beach-worn specimens. The anterior teeth of *C. taurus* also typically lack secondary cusplets, whereas they are present, if frequently small, in *C. cuspidatus*. Lateral *C. taurus* teeth have narrower crowns and fewer cusplets than in *C. cuspidatus*.

The teeth listed here as *C. taurus* are typically identified as *C. acutissima* in the paleontological literature on the basis of the presence of more extensive striations on the lingual face of the crown in the latter species. Reinecke et al. (2011) qualitatively evaluated these differences and found that although they did exist, there was such broad overlap between the Neogene and Holocene forms that they could not be reliably separated into distinct species. Instead, the two appear to represent phyletic evolution of this character within a single lineage, although a more thorough quantitative analysis is needed to confirm these observations.

The striations on the lingual crown face of *C. taurus* teeth from Calvert Cliffs are comparatively sparse and inconspicuous. They are most evident on smaller specimens and become progressively less numerous and obvious on larger teeth. This situation differs from that on specimens from the contemporaneous Pungo River Formation of North Carolina (Purdy et al., 2001; B. W. Kent, personal observations) and the Lower Mica Fine Sand Formation in Saxony, Germany (Reinecke et al., 2011), where striations are more prevalent, even on larger teeth. Too few specimens were available to determine whether they represent a separate *taurus*-like species in Calvert Cliffs or simply regional variation in *C. taurus*. Research on extant populations of *C. taurus* have demonstrated that there is substantial regional variation for both morphological (Lucifora et al., 2003) and molecular (Ahonen et al., 2009) characters, providing some support for the latter explanation.

The teeth of *C. taurus* from Calvert Cliffs are of modest size with a maximum height of about 20 mm. This height differs from those of *C. taurus* in the contemporaneous Pungo River Formation in North Carolina, where maximum size was more than 40 mm (Purdy et al., 2001). As yet, it is not clear if this size disparity is due to differences in the paleoenvironments represented by the Calvert Cliffs and Pungo River sediments or is a consequence of sampling error. Purdy et al. (2001) examined more than 200 *C. taurus* teeth, whereas only nine teeth of this species were available from Calvert Cliffs.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Carcharias taurus* is the rarest sand tiger from Calvert Cliffs, as previously observed by Eastman (1904; as *Odontaspis elegans*), and only nine were examined for this study. Teeth have been collected primarily from the northern half of Calvert Cliffs, and in situ specimens have been recovered from beds 3–4, 8, and 10, as well as in river exposures of beds 1 and 2 (Calvert Formation). The Neogene form of *C. taurus* has been widely reported in the North Atlantic from the early Oligocene (Rupelian) through middle Miocene (Serravallian) of Maryland, North Carolina, and Virginia (Kent, 1994; Müller, 1999; Purdy et al., 2001) and Europe (Radwański, 1965; Nolf, 1988; Antunes et al., 1999a; Ward and Bonavia, 2001; Kocsis, 2007; Marsili et al., 2007; Marsili, 2008; Reinecke et al., 2011; Bor et al., 2012). The species also has been reported from Argentina (Cione et al., 2000, 2005), the Azores (Ávila et al., 2012), the Lesser Antilles (Portell et al., 2008), Mallorca (Vicens and Rodríguez-Perea, 2003), Australia (Fitzgerald, 2004), Japan (Yabumoto and Uyeno, 1994), and Peru (Apolín et al., 2004; Landini et al., 2017).

***Carcharias reticulatus* (Probst, 1879)**

FIGURE 2.8I

Synonymy follows Reinecke et al. (2005, 2011).

DESCRIPTION. The upper anterior teeth have crowns that are narrow and erect but only moderately tall. The coronal apex is acutely pointed, but the crown flares basally in joining the shoulders. The cutting edges are typically incomplete. The labial face is flat and smooth, whereas the convex lingual face has fine basal striations. There is a single cusplet on each shoulder that is tall, slender, and erect to weakly divergent; a much smaller, secondary cusplet is present on some teeth. In profile, the crown is weakly recurved. The root lobes are slender and moderately elongated and meet at a weakly obtuse to broadly acute basal root angle. There is a single nutrient foramen positioned basal to the most elevated portion of the lingual protuberance in a short medial groove.

The lower anterior teeth are similar to upper anteriors (Figure 2.8i) but have thicker, more strongly recurved crowns. The root lobes are also somewhat longer and meet at a less obtuse, or even weakly acute, angle.

The lateral teeth of *C. reticulatus* have narrow crowns like those of *C. taurus* but differ in cusplet morphology. The cusplets are shorter than in anterior teeth but are erect and not mediolingually arched. Also, secondary cusplets are usually present in *C. reticulatus* but only rarely on *C. taurus* lateral teeth. The cutting edges are smooth and complete. The root is robust with widely divergent lobes.

DISCUSSION. The appropriate specific name for these Miocene *Carcharias* teeth is not fully resolved. De Schutter (2011) considers the middle Miocene form *C. reticulatus* to be sufficiently distinct from the similar Oligocene *C. gustrowensis* to retain separate names. Conversely, Reinecke et al. (2011) consider the Oligocene and Miocene forms similar enough to warrant only a single name, *C. gustrowensis*. Neither provides convincing evidence, so pending a more detailed analysis of their respective morphologies, separate names for the Oligocene (*C. gustrowensis*) and Miocene (*C. reticulatus*) forms are recognized here.

This *Carcharias* species is infrequently collected from Calvert Cliffs. The teeth of *C. reticulatus* are not easily confused with those of other Calvert Cliffs *Carcharias*. The anteriors have shorter crowns and taller, more erect cusplets than either *C. taurus* or *C. cuspidatus*. Like *C. taurus*, *C. reticulatus* teeth typically have striations on the lingual face of the crown, although those of *C. reticulatus* are generally somewhat more conspicuous. In overall morphology, *C. reticulatus* teeth are smaller (maximum height of about 20 mm) and also more delicate than those of either *C. cuspidatus* or *C. taurus*. Upper and lower laterals have narrower crowns, two pairs of taller cusplets, and more conspicuous striations than those of *C. taurus*. Upper laterals lack basal crenulations on cutting edges sometimes present in *C. cuspidatus*.

The delicate teeth of *C. reticulatus* are known primarily from broken, incomplete specimens. The distinctive cusplets are particularly vulnerable and rarely intact. The most distinctive feature of incomplete *C. reticulatus* teeth is the narrow crown that quickly flares basally, which is most obvious on anterior teeth but is also present on laterals.

Stratigraphic and Geographic Ranges. This species was previously reported from Calvert Cliffs as *C. reticulata* (Probst) in Kent (1994) and has been collected from beds 3, 4, and 8. This species is never common, and only about 20 teeth were available for this study.

Carcharias reticulatus has been widely reported in the North Atlantic from the early Oligocene (Rupelian) through at least the middle Miocene (Serravallian) and perhaps the early late Miocene (Tortonian). It is a rare species in northwestern Atlantic fossil beds of Maryland, North Carolina, and Virginia (Kent, 1994; Müller, 1999; Purdy et al., 2001). Teeth with this morphology from North Carolina were listed as *Odontaspis* cf. *O. acutissima* (Agassiz) by Purdy et al. (2001), but Reinecke et al. (2011) reevaluated these specimens and assigned them to *C. gustrowensis* (=*reticulatus*). The species is more common in European and Mediterranean fossil beds of Austria, Belgium, Catalonia, France, Germany, the Netherlands, Malta, Slovakia, and Switzerland (Leriche, 1926; Menesini, 1974; Nolf, 1988, planche 44, figs. 8, 9, as *Synodontaspis acutissima*; Ward and Bonavia, 2001; Reinecke et al., 2011; Bor et al., 2012).

Genus *Carcharoides* Ameghino, 1901

The genus *Carcharoides* is an unusual lamniform that possesses distinctly different anterior and lateral tooth morphologies (Antunes, 1969; Müller, 1999; Ward and Bonavia, 2001; Reinecke et al., 2005; Kocsis, 2007). Traditionally, *Carcharoides* has been assigned to the lamnids, primarily on the basis of the presence of lateral teeth with broad crowns and short root lobes (Cappetta, 1987, 2006). Recently, Reinecke et al. (2011) presented a detailed argument for moving this genus to the family Odontaspididae. Their arguments have two components, the overall similarity of the *Carcharoides* dentition to that of other odontaspidids and, more specifically, the structure of the upper intermediate tooth. The upper intermediate teeth of odontaspidids and lamnids are not analogous, with those of the former developing on the cartilaginous bar between the anterior and lateral dental bullae, whereas those of the latter are reduced third anteriors that develop within the anterior bulla (Siverson, 1999; Shimada, 2002). The different developmental origins of odontaspidid and lamnid intermediates are reflected in different root morphologies. The intermediate teeth of *Carcharoides* have a flat basal root face that compares favorably with that of odontaspidids and differs from the larger intermediates of lamnids, which have longer, more obvious root lobes.

Purdy et al. (2001) dismiss *Carcharoides* as a valid genus. They argue that the anterior teeth of *Carcharoides* are actually those of the odontaspidid *Carcharias*, whereas the lateral teeth belong to the carcharhiniform *Triaenodon*. Although there is some superficial resemblance of anterior *Carcharoides* teeth to those of *Carcharias* and lateral *Carcharoides* teeth to those of *Triaenodon*, these assignments are unlikely. Ward and Bonavia (2001) provide three lines of evidence for the validity of *Carcharoides*:

- The teeth of *Carcharoides* have the osteodont histological morphology found in lamniforms, rather than the orthodont histology typically found in carcharhiniforms. This distinction between orders is not absolute (e.g., the extant carcharhiniform *Hemipristis* has pseudo-osteodont teeth, whereas the Neogene *H. serra* has orthodont teeth; Compagno, 1970; Herman et al., 1991), but such exceptions are rare.
- Like other lamniforms, the teeth of *Carcharoides* can be separated into distinctive anterior and lateral tooth morphologies. *Triaenodon* has gradient monognathic heterodonty, without an abrupt transition between anterior and lateral teeth.
- The lower lateral teeth of *Triaenodon* frequently have a pair of cusplets on the mesial shoulder of the tooth. This condition has never been observed in *Carcharoides*, although a secondary cusplet is rarely present on the distal shoulder (Reinecke et al., 2011, pl. 27, fig. 6).

Further, Reinecke et al. (2011) were able to examine a sample of approximately 1,100 *Carcharoides* teeth and construct a dentition that combines anteriors and laterals with compatible morphologies.

Carcharoides catticus (Philippi, 1946)

FIGURE 2.8J,K

Synonymy follows Reinecke et al. (2005, 2011).

Description. At present, only the distinctive upper lateral teeth are known from Calvert Cliffs. These teeth have short, broad, and distally inclined crowns. The cutting edges are smooth and continuous between the crown and cusplets. The cusplets are large, triangular, and dissimilar in size; the mesial cusplet is taller and more erect than the distally inclined distal cusplet. The root is shallow and compressed, with lobes widely divergent.

Discussion. Reinecke et al. (2011) provide extensive documentation for the other tooth positions in the *C. catticus* dentition not yet recorded from Calvert Cliffs. The upper anterior teeth have narrow crowns that are erect or weakly inclined distally. The labial face is flat and extends onto the lingual face of the root a short distance, whereas the lingual face is weakly convex. In profile, the crown is weakly recurved. The cutting edges are smooth and may not extend to the cutting edges on the cusplets on some anterior teeth. The cusplets are tall (up to about 25% of the coronal height), slender, and highly compressed, with smooth cutting edges. The root lobes are moderately elongated and meet at an obtuse basal root angle. There is a single nutrient foramen positioned basal to the most elevated portion of the lingual protuberance in a short medial groove. The lower anterior teeth are similar to upper anteriors but have thicker, more strongly recurved crowns. The root lobes are also somewhat longer and meet at a less obtuse, or even weakly acute, angle. Some lower anterior teeth have cusplets that are lower and rounded. Lower lateral teeth are somewhat narrower than upper laterals, with erect to slightly inclined crowns. The cusplets are large, triangular, and frequently divergent.

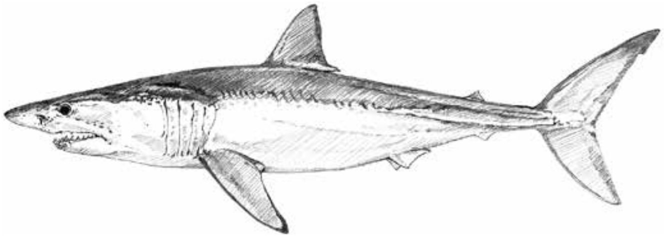
The teeth of this shark are surprisingly delicate, and intact specimens are rare. Even when fragmentary, upper lateral teeth are not easily mistaken for other sharks because of the combination of highly compressed crowns; tall, triangular cusplets; and short roots. Damaged anterior and, to a lesser extent, lower lateral teeth are most easily mistaken for those of *Carcharias* species.

Stratigraphic and Geographic Ranges. This species is rare in Calvert Cliffs, and only four teeth were examined for this study. Calvert Cliffs records are confined to the northern half of the cliffs, although specimens of *C. catticus* have been collected in situ from bed 3 of the Calvert Formation in Virginia (M. Bennett, pers. comm., 2014).

Carcharoides catticus has been widely reported in the North Atlantic from the early Oligocene (Rupelian) through middle Miocene (Langhian). It is a rare species in northwestern Atlantic fossil beds of Maryland, North Carolina, and Virginia (Kent, 1994; Müller, 1999; Purdy et al., 2001, as *Triaenodon obesus*). The species is more common in European and Mediterranean fossil beds of Austria, Belgium, Catalonia, France, Germany, Hungary, the Netherlands, Malta, Slovakia, and Switzerland (Leriche, 1926; Menesini, 1974; Nolf, 1988; Ward and Bonavia, 2001; Kocsis, 2007; Reinecke et al., 2011; Cappetta, 2012; Bor et al., 2012; Everaert, 2014).

Family Lamnidae Müller and Henle, 1838

Genus *Isurus* Rafinesque, 1810



Mako Sharks – Lamnidae

Extant mako sharks in the genus *Isurus* are large, pelagic predators. There are two living species, the shortfin mako (*I. oxyrinchus*) and the longfin mako (*I. paucus*). Much of the known biology of makos is based on that of the abundant and widely distributed *I. oxyrinchus*. Like many other pelagic lamniforms, the shortfin mako is a mesotherm that maintains elevated temperatures for the aerobic muscles, viscera, brain, and eyes, with the greatest elevation occurring in cooler waters at higher latitudes or in deeper waters (Carey and Teal, 1969; Carey, 1982; Block and Carey, 1985; Bernal et al., 2001b). With these elevated temperatures makos can be more active than ectothermic fishes, allowing them to pursue prey at higher speeds with aerobic muscles, rather than more quickly fatigued anaerobic muscles (Katz, 2002). The rarer longfin mako (*I. paucus*) has many of the same morphological adaptations for mesothermy as *I. oxyrinchus*, although it is unclear whether this species maintains an elevated body temperature (Carey, 1982; Compagno, 2002).

Extant shortfin makos are ichthyo- and teuthyophagous, feeding primarily on a range of small, pelagic fishes and squid and, to a lesser extent, on demersal fishes and invertebrates. Larger individuals have proportionally broader teeth and are capable of successfully attacking comparatively large individual fishes, sea turtles, and porpoises (Compagno, 1984, 2002; Castro, 2011). The longfin mako is presumed to have a broadly similar diet, although its comparative rarity precludes a more definitive assessment.

Both extant makos are epipelagic and found worldwide in tropical and warm temperate marine waters (Compagno, 2002). Again, because of its rarity the complete range of *I. paucus* is poorly known. On the basis of fossil tooth abundance in deep-sea sediments, makos (especially *I. oxyrinchus*) were the predominant large epipelagic sharks throughout the Neogene (Belyaev and Glikman, 1970). Only within, at most, the past 4,000 years have they been supplanted in this ecological role by the abundant and ubiquitous blue shark, *Prionace glauca* (Litvinov, 1989, 2007). There are two fossil mako sharks known from Calvert Cliffs, the comparatively common *I. oxyrinchus* and the much rarer *I. retroflexus*.

Isurus oxyrinchus Rafinesque, 1810

FIGURE 2.9A–F

Synonymy follows Purdy et al. (2001), Marsili et al. (2007), and Reinecke et al. (2011).

Description. Anterior *I. oxyrinchus* teeth are elongate, with slender crowns and divergent root lobes. In upper anteriors the crown is distally curved or angled and weakly sigmoidal in profile, and when viewed in profile, the coronal apex is bent labially. The mesial cutting edges are nearly complete on both the first and second anteriors, whereas the distal cutting edge may be either nearly complete or restricted to the apical portion of the crown. The extent of the distal cutting edges varies both ontogenetically and by tooth position (first versus second anterior). On first anterior teeth the distal cutting edge in smaller individuals

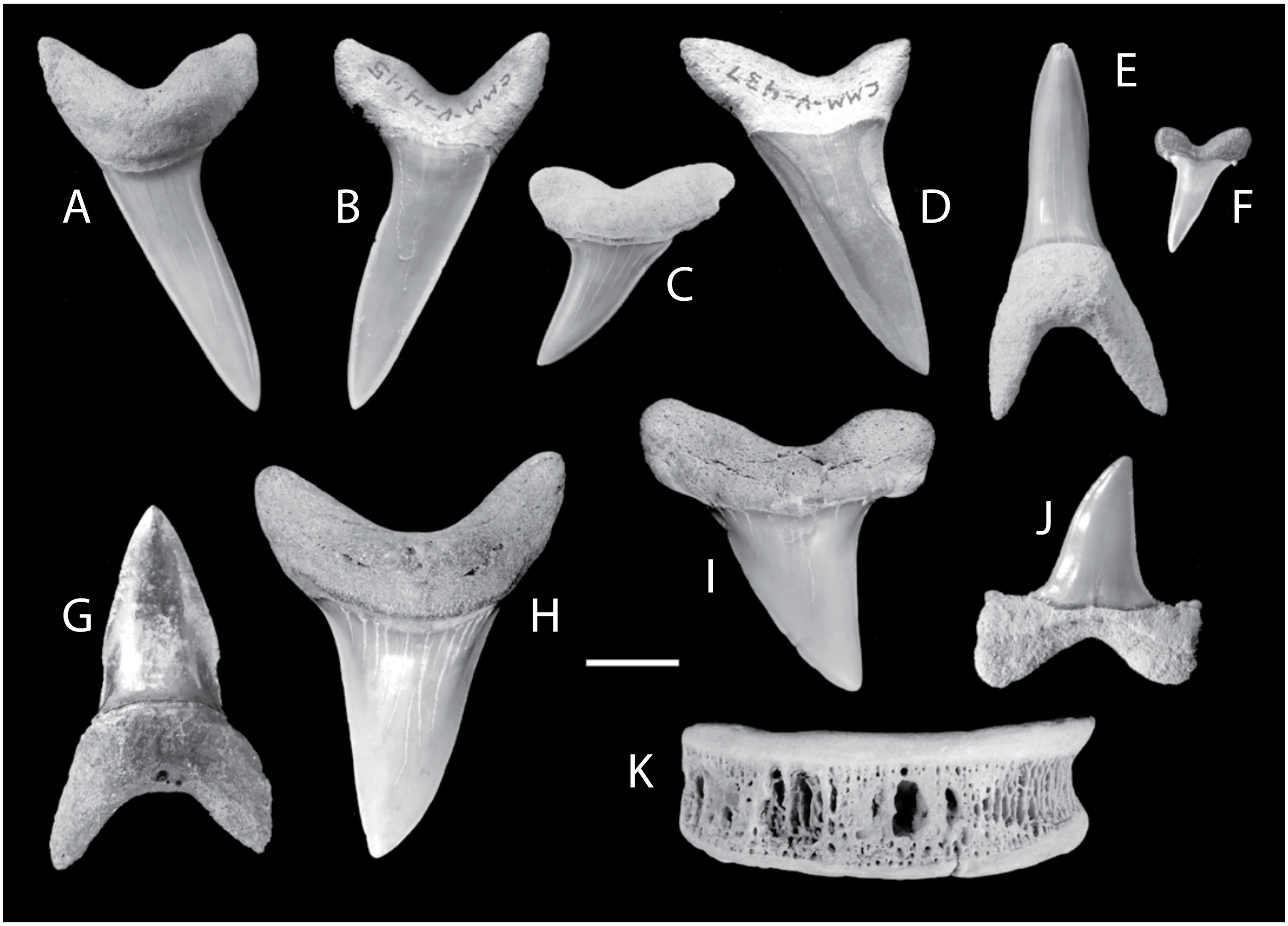


FIGURE 2.9. *Isurus* fossils (1 cm scale bar). (A) *I. oxyrinchus* right first upper anterior tooth; lingual view (CMM-V-445; bed 11, Parkers Creek, Maryland). (B) *I. oxyrinchus* right first upper anterior tooth; labial view (CMM-V-445; bed 11, Parkers Creek, Md.). (C) *I. oxyrinchus* left upper lateral tooth; lingual view (CMM-V-1623; Scientists Cliffs, Md.). (D) *I. oxyrinchus* second upper anterior tooth: labial view (CMM-V-437; bed 12, Parkers Creek, Md.). (E) *I. oxyrinchus* left(?) lower anterior tooth; lingual view (CMM-V-1623; Scientists Cliffs, Md.). (F) *I. oxyrinchus* juvenile right second upper anterior tooth; labial view (UMCP 1003; Matoaka Cottages, Md.). (G) *I. retroflexus* lower anterior tooth; lingual view (CMM-V-7717; beds 3 and 4, New Kent County, Va.). (H) *I. retroflexus* left upper anterior tooth; lingual view (CMM-V-4484; Willows Beach, Md.). (I) *I. retroflexus* right upper lateral tooth; lingual view (CMM-V-1539; Scientists Cliffs, Md.). (J) *I. retroflexus* lower lateral tooth (CMM-V-7028; labial view; bed 12, Scientists Cliffs–Parkers Creek, Md.). (K) *Isurus* sp. vertebral centrum; dorsal perspective (CMM-V-3610; Scientists Cliffs, Md.).

is restricted to the apical half of the crown, becoming nearly complete in larger individuals (Figure 2.9A,B). The distal cutting edge of the second upper anterior is nearly complete at all sizes (Figure 2.9C). The root lobes of anterior teeth are extended and generally meet at an obtuse angle. The lobes are also elongate and comparatively narrow, with rounded ends. Either a single nutrient foramen or a tight cluster of foramina in larger teeth is present just basal to the most elevated portion of the moderately thick lingual protuberance. A nutrient groove is either lacking or broad and indistinct.

Lower anterior teeth have crowns that are more erect and strongly recurved (Figure 2.9D). The distal cutting edge reflects the condition present in upper anteriors. Lower first anteriors have incomplete distal cutting edges on smaller teeth and nearly complete cutting edges on larger teeth. Second lower anteriors have nearly complete distal cutting edges. The roots have a more prominent lingual protuberance, bearing a single or several loosely clustered nutrient foramina, and root lobes meeting at a broadly acute, or weakly obtuse, angle.

Lateral teeth of *I. oxyrinchus* have progressively lower crowns and shorter root lobes meeting at a broadly obtuse angle. The crowns of the upper laterals are angled or distally arched and more compressed (Figure 2.9E). Lower laterals have crowns that are more erect and less compressed. Lateral teeth typically have a single nutrient foramen.

Small, presumably juvenile, teeth of *I. oxyrinchus* are typically more slender and gracile than larger teeth and frequently have a single small cusplet on each shoulder (Figure 2.9F).

Discussion. The teeth of *I. oxyrinchus* resemble those of a second narrow-toothed *Isurus* (*I. retroflexus*) and the broader-crowned species, *Carcharodon hastalis* (see below). Differences between the three species are most obvious in the first and second anterior teeth. The crowns of these *I. oxyrinchus* teeth are narrower and less bladelike than the other two species, and the incomplete distal cutting edge of the *I. oxyrinchus* first upper anterior does not occur on either *I. retroflexus* or *C. hastalis*. In profile, the coronal apex has marked labial curvature, which also occurs in *C. hastalis* but is absent or only weakly expressed in *I. retroflexus*. Likewise, for lower anterior teeth, the combination of narrower crowns, incomplete distal cutting edges on first anteriors, and a strongly recurved profile separates *I. oxyrinchus* from *I. retroflexus* or *C. hastalis*. Lateral *I. oxyrinchus* teeth have narrower crowns and longer root lobes than those of either *I. retroflexus* or *C. hastalis*.

Stratigraphic and Geographic Ranges. The teeth of *I. oxyrinchus* are moderately common along Calvert Cliffs, and more than 60 were available for study. This species is somewhat more prevalent at the northern end of the cliffs and has been collected in place from beds 4, 8, 10, 12, and 14 of Calvert Cliffs and from inland exposures of beds 1 and 2 of the Calvert Formation.

This species may have appeared as early as the late Oligocene (Chattian) and has been widely reported from Belgium, France, the Netherlands, Hungary, Italy, Malta, Poland, Portugal, Chile, Japan, Costa Rica, Cuba, the Lesser Antilles, Angola, Zaire, and the eastern United States (Radwański, 1965; van den Bosch et al., 1975; Cappetta, 1987, 2012; Nolf, 1988; Kent, 1994; Yabumoto and Uyeno, 1994; Iturralde-Vinent et al., 1996; Antunes et al., 1999a; Müller, 1999; Purdy et al., 2001; Ward and Bonavia, 2001; Suarez et al., 2006; Kocsis, 2007; Marsili et al., 2007; Laurito Mora and Valerio-Zamora, 2008; Marsili, 2008; Portell et al., 2008; Bor et al., 2012; Everaert, 2014). Most of these records assign these teeth to *I. desori*. However, there are several problems with the use of the specific name *desori*, and it seems advisable to assign these teeth to the extant species, *I. oxyrinchus* (Purdy et al., 2001; Marsili, 2007a; Ward and Bonavia, 2001 Reinecke et al., 2011; Bor et al., 2012).

***Isurus retroflexus* (Agassiz, 1843)**

FIGURE 2.9G–J

Synonymy follows Reinecke et al. (2011).

Description. The upper anterior teeth of *I. retroflexus* have crowns that are compressed, bladelike, and nearly erect to distally inclined (Figure 2.9G). The cutting edges are smooth and complete and meet at a relatively broad, spatulate apex. In profile, the crown is erect or only weakly bent lingually and lacks a marked labial curvature of the apex. The root is moderately thick, with rounded lobes of modest length that diverge at an obtuse angle. A broad shelf is present on the lingual root face below the neck and extends and broadens laterally on the shoulders. A conspicuous callosity is present on the labial root face, extending out onto the apical surface of the root. Laterally, the callosity is contiguous with the basal shelf on the lingual face of the root. A ridge is frequently present on the shoulders at this junction of the callosity with the lingual shelf. The ridge may be covered with enameloid, forming broad, low mesial and distal heels. Many, particularly larger, teeth have short, vertical wrinkles on the enameloid of the basal portion of the labial face. The root is only moderately thick, with rounded lobes of modest length. One or more nutrient foramina are located medially, basal to the lingual protuberance.

Lower anterior *I. retroflexus* teeth are similar to uppers but are more symmetrical, with a somewhat thicker, more prominent lingual protuberance (Figure 2.9H). In profile, the crown is bent lingually and lacks any conspicuous apical recurvature. The root lobes can be slightly longer, with more narrowly rounded ends, and meet at a smaller angle than in upper anteriors.

Lateral teeth have lower cusps that are distally inclined (Figure 2.9I,J). In profile, the cusp on upper teeth is erect or weakly bent labially, whereas in lowers the cusp is arched lingually. The heels may bear one or a few low, rounded cusplets (Figure 2.9J). The root lobes meet at a very wide obtuse angle and may have a shallow medial concavity. The root lobe ends can range from rounded to rectilinear. Smaller teeth have a single median nutrient foramen located basal to the most elevated portion of the lingual protuberance. Larger teeth usually have several loosely clustered foramina.

Discussion. Purdy et al. (2001) considered *I. retroflexus* a nomen dubium on the basis of uncertainty about Agassiz's original description and figure (Agassiz, 1843) and considered this specimen unidentifiable to species. This classification creates a serious difficulty since there are morphologically distinct Neogene *Isurus* teeth assigned to *I. retroflexus* (Lawley, 1881; Leriche, 1926; Cappetta, 1970; Kent, 1994; Ward and Bonavia, 2001) that are now orphaned. This approach seems overly conservative, as the root morphology of the type specimen is distinctive, and the specific name *retroflexus* is retained for these teeth (Reinecke et al., 2011).

The teeth of *I. retroflexus* resemble those of both *I. oxyrinchus* and *C. hastalis* but differ from these species in crown and root morphology. The short, broad, compressed crowns of *I. retroflexus* anteriors are very different from the taller, narrower crowns of *I. oxyrinchus* but superficially resemble those of *C. hastalis*. But *I. retroflexus* crowns lack the conspicuous labial curvature present in the latter species. At similar tooth sizes, *I. retroflexus* crowns also tend to have broader, more ogival apices. The distinctive roots of *I. retroflexus* have a pronounced lingual shelf and labial callosity that are absent from either *I. oxyrinchus* or *C. hastalis*. Lateral teeth of the three species are more easily confused, but the length of the root lobes and the idiosyncratic shelf and callosities are sufficient to separate *I. retroflexus* from the other species.

Herman (1979) resurrected the genus *Anotodus* Le Hon and argued that this species (as *A. retroflexus*) was actually a giant alopiid. This attribution has been largely ignored by other researchers, although it was recently advocated by Cappetta (2012:242) on the basis of similarities in dental morphology between this species and alopiids. Although *retroflexus* lateral teeth can superficially resemble those of alopiids, this is less true of anteriors. Further, the resemblance is most marked in the largest teeth; smaller teeth (particularly, the tall, narrow anteriors) strongly resemble those of *Isurus*. An analysis of Neogene *Isurus* by Bourdon (2005) documents these similarities in detail and provides strong support for retaining *retroflexus* within *Isurus* and allying it with the extant longfin mako, *I. paucus*.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Isurus retroflexus* teeth are currently known only from the northern portions of Calvert Cliffs. They have been collected in situ from beds 12 and 17 or 19, although they seem more common in bed 12 than anywhere else along the cliffs. This species is less abundant than *I. oxyrinchus* in Calvert Cliffs (only 17 available for study) but nonetheless has a wide geographic distribution in the early Miocene (Burdigalian) through early Pliocene (Zanclean), including the United States (Maryland, Virginia, and North Carolina), Australia, Austria, Belgium, France, Germany, Hungary, Italy, Japan, the Netherlands, Malta, Peru, and Switzerland (Hirota, 1979; Cappetta, 1987, 2012; Nolf, 1988; Kent 1994; Yabumoto and Uyeno, 1994; Ward and Bonavia, 2001; Kocsis, 2007; Marsili et al., 2007, as *Isurus* sp.; Reinecke et al., 2011; Bor et al., 2012; Landini et al., 2017, as *Anotodus* cf. *A. agassizi*).

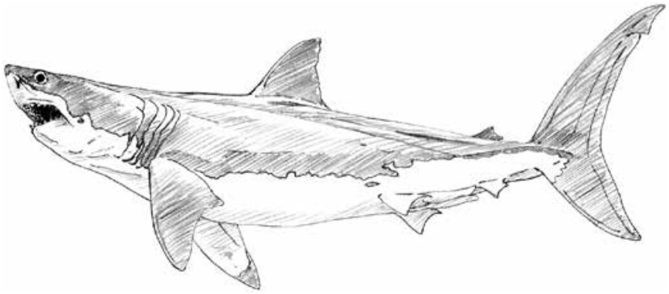
Isurus Vertebral Centra

FIGURE 2.9K

DESCRIPTION. Presumed *Isurus* centra from Calvert Cliffs are short, discoidal, and circular in axial perspective. The dorsal and ventral foramina are ovoid and stop short of the rims. In dorsal or ventral perspective, the walls are concave, recurved near the rims, and septate. The septa are simple and straight medially but undergo complex, reticulating branching near the rims. This branching causes the septa to have an intricate, lacy appearance.

DISCUSSION. The morphology of the vertebral centra from the extant *Isurus* has been well documented (Kozuch and Fitzgerald, 1989; Kraig, 2008) and is consistent with the centrum shown here (Figure 2.9K). Only three presumed *Isurus* centra have been studied from Calvert Cliffs.

Genus *Carcharodon* Smith, 1838



White Sharks – *Carcharodon*

White sharks of the genus *Carcharodon* are the most famous, and one of the most heavily studied, of all living sharks (Compagno et al., 1989, 2005; Compagno, 2002; Castro, 2011). The extant species, *Carcharodon carcharias*, is large, powerful, and archipelagic, combining a high-speed tachypelagic body with robust jaws and a versatile dentition of bladelike cutting teeth (Compagno, 1990b). Although primarily inhabitants of continental and insular shelves, white sharks are capable of cruising long distances and have one of the most extensive geographic ranges of any shark. They occur most commonly in temperate waters, although large adults are occasionally reported from the tropics. White sharks occupy depths from the surf line down to about 1,300 m. Extant white sharks are top predators in marine communities, and the combination of large size, efficient locomotion, and large cutting teeth allows them to successfully subdue a broad range of prey, including bony fishes, sharks, skates, rays, sea turtles, sea birds, seals, sea lions, porpoises, invertebrates (gastropods, cephalopods, and crustaceans), and carrion. Marine mammals are particularly important in the diet of large white sharks, either as predation or scavenging. Maximum size for extant white sharks appears to be 6 m (Compagno, 1984, 1990b, 2002; Compagno et al., 1989, 2005; Wroe et al., 2008; Castro, 2011; Fallows et al., 2013).

Carcharodon has a tooth morphology very similar to that of sharks typically placed in the extinct genus *Cosmopolitodus*. Both groups have dignathic heterodonty with broad compressed crowns on the upper teeth and somewhat narrower, less compressed crowns on the lower teeth. The root lobes are comparatively short. Larger teeth have a cluster of nutrient foramina on the labial root face, basal to the most elevated portion of the lingual protuberance. In some cases, the foramina are contained

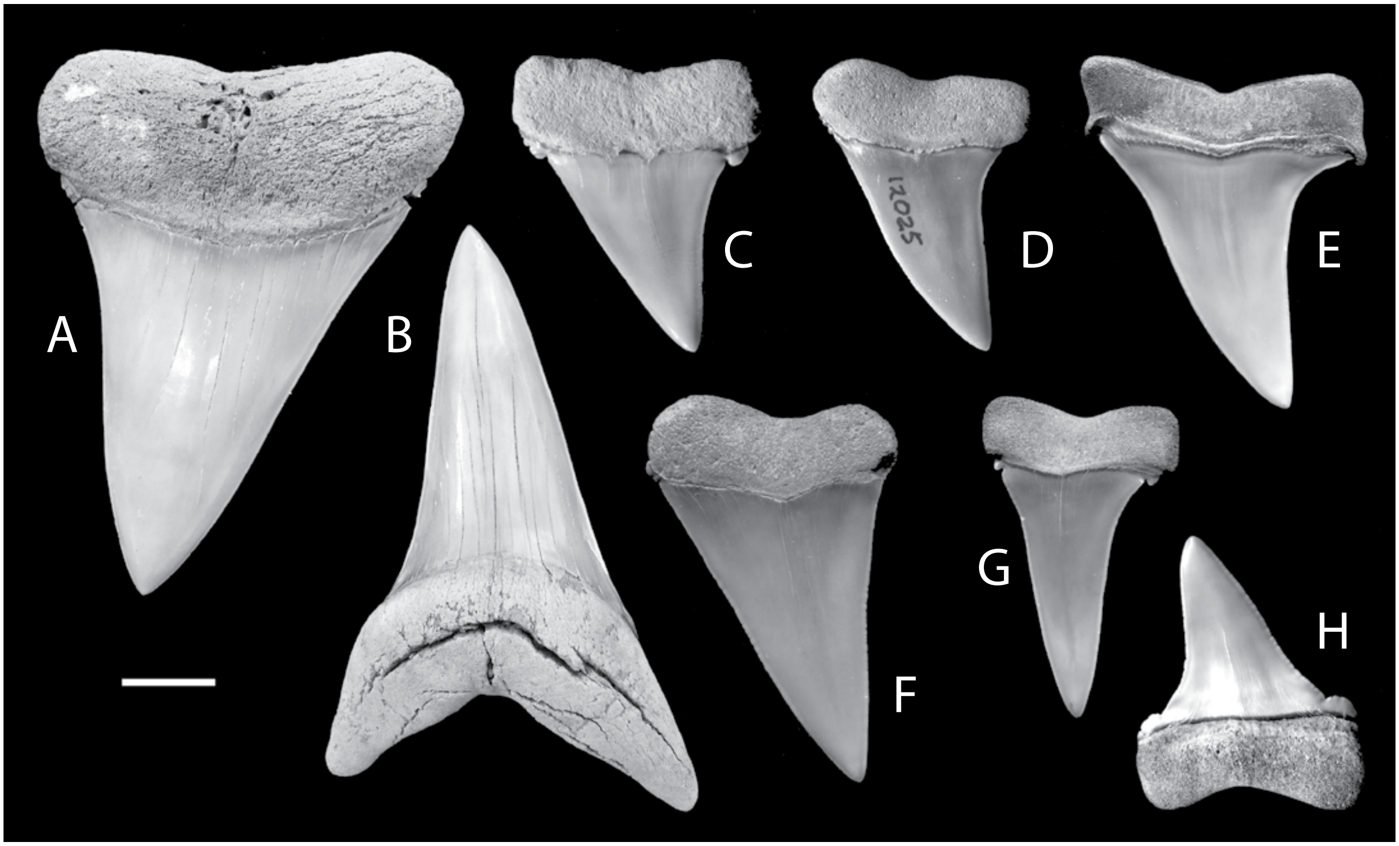


FIGURE 2.10. *Carcharodon* teeth (1 cm scale bar). (A) *C. hastalis* left upper anterior; lingual view (CMM-V-245; Parkers Creek, Maryland). (B) *C. hastalis* left lower anterior; lingual view (CMM-V-245; Parkers Creek, Md.). (C) *C. hastalis* left upper lateral with cusplets; labial view (CMM-V-7569; bed 12, Scientists Cliffs–Parkers Creek, Md.). (D) *C. hastalis* left upper lateral with basal serrations; labial view (UMCP 12025; Matoaka Cottages, Md.). (E) *C. hastalis* left upper lateral with root spurs; labial view (CMM-V-7716; Scientists Cliffs–Warrior's Rest, Md.). (F) *C. subserratus* upper anterior; labial view (CMM-V-3876; Flag Ponds, Md.). (G) *C. subserratus* upper anterior with cusplets; labial view (CMM-V-4173; Flag Ponds, Md.). (H) *C. subserratus* lower lateral with crenulate cusplets; labial view (CMM-V-7802; Windmill Point, Md.).

within a larger external opening (Kent, 1994:64; Cappetta, 2012:211). Differences between *Carcharodon* and *Cosmopolitodus* are almost entirely based on the condition of the cutting edges; the cutting edges are coarsely serrate in *Carcharodon* and smooth or weakly crenulate in *Cosmopolitodus*.

In recent years the evolution of *Carcharodon* from *Cosmopolitodus* has been extensively documented in the Pacific Ocean, with an unserrated ancestor giving rise to increasingly more strongly serrated forms (Stewart, 1999, 2000; Yabe, 2000; Stewart and Perry, 2002; Ehret et al., 2009a, 2009b, 2012). The primary difficulty is in unambiguously distinguishing between *Cosmopolitodus* and *Carcharodon*. The simplest descriptor is the presence or absence of serrated cutting edges on the crown (Cappetta, 2006; Mewis, 2008; Ehret et al., 2009a, 2012). This delineation parallels the marked changes in the triple-layered neoselachian enameloid necessary to produce true serrations (Andreev, 2010; BWK, pers. obs.). Smooth and crenulated cutting edges have essentially identical orientations of fibers in the parallel enameloid bundles, whereas serrations have pronounced bending of these bundles to biomechanically reinforce the notches between serrations. The problem with this distinction is that it ignores a variety of intermediate forms, including teeth with crenulate, partially serrate, and weakly serrate cutting edges (Muizon and DeVries, 1985; Kent, 1994; Mewis, 2008; Ehret et al., 2009a, 2012). A further difficulty is that by the early Pliocene both *Cosmopolitodus* and *Carcharodon* also evolved broader, more triangular crowns. An unresolved question is whether the extant *C. carcharias* (1) arose from a narrow, fully serrated ancestor and independently evolved the broad tooth form or (2) arose from a broad-toothed ancestor with smooth, unserrated cutting edges and independently evolved serrated cutting edges. Retaining *Cosmopolitodus* as a separate genus would make it a paraphyletic stem group to the genus *Carcharodon*. The more parsimonious solution is to make the whole *Cosmopolitodus-Carcharodon* complex a single clade, for which *Carcharodon* would have priority, as has been proposed by Mewis (2008), Cione et al. (2012), and Ehret et al. (2012).

Two species of *Carcharodon* are definitively known from Calvert Cliffs, the abundant *C. hastalis* and the much rarer *C. subserratus*. Those of *C. hastalis* are actually the most abundant large lamnid teeth collected from these beds (reanalyzed data from Visaggi and Godfrey, 2010). Teeth attributed to the extant *C. carcharias* have also been rarely reported from the Calvert Cliffs beds.

***Carcharodon hastalis* (Agassiz, 1843)**

FIGURES 2.10A–E, 2.11

Synonymy follows Marsili et al. (2007) and Reinecke et al. (2011).

Description. This is a large lamnid with relatively broad, compressed teeth. Like the extant *C. carcharias* the dentition has dignathic heterodonty. Upper anterior teeth have tall, moderately broad, triangular crowns with complete, unserrated cutting edges (Figure 2.10A). The mesial margin of the crown is weakly convex to nearly straight, whereas the distal margin is concave to slightly sigmoidal. In profile, the coronal apex is labially recurved. The crown is separated from the root by a narrow neck with roughly parallel sides. The roots have abbreviated lobes that meet at an obtuse angle. Large teeth have a cloacal cluster of nutrient foramina basal to the inconspicuous lingual protuberance. Upper lateral teeth are similar, although the crowns become progressively lower and more distally inclined in tooth row groups closer to the jaw commissure. The root lobes become somewhat longer but meet at increasingly larger obtuse angles.

Lower anterior teeth (Figure 2.10B) are similar to upper anteriors but have somewhat narrower, less compressed crowns, a more prominent lingual protuberance, and longer root lobes meeting at less obtuse angles. As in the upper jaw, lateral teeth have lower crowns, although they have more erect crowns than corresponding uppers. Also, the root lobes of lower lateral teeth (compared to lower anterior teeth) become shorter and meet at a larger angle.

There is considerable variation in many of these characters. As is common with many lamniforms, smaller teeth are more delicate, with narrower crowns and slightly longer root lobes, than larger teeth. Smaller teeth also have a simple cluster of nutrient foramina or, in the smallest teeth, a single foramen. Some teeth, particularly those in lateral files, can have cusplets (Figure 2.10C), basal serrations (Figure 2.10D), or root spurs (Figure 2.10E). These serrations are coarse and comparable in size and shape to those of *C. carcharias* but are restricted to the most basal portions of the cutting edges.

Discussion. The larger, broader teeth of *C. hastalis* resemble those of the later Pliocene species usually identified as *C. xiphodon* (Agassiz). Ward and Bonavia (2001) considered this species name to be a nomen dubium. According to Cione et al. (2012), the next available name for these teeth is *C. plicatilis* (Agassiz), although Cappetta (2006) lists *plicatilis* as a Miocene (rather than Pliocene) species. But Cappetta's stratigraphic placement appears to be an error, as the type locality of *plicatilis* ("du terrain calcaire de Castell-Arquato," i.e., limestones of Castell'Arquato) contains predominately Pliocene sediments. Further, the limestones in this area are from the middle Pliocene (Piacenzian; Roveri and Taviani, 2003). This is consistent with the early to middle Pliocene (Zanclean–Piacenzian) age of this broad-toothed form (listed as *Isurus xiphodon*; Purdy et al., 2001; Ward, 2007; Marsili, 2008). As proposed by Cione et al. (2012), *C. plicatilis* will be used here as the name for the Pliocene *Carcharodon* with broad, triangular crowns and smooth cutting edges.

Ehret et al. (2012) considered *C. hastalis* and *C. plicatilis* (listed as *C. xiphodon*) to represent different forms of a single chronospecies and united them under the senior synonym *C. hastalis*. This approach is overly conservative and ignores the stratigraphically relevant differences in morphology between the Miocene *C. hastalis* and the early to middle Pliocene *C. plicatilis* (Whitenack and Gottfried, 2010; listed as *I. xiphodon*).

An assemblage of 31 large teeth and 18 vertebral centra was collected from Calvert Cliffs south of Parkers Creek (CMM-V-245; Figure 2.11A) and provides insights into the transition between *C. hastalis* and *C. plicatilis*. The teeth represent morphologies attributable to a number of tooth row groups, although there are relatively few of the smaller teeth closer to the jaw commissure. The largest tooth is a lower second anterior from the right side of the jaw with a height of 65.4 mm. The largest upper tooth is a 63.5 mm tall second anterior from the left side. Although the first and second anterior teeth in both jaws were easily allocated to position, lateral teeth were more difficult to assign. The ambiguity in the assignment of lateral teeth was due in part to the small number of tooth groups represented in the association and to the variability in tooth size and shape in known extant *Carcharodon*. Purdy et al. (2001) examined the Calvert Cliffs tooth assemblage (at the time consisting of only 27 teeth) when constructing their artificial tooth sets of *C. plicatilis* from Lee Creek Mine, North Carolina. To evaluate the teeth of the assemblage, they were compared to the Purdy et al., (2001) artificial tooth sets for *C. hastalis* (fig. 27) and *C. plicatilis* (figs. 29, 30; as *I. xiphodon*). The tooth morphologies of the Calvert Cliffs assemblage were also compared with dentitions reconstructed from tooth assemblages of *C. plicatilis* (Lawley, 1881: pl. 5, based on 140 teeth) and *C. subserratus* (=escheri; Mewis, 2008: fig. 14, based on 42 teeth), as well as the associated dentition of *C. hubbelli* (Ehret et al., 2012: fig. 7, based on 222 teeth). The Lawley reconstruction places the largest upper lateral tooth in the first lateral tooth position. The largest upper lateral tooth is actually in the second position, rather than the first (Shimada, 2002), and this was corrected before analysis. The relative sizes,

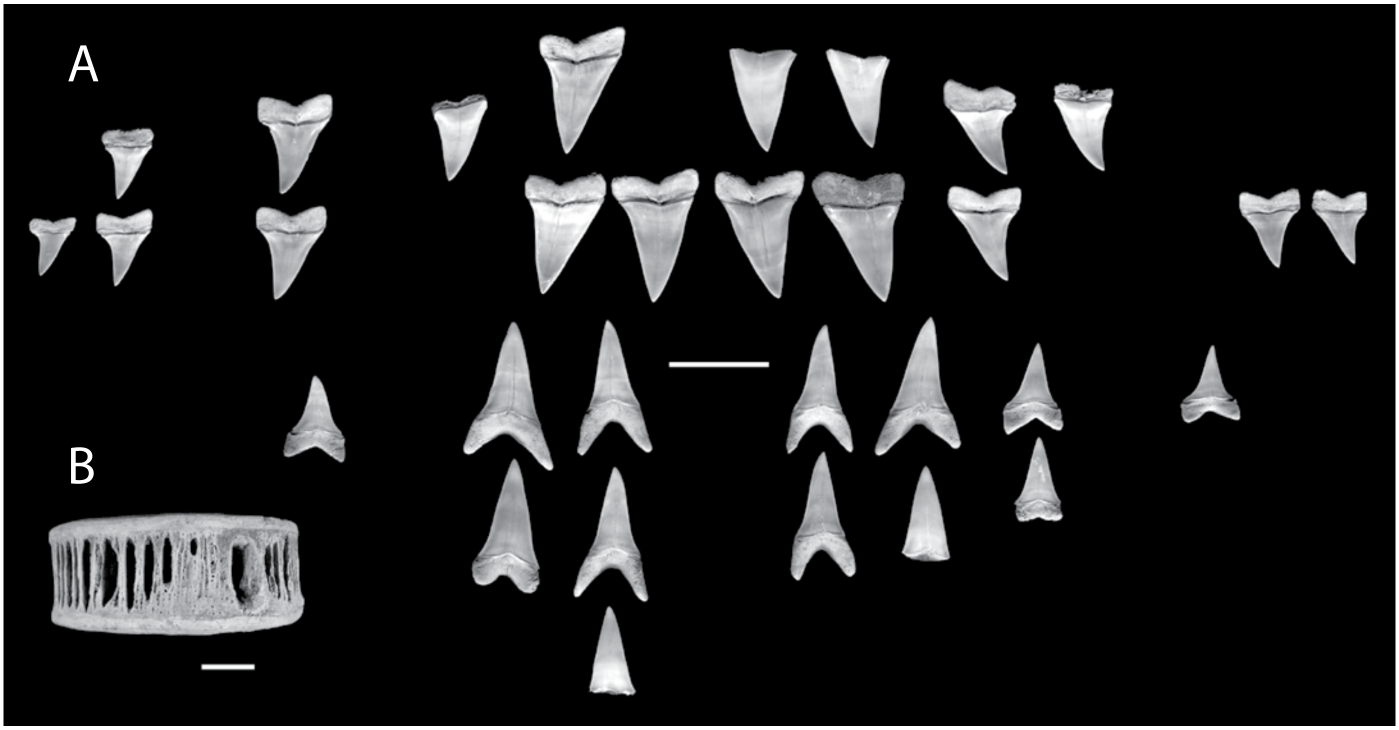


FIGURE 2.11. Associated teeth and centra of *Carcharodon hastalis* (CMM-V-245; Parkers Creek, Maryland). (A) Reconstructed dentition (lingual view; 5 cm scale bar on symphysis). (B) Vertebral centrum (three-quarters view; enlarged 1 cm scale bar).

height-width ratios, and coronal angles were evaluated in these six dentitions to help assign the Calvert Cliffs teeth to positions in the jaws. Anterior teeth were most easily assigned to position, but lateral teeth exhibit greater variability between individuals and species, and the positions of these teeth in Figure 2.11A are more provisional.

An additional thirty-second tooth from the assemblage is not included in the reconstructed dentition. This is a narrow, moderately sized tooth (height = 36.8 mm) that almost certainly represents an upper second anterior of a smaller individual.

The centra from the association are largely intact, discoidal cylinders with straight sidewalls, diameters between 34.3 and 62.0 mm, and diameter-to-length ratios of 2.22–2.80. They have the typical septate condition present in lamniforms, with large numbers of closely spaced septa. The septa are relatively straight and simple, although they have a tendency for one or two dichotomous branchings at their anterior and posterior ends. They are comparable to those of *C. carcharias* described by Kozuch and Fitzgerald (1989) and those of *Carcharodon hubbelli* (Ehret et al., 2009a: fig. 9; 2012: fig. 8). Extant *Isurus* centra have septa with a distinctive pattern of complex reticulated branchings at their anterior and posterior ends (Kozuch and Fitzgerald, 1989). Small areas on a few of the associated centra (Figure 2.11B) resemble this pattern, but it is unclear whether these represent true reticulations or the remnants of an incompletely preserved superficial cartilage. Overall, the morphology of the centra is much closer to *C. carcharias* than to *Isurus* and provides additional evidence for placing these broad-toothed sharks in the genus *Carcharodon*.

Exceptionally large anteriors of *C. hastalis* from Calvert Cliffs resemble the broad, markedly triangular teeth of *C. plicatilis*. This tooth morphology is purportedly also present in smaller individuals of *C. plicatilis* (Purdy et al., 2001). Although a few large teeth with broader crowns are known (e.g., Figure 2.10C), there is no persuasive evidence from Calvert Cliffs for smaller teeth with the *C. plicatilis* morphology. Further, in the associated set of teeth discussed above (Figure 2.11) the upper anteriors have broad, triangular *plicatilis*-like crowns but retain the more rounded root lobes of smaller specimens. The laterals and lower anteriors in the tooth assemblage are of typical *hastalis* morphology. On the basis of the absence of the *plicatilis* tooth morphology in either smaller individuals or the lateral teeth of large individuals, all of these teeth from Calvert Cliffs are referred to *C. hastalis*.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. The teeth of *C. hastalis* have been collected along the length of Calvert Cliffs as beach specimens. Teeth have also been collected in place from beds 3, 10–14, 17 (or 19), and 24 from Calvert Cliffs and river exposures of bed 1. This is the most abundant large shark from Calvert Cliffs, and more than 200 teeth were available for study.

Carcharodon hastalis has a very wide geographic distribution, having been found from the late Oligocene (Chattian) through late Miocene (Messinian) in Belgium, Chile, Cuba, Fiji, Germany, Japan, Malta, the Netherlands, Peru, Poland, Portugal, and Spain, as well as Maryland, North Carolina, and Virginia (Radwański, 1965; Hirota, 1979; Cappetta, 1987, 2012; Nolf, 1988; Kent, 1994; Yabumoto and Uyeno, 1994; Iturralde-Vinent et al., 1996; Antunes et al., 1999a; Müller, 1999; Purdy et al., 2001; Ward and Bonavia, 2001; Vicens and Rodríguez-Perea, 2003; Suarez et al., 2006; Wijnker et al., 2008; Reinecke et al., 2011; Bor et al., 2012; Everaert, 2014; Landini et al., 2017; BWK, pers. obs., USNM 22504).

Carcharodon subserratus **Agassiz, 1843**

FIGURE 2.10F–H

1970 *Isurus* cf. *oxyrinchus* var. *escheri* Rafinesque – Antunes and Jonet, pp. 140–143, fig. 21.
1987 *Isurus escheri* Agassiz – Cappetta, p. 96.
2006 *Carcharodon escheri* (Agassiz) – Cappetta, p. 78.
2008 *Carcharodon escheri* (Agassiz) – Mewis, pp. 23–28, pls. 4, 5.
2009 *Isurus escheri* (Agassiz) – García et al., p. 681, fig. 5c,d.
2015 *Carcharomodus escheri* (Agassiz) – Kriwet et al., pp. 862–870, figs. 10, 11.

Description. This species has teeth that resemble those of similarly sized *C. hastalis*, except for the presence of fine crenulations on the cutting edges. The teeth are exceptionally rare in the cliffs and presently known only from four specimens of moderate size. As with *C. hastalis* teeth of comparable size, the crowns are comparatively narrow, and the root lobes are somewhat elongated. The crenulations are small and inconspicuous and can be easily overlooked during a casual inspection. Partially serrate *C. subserratus* teeth are also known from the Chesapeake Group, some of which also have a simple, triangular cusplet on each shoulder (Figure 2.10G). Specimens with crenulations on the cusplets are also known (Figure 2.10H).

Discussion. The teeth identified here as *C. subserratus* are more commonly listed in the paleontological literature with the specific name of *escheri*, which has produced confusion as to the correct name (Antunes and Jonet, 1970; Cappetta, 1987, 2006, 2012; Bourdon et al., 2005b; Mewis, 2008). The original description of *Carcharodon escheri* (Agassiz, 1843: tbl. 36, figs. 16–21) is of a pair of lateral teeth, one an upper and the other a lower. Purdy et al. (2001) considered the type specimens of this species to represent a crenulated form of *Isurus oxyrinchus* on the basis of the presence of slightly recurved coronal apices that do not occur in *C. plicatilis*. Although this distinction is generally true, lateral teeth with recurved apices do occur in the morphologically similar *C. hastalis* (BWK, pers. obs.), and it seems imprudent to ally the type specimens with *I. oxyrinchus*.

A second difficulty with the specific name *escheri* is that Agassiz earlier named another tooth with crenulated cutting edges (Agassiz, 1843: tbl. 36, figs. 14, 15) *Carcharodon subserratus*. This tooth (NHMUK P. 2356) is taller and narrower than those shown for Agassiz's *C. escheri* and likely represents an upper anterior tooth. The tooth has an unusual indentation near the base of the distal cutting edge, which is associated with a convex distal heel. Further, when viewed in profile, the tooth has unusual depressions on both the labial and lingual faces of the crown and likely represents a slightly pathological specimen. Unfortunately, the locality where this specimen was originally collected (London Clay, Sheppey, UK) is suspect, as it would put this specimen in the early Eocene (Ypresian), rather than the Miocene (Cappetta, 2006, 2012). An Eocene age assignment is unlikely, and this tooth was more likely collected from the Miocene beds of Belgium or the Netherlands (David Ward, Natural History Museum, London, pers. comm., 2016). Despite this confusion about the locality of *subserratus*, Woodward (1889:411) regarded it as the senior synonym of *escheri* on the basis of both page and figure priority. Consequently, the specific name *subserratus* is used here for these crenulated North Atlantic teeth.

The crenulation size of a Calvert Cliffs upper anterior *C. subserratus* (CMM-V-4173; Figure 2.10F) was compared to those of similar-sized upper anterior *C. subserratus* teeth from the Berchem Formation of Antwerp, Belgium (UMCP 10055 and UMCP 11104). Ten randomly selected crenulations were measured on the distal cutting edge of each tooth. Although the crenulations were slightly smaller on the Calvert Cliffs tooth (mean = 0.82 mm) than the Belgian teeth (mean = 1.05 and 0.93), the differences were not significant (one-way ANOVA, $F_{2,27} = 2.35$, $P = 0.115$), and there was broad overlap in crenulation size between the teeth.

Ehret et al. (2012) considered C. *subserratus* to be more closely related to *Isurus* than to *C. hastalis*, primarily on the basis of the shape of the root lobes. However, their arguments are based on comparisons between the broader, triangular crowns and more rectilinear roots of *C. plicatilis* (Pliocene representatives of their chronospecies *C. hastalis*). The more appropriate comparison is between contemporaneous middle Miocene *C. subserratus* and *C. hastalis*. Teeth of these two species have similar morphologies and, except for crenulations on the former species, can be easily confused. A placement of *C. subserratus* in *Carcharodon* is more plausible than an assignment to *Isurus*.

Mewis (2008) reconstructed the dentition of C. *subserratus* on the basis of a partially disassociated assemblage of 42 teeth and 49 vertebral centra from the Miocene of Germany. Teeth within the dentition exhibited substantial variation, including cusplets on some teeth and smooth cutting edges on others. Subsequently, this assemblage was used to erect a new genus for this species (Kriwet et al., 2015; as *Carcharomodus escheri*), but there seems to be little justification for this new, monotypic genus.

Stratigraphic and Geographic Ranges. Fossils of *C. subserratus* are apparently restricted to the North Atlantic, having been previously documented from the middle Miocene through early Pliocene of Belgium, Germany, Portugal, and Spain (Antunes and Jonet, 1970; van den Bosch et al., 1975; Moths, 1998; Andres, 2002; Mewis, 2008; García et al., 2009). In the Mid-Atlantic of the eastern United States, *C. subserratus* is known from only four teeth, one from bed 19 of the Choptank Formation (John Nance, Calvert Marine Museum, Solomons, Maryland, pers. comm., 2016) and three from localities associated with the Choptank and St. Marys Formations (Figure 2.10F–H).

Crenulated *Carcharodon* teeth have also been reported from the Pacific, but these appear to represent an independent acquisition of these modifications to the cutting edges (Nyberg et al., 2006; Cappetta, 2012, as "*Carcharodon*" *escheri*; Ehret et al., 2012).

Fossil *Carcharodon* teeth with coarsely serrated cutting edges have typically been referred to the extant species, *C. carcharias*, although a number of other names have been proposed that are generally considered junior synonyms (Cappetta, 1987, 2006). Newton (1997) used relative warp analysis to determine that 5-MY-old fossil *Carcharodon* teeth were narrower and had larger basal serrations than those of either 3-MY-old fossil teeth or Holocene *C. carcharias* teeth, suggesting that a reanalysis of older fossils was warranted. Subsequently, Ehret et al. (2012) erected the name *C. hubbelli* for a large, well-preserved set of associated teeth and vertebral centra from the late Miocene of Peru that have crowns that are narrower and less prominently serrated than younger *C. carcharias*.

***Carcharodon carcharias* (Linnaeus, 1758)**

FIGURE 2.12A–E

Synonymy follows Marsili (2006) and Adnet et al. (2010).

Description. Great white sharks (*C. carcharias*) are exceptionally rare from Calvert Cliffs and are represented by only three teeth of uncertain origins. The remarkably large specimen shown in Figure 2.12A (CMM-V-7031) is an upper anterior from an old amateur collection. The exact context of this tooth is unknown but is purportedly a beach-collected tooth from the northern half of Calvert Cliffs. This tooth has a relatively broad, triangular crown with coarsely serrate, nearly straight cutting edges. Both faces of the crown are convex, although the labial face is only weakly so. There is a narrow neck on the labial face of the root. The root is moderately thick with cloacal nutrient pores basal to the thickest portion of the root. The root lobes are abbreviated, rounded, and joined at a very large obtuse angle.

The second Calvert Cliffs specimen (Figure 2.12B; CMM-V-5806) was beach collected (Visaggi and Godfrey, 2010) from the northern end of Calvert Cliffs. It consists of a triangular crown of moderate size with coarsely serrated cutting edges. Although the crown is intact, the root is missing. The morphology of the crown is consistent with that of an upper anterior tooth.

The final specimen (Figure 2.12C; USNM 336204) was collected in situ from the Plum Point Member (bed 10) and has previously been illustrated by Purdy (1996: fig. 3D) and Gottfried and Fordyce (2001: fig. 7). The crown is broadly triangular and semi-erect, with relatively coarse serrations. The crown is moderately compressed, and both the labial and lingual faces are weakly convex. The root is partially eroded, and the mesial root lobe is incomplete. The distal root lobe is short and rounded, and the basal root margin is weakly arcuate to broadly obtuse.

Discussion. There is some controversy about the earliest appearance of coarsely serrate *Carcharodon* in the fossil record, with a number of reports from the early through late Miocene (Leriche, 1927; Hatai et al., 1974; Purdy, 1996; Tanaka and Mori, 1996; Stewart, 1999, 2000; Yabe, 2000; Gottfried and Fordyce, 2001; Stewart and Perry, 2002; Boessenecker, 2011; Cione et al., 2012). The specimens from Maryland are some of the oldest known representatives, so their identity and context must be carefully assessed. The largest of the three is a complete upper anterior tooth that is undeniably referable to *C. carcharias* and was reported to have been a beach specimen from the northern half of Calvert Cliffs. The enameloid has a dull, matte patina, and the tips of most of the serrations are worn, both of which are consistent with a beach specimen. But its provenance is suspect because there is no direct documentation of its collection. The specimen is also very large, relatively wide, and triangular, a shape typically seen in Pliocene specimens (e.g., Purdy et al., 2001; Ehret et al., 2012).

The assessment of this tooth is complicated by the documented trade in fossil and Holocene shark teeth by Native Americans. Large teeth of *C. carcharias* were particularly valued and are represented at exceptionally high frequencies in archeological sites from the Chesapeake Bay to Ohio (Colvin, 2011; Lowery et al., 2011). There are a number of Native American sites along the western shore of the Chesapeake Bay, so the possibility that CMM-V-7031 represents an unmodified Native American trade tooth cannot easily be dismissed. Robert Purdy (in Lowery et al., 2011) suggests the Choptank Formation (middle Miocene) in Caroline County, Maryland, on the opposite shore of the Chesapeake Bay from Calvert Cliffs as a likely source of these teeth. A reevaluation of the four *C. carcharias* teeth from this locality (cataloged as USNM 235 and USNM 407) indicates that they are highly variable in color and degree of mineralization and are unlikely to have been derived from the same formation. The teeth were not collected in situ and may themselves represent trade teeth.

The other two specimens are smaller and less complete, with only an isolated crown in CMM-V-5806 and a crown with a nearly complete, but poorly preserved, root in USNM 336204. The identification of these incomplete teeth is difficult, since the Miocene sediments of Calvert Cliffs overlie Paleogene marine sediments. These sediments contain numerous shark teeth that can be reworked into the younger Miocene sediments at

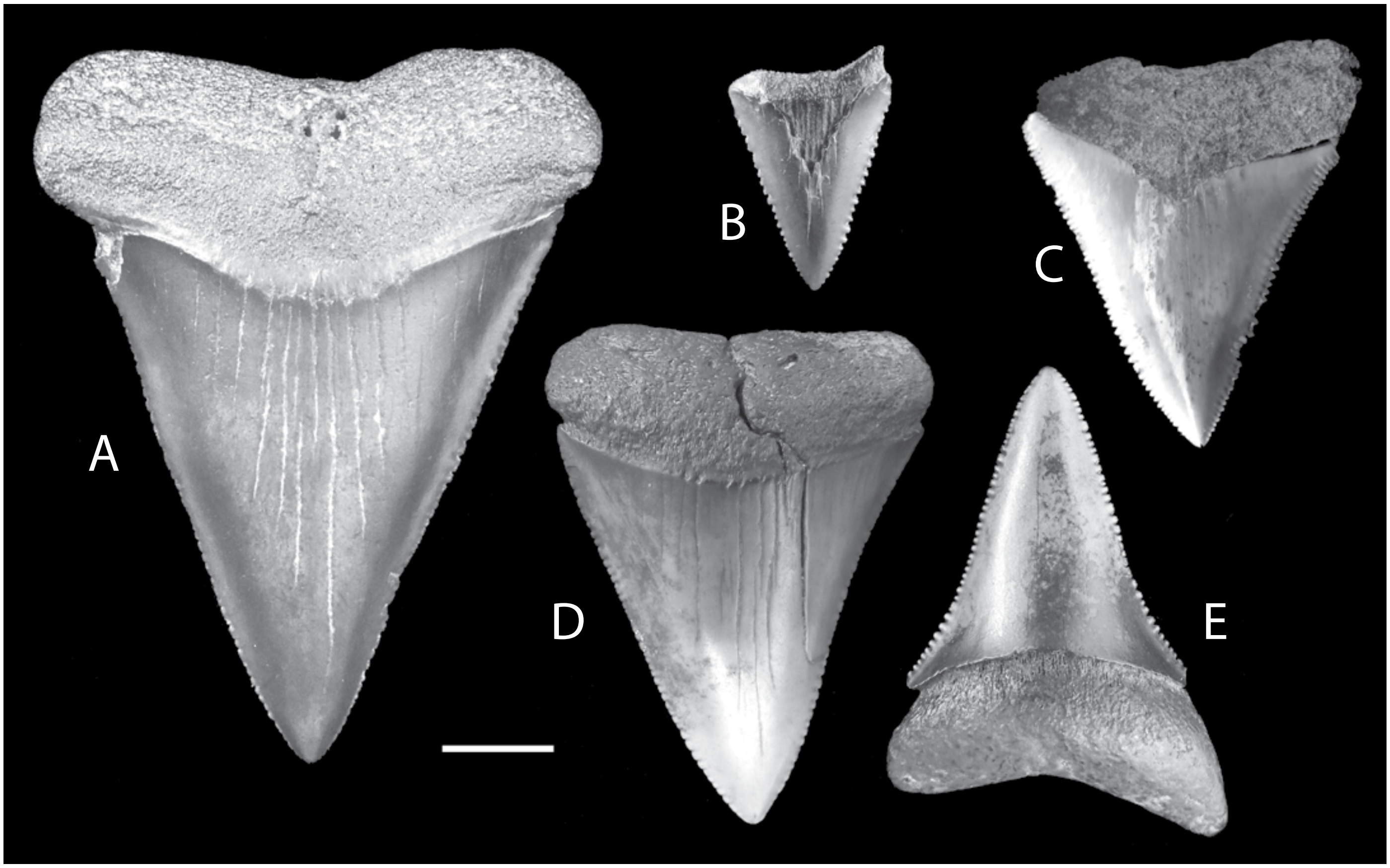


FIGURE 2.12. Purported *Carcharodon carcharias* teeth from the Chesapeake Group (1 cm scale bar). (A) First upper anterior tooth, lingual view (CMM-V-7031; indeterminate location, northern Calvert Cliffs, Maryland). (B) Upper anterior tooth fragment, lingual view (CMM-V-5806; Dares Beach–Plum Point, Md.). (C) Right upper lateral tooth, lingual view (USNM 336204; bed 10, Camp Kaufmann, Md.). (D) Right upper anterior tooth, lingual view (CMM-V-7734; St. Marys/Eastover Formation(?), Southampton County, Virginia). (E) Left lower anterior tooth, lingual view (CMM-V-7734; St. Marys/Eastover Formation(?), Southampton County, Va.).

the extreme northern end of the cliffs (Bayfront Park to Randle Cliff; Shattuck, 1904:lxxii; BWK, pers. obs.). Among the teeth potentially present in these older sediments of the Chesapeake Bay area are those of the rare species *Palaeocarcharodon orientalis* (Sinzow). Intact *C. carcharias* and *P. orientalis* anterior teeth can easily be recognized on the basis of differences in root and enameloid shoulder morphology, but these diagnostic areas are missing on CMM-V-5806. The gross morphology of this tooth is consistent with both *Carcharodon* and *Palaeocarcharodon*. Serrations of the former genus are perpendicular to the cutting edges, whereas those of the latter have a tendency to angle slightly toward the coronal apex. Serrations on CMM-V-5806 are perpendicular to the cutting edge, but since this orientation was also observed in some *P. orientalis* (BWK, pers. obs.), this characteristic is not definitive.

Serration width on CMM-V-5806 was compared with similarly sized teeth of *P. orientalis* from Maryland (CMM-V-4336) and *C. carcharias* from Lee Creek Mine, North Carolina (CMM-V-864). The basal width of 10 randomly selected serrations from both the mesial and distal cutting edges of each tooth were measured and statistically analyzed with a one-way ANOVA. There were no significant differences in serration size among the teeth ($F_{2,57} = 1.670$, $P = 0.197$). The absence of a root on CMM-V-5806 complicates an unambiguous assignment of this tooth to *Carcharodon*. This specimen was collected from the beach and has the dull, abraded enameloid and worn serrations typical of such specimens. The crown is tall and triangular, consistent with an upper anterior of either *C. carcharias* or *P. orientalis*. However, the serrations are more prominent than in the late Miocene (Messinian) *C. hubbelli* from Peru, and an assignment of this specimen to *Palaeocarcharodon* is plausible.

The third specimen (USNM 336204) was collected in situ (bed 10) with very specific locality data and has glossy enameloid and intact serrations, suggesting that it was unlikely to have been reworked from older sediments. The broadly triangular semierect crown is comparable to upper lateral teeth of *Carcharodon* but very different from the narrower, more oblique crowns of upper *P. orientalis* teeth. Further, the distal shoulder of this tooth is nearly intact but has no evidence of the distinctive coarsely serrate cusplet that would be present on a *P. orientalis* tooth (Cappetta, 1987; Case, 1989, 1993; Kent, 1994; Purdy, 1998c).

Ehret et al. (2012) reevaluated USNM 336204 and concluded it is actually a small *C. megalodon* and not *C. carcharias*. They note three unusual features of this tooth: (1) the crown is too thick for *C. carcharias*, (2) the angled basal margin of the crown on the lingual face is inconsistent with *C. carcharias*, and (3) the serrations are somewhat coarser than is typical for *C. megalodon*. Although this identification is plausible, it cannot be verified on the basis of the anecdotal evidence they provide. In particular, the morphology of this tooth has some resemblance to larger neonatal teeth of *Carcharocles* from Calvert Cliffs. Their reassignment of this tooth was tested by comparing it to similarly sized neonatal *Carcharocles* teeth from Calvert Cliffs (Figure 2.14C–F; see the *C. megalodon* section for a more detailed description of these neonatal teeth).

Neonatal teeth of *Carcharocles* have a crown that is particularly thick, largely because of a convex labial face, producing a lenticular cross section on the apical half of the crown. This convexity is most pronounced on small anterior teeth (<20 mm) and declines as tooth size approaches 50 mm. USNM 336204 has a convex labial face and lenticular cross section. Although this compares favorably with that of neonatal *Carcharocles*, a similar, if somewhat less pronounced, lenticular cross section infrequently occurs in *C. carcharias* (BWK, pers. obs.). The coronal thickness of USNM 336204 was compared to that of seven upper neonatal *Carcharocles* teeth of roughly similar size (UMCP 12599-12604, USNM 639784). To compensate for slight differences in tooth size, thickness was expressed as relative coronal thickness (tooth thickness at mid-crown divided by tooth height). Many statistical procedures for comparing a single observation with a sample suffer from an elevated type 1 error rate, so the data were analyzed with the Crawford and Howell (1998) modification of the special-case *t*-test proposed by Sokal and Rohlf (1995:227–229). The relative coronal thickness of USNM 336204 (0.168) was not significantly different from those of the seven neonatal *Carcharocles* teeth examined (mean = 0.187; Crawford-Howell modified *t*-test, $t = 0.711$, $P = 0.504$).

The angular basal coronal margin on the lingual face is common in *Carcharocles* but is also known, if rare, in *C. carcharias* (BWK, pers. obs.). The important distinction between the two is that the angled margin in *Carcharocles* is associated with a broad, chevron-shaped neck covered with orthodentine, whereas in *C. carcharias* the neck is narrow and relatively inconspicuous. The chevron-shaped neck on *Carcharocles* neonatal teeth is distinct but is also quite delicate and is incomplete to absent on many specimens. In some of these specimens, the shape and breadth of the neck are still detectable as a smooth area immediately basal to the enameloid. Unfortunately, the root in USNM 336204 is too poorly preserved to reconstruct the shape of the neck, and the basal margin angle is the only available metric. The basal coronal angle on the lingual face of USNM 336204 (=131°) was compared with the same seven upper neonatal teeth used to examine coronal thickness (UMCP 12599–12604; USNM 639784). There was no significant difference in basal angle between the *Carcharocles* neonatal teeth (mean = 123°) and USNM 336204 (Crawford-Howell modified *t*-test, $t = 0.628$, $P = 0.553$).

The serrations of USNM 336204 were compared with the two upper neonatal *Carcharocles* teeth most similar in overall size (UMCP 12602 and UMCP 12603). Twenty randomly selected serrations from each tooth were measured on photographic enlargements. There was no significant difference in serration size between these three teeth (one-way ANOVA; $F_{2,57} = 0.510$, $P = 0.603$). Serration size in USNM 336204 is fully comparable with that of neonatal *Carcharocles*.

In summary, using the three attributes first suggested by Ehret et al. (2012), USNM 336204 appears to be more closely allied to *Carcharocles* than to *Carcharodon*. The crown is statistically indistinguishable in thickness from those of neonatal *Carcharocles*, although it is among the thinner teeth measured. Likewise, the angled basal coronal margin on the lingual face is not statistically different from those of the neonatal *Carcharocles* examined. Finally, contrary to Ehret et al. (2012), USNM 336204 does not have coarser than expected serrations; there was no significant difference in serration size between this tooth and the two neonatal *Carcharocles* of similar size. Taken as a whole, there is no convincing evidence to retain USNM 336204 within *Carcharodon*. Instead, its overall morphology is consistent with a neonatal, or transitional neonatal-juvenile, *Carcharocles* tooth.

None of the three alleged *C. carcharias* teeth from Calvert Cliffs can be accepted as proof of this species in the late to middle Miocene of the western Atlantic. There is better evidence that late Miocene *Carcharodon* may have been present, if uncommon, in the St. Marys Formation (Tortonian) or Eastover Formation (Messinian) of Virginia on the basis of 13 teeth from site #PQ-BH9812 in Southampton County, Virginia. None of the teeth were collected in situ, but at this site the St. Marys and Eastover Formations are overlain by unfossiliferous Pleistocene/Holocene sands. Further, Pliocene beds from which the teeth could have been derived are not present at either this site (A. Alford, National Network of Public Health Institutues, Washington, D.C., pers. comm., 2015) or nearby USGS core holes (Weems et al., 2010). Finally, these specimens are unlikely to have been Native American trade teeth, as they all have similar, distinctive permineralization that corresponds to that of other St. Marys or Eastover vertebrate fossils from this locality. The difficulty in interpreting these teeth is that they are relatively broad and comparable in morphology to those of *C. carcharias*, rather than late Miocene *C. hubbelli*. However, none of these 13 teeth were collected in context, and despite the absence of younger fossiliferous horizons from which they could have been derived, they do not provide irrefutable evidence for this species in the late Miocene (Tortonian-Messinian). Research is continuing at this site, which could help clarify the ultimate source of these teeth.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Carcharodon carcharias* is not reliably known from Calvert Cliffs, although teeth collected from Virginia suggest there is a slight possibility they could be present in the St. Marys Formation at the southern end of the cliffs. Likewise, Miocene records of *Carcharodon* from other areas are rare and in many cases very poorly documented (Andres, 2006), although several reasonably reliable reports of this genus are known:

- Iturralde-Vinent et al. (1996) reported the presence of *C. carcharias* from the early to middle Miocene of Cuba (Cojímar Formation), although the teeth were not illustrated.
- Reis (2005) lists five lower *C. carcharias* teeth from the early Miocene Pirabas Formation of northern Brazil and illustrates one specimen (fig. 11). This figure is somewhat indistinct, but the morphology seems consistent with that of *Carcharodon*.
- Walsh and Suárez (2005) report *C. carcharias* teeth from a bone bed in the Bahía Inglesa Formation of Chile. Teeth are not illustrated, so the reliability of this identification is unclear. But the teeth were collected below an ash layer in the lower part of the Lechero Member with a K-Ar date of 7.6 ± 1.3 MYA and can be no younger than the late Miocene (Tortonian) and no older than middle Miocene. Walsh and Suárez (2005) also report that *C. carcharias* teeth are much more commonly collected above the ash layer in early Pliocene portions of the Bahía Inglesa Formation. Unfortunately, they do not discuss the possibility that these early Pliocene teeth could have been reworked into older horizons by bioturbational burrowing.
- Cione et al. (2012) describe and illustrate teeth of a *Carcharodon* sp. collected in situ from the late Miocene Paraná Formation of Argentina. Although these teeth are somewhat worn, they conclude that the serrations are larger and more distinct than those of *C. subserratus* but slightly smaller and less well defined than those of Pliocene and extant *C. carcharias*.
- Ehret et al. (2012) recalibrated the stratigraphy of the specimen earlier described as *Carcharodon* sp. (Ehret et al., 2009a), moving it to the late Miocene and naming it as a new species, *C. hubbelli*. This is the single most reliably documented late Miocene *Carcharodon* and firmly establishes fully serrated species of this genus in the eastern Pacific.

Carcharodon (usually as *C. carcharias*) is far more widely, and definitively, known from early Pliocene and younger sediments, including both coasts of North and South America, Japan, Australia, southern and western Africa, and southern Europe (Cappetta, 1987; Kemp, 1991; Scudder et al., 1995; Stewart, 1999, 2000; Yabe, 2000; Purdy et al., 2001; Stewart and Perry, 2002; Walsh and Suárez, 2005; Andres, 2006; Marsili, 2007a; Adnet et al., 2010; Ehret et al., 2012).

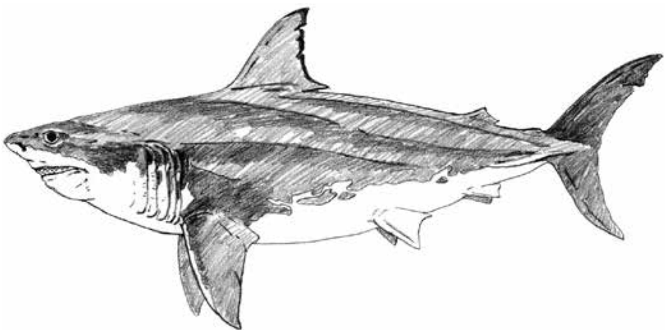
EVIDENCE OF FEEDING. Extant *Carcharodon* are primarily piscivorous as juveniles and shift to marine mammals (e.g., seals, sea lions, cetaceans) as adults (Tricas and McCosker, 1984; McCosker, 1985; Long and Jones, 1996; Estrada et al., 2006). Living *C. carcharias* are primarily described as active predators (Compagno, 1990b), but scavenging on marine mammal carcasses is known for both juveniles and adults (Carey et al., 1982; Dicken, 2008; Fallows et al., 2013). Carey et al. (1982) have even argued that meals of energy-rich mammalian blubber are necessary for large *C. carcharias* to undertake long-distance, open ocean migrations.

Determining whether feeding in extinct *Carcharodon* species was comparable to that of the extant *C. carcharias* is difficult, although bite marks on, or shark teeth associated with, marine mammal skeletons can provide evidence of predatory attacks or scavenging events. In a few cases the predatory/scavenging habits of fossil *C. carcharias* have been documented in the fossil record, and as with observations on extant *C. carcharias*, attacks are principally on cetaceans (Deméré and Cerutti, 1982; Cigala-Fulgosi, 1990; Bianucci et al., 2000; Ehret et al., 2009b). To date, there are no studies documenting piscivory by *C. carcharias* in the fossil record.

The similarity in tooth morphology between serrate and unserrate *Carcharodon* would suggest at least some similarity in diet. Purdy et al. (2001) attribute unserrated bite marks on the humerus of a phocid seal to *C. plicatilis* (listed as *I. xiphodon*). A large upper anterior tooth from the St. Marys Formation (CMM-V-3777; height = 71.0 mm, width = 50.1 mm) was associated with a shark-tooth-marked cetacean skeleton (*Cephalotropis coronatus* Cope, CMM-V-3277). Bite mark evidence for unserrated *Carcharodon* utilizing cetaceans as a food source also has been reported from Argentina (Noriega et al., 2007) and Italy (Bianucci et al., 2010). Collareta et al. (2017b) have described a unique juvenile *C. hastalis* skeleton from Peru with a number of pilchard (*Sardinops* cf. *S. sagax*) fossils in the abdominal region. These teleost fossils were interpreted as ingested prey and indicate the diet of juvenile *C. hastalis* was comparable to that of juvenile extant *C. carcharias*. As previously discussed, there is evidence in the form of a caudal spine embedded in a *C. hastalis* tooth (Figure 2.2) that this species preyed on myliobatiform rays. Curiously, the ubiquitous unserrated *Carcharodon* species were not quickly supplanted by serrated *Carcharodon* species and continued as the most abundant lamnids through the early Pliocene. The presence of numerous other large macrophagous sharks may have simply maintained populations of different *Carcharodon* species at levels low enough to preclude extensive direct competition for resources.

Family Otodontidae Glikman, 1964

Genus *Carcharocles* Jordan and Hannibal, 1923



Megatooth Sharks – *Carcharocles*

The extant great white shark (*Carcharodon carcharias*) has cutting teeth that are broad and compressed and have serrated cutting edges. These teeth are ideally suited to slicing chunks of flesh from large vertebrate prey, such as fishes and marine mammals. A number of fossil lamniforms have teeth with similar morphology and are frequently referred to as "fossil white sharks." In this context, there has been a long, ongoing discussion about whether fossil white sharks represent a monophyletic clade allied with *C. carcharias* or a polyphyletic grade united by the convergent evolution of a common tooth morphology. These discussions are fundamental to understanding how white sharks evolved and their relationship to other lamniform groups. Most of these discussions have focused on the relationship of the large-toothed *Carcharocles megalodon* and its ancestral forms (variously known as megatooth sharks or giant white sharks) to the extant great white shark.

Currently, there are three competing models for the evolution and systematic placement of the megatooth sharks within the Lamniformes:

1. In the *Carcharodon* model, all fossil white sharks represent a single monophyletic clade and should be assigned to the genus *Carcharodon* with the extant *C. carcharias* (Dockery and Manning, 1986; Uyeno et al., 1989; Applegate and Espinosa-Arrubarrena, 1996; Gottfried et al., 1996; Purdy, 1996; Gottfried and Fordyce, 2001; Purdy et al., 2001). In this model white sharks are a clade, and all extinct and extant species are assigned to the family Lamnidae.
2. In the *Carcharocles* model, the megatooth sharks represent a separate lineage from that leading to the extant *C. carcharias* and should be placed in a separate genus. Several genera have been erected for this lineage, including *Carcharocles* (Jordan and Hannibal, 1923), *Procarcharodon* (Casier, 1960), and *Megaselachus* (Glikman, 1964). The genus *Carcharocles* has priority and has been used in preference to the other generic names (Cappetta, 1987:103; Ward and Bonavia, 2001; Bourdon et al., 2005a; Nyberg et al., 2006; Mewis, 2008; Ehret et al., 2009a). In this model the "white shark" tooth form is homoplastic, with the *Carcharocles* lineage placed in a separate family (Otodontidae) from that of the extant *Carcharodon* (Lamnidae).
3. The *Otodus/Megaselachus* model (Zhelezko and Kozlov, 1999; Cappetta, 2006) describes the evolution of megatooth sharks from the genus *Otodus* through the progressive acquisition of serrated cutting edges and loss of lateral cusplets. This model envisions a linear series of chronospecies arising by phyletic gradualism from the ancestral *Otodus obliquus* with smooth, unserrated cutting edges and cusplets. Zhelezko and Kozlov (1999: figs. 25–27) provide a detailed stratigraphic sequence of chronospecies to support their model. All cuspletted forms (regardless of the presence or absence of serrated cutting edges) are referred to the genus *Otodus*. Only the terminal, serrated, and noncuspletted species is placed in the monotypic genus *Megaselachus*, as *M. megalodon*. Cappetta (2006) alters this slightly by including serrate, but weakly cuspletted, species within *Megaselachus*. Both *Otodus* and *Megaselachus* are placed in the family Otodontidae, with *Carcharodon* in the Lamnidae. Cappetta (2012:224) further modified this model by placing all species within this lineage in the genus *Otodus*, containing three subgenera, *Otodus, Carcharocles* and *Megaselachus*.

Much of the discussion about megatooth shark evolution and systematics has focused on the *Carcharodon* and *Carcharocles* models, whereas the *Otodus/Megaselachus* model has received relatively little attention until recently. To some extent this lack of discussion of the third model reflects its status as simply a variant of the second that provides an alternative generic assignment of megatooth sharks. But at a deeper level, the *Otodus/Megaselachus* model hypothesizes a fundamentally different mechanism for megatooth shark evolution based on anagenesis, or phyletic gradualism. Anagenesis occurs by the slow accumulation of mutations over time, producing a linear series of progressively different chronospecies that do not overlap in time. This process differs from cladogenesis, where speciation occurs rapidly by divergent branching events and sister species overlap in time. In general, paleontologists prefer cladogenesis as an evolutionary model since it more closely matches the common speciation models in evolutionary biology, although both anagenesis and cladogenesis have been documented in the fossil record (Freeman and Herron, 2004:679–680; Foote and Miller, 2007:82).

There are several inherent problems with documenting gradual, anagenetic evolution across the large time spans in the megatooth shark fossil record. First, the stratigraphic range of a species in the fossil record is almost always an underestimate of the actual temporal range because of inadequate or biased sampling (Smith, 1994:183–187; Foote and Miller, 2007:171–173). So the obvious question is whether the fossil record of the megatooth sharks is sufficiently detailed to demonstrate anagenesis. Freeman and Herron (2004:680) propose two criteria for distinguishing anagenesis from cladogenesis: (1) the phylogeny of the clade is known, and individual species can be identified, and (2) individual species survive long enough for ancestral and descendant species to temporally co-occur. Fundamental to this methodology is a fossil record that is simultaneously stratigraphically fine grained and geographically broad (Smith, 1994:186; Liow, 2010). This requirement is difficult to meet for rare species, such as the megatooth sharks. Certainly, we have megatooth sharks from many horizons and localities, but rarely do we have tightly correlated contemporary horizons that adequately represent the presumed geographic range of the species present at the time.

A second, related difficulty concerns the temporal resolution implicit in the chronospecies model of anagenesis. Zhelezko and Kozlov (1999: figs. 26, 27) designate stratigraphically distinct species and subspecies on the basis of serration shape and cusplet shape. Unfortunately, they do not discuss the range of variability within either chronospecies or chronosubspecies from specific horizons. Cusplet shape, in particular, is known to be morphologically disparate because of ontogenetic changes and position within the jaws (Menesini, 1974; Gottfried and Fordyce, 2001; Purdy et al., 2001) and the stratigraphic precision of the chronospecies proposed by Zhelezko and Kozlov is untested. In many respects the pattern observed in megatooth sharks closely parallels the situation for the dental evolution of rodents, where definitive separations are impossible due to wide morphological overlap (R. A. Martin, 1993, 1995). Martin proposed the term chronomorph to describe these complex, frequently mosaic, evolutionary changes in rodent tooth morphology. The chronomorph concept implicitly acknowledges the problem of individual variation in describing evolutionary change in dental-based taxa and provides a more plausible framework for investigating evolution in the megatooth sharks than the stratigraphically pristine designation of chronospecies. Operationally, chronomorphs can overlap in time, whereas chronospecies cannot, which allows these two models of anagenesis to be tested with a sufficiently detailed fossil record.

The final problem with the *Otodus*/*Megaselachus* model is the designation of genera and chronospecies within the lineage. Zhelezko and Kozlov (1999) and Cappetta (2006) use *Otodus* for the ancestral portion of the lineage, with *Megaselachus* for the single, terminal species, whereas Cappetta (2012) uses *Otodus* for the entire lineage. Distinctions within a phyletic lineage are, of necessity, based on arbitrary decisions about the degree of differences relative to morphological traits (Benton and Pearson, 2001; Liow, 2010; Aldhebiani, 2017). Further, such distinctions are based on tooth morphology and lack information from the whole body. In such situations it can be particularly difficult to detect anagenetic morphs since the critical differences either are not based on morphological differences (Charlesworth, 1990), or have not been preserved in the fossils.

Despite these difficulties of unambiguously identifying morphs within the megatooth shark lineage, it does provide a useful framework for viewing megatooth shark evolution. Ward and Bonavia (2001) acknowledge the utility of this model but merge it with the second model by using *Carcharocles* for serrated species within this group. Further, they concur with Menesini (1974) that specific names should be based on large, adult individuals. In the discussion that follows, this chronospecies perspective of megatooth shark evolution will be considered a plausible, if currently untestable, variant of the *Carcharocles* model.

The relative merits of the *Carcharodon* and *Carcharocles* models are complex and, in some cases, contentious. Arguments about the generic and familial assignment of megatooth sharks in these two models revolve around several lines of evidence, including dental morphology, vertebral centrum morphology, nutrient foramina morphology, heterochronic change, molecular divergence times, and stratigraphic ranges and first appearances in the fossil record.

DENTAL MORPHOLOGY. Extant *Carcharodon* and *Isurus* are both characterized by the presence of two upper anterior teeth in each half jaw, rather than the three present in the more primitive odontaspids. Applegate and Espinoza-Arrubarrena (1996) argued that *Carcharodon* has a symmetrical first upper anterior tooth, whereas *Isurus* has an asymmetrical first upper anterior. From this observation they concluded that the two upper anteriors in *Carcharodon* represented the first and third tooth positions in odontaspids, whereas those of *Isurus* were derived from the second and third ancestral tooth positions. On the basis of the nonhomology of the upper anteriors in *Carcharodon* and *Isurus*, the two genera could not be closely related.

Applegate and Espinoza-Arrubarrena provided no data to support this supposed difference in symmetry. In the same volume, Hubbell (1996) published data on coronal angle for upper anteriors in *Carcharodon*. A statistical analysis of Hubbell's data for the two anterior tooth positions demonstrates that they are statistically indistinguishable (paired t-test, $t = 0.200$, P 0.843). Shimada (2002) reached the same conclusion with a larger data set, although without statistical analysis. More importantly, Shimada evaluated dental homologies among extant lamniforms and demonstrated that the upper anteriors in *Carcharodon* and *Isurus* were homologous.

Nyberg et al. (2006) tested differences in tooth morphology in a more rigorous way and with more tooth positions (upper anteriors, lower anteriors, upper laterals, and lower laterals) using the generalized Procrustes method and principal components analysis. Both whole-tooth morphology and root morphology were analyzed for all four tooth positions and for four species, *C. megalodon, C. carcharias, C. plicatilis* (listed as *Isurus hastalis*), and the "Sacaco species" (a weakly serrated form subsequently named *Carcharodon hubbelli*; Ehret et al., 2012). For all four tooth positions for both whole-tooth morphology and root morphology, *C. carcharias, C. plicatilis*, and *C. hubbelli* clustered together and had little or no overlap with *C. megalodon* (Nyberg et al., 2006: figs. 4, 5).

The upper intermediate tooth of *C. carcharias* is large and has a crown inclined mesially, rather than distally as in other upper teeth (Applegate and Espinoza-Arrubarrena, 1996; Purdy et al., 2001). This condition is not diagnostic for any other extant lamniform, and Purdy et al. (2001) propose it as a synapomorphy for the genus *Carcharodon* and as a justification for suppressing *Carcharocles* as simply a junior synonym of *Carcharodon*. They provide no cladistic analysis to support this contention, relying instead on the disposition of the upper intermediate tooth in artificial tooth sets assembled from *C. megalodon* teeth.

No intact *Carcharocles* dentition has ever been collected. The best available evidence is based on disassociated assemblages of *Carcharocles* teeth from a single individual that have not been preserved in life position. Reconstructions of dentitions from such tooth assemblages (e.g., Uyeno et al., 1989; Gottfried and Fordyce, 2001; Purdy et al., 2001) use the extant *C. carcharias* dentition (with a reversed upper intermediate) as the model. This reconstructed dentition is then used as evidence to support the presence of a reversed upper intermediate tooth in *Carcharocles*. But in these reconstructions, assignment of an intermediate tooth to the right or left side of the dentition is determined solely by assuming a *Carcharodon*-like dentition with a reversed upper intermediate (Mewis, 2008; Ehret et al., 2009) and circular reasoning used to posit monophyly of *Carcharocles* and *Carcharodon* (Nyberg et al., 2006).

Extant *C. carcharias* have exceptionally large upper intermediate teeth when compared to other lamnids, including unserrated *Carcharodon* (Shimada, 2002; Mewis, 2008:79, fig. 15). Because of the development of teeth within dental bullae in lamniforms, the evolution of a reversed intermediate tooth in *Carcharodon* simply appears to be a developmental constraint of producing a large intermediate tooth within the confined space of the anterior dental bulla (Shimada, 2002: fig. 14). In this sense, a reversed upper intermediate may be an autapomorphy of this species. This possibility is supported by the largely intact fossil of *Carcharodon hubbelli* from the late Miocene of Peru with the teeth preserved in near-life position (Ehret et al., 2009a, 2012). The teeth of this species are unusual in that they are narrower and have weaker serrations than in *C. carcharias*. Further, the intermediate tooth is relatively small and has a distally directed crown. Overall, this specimen shares characteristics with both *C. hastalis* and *C. carcharias*.

Siverson (1989) stated that *C. megalodon* lacks the obvious dignathic heterodonty present in *C. carcharias*. Purdy et al. (2001:125) disagreed with this contention, arguing that it is present in *C. auriculatus* (Dockery and Manning, 1986: pls. 2, 3) and is "very marked" in juveniles and associated tooth sets (Purdy et al., 2001: figs. 34, 35). A visual inspection of the figures in these two publications indicates that there are differences in tooth shape when viewed from the lingual surface, but these differences are relatively subtle. The morphometric analysis of tooth shape by Nyberg et al. (2006) found that although anterior teeth could be assigned to the correct jaw on the basis of either whole-tooth morphology or root morphology, there was a high degree of overlap in both tooth and root morphology for lateral teeth. Although there are differences in coronal curvature between upper and lower teeth when viewed in profile, these are generalized lamniform symplesiomorphies, rather than synapomorphies of *Carcharodon* (sensu lato). On the basis of the currently available evidence, both Siverson (1989) and Purdy et al. (2001) were partially correct. The anterior teeth of *C. megalodon* can be reliably assigned to upper and lower jaws, although differences are not as obvious as in *C. carcharias*.

VERTEBRAL CENTRA. The large discoidal centra of *C. megalodon* are infrequently collected. The most complete set consists of about 150 associated specimens from Antwerp, Belgium (Leriche, 1926; Gottfried et al., 1996). Although this is a large number of centra from a single individual, the entire vertebral column is not present. The best estimates for the total number of centra in the entire vertebral column range from 190 to 200 centra (Gottfried et al., 1996; Gottfried and Compagno, 2006). This large number of centra is roughly comparable to the number in *C. carcharias*, providing some support for allying *C. megalodon* and *C. carcharias* in a single genus. Unfortunately, this argument is comparatively weak on two counts.

First, *C. carcharias* is the paradigm used for making these estimates. This paradigm implicitly assumes that the two species have similar numbers and proportions of precaudal and caudal centra. This assumption fundamentally constrains the reconstructed *C. megalodon* vertebral column to be a derivative version of that in *C. carcharias*. Under these circumstances, a similar number of centra would not be particularly surprising.

Second, claims of similarity in centra counts ignore disparities between *C. megalodon* and extant lamnids. Gottfried et al. (1996) estimate that *C. megalodon* had 130 precaudal centra. Comparable numbers for extant species are consistently lower, with 84–91 for *Lamna nasus*, 108–112 for *Isurus* spp., and 103–108 for *C. carcharias*. Likewise, the estimated total number of 190–200 centra is generally higher than those of these same extant lamnids: 150–162, 187–197, and 172–187, respectively (Springer and Garrick, 1964). By this criterion, *C. megalodon* would be more closely related to *Isurus* than to *Carcharodon*.

Vertebral centra counts in and of themselves are of limited utility in reconstructing taxonomic relationships since they represent a single, somewhat variable character without a clear phylogenetic signal. Conversely, details of morphology (Kozuch and Fitzgerald, 1989) and mineralization patterns (Gottfried and Compagno, 2006) of the centra are far more useful, as there are a number of taxonomically relevant characters present. Gottfried and Compagno (2006) provided the first qualitative comparison of the internal mineralization pattern of the centra and reported that they are comparable in *C. megalodon* and *C. carcharias*. This observation supports the congener status for these two species, although they did not place these conclusions in a phylogenetic context. Kraig (2008) used computerized tomography to evaluate internal structures more thoroughly, using cladistic techniques to assess the distribution of the external and internal structures of centra in lamniforms. In her analysis, *C. carcharias* aligned with *Isurus*, rather than with *C. megalodon*. This alignment is consistent with separate origins of *C. megalodon* and *C. carcharias*. Curiously, she also found that *C. megalodon* and the older *C. auriculatus* formed a clade that was a sister group to *Lamna nasus*. This association has not previously been hypothesized for the origins of *C. megalodon* and is diametrically opposed to the simpler vertebral count data shown above. The strength of this association is unclear; although a total of 35 characters were used in the analysis, many are based on ratios or covarying morphological features. This interdependence of features would reduce the number of independent characters and phylogenetic resolution to an unknown extent. But these results do provide new insights into lamniform relationships and merit a more extensive study that includes a larger number of species. An analysis that incorporated both vertebral characters, such as those in Kraig (2008), and dental characters (e.g., Shimada, 2005; Mewis, 2008) would likely provide even better resolution.

NUTRIENT FORAMINA. As discussed in the introduction to this chapter, the evolution of large tooth size is under strong fractal constraints arising from the need to produce a greatly elaborated capillary system within developing teeth. In *C. megalodon* teeth, the nutrient foramina are dispersed in an arc over the lingual face of the root and are added in a straightforward and predictable way during development (Kent, 1994). Small individuals have teeth with a single, medial nutrient foramen located at the thickest portion of the root. In progressively larger teeth, additional foramina are added laterally. If *C. carcharias* arose from *C. megalodon*, the nutrient foramina of *C. carcharias* should increase in number by following the same developmental pathway, with perhaps a different terminal condition. The smallest teeth in *C. carcharias* have a single medial pore, although it is located closer to the basal margin of the root than in *C. megalodon*. As tooth size increases, additional pores are added as a tight cluster. In the largest teeth, the pore cluster frequently fuses to form a single large opening. This cloacal pore condition in the largest teeth (Kent, 1994), and the developmental sequence that produces it, is very different than the pattern in *C. megalodon* but is like that of fossil smooth-edged *Carcharodon* and, to a lesser extent, *Isurus*.

HETEROCHRONIC CHANGES. Gottfried and Fordyce (2001) and Purdy et al. (2001) argue that the apparent differences between *C. megalodon* and *C. carcharias* are simply size-related ontogenetic effects and that similarly sized teeth of the two species are comparable in shape and serration size. In this view, the two species share the same developmental pathway, and morphological differences arise by heterochronic mechanisms. Unfortunately, heterochrony can be difficult to evaluate in fossils since it reflects a three-way interaction between age, size, and shape. With isolated fossil shark teeth age cannot be determined, and heterochronic processes cannot be directly evaluated. McKinney and McNamara (1991) proposed the simplifying assumption that if size and age are correlated, then allometric relationships are a reasonable proxy for heterochronic relationships.

Nyberg et al. (2006) used this assumption and were able to test both of these suppositions about heterochronic relationships between *C. megalodon* and *C. carcharias*. Ontogenetic changes in tooth morphology were evaluated for three species, *C. megalodon*, *C. carcharias*, and *C. plicatilis* (listed as *I. hastalis*). Nyberg et al. (2006) used the relationship between two derived variables, approximated tooth area (=size metric) and aspect ratio (=shape metric), to test for similarities in developmental trajectories. They restricted this portion of their study to upper and lower anteriors since these tooth positions exhibited less intraspecific variation. Data were analyzed with reduced major axis regression. For both upper and lower anteriors, *C. carcharias* and *C. plicatilis* shared similar slopes and *y* intercepts and were very different in both respects from *C. megalodon* (Nyberg et al., 2006: figs. 6, 7).

Serration size was measured in three megatooth species (*C. auriculatus*, *C. subauriculatus*, and *C. megalodon*), *C. carcharias*, and a weakly serrated species (subsequently named *Carcharodon hubbelli*; Ehret et al., 2012). The serrations of *C. carcharias* and *C. hubbelli* were wider and more variable than in the three megatooth species. Further, they were triangular in shape and unlike the lobed serrations of *C. auriculatus*, *C. subauriculatus*, and *C. megalodon* (Nyberg et al., 2006: figs. 8, 9).

FIRST APPEARANCES IN THE FOSSIL RECORD. Muizon and DeVries (1985) argued that weakly serrate teeth known from the late Miocene of Peru, rather than *C. megalodon*, were ancestral to *C. carcharias*. Purdy (1996), Gottfried and Fordyce (2001), and Purdy et al. (2001:121) refute this interpretation on the basis of a single, well-documented tooth collected in situ (USNM 336204) from the middle Miocene of Maryland. If correctly identified, this tooth is older than the purported ancestral partially or weakly serrate teeth known from the late Miocene of Peru (Muizon and DeVries, 1985; Ehret et al., 2009a, 2012) or the latest Miocene to earliest Pliocene (Yabe, 2000) and early Pliocene (Kemp, 1991: pl. 19H). Arguments based on first appearances in the fossil record are always tenuous, as a single new record can extend the stratigraphic range of a species by millions of years. Further, as discussed above (see *Carcharodon* section), USNM 336204 is most likely referable to *Carcharocles* rather than *Carcharodon*, and the oldest reliably dated serrated *Carcharodon* (*C. hubbelli*) is from the late Miocene. Finally, because of the vagaries of preservation in different localities, a descendant species can appear earlier in the fossil record than the presumed ancestral one (Foote and Miller, 2007:155–156). Consequently, the argument that *C. megalodon* must be placed in the genus *Carcharodon* (i.e., *Carcharodon* model) because it appears in the fossil record before its presumed ancestral form among unserrated *Carcharodon* (*Carcharocles* model) is not supported.

MOLECULAR DIVERGENCE TIMES. A. P. Martin (1995) and Martin et al. (2002) used molecular clock data to estimate that *Isurus* and *Carcharodon* diverged from a common ancestor approximately 60 MYA. This estimate predates the appearance of the oldest known megatooth shark and precludes a hypothesized origin of *C. carcharias* from *Isurus* tens of millions of years later in the Miocene. This date is an apparently strong piece of evidence for the *Carcharodon* model, but there are two difficulties with this interpretation.

First, the molecular data were based on extant *Isurus* and *Carcharodon*. As discussed above, unserrated *Carcharodon* teeth previously placed in the genus *Cosmopolitodus* are morphologically closest to *C. carcharias*. Further, a cladistic analysis of tooth morphology in large-toothed lamniforms places unserrated *Carcharodon* and *C. carcharias* in a clade that is the sister group to *Isurus* (Mewis, 2008). This placement would mean that molecular dates would reflect divergence between *Isurus* (sensu stricto) and unserrated *Carcharodon* + *C. carcharias*, not between *Isurus* + unserrated *Carcharodon* and *C. carcharias*. In this scenario, a more ancient molecular divergence time between extant *Isurus* and *Carcharodon* would be more plausible.

Second, a reliable, universally accepted molecular clock for dating ancient events has proved elusive. Numerous complications can adversely affect the reliability of molecular divergence times, with different systems producing widely different estimates (Heads, 2005; Ware and Grimaldi, 2011; White and Last, 2012). The 60 MYA divergence time of *Isurus* and *Carcharodon* must be accepted with an appropriate level of caution, and Bernal et al. (2001a) used a recalibrated molecular clock to obtain a 43 MYA divergence time between these two genera.

As reviewed here, the best available evidence makes the *Carcharodon* model of megatooth shark evolution untenable, and the *Carcharocles* and *Otodus/Megaselachus* models are better representations of the evolutionary history of this group. As discussed above, these two models have a number of similarities but differ in the generic organization of the lineage. The taxonomy of the *Carcharocles* model follows that of a number of researchers (Casier, 1960; Cappetta, 1987; Nyberg et al., 2006; Mewis, 2008; Ehret, 2010) who have argued for placement of these species in a separate extinct family (Otodontidae) and genus (*Carcharocles*). In the *Otodus/Megaselachus* model, Cappetta (2006) advocated the use of *Megaselachus* for megatoothed sharks, although he later (2012:224) used *Megaselachus* as a subgenus of *Otodus*. In this later scenario, the subgenus *Megaselachus* is separated from the older subgenus *Carcharocles* not only by the presence of teeth with cusplets that are greatly reduced or absent but, more importantly, by having smaller, more uniform serrations and parallel basal crown and root margins on the labial face of the tooth. Unfortunately, all of these characters are quite variable and not as definitive as proposed. For example, Nyberg et al. (2006: fig. 9A–C) compiled serration size data for three specimens of *C. auriculatus*, two specimens of *C. subauriculatus* (=*C. chubutensis*; see below), and four specimens of *C. megalodon*. These data were reanalyzed with a one-way ANOVA of the three *Carcharocles* species (*C. auriculatus*, mean = 0.676, variance = 0.014; *C. chubutensis*, mean = 0.696, variance = 0.005; *C. megalodon*, mean = 0.752, variance = 0.013). Significant differences in serration sizes were present ($F_{2,93} = 4.91$, $P = 0.009$), although subsequent Tukey HSD pairwise comparisons indicated that the significant differences ($P < 0.05$) were localized between *C. auriculatus* and *C. megalodon*. But the differences in serration size were in the opposite direction from that predicted by Cappetta. Further, the two species had similar variances, which is contrary to the expectation of greater uniformity of serration size in *C. megalodon*. The variance is smaller in the teeth of *C. chubutensis*, but this may simply reflect the smaller sample size for this species.

Cappetta's model of megatooth shark evolution based on a single genus (*Otodus*) and three subgenera (*Otodus*, *Carcharocles*, and *Megaselachus*) explicitly acknowledges the role of phyletic evolution in this lineage, but the subgeneric distinctions between *Carcharocles* and *Megaselachus* are based on variable and, in some cases, poorly documented differences (see above; see also Bor et al., 2012:38). Further, Cappetta's assignment of all species within the lineage to a single genus requires an expansion of *Otodus* far beyond its original intent and provides no additional clarity on evolutionary relationships. The more common usage of *Carcharocles* separates this genus from the genus *Otodus* (=Cappetta's *Otodus* subgenus) by the presence of serrations and combines Cappetta's *Carcharocles* and *Megaselachus* subgenera into a single genus. The appearance of fully formed serrations, as opposed to the crenulate edges of some *Otodus*, is the most reliable character separating the basal and terminal species in the megatooth shark lineage. The use of this character is supported by recent research showing that fully functional serrations are characterized by fundamental changes in the arrangement of fibers in the parallel bundled enameloid layer of neoselachian teeth (Andreev, 2010).

At present, the question of whether the transition from *Otodus* to *Carcharocles* is phyletic (as assumed by Cappetta, 2012) or arose by cladogenesis is unresolved. The distributional data for *Otodus* and *Carcharocles* currently lack both the stratigraphic precision and the geographic breadth to fully address this question, although two recent studies have provided some insights.

- King et al. (2013) examined the evolution of serrations in this lineage across a series of strata. Each stratum contained a range of cutting edge morphologies with serrations becoming larger or more pronounced in younger horizons. This is the strongest evidence for phyletic evolution within this lineage, although it assumes that each stratum represents a time-averaged sample of a local breeding population. An alternative scenario is that each stratum reflects the convergence of separate populations on a common feeding area.
- Pimiento and Balk (2015) have documented geographically distinct populations of *C. megalodon*, rather than a single global population. Such discrete populations would facilitate cladogenesis if they represented different breeding populations, but as yet, it is unclear whether these differences have a genetic basis or are ecophenotypic. Furthermore, on the basis of fossils alone, there is no easy way to distinguish evolutionary differences from ecophenotypic ones.

Phyletic evolution, as seems apparent in the megatooth shark lineage (Zhelezko and Kozlov, 1999; Ward and Bonavia, 2001; Cappetta, 2006, 2012; King et al., 2013; Shimada et al., 2016), is typically found in widespread pelagic groups with few reproductive barriers (Benton and Pearson, 2001; Hull and Norris, 2009). This pattern is consistent with the widespread distribution of megatooth shark chronomorphs, although the work by Pimiento and Balk (2015) suggests that some barriers may have been present.

Unfortunately, there are problems with straightforward interpretations of such trends in phyletic lineages, including (1) rates of evolutionary change that are surprisingly slow and (2) the difficulty of identifying cryptic species that may be present (Hull and Norris, 2009; Geary et al., 2010; Liow, 2010; Saylo et al., 2011). One unusual characteristic of the megatooth lineage is its longevity of about 60 MY (using data in Cappetta, 2012; Pimiento and Clements, 2014). Even less dramatic changes, such as the loss of vestigial cusplets during the early Miocene, required about 4 MY (on the basis of specimens collected in situ from the Calvert Formation; see below). Such slow directional change in a lineage is not easily explained, as it is difficult to envision a selective pressure that could act continuously over such long time periods. Likewise, research on extant elasmobranchs has demonstrated that cryptic species are quite common (Sole-Cava and Levy, 1987; Eitner, 1995; Heemstra, 1997; Pank et al., 2001; Gardner and Ward, 2002; Sandoval-Castillo et al., 2004; Keeney and Heist, 2006; Quattro et al., 2006; Castilho et al., 2007; Corrigan et al., 2008; Boomer et al., 2010). Cryptic species are highly likely to exist in fossil sharks because chronomorphs are based almost exclusively on teeth, which form a tiny portion of the entire body.

Resolving the unanswered questions about the megatooth shark lineage may require a new, more inclusive model to explain evolution within this group. A useful analogy for such a model can be found in the detailed evaluation of a long-lived (18 MY) lineage of graptolites (Urbanek et al., 2012). In this species complex a basic lineage evolved phyletically and periodically produced short-lived sister clades that themselves exhibited phyletic evolution, as well as convergence with other clades. Although the exact mode of evolution described by Urbanek and colleagues may be inappropriate for megatooth sharks, a composite evolutionary model combining both anagenesis and cladogenesis is both possible and consistent with the findings of King et al. (2013; broad overlap of chronomorphs) and Pimiento and Balk (2015; geographically distinct intraspecific groups) discussed above. Sorting out the details of evolution in the megatooth sharks will require extensive research with rigor comparable to these two studies. This work will also likely require the application of statistical approaches to distinguish different modes of evolution (Hunt, 2006).

Because of these unresolved issues surrounding the evolution of the megatooth sharks the genus name *Carcharocles* is used here for serrated member of the megatooth lineage. This follows the widespread usage of this genus by a number of researchers (Casier, 1960; Cappetta, 1987; Antunes et al., 1999a; Müller, 1999; Aguilera and Rodrigues de Aguilera, 2001; Apolín et al., 2004; Nyberg et al., 2006; Kocsis, 2007; Mewis, 2008; Portell et al., 2008; Cicimurri and Knight, 2009b; García et al., 2009; Ehret, 2010; Pimiento et al., 2010, 2013a, 2013b; Visaggi and Godfrey, 2010; Cione et al., 2011; Pimiento and Clements, 2014; Pimiento and Balk, 2015; Carrillo-Briceño et al., 2016), including researchers such as Ward and Bonavia (2001) who accept that the group evolved phyletically. The use of *Otodus* and *Carcharocles* for the ancestral and descendant members of the lineage, respectively, provides taxonomic stability while additional research is pursued. Conversely, using *Otodus* for the entire lineage (or *Otodus* for earlier species and *Megaselachus* for the terminal species) provides no new information and requires assumptions that have not been fully tested.

Two different *Carcharocles* tooth morphologies occur in Calvert Cliffs. Weakly cuspletted *Carcharocles* teeth are collected from the northern half of Calvert Cliffs, where the species co-occurs with the more common *C. megalodon*. Identification of these two tooth forms to species is problematic because of ontogenetic changes in tooth morphology, with cusplets occurring more commonly on both lateral teeth and from those of smaller individuals (Menesini, 1974; Purdy et al., 2001; Ward and Bonavia, 2001). There are two plausible names for these weakly cuspletted teeth. Purdy et al. (2001) argue that the specific name *subauriculatus* (Agassiz, 1839) has priority, partially because this name is based on anterior teeth, rather than lateral teeth. However, the original illustrated specimens of *C. subauriculatus* (Agassiz, 1843: tbl 30a, figs. 11–13) lack cusplets, and only one (fig. 12) has a small, inconspicuous notch on the cutting edge to separate the cutting edge from a cusplet. In his description Agassiz actually separated *C. subauriculatus* from *C. megalodon* on the basis of a more triangular crown with nearly straight cutting edges and considered the tooth with a faint notch (fig. 12) to be closer to *C. megalodon* than to the definitive *C. subauriculatus* specimen (figs. 11, 11'). Further, Cappetta (2006:220) notes that the original locality data for *C. subauriculatus* (Tertiary of Maastricht, the Netherlands) is dubious and, like Leriche (1926), places *subauriculatus* in synonymy with *C. megalodon*. Leriche (1926) uses the specific name *chubutensis* (Ameghino, 1906) for weakly cuspletted teeth, and this name was retained as a valid species by Cappetta (2006). The type specimen of *chubutensis* is based on a lateral tooth but is consistent with the morphology of the cuspletted teeth from Calvert Cliffs, and that name is used here.

Carcharocles chubutensis **(Ameghino, 1906)**

FIGURE 2.13

Synonymy follows Purdy et al. (2001; under *Carcharodon subauriculatus*) and Marsili et al. (2007; under *Carcharodon subauriculatus*), with the following additions:

2006 *Megaselachus chubutensis* (Ameghino, 1906): Cappetta, p. 51.
2010 *Carcharocles chubutensis* (Ameghino, 1906): Cook et al., p. 80, fig. 2B,C.

Description. The cuspletted teeth of *C. chubutensis* are smaller than those of the more famous *C. megalodon*. The crown of upper teeth has a relatively wide, compressed cusp with a broadly ogival apex, and weakly sigmoidal, moderately coarsely serrate, cutting edges (Figure 2.13A). The lingual face is convex, whereas the labial face is flat to weakly concave. In profile, the coronal apex is arched labially. On each shoulder is a low, broad, serrated cusplet that is separated from the main cusp by a shallow notch. Between the crown and root on the lingual surface is a broad, chevron-shaped neck covered with a thick layer of orthodentine (=bourlette of Kent, 1994). The root lobes are moderately elongated with shallow concavities on the mesial and distal margins. There is a broadly U-shaped basal root margin. The nutrient foramina are scattered in a broad arc over the thickest portion of the lingual protuberance. In anterior positions, the crown is tall and erect or weakly inclined distally. In lateral tooth positions, the crown becomes lower and more distally inclined, whereas the root lobes become more widely separated, with an obtusely angled basal margin (Figure 2.13B,C,E).

Lower teeth are similar to upper teeth, although with somewhat narrower cusps and less widely separated root lobes. The labial face of the crown is usually weakly convex, with the lingual face more strongly convex. Viewed in profile, the crown is straight or slightly bent lingually. The root is somewhat more robust but is otherwise similar to those of upper teeth. Lower lateral teeth resemble upper lateral teeth in overall morphology but retain a slightly more robust root (Figure 2.13D).

Discussion. *Carcharocles chubutensis* teeth never reach the remarkable sizes of the more famous *C. megalodon*, but because of its comparative rarity, the maximum size for this species from Calvert Cliffs is difficult to determine. Case (1980) reported a maximum tooth height of 130 mm for *C. chubutensis* from the Trent Marl in North Carolina, but no teeth of this size are known from Calvert Cliffs. Teeth in excess of 100 mm have been collected from the cliffs, and the largest measured tooth (USNM 392158) is an upper anterior from bed 14. The height of this tooth is 106.9 mm, although the coronal apex is damaged; the reconstructed height of the intact tooth is about 110 mm. A fragment (CMM-V-4459; Figure 2.13E) is the largest lateral tooth available and has a width of 86 mm and an incomplete crown. Comparisons with intact upper lateral *C. megalodon* teeth of the same size and shape produce estimated heights of 89–92 mm.

The smaller maximum size of *C. chubutensis* from Calvert Cliffs may simply reflect immature individuals, rather than a separate species, since cusplets are more commonly present on smaller teeth (Menesini, 1974; Purdy et al., 2001; Ward and Bonavia, 2001). The difficulty in assessing this possibility is that there is no direct evidence for the maximum sizes of different life stages in *Carcharocles*. Gottfried et al. (1996) assumed similar ontogenetic trajectories in *C. megalodon* and *C. carcharias* to infer total body lengths of 3.6–4.2 m for the neonatal–immature adult transition and about 10.5 m for the immature adult–mature adult transition in males and 13.3 m in females. Pimiento et al. (2010) used transitions sizes of 4 and 10.5 m, along with position-specific regression equations from *C. carcharias* (Shimada, 2003), to reconstruct the life stages for *C. megalodon* teeth and inferred the presence of a nursery area in the Miocene of Panama. Applying this same methodology, the largest *C. chubutensis* tooth examined from Calvert Cliffs (USNM 392158, a first or second upper anterior) has a reconstructed coronal height of 90 mm, and using the regression equations for the first and second upper anteriors of *C. carcharias* (Shimada, 2003), this would represent an individual with a total body length of 10.4–10.8 m. Other possible methods of reconstructing body lengths from anterior teeth using either the midline tooth height (Gottfried et al., 1996) or root width (C. Jeremiah in Renz, 2002) produce estimates of 10.3 and 12.2 m, respectively.

Unfortunately, the life stage sizes inferred by Gottfried et al. (1996) and Pimiento et al. (2010) largely ignore some serious difficulties. The most obvious is that *C. megalodon* is dramatically larger than *C. carcharias*. Extrapolations far beyond the available data are always risky because they ignore a number of possible confounding factors (Schmidt-Nielsen, 1984; Glazier, 2005). Gottfried et al. (1996: tbl. 1, footnote c) recognized this difficulty, and on the basis of a general trend for a reduced relative fetal size in larger sharks, proposed that the largest neonates could have had smaller total body lengths of 2–3 m in *C. megalodon*. They made no comparable prediction of the juvenile-adult transition, but 6–7.5 m would seem plausible. These scaling difficulties also are complicated by the presence of mesothermy in *C. carcharias* (Block and Finnerty, 1994; Goldman, 1997; Carlson et al., 2004; Bruce, 2009). The metabolic condition of *C. megalodon* is unknown, although Purdy (1996) speculates that on the basis of its warm temperate distribution *C. megalodon* was an endotherm. Scaling relationships are known to differ between ectotherms and endotherms (McNab, 2002; Suarez et al., 2004; Glazier, 2009), further complicating any straightforward determination of life stage sizes in *C. megalodon*. Finally, the fundamental assumption of Gottfried et al. (1996) was that *C. megalodon* and *C. carcharias* had similar developmental trajectories. Nyberg et al. (2006: figs. 6, 7) evaluated size-related changes in the upper and lower anterior teeth of these two species and found that they were very different, casting further doubt on current size estimates for different life stages in *C. megalodon*.

Despite these complications, extrapolations from *C. carcharias* scaling of life history stages are, at present, the best available estimates for the sizes of neonatal, juvenile, and adult *Carcharocles*. On the basis of these relationships it seems likely that the largest *C. chubutensis* teeth from Calvert Cliffs represent mature individuals and a separate chronomorph of *C. megalodon* that overlaps in time for approximately 4 MY (beds 3–14 of the Calvert Formation) in Calvert Cliffs. Cuspletted teeth that are less than half the dimensions of the largest teeth are relatively common but may represent small individuals of either *C. chubutensis* or *C. megalodon* (Figure 2.13C,D).

Stratigraphic and Geographic Ranges. *Carcharocles chubutensis* teeth appear to be restricted to the northern half of Calvert Cliffs and appear to be most prevalent in the

FIGURE 2.13. *Carcharocles chubutensis* teeth (1 cm scale bar). (A) Right upper anterior tooth, lingual view (CMM-C-205 [voucher cast]; bed 3, Pamunkey River, Virginia). (B) Left upper lateral tooth, lingual view (CMM-C-206 [voucher cast]; bed 3, Pamunkey River, Va.). (C) Juvenile(?) *C. megalodon/chubutensis* right upper lateral tooth, labial view (CMM-V-818; Popes Creek, Maryland). (D) Juvenile(?) *C. megalodon/chubutensis* right lower lateral tooth, lingual view (CMM-V-124; Popes Creek, Md.). (E) Right upper lateral tooth, labial view (CMM-V-4459; bed 10, Plum Point, Md.).

lower Calvert Formation (bed 4 and below; Purdy et al., 2001; BWK, pers. obs.), with in situ specimens known from beds 3, 4, 10, 12, and 14. In the general Chesapeake Bay area, *C. chubutensis* teeth have also been collected in situ from bed 1 of the Calvert Formation of Virginia. *Carcharocles chubutensis* teeth are uncommon, and only about 40 were available for study. Most of these were small (heights of 4–7 cm), and only three had a vertical height of at least 100 mm.

Elsewhere, *C. chubutensis* has been reported from early to middle Miocene (Aquitanian to Langhian) beds of Argentina, Baja California, Brazil, Egypt, Germany, Florida, Italy, Panama, and North Carolina (Ameghino, 1906; Kimmel and Purdy, 1984; Dülge and Engelhard, 1988; Müller, 1999; González-Barba and Thies, 2000; Hulbert, 2001; Purdy et al., 2001; Marsili et al., 2007; Costa et al., 2009; Cook et al., 2010; Pimiento et al., 2013b; Pimiento and Balk, 2015). In younger sediments *C. chubutensis* is replaced by the larger *C. megalodon*, possibly because of the evolution of larger cetacean prey beginning in the middle Miocene (Pyenson and Vermeij, 2016).

Carcharocles megalodon (Agassiz, 1843)

FIGURE 2.14

Synonymy follows Purdy et al. (2001) and Reinecke et al. (2011).

Description. The enormous teeth of *C. megalodon* are the most avidly pursued fossil from Calvert Cliffs. At heights in excess of 150 mm, they are the largest chondrichthyan teeth and, except for *C. chubutensis*, are not easily confused with other Calvert Cliffs teeth. In general, the descriptions of teeth from the two *Carcharocles* species are similar, although they differ in some details. Specifically, both the upper (Figure 2.14A) and lower (Figure 2.14B) teeth of *C. megalodon* tend to be somewhat broader, with more spatulate coronal tips than those of *C. chubutensis*, although this really becomes obvious only in larger specimens. The shoulders lack cusplets, although in some cases there is a low, vestigial cusplet that joins the coronal cutting edge without an intervening notch. In other respects the two species are comparable.

Small, heart-shaped *Carcharocles* teeth are infrequently collected from Calvert Cliffs (Figure 2.14D,E). These teeth have thick crowns with convex labial and lingual surfaces, producing a lenticular cross section in the apical half of the crown. Basally, the lingual face becomes more weakly convex, whereas the labial face is more complex, with convex lateral margins and a medial triangular depression. This triangular area is contiguous, with a broad shallow depression on the labial root face that extends to a broad concavity on the basal margin of the tooth. Both the mesial and distal cutting edges are completely serrated and are weakly convex to nearly straight. On some specimens, the cutting edges are broadly undulating, with a shallow concavity at mid-crown (Figure 2.14G). Presumed upper and lower teeth are distinguished by the position of the coronal apex when viewed in profile. In upper teeth, the coronal apex is arched labially. This curvature is most obvious in teeth > 30 mm in height and subtler in smaller teeth. Lower teeth have a crown that is erect or bent lingually in profile and varies little across the size range examined. Roots are relatively short and separated into lobes by a shallow to deep concavity of the basal root margin. Maximum size for these teeth is about 50 mm.

Discussion. The huge size of *C. megalodon* teeth makes them unmistakable, and they have been extensively discussed in both the popular and professional literature. Less clear are the scaling relationships in tooth morphologies that govern shape changes across the enormous size range of these teeth. Of particular interest are the comparatively small, heart-shaped teeth (Figure 2.14C–E). These unusual teeth are sometimes referred to as "Hubbell teeth" (not to be confused with the late Miocene lamnid *Carcharodon hubbelli* Ehret et al., 2012) and were first reported in the literature by Applegate and Espinosa-Arrubarrena (1996:32, fig. 11, nos. 3–5). Teeth with this morphology have been described as being either slightly pathological (Purdy et al., 2001:134) or from neonatal individuals (Renz, 2002:89; Pimiento et al., 2010). Of these two possibilities, a neonatal origin of the teeth is the more plausible as the teeth are typically symmetrical and of consistent morphology (unusual for pathological teeth) and restricted to smaller sizes. Pimiento et al. (2010) argue that there is a progression in morphology from the smallest neonatal teeth to the more typical juvenile teeth but provide little evidence to support this premise. On the basis of scaling relationships (Shimada, 2003) and ontogeny of the modern *C. carcharias* they separate neonates from juveniles at a total length of about 4 m. Upper anterior teeth for sharks of this size would have crown heights of 33–35 mm (=total height of about 50 mm), whereas lower anterior teeth would have crown heights of 27–30 mm. Lateral teeth for sharks of 4 m length would have smaller teeth with maximum crown heights of about 27–29 mm for upper laterals and 21–22 mm for lower teeth. On the basis of these criteria, more than 30 neonatal teeth were available for study from Calvert Cliffs, and changes in morphology with increasing tooth size can be easily traced across a size range of 15–50 mm.

The tooth size for the neonatal-juvenile transition is highly variable, as previously suggested by Pimiento et al. (2010). Even the smallest teeth examined had the distinctive convex labial crown face and bilobed roots of neonates, but the changes in these two characteristics were decoupled in larger teeth. Some teeth (Figure 2.14F) are of comparatively small size but have a fully adult morphology for this tooth position. Conversely, some teeth (e.g., CMM-V-366; upper lateral tooth fragment, width = 72.5 mm) have an adult coronal morphology but retain the bilobed neonatal root structure.

Stratigraphic and Geographic Ranges. The teeth of *C. megalodon* are most commonly collected as beach specimens, and although they occur along the length of Calvert Cliffs, they are most often found from the middle of Calvert

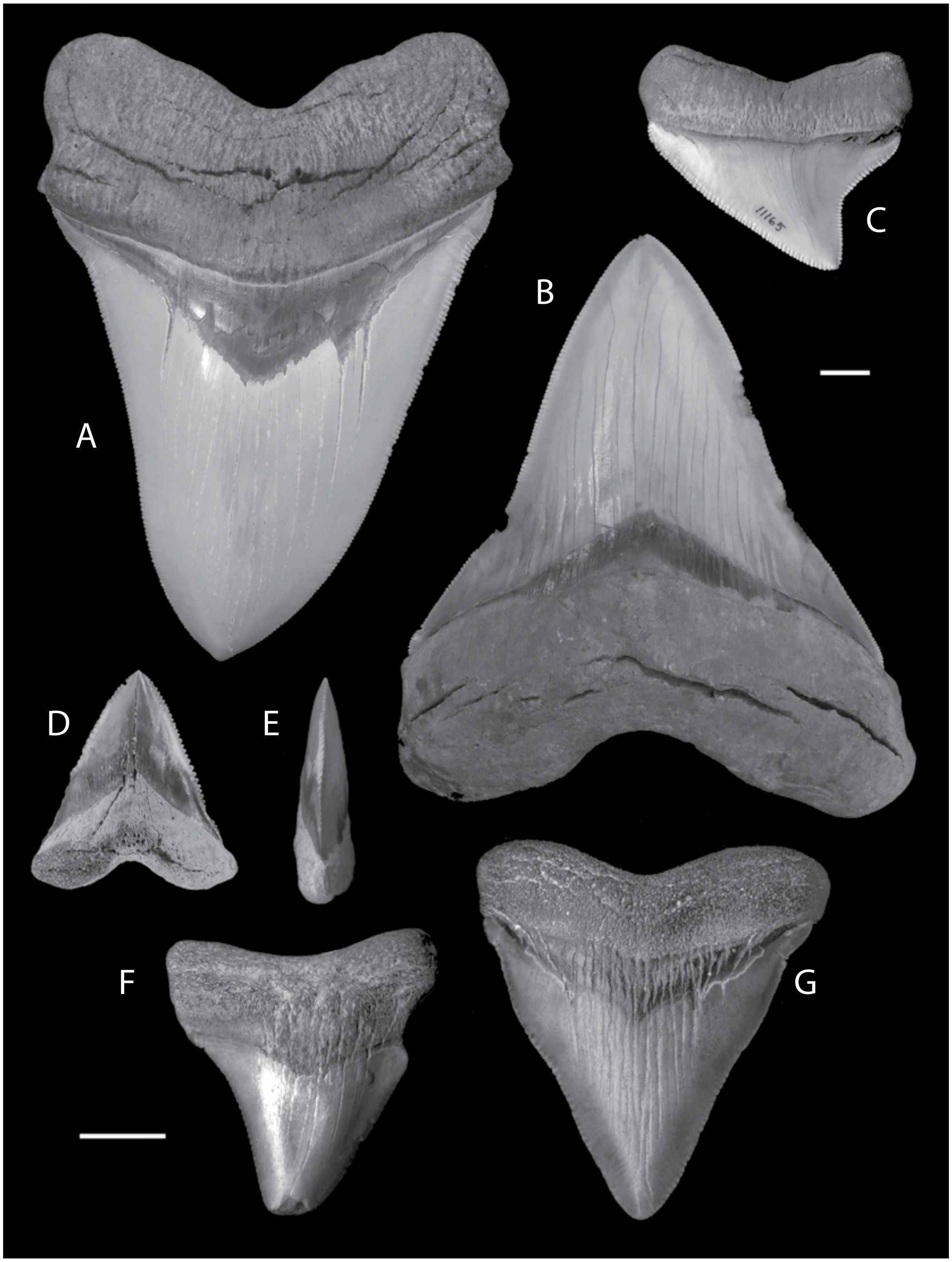


FIGURE 2.14. *Carcharocles megalodon* teeth (separate 1 cm scale bars for A–C and D–G). (A) Left upper anterior tooth, lingual view (UMCP 10061; Matoaka Cottages, Maryland). (B) Left lower lateral tooth, lingual view (UMCP 10060; Western Shores, Md.). (C) Left upper lateral tooth, labial view (UMCP 11165; Matoaka Cottages, Md.). (D) Lower neonatal tooth, lingual view (UMCP 11397; Matoaka Cottages, Md.). (E) Lower neonatal tooth, lateral view (UMCP 11397; Matoaka Cottages, Md.). (F) Upper lateral tooth, lingual view (UMCP 12599; Bayfront Park, Md.). (G) Upper neonatal/juvenile tooth, lingual view (UMCP 12600; north of Calvert Cliffs Nuclear Power Plant, Md.).

Cliffs northward. Teeth found in place are known from beds 3–5, 8, and 10–14. Although large *C. megalodon* teeth are quite rare, smaller specimens are not, and more than 150 teeth were examined for this study.

Carcharocles megalodon is a cosmopolitan species, and teeth have been very widely reported from early Miocene (Burdigalian) through late Pliocene (Piacenzian) formations from many countries, including Argentina, the Azores, Australia, Austria, Belgium, Congo, the Czech Republic, France, Germany, India, Italy, Japan, Lesser Antilles, Madagascar, Mallorca, Malta, the Netherlands, New Zealand, Panama, Peru, Poland, Portugal, Spain, Tunisia, United States, and Venezuela (Radwański, 1965; Cappetta, 1970; Keyes, 1972; Hirota, 1979; Cappetta, 1987; Nolf, 1988; Kemp, 1991; Yabumoto and Uyeno, 1994; Antunes et al., 1999a; Müller, 1999; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Vicens and Rodríguez-Perea, 2003; Apolín et al., 2004; Marsili, 2008; Portell et al., 2008; Rögl et al., 2008; Pimiento et al., 2010; Schultz et al., 2010; Cione et al., 2011; Reinecke et al., 2011; Ávila et al., 2012; Cappetta, 2012; Bor et al., 2012; Andrianavalona et al., 2015; Pimiento and Balk, 2015; Reolid and Molina, 2015; Landini et al., 2017). By evaluating post-Miocene records for *C. megalodon*, Pimiento and Clements (2014) were able to produce a most likely estimate of the *C. megalodon* extinction at ~2.6 MYA.

Carcharocles Vertebral Centra

FIGURE 2.15A–C

DESCRIPTION. Likely *Carcharocles* centra from Calvert Cliffs are round or weakly ovoid in axial view and septate and have thickened rims. The septa are simple and straight and may bifurcate as they approach the rims. The interseptal spaces are ovoid and relatively broad. When viewed from either dorsal or ventral perspective, the centra have straight lateral margins, although the distal edges of the septal walls are thin and easily damaged, making this character difficult to observe. The rim margins are straight or weakly recurved. The dorsal and ventral foramina are ovoid and reach almost to the rims.

DISCUSSION. Although the teeth of *C. megalodon* are widely known, other skeletal elements are infrequently collected and even more rarely described in the literature (Leriche, 1926:426; Gottfried et al., 1996: fig. 1C; Kraig, 2008:19–21). Bartsch and Barwick (1941) erroneously listed vertebrae from Calvert Cliffs as those of *C. megalodon*, although Gottfried et al. (1996) reevaluated those centra and identified them as being consistent with the centra of *Cetorhinus*. Centra attributable to *C. megalodon* are quite rare, and only two were examined for this study.

Large *Carcharocles* vertebrae can be easily mistaken only for those of *Cetorhinus*. However, *Cetorhinus* centra have much more delicate septa that are rarely preserved and an axial foramen that is lacking in *Carcharocles* centra. *Carcharocles* centra differ from those of other large lamniforms, such as *Isurus* and *Carcharodon*, in having thicker rims and larger interseptal spaces.

Carcharocles Morphology and Biology

Carcharocles megalodon was among the largest marine predators in the Earth's history, and numerous attempts have been made to reconstruct both its appearance and body size. Unfortunately, the absence of intact, well-documented skeletons precludes simple, direct interpretations of either body shape or size. Instead, *C. megalodon* reconstructions must rely on the application of general principles of functional morphology and scaling relationships.

RECONSTRUCTED MORPHOLOGY. The physical appearance of *C. megalodon* has generally been reconstructed using *C. carcharias* as a model, with one of the most rigorous of these reconstructions (Gottfried et al., 1996) being based on statistical extrapolations of *C. carcharias* morphology. This evidence was used for a skeletal reconstruction at the Calvert Marine Museum (Figure 2.15) at the southern end of Calvert Cliffs in Solomons, Maryland. But if (as discussed above) the preponderance of evidence supports an evolutionary lineage for *C. megalodon* that is separate from that of *C. carcharias*, how realistic are these morphological reconstructions? An assessment requires a two-pronged approach: (1) a biomechanical evaluation of the likely overall morphology of a very large, axially swimming shark and (2) a review of how different specific morphological details map onto phylogenetic relationships within the lamniforms.

Carcharocles was a macrophagous carnivore feeding on prey that were likely both widely dispersed and evasive, requiring a body morphology capable of covering long distances efficiently (Webb, 1988; Vermeij, 2016; Ferrón et al., 2017). Large axial swimmers (such as *Carcharocles*) must operate at very high Reynolds numbers, which, in turn, places strong physical constraints on plausible body morphologies. These constraints are so restrictive that numerous large, axial swimmers (e.g., lamnid sharks, tunas, odontocete whales, ichthyosaurs) have all evolved biomechanically similar thunniform body morphologies (Webb, 1988; Weihs, 1989; McGowan, 1991; Motani et al., 1996; Wilga and Lauder, 2004). All of these groups are characterized by (1) a relatively rigid fusiform body with large anterior depth, (2) a lunate, high-aspect-ratio caudal fin with lateral keels on the caudal peduncle, (3) reduced second dorsal and anal fins of the posterior half of the body, (4) a spacing between the first (or only) dorsal fin and caudal fin of about 40% the fork length, and (5) long pectoral fins. Many thunniform swimmers are also at least partially endothermic, either through mesothermy (e.g., tunas, lamnid sharks) or true endothermy (e.g., cetaceans). Because of its enormous size, *C. megalodon* could also maintain an elevated body temperature as a gigantotherm (Paladino et al., 1990) in conjunction with either an ectothermic or a mesothermic metabolism.

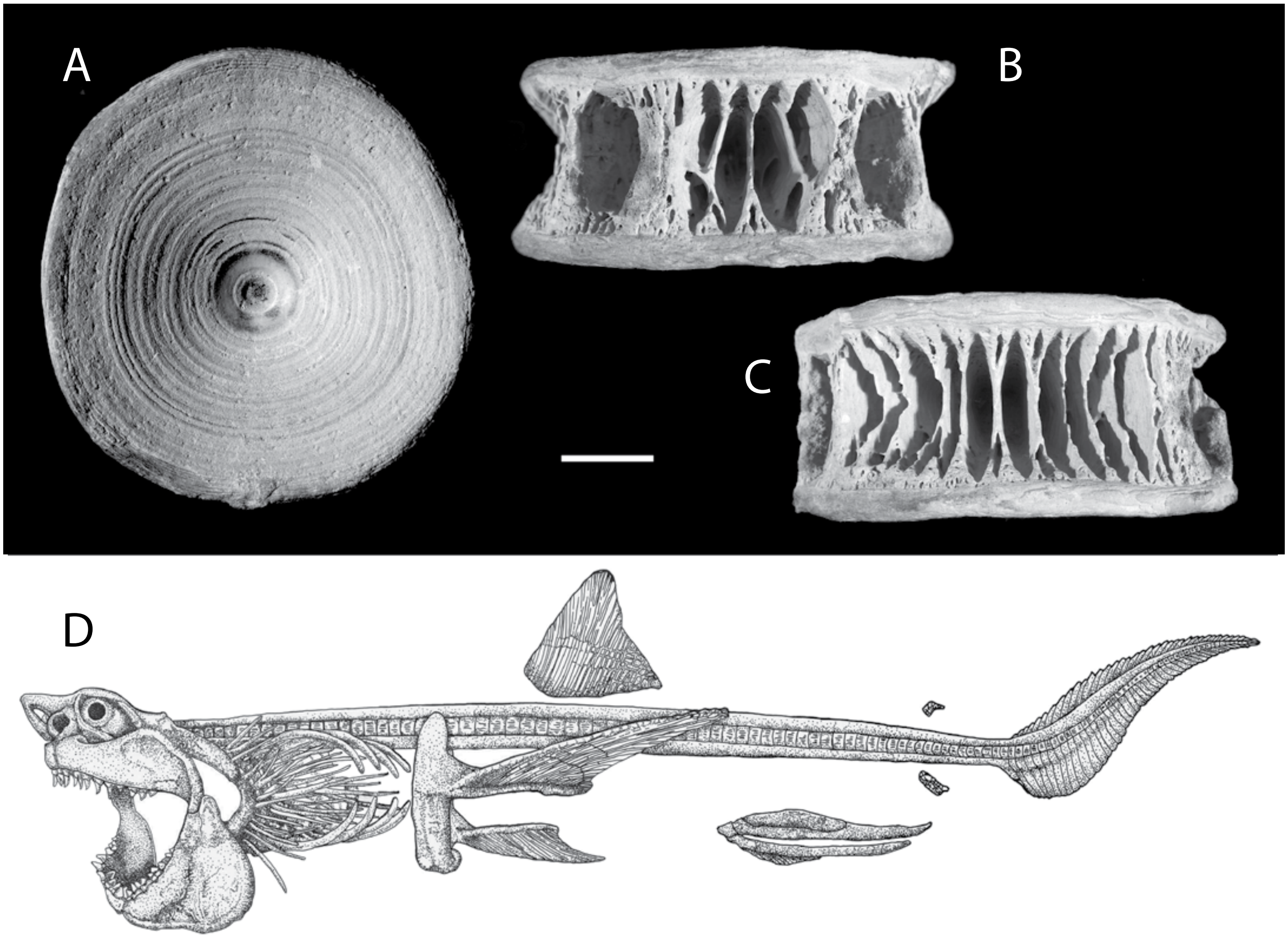


FIGURE 2.15. *Carcharocles* skeleton (1 cm scale bar for A–C). (A) Vertebral centrum; axial view (CMM-V-4739; Scientists Cliffs(?), Maryland). (B) Vertebral centrum; ventral view (CMM-V-4739; Scientists Cliffs(?), Md.). (C) Vertebral centrum; lateral view (CMM-V-4739; Scientists Cliffs(?), Md.). (D) Skeletal reconstruction of *Carcharocles megalodon* at the Calvert Marine Museum, Solomons, Md. (courtesy of Calvert Marine Museum; drawing by Connie Barut-Rankin).

The two large, relatively docile planktivores, the whale shark (*Rhincodon*; Orectolobiformes) and basking shark (*Cetorhinus*; Lamniformes), are the only living sharks comparable in size to *C. megalodon*. Despite operating at comparably low speeds, these large sharks also have a thunniform body plan. Motani et al. (1996: fig. 2a) found a strong correlation in sharks between the fineness ratio of the body (maximum body depth divided by precaudal length) and the caudal fin height-length ratio (analogous to caudal fin aspect ratio). Further, they found that *Rhincodon* and *Cetorhinus* clustered with the lamnids at one extreme of the shark body and caudal fin morphology spectrum. At such large body sizes, even the slow-moving basking and whale sharks apparently need a thunniform body form to maintain high swimming efficiency for long-distance cruising (Wilga and Lauder, 2004). The fossils of *C. megalodon* are very widely distributed and are known from deep-sea sediments (Séret, 1987; Roux and Geistdoerfer, 1988; Purdy, 1996), which would be consistent with a coastal to oceanic lifestyle where the ability to efficiently move long distances would be critical. Zoogeographical research on extant sharks reinforces the inference since broad geographic ranges are correlated with large (>3 m) size, pelagic habits, and coastal to oceanic habitats (Musick et al., 2004; Stevens, 2010).

There is an alternative body morphology for large coastal to oceanic sharks that is less efficient but nonetheless possible. Carcharhiniform swimming (Thompson and Simanek, 1977; Webb, 1988) is a form of carangiform swimming widespread in carcharhinid and sphyrnid sharks, although it also occurs in lamniforms, such as *Carcharias*, *Odontaspis*, and *Alopias*. Carcharhiniform swimmers are less specialized than thunniform swimmers with (1) less body depth, (2) great flexibility, (3) a lower-aspect-ratio caudal fin, (4) a thicker caudal peduncle lacking lateral keels, (5) larger second dorsal and anal fins, (6) a more flattened head, and (7) a lack of mesothermy. Within this group there is a broad range of morphologies, with some carcharhinids approaching thunniform swimmers in fineness ratio and caudal fin height-length ratio (Motani et al., 1996). Some carcharhinids have even independently evolved thunniform features, such as the caudal keels of *Galeocerdo* (Compagno, 1984). The lamniforms within this body morphology are also diverse. Odontaspids have low fineness ratios and caudal fin height-length ratios (Motani et al., 1996) and are comparatively sluggish swimmers (Compagno, 1984, 1990b). Further, the low caudal fin height-length ratio in these sharks is due to a low heterocercal angle (=elevation of the dorsal lobe relative to the body axis), a feature associated with a diet of small prey in lamniforms (Kim, 2009). The alopiids are an unusual group with a morphology that is difficult to assign to a single group. The unique, exceptionally long dorsal lobe of the caudal fin is used to stun small schooling fish and is held at a relatively low angle, like most carcharhiniform swimmers. Like this group, alopiids also have flattened heads and lack caudal keels. But they have reduced second dorsal fins and anal fins and partial endothermy (in *A. vulpinus*) like thunniform swimmers (Compagno, 2002; Sepulveda et al., 2005). Further, one species (*A. superciliosus*) has a shorter dorsal lobe and has evolved a caudal fin functionally comparable to the thunniform lamnids (Kim, 2009).

One final possibility is an elongate, anguilliform body plan. This morphology occurs in a few large, primarily coastal, amniotes, such as primitive ichthyosaurs and the cetacean *Basilosaurus*. But the slow swimming speeds associated with this body morphology would require that these animals either feed on slow or immobile prey or capture prey from ambush (Motani et al., 1996; Massare, 1998; McHenry, 2009:437; Corrie, 2013:54). This lifestyle is inconsistent with the global, coastal to oceanic distribution of *Carcharocles* and is very unlikely to have been present in this genus.

On the basis of the need to move long distances and the physical constraints on operating at high Reynolds numbers, the most likely body shape of *Carcharocles* would be that of a thunniform swimmer. A specialized form of carcharhiniform swimmer with a body morphology approaching that of thunniform swimmers is possible, although none of the sharks with these adaptations have ever approached the tremendous size of *Carcharocles*. The physical constraints of such a large body may simply require the inherent efficiency of the thunniform body plan to be biologically viable.

Biomechanical constraints on morphology are, to a large extent, independent of evolutionary history. So the caudal fins of a lamnid shark and an odontocete whale push the body forward in fundamentally similar ways; the caudal fin has a high lift-to-drag ratio and generates hydrodynamic lift that pushes the body forward. The same is not true of the internal morphological details of how these two caudal fins are constructed. For example, the *Carcharodon* caudal fin contains phylogenetic signals about how it evolved, which, in turn, allows an assessment of which characters are plesiomorphic and which are apomorphic. Generalized lamniforms synapomorphies, such as plesodic pectoral fins, were almost certainly present in *Carcharocles*. On the other hand, derived characters restricted to the extant lamnids are unlikely to be found in an independent *Carcharocles* lineage. Unfortunately, the unsettled phylogeny of extinct lamniforms complicates definitive assessments of some skeletal features.

A number of skeletal attributes likely differed between *Carcharodon* and *Carcharocles*, although many of them would be difficult to observe on a skeleton, let alone a soft-tissue reconstruction. For example, lamniforms are characterized by a reduction of the labial cartilages, which are present in *Mitsukurina*, *Odontaspis*, and *Carcharias* but lacking in more derived groups (Shimada et al., 2009). Because lamniform phylogeny is not fully resolved, particularly with respect to extinct genera, labial cartilages may have been present in *Carcharocles*. Fortunately, their presence or absence would have no outward manifestation on a whole-body reconstruction. Likewise, *Carcharodon* and other lamnids have the palatoquadrate attached to the chondrocranium by a single palatonasal ligament, whereas less derived macrophagous lamniforms (e.g., *Alopias*) have both a palatonasal ligament and a pair of ethmopalatine ligaments (Wilga, 2005). The two forms of jaw suspension have subtle differences in the size of the ligament attachment areas of the palatoquadrate and chondrocranium that would be difficult to observe on a skeleton. These differences could have important consequences for jaw movements during prey capture but would have no discernible effect on a static reconstruction. Likewise, any number of other skeletal details (e.g., the number of fin rays in the pectoral fins, the curvature of the palatoquadrate, and Meckel's cartilages) either are difficult to assess without better information from extant species or would produce minimal changes in reconstructions. Overall, only two morphological features of the skeletal reconstruction shown in Figure 2.15D (i.e., the rostrum and the caudal fin) reflect derived features unlikely to have been present in *Carcharocles* and distinctive enough to affect whole-body reconstructions.

The rostrum in the Gottfried et al. (1996) reconstruction is a straightforward extrapolation of rostral morphology in *C. carcharias*. The rostrum of *C. carcharias* is shorter than in other lamniforms and appears to be an autapomorphy (Compagno, 1990a; Mollen, 2010). When the *C. carcharias* rostrum is extrapolated to a much larger body size, it becomes shorter and more robust, producing the distinctive pug-nosed head profile of this reconstruction. The majority of lamniforms have a somewhat longer rostrum, which seems to be a more likely condition for *Carcharocles*.

The caudal fin of *C. carcharias* (and as reflected in the skeletal reconstruction of *C. megalodon* in Figure 2.15D) has both a high heterocercal angle (=the angular elevation of the dorsal lobe of the tail relative to the body axis) and a high hypochordal angle (=the angle of the hypochordal cartilages of the tail relative to the vertebral column in the caudal fin). This combination is a synapomorphy of the family Lamnidae and is not known in any other lamniforms. The only lamniform with roughly comparable caudal fin morphology is the basking shark (*Cetorhinus maximus*). The semilunate caudal fin of this species also has a high heterocercal angle but has a lower hypochordal angle and a correspondingly smaller ventral lobe (Kim, 2009). Despite the difference in morphology, the *Cetorhinus* caudal fin nonetheless has an elevated height-length ratio comparable to that of extant lamnids (Motani et al., 1996: fig. 2). Further, the orectolobiform whale shark, *Rhincodon typus*, has independently evolved a semilunate caudal fin with a high height-length ratio fully comparable to that of cetorhinids and lamnids (Motani et al., 1996: fig. 2). As discussed above, a thunniform body morphology, including a high-aspect-ratio caudal fin, appears to be a prerequisite for a very large axial swimmer. Either a lunate caudal fin (as in lamnids) or a semilunate caudal fin (as in *Cetorhinus* and *Rhincodon*) is a plausible morphology, although the structural details in *Carcharocles* may differ from these extant species. In particular, the lunate caudal fin of lamnids uses a uniquely elevated hypochordal angle to support the longer ventral lobe. *Carcharocles* would need to either independently evolve a high angle on the hypochordal cartilages or support an elongated ventral lobe using other mechanisms. An independently derived high hypochordal angle is certainly plausible. The bigeye thresher (*A. superciliosus*) has a relatively elongated dorsal lobe but has evolved a high hypochordal angle and a caudal fin functionally analogous to that of the lamnids (Kim, 2009). Other morphological modifications, such as a fusion or heavier mineralization of fin rays, an increase in the density of connective tissues, or an increase in the aspect ratio of the lobe (Weihs, 1989; Sfakiotakis et al., 1999; Lingham-Soliar, 2005a–c), have been shown to stiffen caudal fin lobes in thunniform swimmers. In lieu of steeply angled hypochordal cartilages, one or more of these mechanisms could have been present in *Carcharocles* to support an elongated ventral lobe. A semilunate caudal fin, like that of *Cetorhinus* and *Rhincodon*, would have required less extreme structural modifications and may be even more likely as a caudal fin morphology for *Carcharocles*. In *Cetorhinus* the caudal vertebral skeleton is relatively weakly mineralized, commensurate with the less active lifestyle of this planktivore. Such a condition would be unlikely for a presumably more active macrophage, like *Carcharocles*, where more extensive mineralization would have been necessary.

All extant lamniforms with a low heterocercal angle (e.g., *Carcharias*, *Odontaspis*, and most *Alopias*) feed on comparatively small prey (Kim, 2009). These sharks also have low fineness ratios and caudal fin height-length ratios (Motani et al., 1996). Lamniforms with high heterocercal angles are all coastal to oceanic cruising forms but can have two different lifestyles, either as predators of comparatively large prey (*Carcharodon*, *Isurus*, *Lamna*) or as microphagous filter feeders (*Cetorhinus*). All of these sharks also have large fineness ratios and caudal fin height-length ratios (Motani et al., 1996).

ESTIMATED BODY SIZE. There have been a number of attempts to determine the maximum body length for *C. megalodon*. The most reliable means of determining length is an intact skeleton, but none is yet available. In the absence of intact skeletons, estimates must be based on tooth parameters, such as enameloid height of the first upper anterior tooth (=13 m; Randall, 1973), anterior tooth height measured along the midline of the tooth (=15.9 m; Gottfried et al., 1996), length of the mesial cutting edge (=15.1 m, Shimada, 2003; 16.8 m, Pimiento et al., 2010; ~18 m, Pimiento and Balk, 2015), and tooth width (=15.5 m; C. Jeremiah in Renz, 2002). These estimates are based on the largest specimens available at the time and may not reflect the largest individuals. Other, less rigorous estimates push the maximum length to at least 24 m (Papson, 1992).

Length estimates produced as extrapolations far beyond the size range of extant analogs all implicitly assume that size relationships are linear at all scales and that there are no ceiling effects due to biomechanical or physiological constraints. There is some evidence that the extant whale shark (*Rhincodon typus*) may reach 20 m (Chen et al., 1997; Compagno, 2002), so neoselachians are under no apparent biomechanical constraints on building a cartilaginous skeleton of a size comparable with some of the larger estimates for *C. megalodon*. But physiological constraints, such as on the cardiovascular system, could be a very different matter. *Rhincodon* is a slow-moving filter feeder and would make comparatively low demands on its cardiovascular system. Yet there are strong selective pressures for filter-feeding sharks to be as large as possible since swimming speed and efficiency both increase with body size (Vogel, 1988:310–312; McMahon and Bonner, 1993:187–191; Alexander, 1998). So a slow-moving 20 m whale shark is probably at the maximum size for a shark of this lifestyle.

The higher-speed locomotion of a macrophagous shark of comparable size would put far higher demands on the cardiovascular system. Sharks have a comparatively simple, single-circuit cardiovascular system in which blood must pass through both the gill capillaries and body capillaries before returning to the heart (Muñoz-Chápuli, 1999). Large, active sharks have evolved adaptations to improve blood flow during high-speed locomotion, including more efficient cardiac pumping, venous pumps, and larger gills (Emery et al., 1985; Emery and Szczepanski, 1986; Lai et al., 1997, 2004; Satchell, 1999). Although these allow for higher activity levels in extant lamnids, such as the shortfin mako (*I. oxyrinchus*) and great white shark (*C. carcharias*), which reach maximum sizes of about 6 m, it is unclear whether they would be adequate for a truly gigantic, fast-swimming shark of about 20 m.

A *C. megalodon* of 20 m or more could face additional, unexpected difficulties in capturing prey. As already noted, swimming speed increases with body length. But swimming speed is also inversely related to maneuverability, and a predator that becomes substantially larger than its prey loses the ability to capture elusive prey (Alexander, 1998; McKenzie et al., 2007; Lucifora et al., 2009). Gigantic filter feeders, such as *Rhincodon*, are under no such constraint since they feed on prey with such limited powers of locomotion that they are essentially immobile. Smaller *C. megalodon* would certainly be capable of pursuing and capturing a broad range of prey species, but at larger sizes scavenging may have become a more energetically viable foraging strategy. If *C. megalodon* ever reached the length of 20 m or more, as sometimes proposed, they may have been relatively slow moving, obligate scavengers that used their sheer size to intimidate smaller scavengers. This interpretation is supported by a recently published model on the evolution of giant marine predators (Ferrón et al., 2017) that found that even with a mesothermic thermal strategy large *C. megalodon* would be at the lowest activity levels possible for a macrophagous predator. This low activity level would interfere with the ability of *C. megalodon* to pursue actively swimming prey but would have less impact on scavenging.

EVIDENCE OF FEEDING. As a top carnivore, *C. megalodon* undoubtedly preyed on a broad range of prey. The best available evidence is the presence of large bite marks in marine mammal bones (Purdy, 1996; Renz, 2002; Godfrey and Altman, 2005; Aguilera et al., 2008; Kallal et al., 2010; Collareta et al., 2017a). In most cases, the marks are large, deep gashes, although in exceptional cases, fine parallel grooving produced by the serrated cutting edges is visible (Figure 2.16A). As with most bite mark data, it is not always clear whether these bite marks reflect predation, failed predation, or scavenging by *C. megalodon*. The distribution of large (≥4 mm wide) bite marks on a cetotherid whale from Calvert Cliffs (Newell, 1998; Figure 2.16B) appears to be evidence of an attack on a live whale. The bite marks are concentrated in the thoracic region, rather than on the flanks, where the large swimming muscles are present. Using biomechanical principles, predatory strikes on prey should be directed at the center of mass, as it is the most predictable target on the prey's body. For piscoid prey the center of mass corresponds to the deepest portion of the body, about one-third of the body length from the anterior end (Webb and Skadsen, 1980; Webb, 1984). This position matches the highest concentration of bite marks on the whale skeleton and is consistent with this predicted attack strategy. This region contains numerous visceral organs, such as the heart and lungs, and a bite in this area would quickly subdue the prey. But the thoracic viscera are also protected by numerous rib and forelimb bones that could deter attacks and protect vital organs. The teeth of *C. megalodon* are particularly robust and appear adapted for surviving impacts against bones (Farlow et al., 1991; Kent, unpubl. data).

This apparent attack strategy by *C. megalodon* is very different from the placement of attacks by the extant *C. carcharias*, which avoids this area in cetaceans and instead attacks other body areas, including the abdomen and caudal peduncle. These areas have major blood vessels and swimming muscles, and damage to these areas would quickly disable the prey (Long and Jones, 1996). This is a very efficient attack strategy, but the caudal area of cetaceans, in particular, would be a less predictable target than the center of mass and would require more rapid neuronal processing in the brain to be successful. Lamnids are known to maintain elevated brain temperatures, which would facilitate their ability to track the complex movements of the caudal area during an attack (Bernal et al., 2012). Further, although a caudal attack is plausible for *C. carcharias* feeding on smaller, porpoise-sized cetaceans, such an attack on much larger whales by *C. megalodon* would expose the shark to possible damage from the powerful caudal fluke (Collareta et al., 2017a).

Genus Parotodus Cappetta, 1980

The higher taxonomic classification of the genus *Parotodus* is, at present, not fully resolved (Bourdon, 2008; Shimada et al., 2016). There is little doubt that *Parotodus* is a lamniform, but several possible familial alignments have been proposed in the literature. None of these proposals is supported by strong evidence, although the reason is primarily the lack of any information from nondental sources.

- For Lamnidae (e.g., Purdy et al., 2001), the assignment allies *Parotodus* with extinct and extant members of *Carcharodon*, *Isurus*, and *Lamna*. This approach is a conservative one that forces extinct species into morphologically less diverse extant taxa. This assignment is possible but ignores consistent morphological details that separate *Parotodus* from extant lamnids.
- For Cardabiodontidae (Siverson, 1999), the assignment places *Parotodus* with the Late Cretaceous genus *Cardabiodon*. Because there are tens of millions of years between the latest *Cardabiodon* in the Cenomanian and the earliest *Parotodus* in the Oligocene, the cardabiodontids would be a Lazarus taxon (Jablonski, 1986) that reappears after an extended absence from the fossil record. This does not preclude the alliance of *Parotodus* with *Cardabiodon* since new discoveries could bridge this gap. But when combined with differences in tooth morphology, this disjunct distribution makes this assignment possible but unlikely. In later research, Siverson discussed morphological differences between these two genera and the problems with the assignment of *Parotodus* to the Cardabiodontidae (Siverson and Lindgren, 2005).
- For Alopiidae (Herman, 1979; Purdy et al., 2001), the assignment is based on the superficial similarity between the teeth of *Parotodus* and those of some extant thresher sharks, including the absence of marked size differences between anterior and lateral teeth. Such similarities must be viewed with caution because of the huge size differences

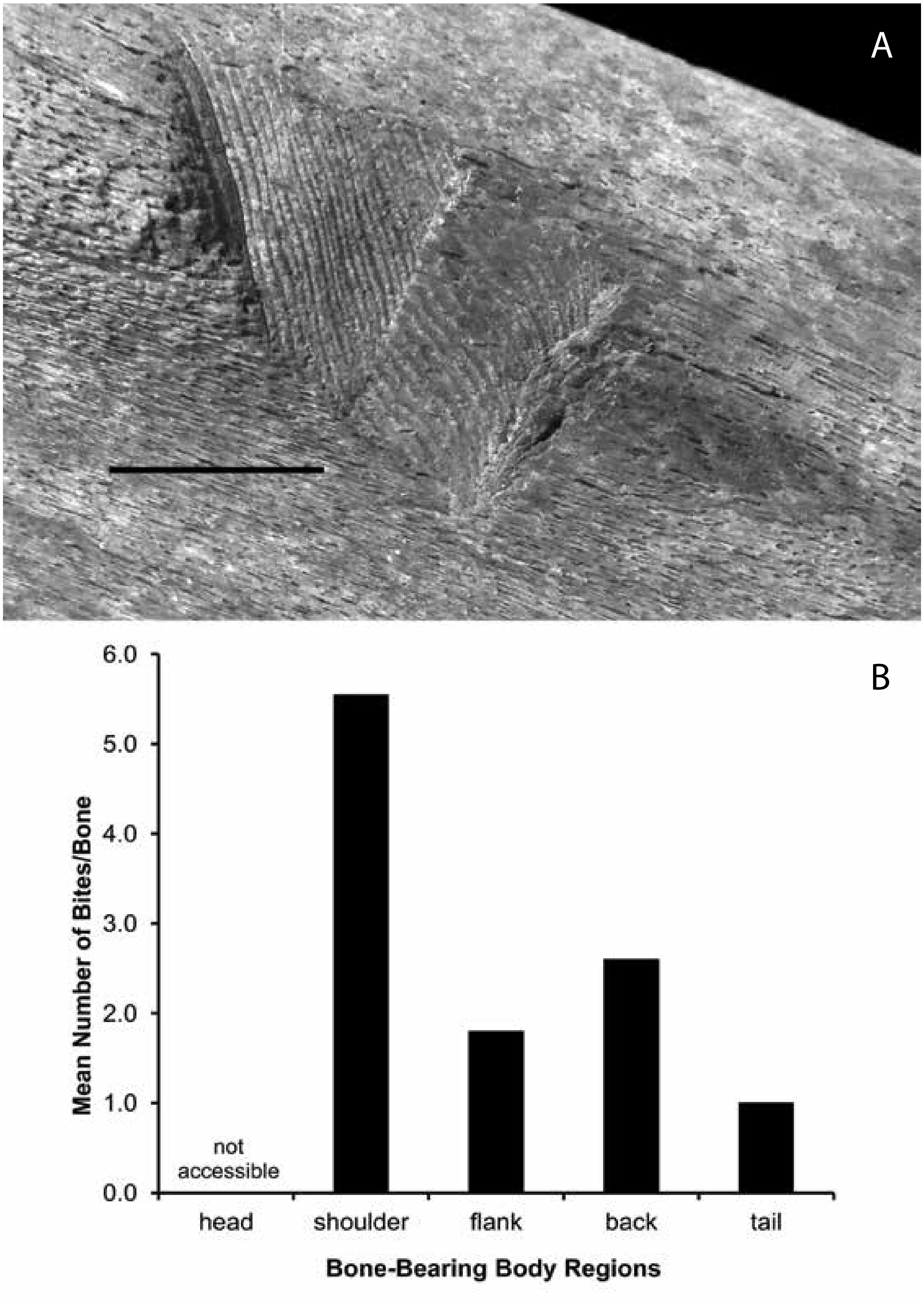


FIGURE 2.16. Cetacean bone damage attributable to *Carcharocles*. (A) Close-up of a bite mark with distinctive serration striations on a cetothere mandible from Calvert Cliffs (CMM-V-3095; Little Cove Point/Driftwood Beach, Maryland; 1 cm scale bar). (B) Distribution of large bite marks on a *Pelocetus calvertensis* skeleton from Calvert Cliffs (USNM 11976; Newell, 1998).

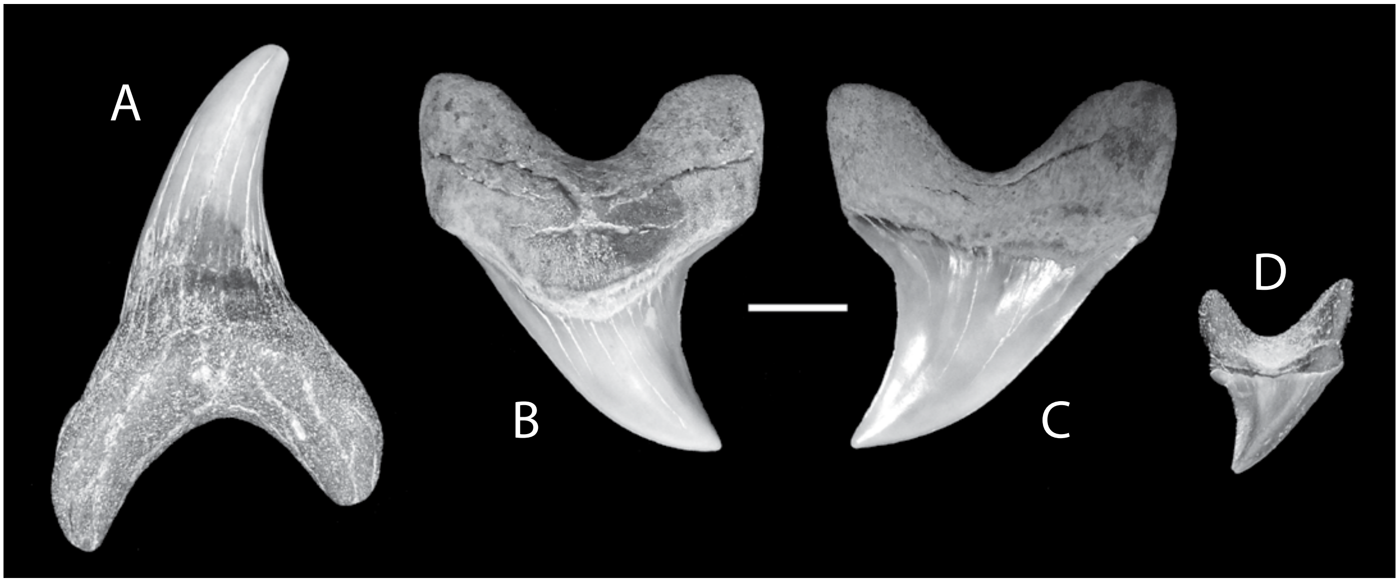


FIGURE 2.17. *Parotodus benedenii* teeth (1 cm scale bar). (A) Lower anterior tooth; lingual view (CMM-V-1633; Scientists Cliffs, Maryland). (B) Upper lateral tooth; lingual view (CMM-V-7803; Plum Point, Md.). (C) Upper lateral tooth; labial view (CMM-V-7803; Plum Point, Md.). (D) Lateral tooth; labial view (CMM-V-18; Bayfront Park, Md.).

between extant *Alopias* teeth and *Parotodus* teeth. Allometric (i.e., size-related) changes in shape due to scaling phenomena are widely known in animals, including sharks (Huber et al., 2006; Nyberg et al., 2006). Two giant *Alopias* are known from the Miocene, but although their teeth approach those of *Parotodus* in size, they have fundamentally different patterns of tooth vascularization.

- For Otodontidae (Glikman, 1964; Cappetta, 1987, 2006), the assignment is based on relatively generalized dental characters, such as large size, a robust crown and root, and a wide neck that allies *Parotodus* with *Otodus* and *Carcharocles*. These characters are not unique and occur in varying degrees in other large lamniform teeth, such as those of *Cardabiodon*, *Cretolamna*, and *Cretoxyrhina*. The one character that allies *Parotodus* with other otodontids is the presence of nutrient foramina in a broad mesiodistal arc over the thickest portion of the root (i.e., dispersed pores of Kent, 1994). This differs from the mesiobasal cluster of foramina in other large lamniforms.

Mewis (2008) performed a phylogenetic analysis of tooth morphology in fossil lamniforms to evaluate the relationships among unserrated *Carcharodon*, *C. carcharias*, and *Carcharocles*. The consensus tree from this study had *Parotodus* as the sister group of a clade containing the Otodontidae and the Lamnidae. Unfortunately, it is difficult to assess the reliability of this study with respect to the status of *Parotodus* since (as Mewis acknowledges) the alopiids were not included in the analysis, and many character states for *P. benedenii* were listed as undefined. Consequently, this study does little to resolve ambiguities over the familial placement of *Parotodus*.

At the present time, the rather meager available evidence supports the retention of *Parotodus* within the Otodontidae. The similarities in gross tooth morphology, along with the distinctive vascularization in these three genera, are consistent with their confamilial status. A thorough evaluation of tooth morphology in *Parotodus*, including a more comprehensive phylogenetic analysis of dental morphology comparable to that of Mewis (2008), is clearly needed.

Parotodus benedenii (Le Hon, 1871)

FIGURE 2.17

Synonymy follows Purdy et al. (2001), Marsili et al. (2007), and Reinecke et al. (2011).

Description. The teeth of this species can be large and remarkably robust. The crown is thick and triangular and either curved distally in upper teeth or distally curved to erect in lower teeth (Figure 2.17A). In profile, the crowns of upper teeth are curved labially, whereas those of lower teeth are erect or inclined lingually. The cutting edges are smooth and unserrated. The crown is separated from the root on the lingual face by a broad neck that retains a comparatively consistent width out onto the mesial and distal shoulders of the tooth. The root is very thick, and lower teeth have a particularly massive root because of a large lingual protuberance. The basal margin of the root is broadly concave, and the root lobes are elongated and have rounded ends. Small teeth have a single nutrient foramen on the most elevated portion of the lingual protuberance. In progressively larger teeth, additional foramina appear laterally. In large teeth the nutrient foramina are disposed in a broad mesiodistal arc over the thickest portion of the root, although these foramina are typically small and can be difficult to observe.

Lateral teeth of both the upper and lower jaws have somewhat lower crowns. The height and width of lateral teeth are similar (Figure 2.17B,C) but otherwise resemble the taller anteriors. Crowns in both jaws become distally curved and, in profile, become more erect. Roots of lower teeth lose the prominent lingual protuberance, although they are still thicker than those of comparable upper teeth. Some lateral teeth near the commissure may bear low, broad cusplets, particularly on the distal shoulder (Figure 2.17D).

DISCUSSION. Kent and Powell (1999) reconstructed the dentition of *P. benedenii* on the basis of an assemblage of 114 teeth as having 14 upper and 13 lower tooth positions (USNM 489114). Position assignments were based on patterns of changes to crown and root morphology derived from extant lamnid and alopiid dentitions. The most speculative position assignment was for a moderately sized coronal fragment that was more compressed than anterior teeth and more erect than lateral teeth. Two possible assignments for this fragment were proposed, either a tooth from another individual or an upper intermediate (=third anterior) tooth. The general rarity of *P. benedenii* would make a second individual unlikely. Further, in bivariate plots of a variety of coronal parameters (corrected to minimize the effect of size as a confounding factor) the fragment consistently graphed as an outlier from both anterior and lateral teeth. Using these observations, it was designated as an upper intermediate tooth.

Ward and Bonavia (2001) proposed a third alternative, that the coronal fragment represented a symphyseal tooth. This interpretation is unlikely, as the morphology of this fragment is unlike the symphyseals in an associated set of about 30 *P. benedenii* teeth from the early Miocene Batesford Limestone of Victoria, Australia (Kemp, 1991: pl. 32). Kemp tentatively identifies one of these teeth (pl. 32D) as a lower symphyseal and a second (pl. 32E) as an upper symphyseal. Purdy et al. (2001) agree with the assignment of these two teeth on the basis of the relative compression of the crowns. The morphology of these two teeth is consistent with symphyseals reported from associated dentitions of other large lamniform sharks (Shimada, 2002, 2007; Siverson, 1999) and very different from the coronal fragment identified as an upper intermediate tooth in USNM 489114.

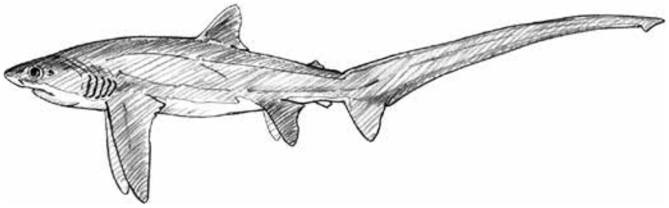
One final, more speculative interpretation of this tooth is that it actually represents the upper first anterior, and the two anterior files reported by Kent and Powell represent the second and third files, respectively.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. The teeth of *P. benedenii* are very rare along Calvert Cliffs (six specimens), having been collected primarily on beaches associated with the Calvert and Choptank Formations. In situ specimens are known only from beds 3 and 10. At inland sites in the Mid-Atlantic area, specimens are also known in situ from bed 1 of the Calvert Formation, as well as from the Eastover Formation (indeterminate horizon; late Miocene). *Parotodus benedenii* has been widely reported from early Oligocene through early Pliocene fossil beds of Europe (Belgium, Germany, Hungary, Italy, Malta, the Netherlands, Portugal, Slovakia, and Switzerland), Africa (Angola and South Africa), the Azores, and the United States (Maryland, North Carolina, and Virginia), along with Australia, Japan, and New Zealand in the western Pacific (Davies, 1964; van den Bosch et al., 1975; Osawa et al., 1978; Kuga, 1985; Cappetta, 1987, 2012; Nolf, 1988; Kemp, 1991; Yabumoto and Uyeno, 1994; Kent and Powell, 1999; Purdy et al., 2001; Ward and Bonavia, 2001; Reinecke et al., 2005, 2011; Kocsis, 2007; Marsili et al., 2007; Marsili, 2008; Ávila et al., 2012; Bor et al., 2012; Cappetta, 2012; Everaert, 2014). In addition to published records of *P. benedenii*, specimens are also known from California, South Carolina, and Peru (BWK, pers. obs.).

Miocene specimens of *P. benedenii*, such as those from Calvert Cliffs, are typically smaller and slightly more gracile than the massive specimens recovered from the early Pliocene (Cappetta, 1987, 2012).

FAMILY ALOPIIDAE BONAPARTE, 1838

Genus *Alopias* Rafinesque, 1810



Thresher Sharks – Alopiidae

The thresher sharks belong to the macroceanic ecomorphotype (Compagno, 1990b), large, active, neritic to epipelagic sharks found in tropical and temperate oceans worldwide. They are easily recognized because of their distinctive body profile with a stout, fusiform body; a relatively short, broad head; a small mouth; and an elongated, scythe-like dorsal lobe of the caudal fin. Living threshers reach a length of at least 5.7 m (and perhaps up to 6.5 m), although because the dorsal lobe of the caudal fin is approximately as long as the body itself, maximum weights are considerably less than would be expected on the basis of total length. Extant threshers are specialized predators of small schooling squid and fishes (e.g., sardines, herring, anchovies, mackerels, and bluefishes) and also benthic fishes (e.g., flounder and hake) and pelagic crustaceans. They swim around schools of prey in circles of decreasing size, herding them into compact masses, and then use the dorsal lobe of the tail to stun and cripple prey. Threshers then turn and consume the disabled prey (Compagno, 1984, 2002; Aalbers et al., 2010; Castro, 2011).

The dentition is unusual for a macrophagous lamniform in that there are no greatly enlarged anterior teeth. Instead, the dentition of comparatively small teeth has weak gradient homodonty, with anterior teeth only slightly larger than the lateral teeth. Because threshers ingest crippled prey that have limited ability to escape, their teeth are relatively small and numerous. Two extant species, the pelagic thresher (*A. pelagicus*) and the common thresher (*A. vulpinus*), have an elevated and variable number of tooth row groups, ranging from 41–45 in the upper jaw and 37–38 in the lower jaw in *A. pelagicus* to 32–52 in the upper jaw and 25–50 in the lower jaw of *A. vulpinus*. The third extant species, the bigeye thresher (*A. superciliosus*) has larger teeth and a lower tooth count of 22–27 in the upper jaw and 20–24 in the lower jaw. The larger teeth of *A. superciliosus* allow it to prey on larger prey, such as lancet fishes and small billfishes. The exceptionally large eyes of *A. supercilious* also allow this species to forage in deeper water such as the outer continental shelves and upper continental slopes (Compagno, 2002).

Four species of *Alopias* are known from Calvert Cliffs, two small-toothed species (maximum tooth height about 15 mm) and two giant-toothed species (maximum tooth height > 40 mm). The small-toothed species have teeth that are similar in size and overall morphology and are allied with extant thresher shark species.

***Alopias* cf. *A. vulpinus* (Bonnaterre, 1788)**

FIGURE 2.18A–C

Synonymy follows Purdy et al. (2001) and Reinecke et al. (2011).

Description. The most common *Alopias* from Calvert Cliffs is *A.* cf. *A. vulpinus*. The teeth are small, reaching a maximum size of about 15 mm in either height or width. The crown is broad, triangular, and erect in anterior files (Figure 2.18A,B). The cutting edges are smooth and complete. The crowns are compressed and erect in profile. The root has an arched basal margin and extended root lobes with rounded ends. The lingual face of the root has a modest lingual protuberance bearing a single nutrient foramen. The labial face of the crown is flat and overhands the labial root face and the proximal portions of the root lobes in the form of distinctive callosities. The callosities are generally smooth, although a few fine, vertical plicae may be present. The basal root margin is widely concave, and the root lobes are rounded. In anteriors, the tooth height and width are roughly equal.

Lateral teeth resemble anteriors but have a crown that is curved distally (Figure 2.18C). The crown is lower than in anterior teeth, and overall, the tooth height is somewhat less than the tooth width.

Discussion. Miocene teeth of this morphology are frequently listed as *A. latidens* (Cappetta, 1987; Kent, 1994; Müller, 1999) on the basis of the presence of very broad crowns, although Purdy et al. (2001) note that coronal width in extant *A. vulpinus* teeth can be quite variable. No extant *A. vulpinus* dentition of comparable size was available for study, but differences in relative coronal width (=coronal width measured at the inflection point on the distal cutting edge divided by the total tooth width) were compared using 12 *A.* cf. *A. vulpinus* teeth from Calvert Cliffs and 14 teeth from comparable tooth positions from the illustrated dentition of an extant 4 m [13 ft] *A. vulpinus* (Bourdon, 2008–2009, photographically enlarged). There was no significant difference in relative coronal width between *A.* cf. *A. vulpinus* (mean = 0.37) and *A. vulpinus* (mean = 0.39; t = 1.61, P = 0.12). Purdy et al. (2001) note that the labial callosity is rounded and plicate in *A.* cf. *A. vulpinus* from the Pungo River and Yorktown Formations. This condition is less pronounced in the teeth from Calvert Cliffs, where the callosity is typically thinner and fine, inconspicuous plications are only infrequently present.

Stratigraphic and Geographic Ranges. The teeth of *A.* cf. *A. vulpinus* are infrequently collected from Calvert Cliffs, although they represent the most abundant thresher shark species. This species is known from the Calvert, Choptank, and St. Marys Formations, although it is more common on the northern and middle portions of the cliffs (Visaggi and Godfrey, 2010). The only specimens found in situ were from beds 10, 12, and 17. More than 20 teeth were examined for this study.

This species (sometimes listed as *A. latidens*) has previously been reported from the Miocene of Belgium, France, Italy, and Maryland (Cappetta, 1987; Kent, 1994; Bourdon, 2006–2009). It has also been reported from the late Oligocene (Chattian; Steurbaut and Herman, 1978; Nolf, 1988; Baut and Génault, 1999; Reinecke et al., 2005), but it is unclear whether these teeth are conspecific or a separate species, *A. latidens*.

The extant common thresher (*A. vulpinus*) is a circumglobal, temperate to occasionally tropical species that occurs primarily in oceanic waters. *Alopias vulpinus* is largely piscivorous but also consumes pelagic cephalopods and crustaceans (Gubanov, 1972; Compagno, 1984, 2002; Compagno et al., 2005; Castro, 2011).

***Alopias* cf. *A. superciliosus* (Lowe, 1840)**

FIGURE 2.18D

Synonymy follows Reinecke et al. (2011; as *A. exigua*).

Description. The second species of small-toothed thresher known from Calvert Cliffs is much less common than *A.* cf. *A. vulpinus*. The teeth of this species are similar in size to

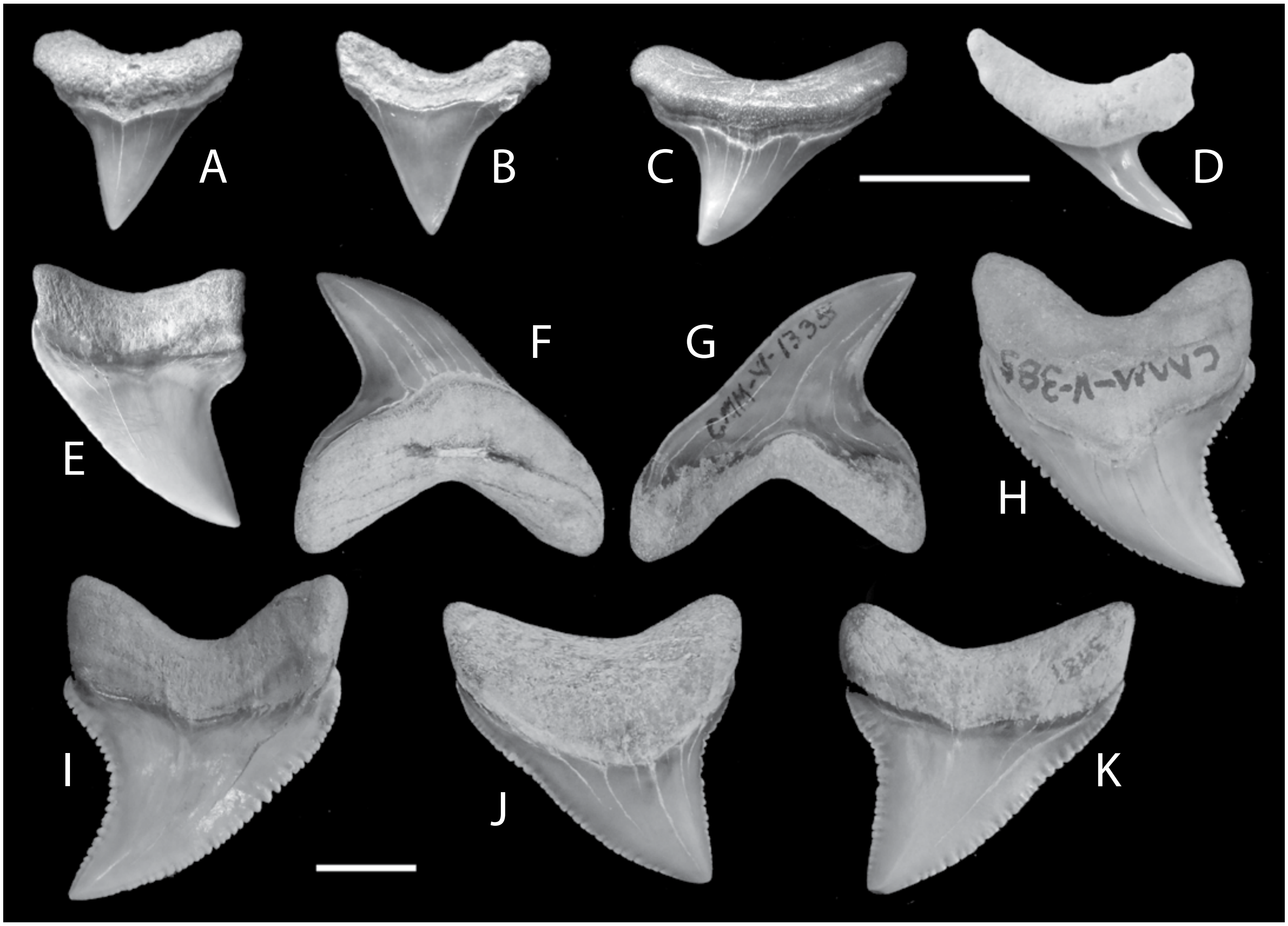


FIGURE 2.18. *Alopias* teeth (separate 1 cm scale bars for A–D and E–K). (A) *Alopias* cf. *A. vulpinus* anterior tooth; lingual view (CMM-V-823; bed 10, Plum Point, Maryland). (B) *A.* cf. *A. vulpinus* anterior tooth; labial view (CMM-V-823; bed 10, Plum Point, Md.). (C) *A.* cf. *A. vulpinus* lateral tooth; lingual view (CMM-V-767; bed 10, Willows, Md.). (D) *A.* cf. *A. superciliosus* lateral tooth; lingual view (CMM-V-7694; bed 3, Pamunkey River, Virginia). (E) *A. grandis* partially crenulate upper anterior tooth; labial view (CMM-V-7804; Randle Cliff, Md.). (F) *A. grandis* left lower lateral tooth; lingual view (CMM-V-1335; Chesapeake Beach, Md.). (G) *A. grandis* left lower lateral tooth; labial view (CMM-V-1335; Chesapeake Beach, Md.). (H) Serrated *Alopias* sp. right upper anterior tooth; lingual view (CMM-V-385; bed 12, Parkers Creek, Md.). (I) Serrated *Alopias* sp. right upper anterior tooth; labial view (CMM-V-385; bed 12, Parkers Creek, Md.). (J) Serrated *Alopias* sp. right upper lateral tooth; lingual view (CMM-V-3981; Parkers Creek, Md.). (K) Serrated *Alopias* sp. right upper lateral tooth; labial view (CMM-V-3981; Parkers Creek, Md.).

those of *A.* cf. *A. vulpinus* but are much more gracile (Figure 2.18D). The crown is narrow to only moderately broad and distally inclined, with smooth cutting edges. The cutting edges are somewhat variable, ranging from incomplete (restricted to the apical half of the crown) to complete. Incomplete cutting edges occur primarily on the narrow, relatively erect anterior teeth, with complete cutting edges that extend out onto the enameloid shoulders becoming more prevalent on lateral teeth. In profile the crowns are bent lingually, or slightly reflexed. The labial face of the crown overhangs the root to form long, narrow callosities. The root is more delicate than in *A. latidens*, with a concave basal margin and elongate root lobes with rounded ends. The mesial root lobe is frequently longer than the distal lobe and roughly aligned with the mesial edge of the crown. The lingual protuberance has one (or sometimes two) nutrient foramina within a deeply incised nutrient groove.

Discussion. There is some controversy over the exact designation for these teeth. The name *A. exigua* has been widely used for narrow-crowned Neogene *Alopias*, but Purdy et al. (2001) and Ward and Bonavia (2001) rejected it on the grounds that the type specimens represent a mixture of different species. Instead, they allied these teeth (as *A.* cf. *A. superciliosus*) with the extant bigeye thresher (*A. superciliosus*). Reinecke et al. (2011) reevaluated the type specimens of *A. exigua* and compared them with a comparatively large sample of teeth from the Miocene of Germany. They concluded that *A. exigua* was a valid species and applied this name to Miocene teeth with narrow crowns. Further, they separate *A. exigua* from *A. superciliosus* by the absence of the distinct distal heels and shallower roots that characterize the latter species. But these characters are quite variable in extant *A. superciliosus*, and it is unclear if they are actually adequate for separating the two species. Finally, the teeth of *A. superciliosus* are sexually dimorphic, with anterior teeth of females having comparatively broader, more bladelike crowns than the narrower, more flexuous crowns of male anteriors (Gruber and Compagno, 1981). This difference is never noted by Reinecke et al. (2011), although it does appear to be present in their illustrated specimens (e.g., pl. 44, fig. 2). Bor et al. (2012) recognize two different tooth morphologies from the Miste Beds (Langhian) of the Netherlands, listing them as separate, co-occurring species, *A. exigua* and *A. superciliosus*. But like Reinecke et al. (2011), they do not consider the possibility of sexual dimorphism.

Unfortunately, the range of variability has never been fully documented in either *A. exigua* or *A. superciliosus*. Coupled with the small number of specimens from Calvert Cliffs, a definitive assessment of these teeth is difficult. Pending a more extensive, quantitative analysis, the small, narrow-toothed threshers from the Calvert Cliffs beds will be allied with *A. superciliosus* (the senior synonym), as *A.* cf. *A. superciliosus*.

Stratigraphic and Geographic Ranges. Teeth of *A.* cf. *A. superciliosus* are quite rare from Calvert Cliffs, and only five were available for study. Fossil teeth of this morphology have also been reported from Barbados, Belgium, France, Germany, Italy, Japan, Malta, the Netherlands, Portugal, Venezuela, Maryland, Virginia, and North Carolina (Cigala-Fulgosi, 1983, 1988; Cappetta, 1987, 2012; Nolf, 1988; Kent, 1994; Yabumoto and Uyeno, 1994; Antunes et al., 1999; Aguilera and Rodrigues de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Bourdon, 2006–2009; Reinecke et al., 2011; Bor et al., 2012).

Living bigeye threshers (*A. superciliosus*) are a coastal to oceanic, tropical and temperate shark that ranges from shallow, nearshore waters to depths of more than 700 m. The diet consists of pelagic teleost fishes and cephalopods (Compagno, 1984, 2002; Compagno et al., 2005; Castro, 2011).

The giant-toothed *Alopias* not only have teeth that are considerably larger than those of *A.* cf. *A. vulpinus* and *A.* cf. *A. superciliosus* but also have crowns that are broader and taller (Figure 2.3B). The root is highly compressed, with much shorter root lobes, and in many respects more closely resembles the roots of similarly sized lateral teeth of *Isurus* and *Carcharodon*. The roots of large *Alopias* differ from these latter genera in having a typically arched basal root margin and a single nutrient foramen. In *Isurus* the basal root margin is relatively straight with a medial indentation, whereas in *Carcharodon* the basal root margin is obtusely angled to nearly straight. Both of these genera usually have two or three clustered nutrient foramina.

Kozlov (2001) transferred the giant-toothed *Alopias* to the genus *Trigonotodus*. Members of this genus, including *T. alteri* from the late Oligocene, have short, relatively narrow, erect crowns; elongated root lobes; obvious callosities on the labial root face; and a conspicuous cusplet on each shoulder. The giant-toothed threshers do not easily fit into the *Trigonotodus* tooth morphology, and both Cappetta (2006) and Maisey (2012) doubt that *Trigonotodus* is actually an alopiid. The teeth of *Trigonotodus* are more consistent with those of the littoral habitus of Compagno (1990b: 54–55) and rather different from the conspicuously taller and broader crowns of giant *Alopias* teeth. Further, the root lobes of giant *Alopias* teeth are more abbreviated and compressed and lack prominent cusplets. A few specimens may have weak vestigial cusplets or long, low distal heels, but since these are also known from small-toothed *Alopias* (e.g., *A.* cf. *A. vulpinus* and *A.* cf. *A. superciliosus*; BWK, pers. obs.), their presence is unremarkable. Overall, the similarity in morphology to the ubiquitous small-toothed *Alopias* makes the assignment of the Calvert Cliffs giant threshers to this genus highly likely.

***Alopias grandis* (Leriche, 1942)**

FIGURE 2.18E–G

1942 *Alopecias grandis* Leriche: Leriche, p. 73, pl. 5, figs. 21–22.
2001 *Trigonotodus grandis* (Leriche), Kozlov, pp. 89–91, figs. 2, 3.

Description. The large teeth of *A. grandis* have broad, smooth-edged, distally curved crowns. The crown is relatively tall with an ogival apex. The mesial cutting edge is moderately to strongly convex, although in some teeth the cutting edge is weakly sigmoidal. The distal cutting edge is broadly concave. Both coronal faces are smooth; the lingual face is flat, whereas the labial face is convex. In profile, the crowns are erect or nearly so. The root is compressed, with root lobes that are short. On the labial face of the root the enameloid does not extend out onto the root lobes, although there may be an indistinct layer of orthodentine forming a thin callosity in this area. A single nutrient foramen is located on the midline of the tooth and on or just basal to the weakly developed lingual protuberance. The basal margin of the root is typically arched, although it becomes obtusely angled in some specimens.

Anterior teeth (Figure 2.18E) have taller, hooked crowns and narrower roots than lateral teeth. Lateral teeth are quite variable in coronal width, ranging from moderately wide (Figure 2.18F,G) to nearly triangular.

Discussion. The teeth of *A. grandis* resemble those of *A.* cf. *A. vulpinus* but are larger (≥40 versus ≤15 mm) in both height and width. The crown is proportionally larger and more ogival than in *A.* cf. *A. vulpinus*, with a mesial cutting edge that is more strongly convex than the curved, triangular crown of *A.* cf. *A. vulpinus*. The root of *A. grandis* is more compressed, with root lobes that are shorter and somewhat deeper.

Cappetta (1970, 2006, 2012) and Kent (1994) incorrectly interpreted these teeth as either intermediate or lateral teeth of *Isurus* or unserrated *Carcharodon*. With larger sample sizes of well-preserved teeth the differences between *A. grandis* and these lamnid laterals are readily apparent. The confusion arises in part because a few specimens may have a basal root margin that tends toward broadly angled, rather than arched. In this respect, the root superficially resembles those of *Carcharodon* and some *Isurus* upper laterals, although in these two genera the angle of the basal root margin is generally greater than in *A. grandis*. Further, the broader, spade-like apex and strongly convex mesial margin of the crown of *A. grandis* is distinctive.

Although monognathic heterodonty is present, there are no clear indications of either dignathic or gynandric heterodonty. Some teeth have slightly broader crowns that may be erect when viewed in profile, whereas other teeth have somewhat narrower crowns that are erect to weakly inclined lingually. But there is also substantial overlap in these characters, and their significance is unknown.

A few *A. grandis* specimens are known that have weak, irregular crenulations on the cutting edges (Figure 2.18E). These crenulations are difficult to detect in a cursory examination and may occupy the entire cutting edges or only portions of the edges.

Stratigraphic and Geographic Ranges. Because of their rarity, *A. grandis* teeth are almost unknown in the paleontological literature but have been documented by amateur collectors from the late Oligocene through middle Miocene. *Alopias grandis* teeth are rare along Calvert Cliffs, with only 10 available for study. They have been collected on beaches associated with the Calvert and Choptank Formations and in situ from beds 3, 10, and 12.

Teeth of *A. grandis* have been collected from the eastern United States in Miocene sediments on the Potomac River and its tributaries in Maryland and Virginia (Leriche, 1942; Cappetta, 1970; Kent, 1994; M. Bennett, pers. comm., 2011, 2015), Hertford and Beaufort Counties in North Carolina (Gary Greaser, Buried Treasure Fossils, Richmond, Texas, pers. comm., 2011; M. Bennett, pers. comm., 2016). *Alopias grandis* teeth are also known from the late Oligocene (Chattian) Ashley and Chandler Bridge Formations in Charleston, Dorchester, and northern Beaufort Counties in South Carolina (Weems and Lewis, 2002: fig. 9; Steven Alter, Steve's Fossil Shark Teeth, Inc., White Bird, Idaho, pers. comm., 2015).

In Europe, *A. grandis* have been reworked into the early Pliocene Kattendijk Formation (early Zanclean) in Belgium from older early to earliest middle Miocene sediments (late Aquitanian, Burdigalian, or early Langhian; Pieter De Schutter, National Institute of Criminalistics and Criminology, Brussels, Belgium, pers. comm., 2012; Everaert, 2014). They have also been found in the Middle Globigerina beds (Burdigalian; Ward and Bonavia, 2001) of Malta (D. Ward, pers. comm. 2015).

Alopias grandis has also been reported from Barbados (Casier, 1966) and Peru (M. Bennett, pers. comm., 2016) and from deep-sea sediments of the central Pacific Ocean (Belyaev and Glikman, 1970).

Serrated *Alopias* species

FIGURE 2.18H–K

Description. See Kent and Ward (this chapter's Addendum) for the complete description of this new species.

Discussion. The second giant-toothed *Alopias* from Calvert Cliffs (Figure 2.18H–K) resembles *A. grandis* but has coarsely serrated cutting edges. These serrations are substantially larger and more distinctive than those of the weakly crenulate specimens of *A. grandis* (Figure 2.18E) discussed above.

Stratigraphic and Geographic Ranges. See Kent and Ward (this chapter's Addendum).

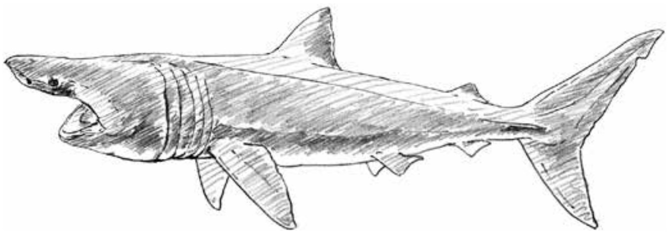
Alopias grandis and the related serrated species are particularly rare, and there are no known sets of associated teeth from these species. Without such evidence it is impossible to reconstruct the dentition of these species or even speculate on how tooth row counts may have differed from those of extant *Alopias*. Their lifestyle was probably unlike that of extant, small-toothed thresher sharks on the basis of differences in tooth morphology. The tall, compressed, smooth-edged or serrated crowns (Figure 2.3B) and compressed roots with reduced root lobes likely would produce biomechanical properties more like those of *Carcharodon* upper laterals than small-toothed *Alopias*. How these differences in tooth morphology would have been reflected in overall body morphology is unknown, although the bladelike cutting teeth of the giant-toothed *Alopias* may have obviated the need for the greatly elaborated sickle-like tail of living threshers.

Extant small-toothed *Alopias* are primarily open-ocean, epipelagic species, and a similar distributional pattern apparently occurs with the giant threshers as well. Along Calvert Cliffs, the distributions of both *A. grandis* and the serrated species parallel that of the common small-toothed thresher (*A.* cf. *A. vulpinus*, 77 of 79 teeth; data from Visaggi and Godfrey, 2010, listed as *A. latidens*) and reflect primarily open shelf marine environments (Kidwell, 1989: fig. 2). Likewise, the distribution of *A. grandis* and serrated *Alopias* teeth along the Potomac River in Virginia, as well as in North and South Carolina, also reflects open marine shelf habitats (Miller, 1982; Idris and Henry, 1995; Powars et al., 2005).

Conversely, the younger St. Marys Formation (beds 22 and 23, early to middle Tortonian) at the southern end of Calvert Cliffs represents marginal marine environments that would be unlikely habitats for primarily epipelagic sharks such as *Alopias*.

FAMILY CETORHINIDAE GILL, 1862

Genus *Cetorhinus* Blainville, 1816



Basking Sharks – Cetorhinidae

The sole extant basking shark, *Cetorhinus maximus* (Gunner), is a derived tachypelagic, ram-feeding planktivore that consumes planktonic crustaceans, such as shrimp and copepods, and teleost fish eggs by filtering them on long, numerous gill rakers. *Cetorhinus maximus* occurs in cold temperate to boreal waters and is found in nearshore waters to well offshore. The basking shark is the second largest living elasmobranch, reaching lengths of at least 11 m and perhaps in excess of 15 m. Their biology is poorly understood, although they have been found to direct their movements to track plankton-rich patches and to shed their gill rakers before overwintering in deeper waters (Matthews and Parker, 1950; Compagno, 1984, 1990b, 2002; Sims and Merrett, 1997; Sims and Quayle, 1998; Compagno et al., 2005; Castro, 2011).

The teeth of *Cetorhinus* are small and superficially resemble those of other large filter-feeding sharks, the lamniform megamouth shark (*Megachasma*), and the orectolobiform whale shark (*Rhincodon*) in having short, recurved crowns and shortened root lobes (Cappetta, 1987; Compagno, 1990a).

Cetorhinus sp.

FIGURE 2.19A

DESCRIPTION. *Cetorhinus* is presently known from Calvert Cliffs exclusively in the form of vertebral centra. The centra are large and are ovoid when viewed axially. The maximum diameter for these centra is more than 9 cm. The articular faces consist of deep conical surfaces with concentric growth lines on the articular surfaces of the cones. The anterior and posterior cones of each centrum typically join apically at an ovoid axial perforation. The radial, cartilaginous septa that form the body of the centra are thin and fragile.

DISCUSSION. The septa on *Cetorhinus* centra are rarely preserved, and these centra are typical represented by isolated articular cones (Gottfried, 1995), although a partial skeleton of a juvenile with well-preserved centra is known (Hovestadt and Hovestadt-Euler, 2012).

The *Cetorhinus* centra from Calvert Cliffs cannot be reliably assigned to a species since the two named species, *C. parvus* Leriche (middle Eocene to middle Miocene) and *C. maximus* (Gunnerus) (middle Miocene to Holocene), both occur during this time (Leriche, 1926; Herman, 1979; Cione and Reguero, 1998; Hovestadt and Hovestadt-Euler, 2012).

The absence of either *Cetorhinus* teeth or gill rakers from Calvert Cliffs is troubling since these are far more common as fossils than the centra (Leriche, 1908; Jordan and Hannibal, 1923; Jonet, 1947; Uyeno and Matsushima, 1974; Herman, 1975, 1979; Schultz, 1978; Bendix-Almgreen, 1983; van den Bosch, 1984; Nakagawa and Yasuno, 1985; Cappetta, 1987; Bellwood and Schultz, 1991; Baut, 1993; Génault, 1993; Long, 1993; Yabumoto and Uyeno, 1994; Cione and Reguero, 1998; Purdy et al., 2001; Hovestadt and Hovestadt-Euler, 2012). The lack of either teeth or gill rakers of *Cetorhinus* from Calvert Cliffs is likely the result of collecting bias rather than a true absence. Teeth are relatively nondescript and small (maximum height about 7 mm). They have a stout, arched crown with weak cutting edges, with short, thick root lobes (van den Bosch, 1984; Cappetta, 1987; Reinecke et al., 2011). *Cetorhinus* gill rakers are much larger than the teeth (up to 60 mm for *C. parvus* and 200 mm for *C. maximus*) but very elongated and easily damaged. The gill rakers have a compressed, fan- to comma-shaped proximal body attached to a slender, prolonged distal rod. The distal rod and adjacent portions of the proximal body are covered with smooth enameloid. The enameloid-free portion of the proximal body consists of osteodentin (Herman, 1979; van den Bosch, 1984; Cione and Reguero, 1998; Cappetta, 1987; Hovestadt and Hovestadt-Euler, 2012). *Cetorhinus* gill rakers are likely present in Calvert Cliffs, although the largely unconsolidated sediments of these formations would make their collection unlikely without careful excavation.

Dermal thorns are also known from *Cetorhinus* (van den Bosch, 1984; Cione and Reguero, 1998; Hovestadt and Hovestadt-Euler, 2012). Thorns from the Calvert Formation compare favorably with those from the late Oligocene Chandler Bridge Formation assigned by Cicimurri and Knight (2008) to *Cetorhinus*, although, as noted previously, these are more plausibly assigned to *Squatina* (which see).

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Cetorhinus* centra have been reliably collected as beach specimens from the northern portion of Calvert Cliffs and likely derived from the Calvert and Choptank Formations. Vertebrae collected in situ have come from beds 10–13.

Fossil *Cetorhinus* are widely distributed, although rarely collected, in Eocene through Pleistocene sediments of Antarctica, Japan, Chile, California, North Carolina, Virginia, Maryland, Austria, Belgium, Romania, Denmark, France, Germany, Italy, the Netherlands, and Switzerland (Leriche, 1908; Jordan and Hannibal, 1923; Jonet, 1947; Uyeno and Matsushima, 1974; Herman, 1975, 1979; Schultz, 1978; Bendix-Almgreen, 1983; van den Bosch, 1984; Nakagawa and Yasuno, 1985; Cappetta, 1987, 2012; Nolf, 1988; Bellwood and Schultz, 1991; Baut,

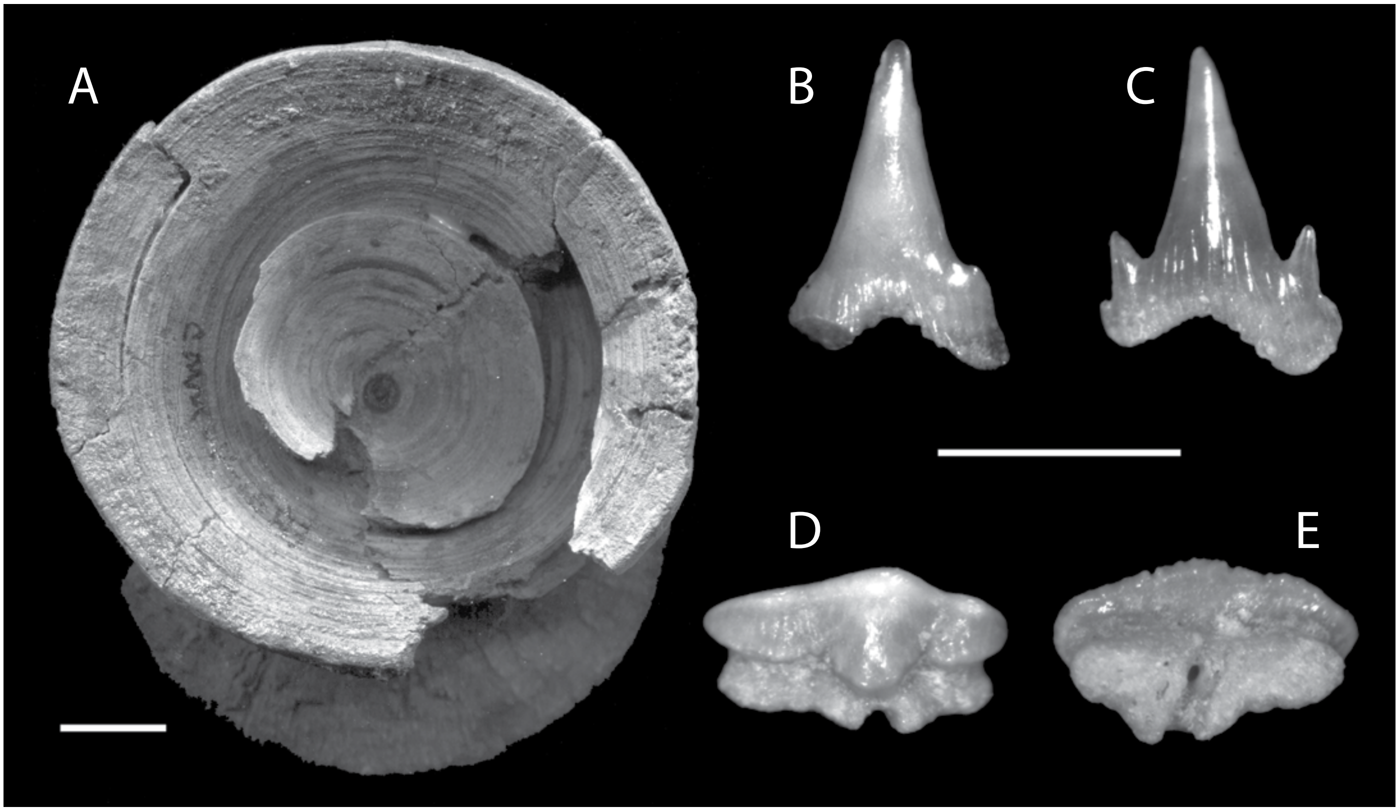
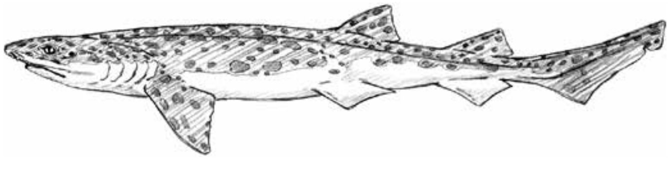


FIGURE 2.19. *Cetorhinus*, Scyliorhinid, and *Mustelus* fossils (1 cm scale bar for A; 1 mm scale bar for B–E). (A) *Cetorhinus* vertebral centrum; axial view (CMM-V-1683; bed 12, Parkers Creek, Maryland). (B) Scyliorhinid sp. anterior tooth; labial view (CMM-V-7719; bed 3B, New Kent County, Virginia). (C) Scyliorhinid sp. anterolateral tooth; labial view (CMM-V-7719; bed 3B, New Kent County, Va.). (D) *Mustelus* sp. tooth; lingual view (CMM-V-7741; bed 3B, New Kent County, Va.). (E) *Mustelus* sp. tooth; labiobasal view (CMM-V-7741; bed 3B, New Kent County, Va.).

1993; Génault, 1993; Long, 1993; Yabumoto and Uyeno, 1994; Gottfried, 1995; Cione and Reguero, 1998; Purdy et al., 2001).

ORDER CARCHARHINIFORMES COMPAGNO, 1977

FAMILY SCYLIORHINIDAE GILL, 1862



Cat Sharks – Scyliorhinidae

The Scyliorhinidae (or cat sharks) is the largest family of benthic sharks, with at least 17 extant genera and 160 species. The cat sharks are generally small sharks; most species are less than 80 cm in length, and the largest is about twice as long. They have distinctive catlike eyes and a slender, elongated body. Their teeth are small and relatively delicate, with a slender crown and, in many cases, lateral cusplets. Their biology is poorly known, but they are generally believed to prey on small fishes and invertebrates (Bass et al., 1975; Compagno, 1984, 1988, 2002; Musick et al., 2004; Compagno et al., 2005; Castro, 2011).

Recent molecular studies evaluating relationships in the Carcharhiniformes have produced evidence that the Scyliorhinidae as presently defined is paraphyletic (Human et al., 2006). The family Scyliorhinidae (sensu stricto) is restricted to the genera *Scyliorhinus* and *Cephaloscyllium*, whereas other genera are more closely allied with other carcharhiniforms (Iglesias et al., 2005). This discovery greatly complicates the familial assignment to extinct "scyliorhinid" genera since tooth morphology is very conservative among these sharks. In addition to slender crowns and cusplets, scyliorhinid-like teeth typically have a callosity on the labial face and longitudinal ridges on the basal portions of the crown and cusplets (Bass et al., 1975; Herman et al., 1990; Soldo et al., 2000). Given the currently unsettled state of scyliorhinid systematics and the high morphological overlap of teeth in this group, the specimens from Calvert Cliffs are assigned only to familial status.

Scyliorhinid sp.

FIGURE 2.19B,C

Description. These teeth are minute, with the largest ≤1.5 mm in height. Anterior teeth (Figure 2.19B) have an erect, narrow crown that is weakly inclined lingually. The coronal cutting edges are weakly developed and complete or nearly so. The shoulders bear weakly convex heels or low cusplets. The labial coronal face is slightly to moderately convex, whereas the lingual face is more strongly convex. The labial face of the crown extends basally over the surface of the root as a pronounced callosity. Short, distinct ridges are present along the basal portion of the labial face of the cusp and laterally on the lingual face. Lateral teeth (Figure 2.19C) are similar but have more widely angled root lobes and a tall, sharp cusplet on each shoulder.

The roots are poorly preserved on the available specimens and cannot be adequately described.

Discussion. Several scyliorhinid teeth have been reported from the Miocene, including specimens from *Scyliorhinus joleaudi* Cappetta, *Pachyscyllium dachiardii* (Lawley), and *Premontreia distans* (Probst) (Marsili, 2007c; Reinecke et al., 2011; Vialle et al., 2011; Bor et al., 2012; Underwood and Schlogl, 2013), but those from Calvert Cliffs cannot be unambiguously assigned to any of these species. The teeth from Calvert Cliffs have some resemblance to those of the extant genus *Apristurus* in having slender cusps and cusplets with basal ridges (Herman et al., 1990; Marsili, 2007c). But the absence of cusplets on the anterior teeth of the scyliorhinid teeth from Calvert Cliffs, along with the absence of typically bathyal shark species (e.g., Marsili, 2007c; Vialle et al., 2011; Underwood and Schlogl, 2013) in Calvert Cliffs sediments, would make such a generic assignation unlikely.

There is also some resemblance to the teeth of *Scyliorhinus canicula* (Herman et al., 1990: pls. 31, 32), although too few specimens are available for a definitive identification.

Purdy et al. (2001: fig. 44a–h) report a scyliorhinid from the Pungo River Formation in North Carolina. These teeth, like those of most other Neogene scyliorhinids, are considerably larger than the specimens from Calvert Cliff. Further, the cusplets on the Pungo River teeth are arched medially, which is not observed in the specimens from the Calvert Formation.

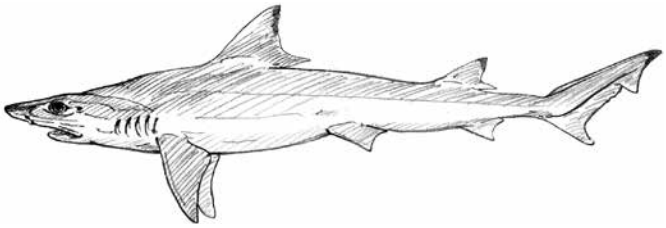
The assignment of these teeth to the scyliorhinids is based on the carcharhiniform tooth morphologies defined by Compagno (1988:35). The scyliorhinid tooth type is characterized by strong, longitudinal ridges on the crown; a pronounced labial callosity with a medially indented basal margin; cusplets typically present; serrations lacking; and a deep, often trilobate, root. The teeth from the Calvert Formation are consistent with these characteristics, although the root characteristics cannot be fully assessed.

The available specimens are all of very small size, and at present, it is unclear whether they represent juvenile or adult teeth.

Stratigraphic and Geographic Ranges. Teeth of the morphology shown in Figure 2.19B,C are known only from a few poor-quality beach specimens from the extreme northern end of Calvert Cliffs and from nine specimens collected in bed 3 of the Calvert Formation at inland sites in the Mid-Atlantic region.

FAMILY TRIAKIDAE GRAY, 1851

Genus *Mustelus* Linck, 1790



Smooth Hounds: Triakidae

The smooth hounds are a modestly diverse group of about two dozen extant species. They are small sharks with a maximum length of about 1.5 m. They are littoral, cancritrophic (=crustacean-feeding) sharks that use their crushing dentitions of low, rounded teeth to feed on crustaceans and occasionally other benthic invertebrates and small bony fishes (Compagno, 1984, 1988, 1990b, 2002; Castro, 2011). The teeth are unusual for a shark in having a domed crown with a transverse ridge, a pronounced labial lip with vertical plicae, and an obvious uvula. This tooth morphology is convergent with some batoids, such as *Pristis, Rhynchobatus*, and *Rhinobatos* (Cappetta, 1987). Despite having an unusual dentition for a shark, recent molecular evidence suggests that the genus *Mustelus* is actually paraphyletic (López et al., 2006).

Extant *Mustelus* are very difficult to identify to species and can require the use of both morphological and molecular techniques (Boomer et al., 2012; Giresi et al., 2013; Pérez-Jiménez et al., 2013). Identification of teeth to species is even more problematic because of a scarcity of definitive characters. Compagno (1984:398–399; 1988:220) describes three different tooth morphologies in *Mustelus*: (1) crown has short, erect cusp and cusplets, (2) crown has low, blunt cusp, and (3) crown is broad, rounded, and lacking a cusp. Unfortunately, the range of intra- and interspecific variation in tooth morphology of extant *Mustelus* is very poorly documented, which greatly complicates the identification of isolated teeth to species.

Mustelus sp.

FIGURE 2.19D,E

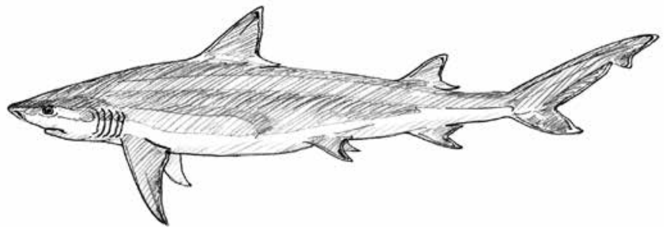
Description. The teeth are broad (<1.5 mm) and low crowned. The crown is elliptical in occlusal view and has the lingual and labial faces separated by a transverse ridge. The labial face of the crown overhangs the root, forming a prominent lip. The lip and basal portions of the labial face are ornamented with closely spaced, irregular plicae. The lingual face has a conspicuous uvula and plicae similar to those of the labial face. The root has an obvious lingual protuberance basal to the uvula, a flat basal face, and wide nutrient groove.

Discussion. Müller (1999: fig. 17/1–4, pl. 5, figs. 3–6) recorded an unnamed *Mustelus* species (*Mustelus* sp. 2) from the St. Marys Formation of Maryland, the Eastover Formation of Virginia, and the Yorktown Formation of North Carolina. Purdy et al. (2001) reported *Mustelus* teeth from the Pungo River Formation of North Carolina. These specimens are very close to those from the Calvert Formation, and they plausibly represent the same species, although the range of variation within Neogene species is currently undocumented.

Stratigraphic and Geographic Ranges. *Mustelus* teeth are rarely reported as fossils because of their very small size and nondescript shape. Along Calvert Cliffs they are known with certainty only from the Little Cove Member (beds 22/23) of the St. Marys Formation. They are also known from bed 3 of the Calvert Formation and bed 24 of the St. Marys Formation at river and inland sites of the Mid-Atlantic region. Neogene records of *Mustelus* from other areas are uncommon but include the late Miocene (Messinian) of Portugal (Balbino, 1995), late Miocene–early Pliocene of Costa Rica (Laurito Mora, 1999), and the early Pliocene (Zanclean) of France (Cappetta, 1987) and Italy (Cappetta and Cavallo, 2006; Marsili, 2008).

Family Hemigaleidae Haase, 1979

Genus *Hemipristis* Agassiz, 1843



Snaggletooth Sharks – Hemigaleidae

There is a single extant species in this genus, *H. elongatus* (Klunzinger, 1871), a nearshore shark occurring in a broad arc from the east coast of Africa, the Red Sea, Persian Gulf, India, the Philippines, and northern Australia. The teeth of *H. elongatus* are relatively large compared to those of other carcharhiniforms of similar body lengths and have a distinctive cutting-clutching dentition of dignathic heterodonty, with triangular upper teeth and awl-like lower teeth. *Hemipristis elongatus* is piscivorous, feeding on a range of bony and cartilaginous fishes. Maximum size for this species is about 2.4 m (Compagno, 1984). The teeth of *H. elongatus* are unusual in that the orthodont tooth condition that typifies carcharhiniform teeth has been modified by a unique secondary infilling of osteodentin (i.e., the pseudo-osteodont condition of Herman et al., 1991).

The snaggletooth sharks (*Hemipristis* spp.) first appear in the Eocene, and although widespread, the genus was never particularly diverse. The earliest species, *H. curvatus*, is known from Egypt, western Africa, Peru, and the eastern United States (White, 1956; Cappetta, 1987; Ward and Wiest, 1990; Kent, 1994).

There is a single snaggletooth shark species, *H. serra*, known from all along Calvert Cliffs. The teeth of this species are both abundant and the largest carcharhiniform in the Chesapeake Group.

Hemipristis serra Agassiz, 1843

FIGURE 2.20

Synonymy follows Purdy et al. (2001), Marsili et al. (2007), and Reinecke et al. (2011).

Description. Upper anterior teeth are relatively narrow and erect (Figure 2.20A). Both cutting edges are coarsely serrated, except for a distinctive smooth apical tip. The serrations are unusual in two respects; they are obliquely angled with respect to the coronal margin and are somewhat larger on the distal edges of the crown. The mesial cutting edge is weakly convex to nearly straight, whereas the distal cutting edge is straight to weakly sigmoidal. The lingual surface of the root is high, with a protuberance of modest size, and has a broad, but shallow, nutrient groove with one or more nutrient foramina. The basal margin of the root is strongly arched, whereas root lobes are comparatively short and rounded.

Lower *H. serra* teeth are very different in morphology, with a thick, narrow crown and a thicker, more robust root (Figure 2.20B). Unlike the serrated cutting edges of upper teeth, those of the lowers are unserrated and limited to roughly the apical third of the crown. One or more large, slender serrations occur on the mesial and distal shoulders.

Upper lateral teeth are broader and more triangular than anterior teeth (Figure 2.20C). Like upper anterior teeth, both cutting edges are coarsely serrated, except for the smooth apex. The mesial heel is weakly convex and transitions smoothly into a convex, serrated mesial cutting edge. The distal cutting edge is strongly concave and serrate. The distal serrations are particularly large, with the largest adjacent to the smooth tip and

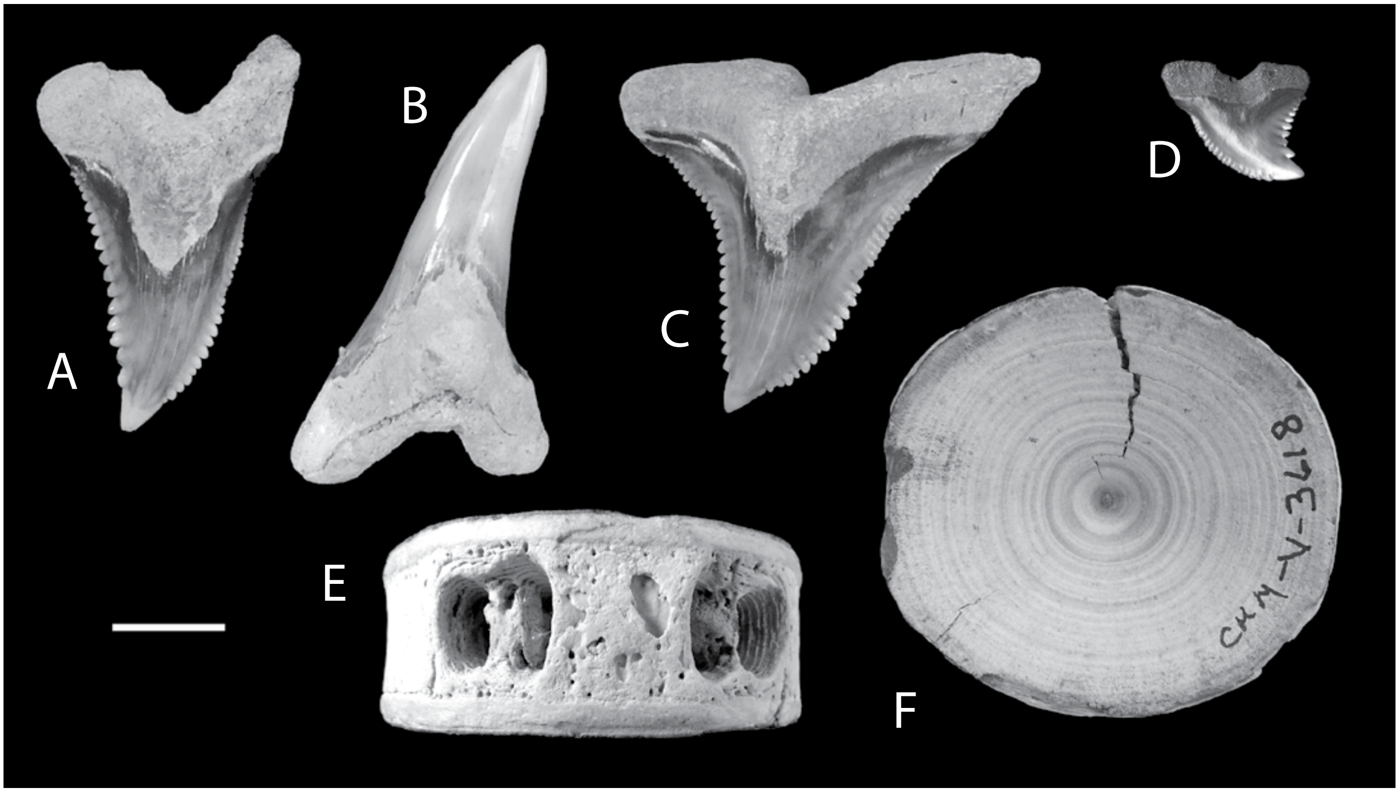


FIGURE 2.20. *Hemipristis serra* fossils (1 cm scale bar). (A) Upper anterior tooth; lingual view (CMM-V-704; Parkers Creek, Maryland). (B) Lower anterior tooth; lingual view (CMM-V-699; Parkers Creek, Md.). (C) Upper lateral tooth; lingual view (CMM-V-699; Parkers Creek, Md.). (D) Upper posterolateral tooth; labial view (UMCP 2171; Matoaka Cottages, Md.). (E) Vertebral centrum; ventral view (CMM-V-3618; Flag Ponds, Md.). (F) Vertebral centrum; axial view (CMM-V-3618; Flag Ponds, Md.).

decreasing in size basally. The lingual face of the root has a moderately large protuberance with a wide, shallow nutrient groove. The basal margin of the root is straight, except for a shallow medial concavity. The mesial root lobe is extended and pointed, whereas the distal lobe is short and rounded or rectilinear. Near the jaw commissure, the crowns of upper teeth become lower and broader (Figure 2.20D).

Lower lateral teeth have crowns that are lower and more distally inclined than lower anteriors, with the serrations expanding apically onto the basal half of the crown.

Hemipristis serra vertebral centra are short, cylindrical, and aseptate, with thick rims and straight to weakly concave sides (Figure 2.20E,F). The dorsal and ventral foramina are rectilinear to ovoid, and each is bisected by prominent diagonal lamella extending to the surface of the centrum. Pores of moderate to large size are common, with some following the outlines of the foramina and rims and others scattered over the surface between these structures. In axial perspective the central are circular to ovoid, with a width greater than the height.

DISCUSSION. Chandler et al. (2006) document both ontogenetic and phyletic changes in tooth morphology in *H. serra*. Immature teeth are small in size and have smooth or very weakly serrated mesial cutting edges and a few, large serrations of the distal cutting edges. Immature specimens were comparatively rare in the samples examined in this study, but this is not unexpected given the strong preservational bias against immature individuals in the fossil record (Raup, 1977; Smith, 1994:108–117). Adult teeth are more strongly serrated, with the unserrated tip of the crown becoming proportionally smaller as tooth size increases.

Hemipristis serra vertebral centra were first described on the basis of centra collected in association with teeth from the Calvert Formation (USNM 467531; Purdy et al., 2001: fig. 48a). Burris (2004: fig. 10) used radiography to investigate the internal morphology of *H. serra* centra as part of a cladistic analysis of carcharhiniform vertebral centra.

Recently, a partial skeleton of *H. serra* has been collected from the Calvert Formation. This skeleton is in a private collection and consists of a large number of vertebrae and teeth, along with fragments of cartilage (Stephen Godfrey, Calvert Marine Museum, Solomons, Maryland, pers. comm.).

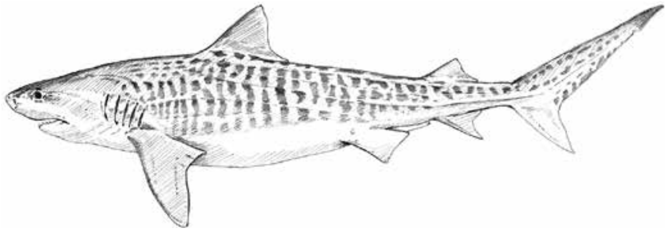
STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Hemipristis serra* teeth are widely distributed as beach specimens in the Calvert, Choptank, and St. Marys Formations. Teeth have been collected in place from beds 3–5, 8, 10–14, and 17–19 of Calvert Cliffs, as well as from local inland exposures of beds 1 and 2. More than 150 teeth were examined for this study.

The species is very widely distributed in warmer-water formations worldwide from the late Oligocene (Chattian) through Pleistocene formations of the Atlantic Ocean, Caribbean Sea, Mediterranean Sea, Indian Ocean, and Pacific Ocean (Radwański, 1965; Longbottom, 1979; Gillette, 1984; Cappetta, 1987; Kent, 1994; Yabumoto and Uyeno, 1994; Scudder et al., 1995; Iturralde-Vinent et al., 1996; Antunes et al., 1999b; Müller, 1999; Sánchez-Villagra et al., 2000; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Vicens and Rodríguez-Perea, 2003; Kocsis, 2007; Marsili et al., 2007; Portell et al., 2008; Cicimurri and Knight, 2009b; Laurito Mora and Valerio-Zamora, 2008; Schultz et al., 2010; Costa et al., 2009; Cione et al., 2011; Bor et al., 2012; Cappetta, 2012; Pimiento et al., 2013a, 2013b; Andrianavalona et al., 2015). Most records for *H. serra* are from the Miocene, and this species appears to have been particularly abundant during that epoch.

The extant *H. elongatus* is a much smaller shark than *H. serra* and is restricted to the tropical Indo-West Pacific. This species is primarily piscivorous, although it will take a broader range on prey when available. Little has been inferred about the diet of *H. serra*, although a diet comparable to that of *H. elongatus* but including larger prey is likely. Large *H. serra* teeth have been found in association with a *Squalodon* skeleton (USNM 183055), although it is unclear whether this represents scavenging or predation on other scavengers attracted to the whale carcass.

FAMILY CARCHARHINIDAE JORDAN AND EVERMANN, 1896

Genus *Galeocerdo* Müller and Henle, 1837



Tiger Sharks – *Galeocerdo*

Tiger sharks in the genus *Galeocerdo* are represented by a single extant species, *G. cuvier*. This is a large, cosmopolitan species in tropical to warm temperate oceans. Tiger sharks are found primarily on continental shelves, and although they have been observed farther offshore around islands, they are not truly pelagic sharks. *Galeocerdo cuvier* is remarkably eurytrophic and has been known to consume an astonishing range of prey, including a variety of invertebrates (e.g., scyphozoans, gastropods, cephalopods, and decapod crustaceans), numerous species of bony fishes, sharks, skates and rays, marine reptiles (sea turtles, sea snakes, and marine iguanas), marine birds, marine mammals (seals, sea lions, and small cetaceans), and carrion. Large individuals purportedly reach a length of 9.1 m, although this has not been reliably established. The largest confirmed lengths are about 5.5 m (Compagno, 1984, 2002; Compagno and Niem, 1998; Castro, 2011). Tiger sharks can be so abundant, and the risk of tiger shark predation so high, that some prey, such as bottlenose dolphins (*Tursiops aduncus*), are known to alter their foraging behavior to avoid habitats where tiger sharks are more common (Heithaus and Gill, 2002).

The teeth of *G. cuvier* are distinctive and not easily confused with those of other sharks. The crown is compressed and distally directed with compound serrations on the cutting edges and a strongly arcuate mesial margin. There are large compound serrations of graded size on the distal heel and a prominent notch between the distal cutting edge and heel. The root is compressed with short, rounded root lobes and a low lingual protuberance with a weak nutrient groove. This tooth shape is adapted for slicing tissues in both mesial and distal directions, although by different mechanisms. As the tooth is pushed mesially, prey tissues are forced along the arched mesial cutting edge toward the coronal apex. As the tooth is pulled distally, tissues are forced into the notch between the crown and the distal heel. The notch has a thin, sharp edge and seems particularly well adapted for cutting tough, fibrous tissues. This dual-action slicing mechanism may be partially responsible for the ability of *G. cuvier* to feed on an exceptionally broad range of prey (Motta, 2004). Unlike many other carcharhiniforms, the dentition of *G. cuvier* lacks dignathic and gynandric heterodonty, having only weak gradient heterodonty (Compagno, 1984; Cappetta, 1987).

Galeocerdo has traditionally been placed in the family Carcharhinidae (Compagno, 1984, 2002; Cappetta, 1987; Compagno and Niem, 1998). An analysis of carcharhiniform relationships by López et al. (2006) provided some evidence for placing *Galeocerdo* either as a basal member of the Hemigaleidae or as the sister group to the hemigaleid-carcharhinid clade. Using these results, Maisey (2012) opted to ally *Galeocerdo* with the hemigaleids. Herman et al. (1991) also note that the root vascularization of *G. cuvier* is atypical for a carcharhinid but make no further comment on the familial assignment of tiger sharks. With only a single study supporting a familial realignment of *Galeocerdo*, additional evidence is needed to more fully assess this possibility. Pending such studies, *Galeocerdo* is retained here as a carcharhinid.

The earliest *Galeocerdo* are recorded from the early Eocene of Morocco (Arambourg, 1952; Cappetta, 1987; Sepkoski, 2002), commensurate with the comparatively basal position of this genus within the carcharhinids (Naylor, 1992). The genus is never particularly specious, with typically one or at most two contemporaneous species.

Traditionally, two species, *G. aduncus* and *G. contortus*, have been reported from the Miocene, frequently co-occurring in the same formations (Cappetta, 1987; Kent, 1994; Purdy, 1998a; Purdy et al., 2001; Kocsis, 2007; Marsili et al., 2007; Visaggi and Godfrey, 2010). Ward and Bonavia (2001) noted that the two species typically occur together and remarked on the similarities of the two tooth morphologies to the heterodont dentitions of the extinct carcharhinid genus *Physogaleus*. From these observations they concluded that both tooth forms belonged to a single species, *P. aduncus* (which has priority). In this interpretation the broader *aduncus* morph is derived from females, whereas the narrower *contortus* morph is referable to males. There are some advantages to this classification, principally since the *contortus* tooth morphology was never entirely consistent with placement in *Galeocerdo*. But there are also a number of problems raised by this assignment. In particular, there are a number of localities where only one of these two morphologies is present (Radwański, 1965; Hirota, 1979; Kemp, 1991; Iturralde-Vinent et al., 1996; Antunes et al., 1999a, 1999b; Vicens and Rodríguez-Perea, 2003; Apolín et al., 2004; Rögl et al., 2008; Cicimurri and Knight, 2009b; Vialle et al., 2011). The reliability of some of these records is unknown and may simply reflect the unavailability of large numbers of specimens for studies. Others are based on large sample sizes (e.g., Kemp, 1991) and are more likely to reflect the actual absence of a second species.

The problem with interpreting *aduncus* and *contortus* teeth is compounded by the presence of three tooth morphologies in Miocene sediments, such as those of Calvert Cliffs. One is the typical *aduncus* morphology (Figure 2.21A,B): a broad, compressed, and distally directed crown with simple serrations on the cutting edges, large compound serrations of graded size on the distal heel, a prominent notch between the distal cutting edge and heel, and a low lingual protuberance with a weak nutrient groove. The *contortus* morphology (Figure 2.21E,F) differs in several important respects: the crown is slender, lingually twisted, and distally directed with simple serrations on the cutting edges, and there are moderately sized simple serrations on the distal heel, an arched or weakly notched junction between the distal cutting edge and heel, and a prominent lingual protuberance with a weak to moderate nutrient groove. The third tooth morphology (Figure 2.21C,D) is intermediate in form between the two: the crown is slender, lingually twisted, and distally directed with simple serrations on the cutting edges, large compound serrations of graded size on the distal heel, a prominent notch between the distal cutting edge and heel, and a low lingual protuberance with a weak nutrient groove. All three tooth morphologies co-occur along the length of Calvert Cliffs in the expected range of graded sizes and shapes for anterior through posterior tooth positions. Although all three are frequently collected, the *contortus* tooth form is typically the least common at localities along the cliffs (reevaluation of samples from Visaggi and Godfrey, 2010).

The most plausible interpretation is that two of these tooth forms (Figure 2.21A,B and 21C,D) represent a single species (*G. aduncus*), whereas the third tooth form (Figure 2.21E,F) is from a second species (*Physogaleus contortus*; see below). This interpretation is consistent with previous research in which adequate sample sizes are present; for example, Kemp (1991) illustrates a large number of *G. aduncus* teeth (both broad and narrow forms) from the Miocene of Australia but none of the *P. contortus* morphology. Applegate (1978, 1992) has advocated the presence of dignathic heterodonty in *G. aduncus* with broad teeth in the upper jaw and narrow teeth in the lower jaw. Further, Applegate (1992) argues that heterodonty in *Galeocerdo* is traceable as far back as the early Eocene and is widely distributed among other carcharhinids. In this interpretation of the *Galeocerdo* fossil record, the nearly homodont dentition of *G. cuvier* is a relatively recent derivation.

A second plausible interpretation of the two tooth morphologies in *G. aduncus* is that they represent gynandric heterodonty (Cicimurri and Knight, 2009b). A number of other carcharhiniforms are known to have sexual dimorphisms in tooth morphology, for example, *Carcharhinus* (Bass et al., 1973), *Iago* (Compagno and Springer, 1971), *Physogaleus* (Cappetta, 1980), and *Prionace* (Litvinov and Laptikhovsky, 2005), so such an interpretation is conceivable. In this model of the *G. aduncus* dentition, broad teeth would be the female tooth form, whereas narrow teeth would have been from males (D. Ward, pers. comm.).

Unfortunately, there are no intact dentitions of *G. aduncus* on hand to test these two competing hypotheses. The most intact specimen available is a *Galeocerdo* jaw fragment with six teeth of the narrow morphology from Calvert Cliffs (Figure 2.21G). This specimen could be interpreted as a portion of the Meckel's cartilage or part of either the palatoquadrate or Meckel's cartilage of a male individual (Gottfried, 1993). Only more complete specimens can resolve this matter.

***Galeocerdo aduncus* Agassiz, 1943**

FIGURE 2.21A–D,G

Synonymy follows Ward and Bonavia (2001; as *Physogaleus aduncus*, in part), Marsili et al. (2007), and Reinecke et al. (2011).

Description. The teeth of this species exist in two morphologies (i.e., broad and narrow), although it is unclear whether this represents dignathic or gynandric heterodonty. The broad tooth morphology (Figure 2.21A,B) has a relatively wide, compressed crown that is angled distally. The crown has simple serrations on the arched mesial and angled distal cutting edges. The distal margin of the crown is divided by a deep, prominent notch that separates the distal margin of the crown from the distal heel. The distal heel bears large compound serrations that progressively decrease in size away from the notch. The root is compressed, with short, rounded root lobes and an arched basal margin and a low lingual protuberance with a weak nutrient groove.

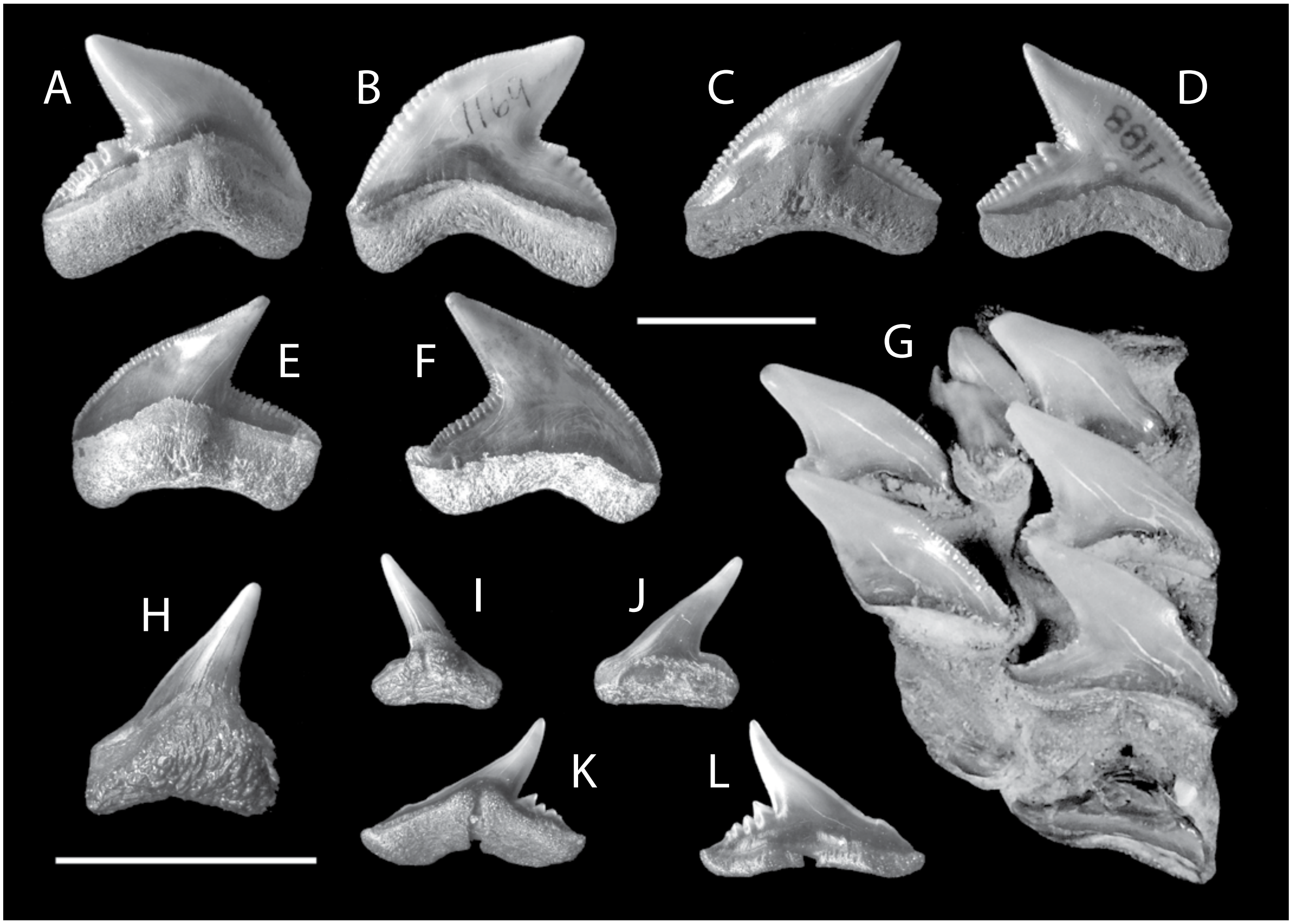


FIGURE 2.21. *Galeocerdo* and *Physogaleus* fossils (separate 1 cm scale bars for A–G and H–L). (A) *Galeocerdo aduncus* anterolateral tooth, broad form; lingual view (UMCP 1169; Matoaka Cottages, Maryland). (B) *G. aduncus* anterolateral tooth, broad form; labial view (UMCP 1169; Matoaka Cottages, Md.). (C) *G. aduncus* anterolateral tooth, narrow form; lingual view (UMCP 1188; Matoaka Cottages, Md.). (D) *G. aduncus* anterolateral tooth, narrow form; labial view (UMCP 1188; Matoaka Cottages, Md.). (E) *Physogaleus contortus* anterolateral tooth; lingual view (UMCP 999; Matoaka Cottages, Md.). (F) *P. contortus* anterolateral tooth; labial view (UMCP 999; Matoaka Cottages, Md.). (G) *G. aduncus* jaw fragment (CMM-V-21; Scientists Cliffs, Md.). (H) *P. contortus* anterior tooth; lingual view (CMM-V-7742; Bayfront Park, Md.). (I) *Physogaleus hemmooriensis* anterior tooth; lingual view (CMM-V-7729; Bayfront Park, Md.). (J) *P. hemmooriensis* anterior tooth; labial view (CMM-V-7729; Bayfront Park, Md.). (K) *P. hemmooriensis* anterolateral tooth; lingual view (CMM-V-7729; Bayfront Park, Md.). (L) *P. hemmooriensis* anterolateral tooth; labial view (CMM-V-7729; Bayfront Park, Md.).

The narrow tooth morphology (Figure 2.21C,D) resembles the broad tooth morphology in overall form, particularly in the structure of the root. The principal difference is in the structure of the crown, which in the narrow form is more gracile. The mesial cutting edge is less strongly arched than in the broad tooth form and is deflected lingually. Like the broad tooth form of *G. aduncus*, the narrow form has simple serrations on the coronal cutting edges and large compound serrations of graded size on the distal heel that are separated from the distal cutting edge by a deep prominent notch. The root is compressed with short, rounded root lobes, an arched basal margin, and a low lingual protuberance with a weak nutrient groove.

DISCUSSION. Purdy et al. (2001) place this species in synonymy with the extant *G. cuvier* on the basis of similarities in morphology. Marsili et al. (2007) dismiss this assignment because of the presence of simple, rather than complex, serrations on the mesial and distal cutting edges of the crown and the distal heel. Costa et al. (2009) report teeth with compound serrations on the medial and basal portions of the crown, although it is impossible to determine from their illustrated tooth whether compound serrations occur on both the mesial cutting edge and the cutting edges of the distal heel. In extant *G. cuvier*, compound serrations are present on all cutting edges on the tooth. In *G. aduncus* from Calvert Cliffs, compound serrations are restricted to the distal heel. The serrations on both the mesial and distal edges of the crown are somewhat irregular and variable in size but are simple in structure. Further, unlike *G. cuvier*, *G. aduncus* has a heterodont dentition, although the exact nature of the heterodonty is unclear.

Stratigraphic and Geographic Ranges. *Galeocerdo aduncus* is a common species in Calvert Cliffs, with more than 200 specimens examined for this study. Teeth of this species have been collected in all three Calvert Cliffs formations, with in situ specimens from beds 3–5, 8, 10–14, and 17. Specimens are also known from beds 1 and 2 in inland sites in the Mid-Atlantic region. This species is present from the early Oligocene (Rupelian) through late Miocene (Messinian) worldwide, including Europe, the Mediterranean, Zaire, the eastern and western coasts of the United States, the Caribbean, Ecuador, Peru, Baja California, Australia, India, and Japan (Dartevelle and Casier, 1959; Mehrotra et al., 1973; Applegate, 1978; Itiogawa et al., 1985; Cappetta, 1987; Nolf, 1988; Kemp, 1991; Yabumoto and Uyeno, 1994; Iturralde-Vinent et al., 1996; Müller, 1999; Schultz et al., 2010; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Vicens and Rodríguez-Perea, 2003; Apolín et al., 2004; Kocsis, 2007; Marsili et al., 2007; Cicimurri and Knight, 2009b; Reinecke et al., 2011; Vialle et al., 2011; Bor et al., 2012; Cappetta, 2012; Landini et al., 2017).

Genus *Physogaleus* Cappetta, 1980

Sharks in the extinct genus *Physogaleus* are known from the late Paleocene through middle Miocene. The teeth of this genus are characterized by a distally inclined crown that slightly overhangs the labial face of the root and may have a few basal serrations on the mesial cutting edge. The distal heel typically has one or more large serrations that decrease in size distally and is separated from the distal cutting edge of the crown by a distinct notch. The root is robust, with a prominent lingual protuberance bearing a deep nutrient groove that forms a conspicuous notch on the relatively straight basal root margin (Cappetta, 1980; Reinecke et al., 2005; Reinecke and Hoedemakers, 2006). The dentition of this genus is generally believed to exhibit gynandric heterodonty in the lower anterior files, where male lower anterior teeth have slender, sigmoidal crowns, whereas those of females have somewhat broader, more compressed crowns (Cappetta, 1987). There is some disagreement on whether this heterodonty is actually due to a sexual dimorphism (Reinecke and Hoedemakers, 2006).

Physogaleus contortus (Gibbes, 1849)

FIGURE 2.21E,F,H

Synonymy follows Ward and Bonavia (2001; as *Physogaleus aduncus*, in part), Marsili et al. (2007; as *Galeocerdo contortus*), and Reinecke et al. (2011).

Description. The teeth of *P. contortus* are small to moderate in size and have a distinctive morphology that is generally similar in both jaws. The crown is slender and distally angled, with a sigmoidal apex. Viewed apically, the crown is twisted with the mesial cutting edge displaced lingually. The cutting edges on the crown and distal heel are serrate, with slightly larger serrations on the latter. The junction between the distal cutting edge and the distal heel can be arcuate or weakly notched. The root has moderately elongated root lobes, with an arched basal margin, and a weak nutrient groove on an elevated lingual protuberance. Weak gradient monognathic heterodonty is present. Anterior teeth have more erect crowns and shorter root lobes. Some anteriors also have crowns that are nearly as thick as they are broad at the base, but it is unclear whether these represent male lower teeth or are found in both genders. Toward the jaw articulation the teeth become progressively lower, with more acutely angled crowns and a less elevated lingual protuberance.

Discussion. *Physogaleus contortus* was originally assigned to the genus *Galeocerdo*, although this assignation was never entirely plausible. A number of characters in this species are at variance with most other *Galeocerdo* species: (1) a slender, finely serrate crown, (2) the absence of large, compound serrations on the distal heel, (3) the absence of a distinct notch separating the distal cutting edge from the distal heel, and (4) a thicker, more prominent lingual protuberance. As already discussed (see above), the crown resembles the narrow tooth form of *G. aduncus*, but the other three characters are sufficient to separate the two.

This species has been assigned to *Physogaleus*, in agreement with a number of other researchers (Reinecke et al., 2005: text-fig. 13, pl. 36; Reinecke and Hoedemakers, 2006; D. Ward, pers. comm.). As a derived *Physogaleus, P. contortus* has evolved a tooth morphology somewhat different from that of more typical members of this genus. The addition of serrations on the cutting edges, the modification of the root shape, and the suppression of heterodonty are all consistent with observable trends in *Physogaleus* during the Eocene and Oligocene (Reinecke et al., 2005; Reinecke and Hoedemakers, 2006). *Physogaleus contortus* is the largest member of the genus (Reinecke et al., 2005). Although of only modest size compared to many other sharks in Calvert Cliffs, *P. contortus* reflects the evolution of gigantism in *Physogaleus*.

The paleobiology of *P. contortus* is largely unknown, although the slender twisted crown is consistent with a largely piscivorous diet. The skeleton of an unnamed sperm whale from the lower Calvert Formation of Popes Creek, Maryland (Popes Creek Sand bed; USNM 489195) has 37 associated

P. contortus teeth. Although the teeth are exceptionally large, these sharks were far too small to have attacked and killed such a substantial prey. Typically, such an association of teeth would be attributed to scavenging, although this is difficult to confirm. On the basis of the tooth morphology of *P. contortus*, it seems equally plausible that this tooth concentration represents *Physogaleus* preying on small scavenging fishes that had been attracted to the carcass.

Stratigraphic and Geographic Ranges. The teeth of *P. contortus* are common along the cliffs, and about 180 teeth have been studied. *Physogaleus contortus* teeth have been found in situ in a number of beds, including 3–5, 8, 10–15, and 17, and river teeth have also been collected from bed 1. The worldwide distribution of this species is more difficult to document since the narrow tooth form of *G. aduncus* is frequently listed as *G. contortus*. Teeth are known from the early and middle Miocene (Burdigalian-Langhian or perhaps Serravallian) of the eastern Unites States (Maryland, North Carolina, and Virginia), Cuba, Panama, Peru, Germany, and Hungary (Gillette, 1984; Iturralde-Vinent et al., 1996; Müller, 1999; Purdy et al., 2001; Kocsis, 2007; Marsili et al., 2007; Reinecke et al., 2011; Pimiento et al., 2013a; Landini et al., 2017). Reinecke et al. (2011) also list *P. contortus* from the late Oligocene (Chattian) of South Carolina on the basis of Cicimurri and Knight (2009b). The only narrow tooth form illustrated by Cicimurri and Knight (fig. 5F) appears to have compound serrations of graded sizes on the distal heel; this morphology is more consistent with *G. aduncus* than with *P. contortus*.

Physogaleus hemmooriensis **Reinecke and Hoedemakers, 2006**

FIGURE 2.21I–L

Synonymy follows Reinecke et al. (2011).

Description. Anterior teeth have tall, sinuous crowns and narrow roots with reduced lobes (Figure 2.21I,J). The mesial margin is sinuous to weakly concave, whereas the distal margin is convex. The cutting edges are smooth and extend onto the mesial and distal heels. The distal shoulder may have a long, low cusplet or broad blade. The root is thick, with a prominent medial nutrient groove and one or more foramina.

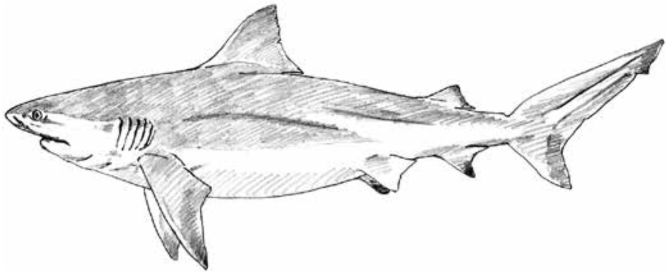
In anterolateral teeth the crown is slender and oblique, with a long, sinuous to noticeably concave mesial margin (Figure 2.21K,L). A slightly convex, irregularly crenulated mesial heel is present. The distal cutting edge of the cusp is convex and meets the distal heel at a conspicuous notch. The distal heel is short and bears two to four large serrations that decrease in size distally. The root lacks a marked lingual protuberance and is relatively thin. A deep nutrient groove and a basal notch are present. The basal margin of the root is weakly sinuous, concave medially, and convex on the root lobes.

Discussion. These teeth have been assigned to *P. hemmooriensis* on the basis of comparing descriptions of teeth of this genus with those of the generally similar teeth in the genera *Chaenogaleus, Galeorhinus*, and *Paragaleus* (Cappetta, 1987; Reinecke and Hoedemakers, 2006; Reinecke et al., 2011). The anterolateral teeth of all three of these genera have shorter cusps and a larger number of cusplets on the distal heel. *Galeorhinus* teeth also have a pronounced labial callosity. This thickening of the basal edge of the enameloid can occur in some *Chaenogaleus* and *Paragaleus* as well. These latter two genera occasionally have distinct serration on the mesial heel, which is lacking in *P. hemmooriensis*.

The medial teeth of *P. hemmooriensis* have not been collected from Calvert Cliffs. Reinecke and Hoedemakers (2006) describe these teeth as having nearly symmetrical crowns with one to rarely three serrations on each shoulder. In this respect, medial teeth differ from anterior and anterolateral *P. hemmooriensis* teeth, which never have mesial serrations. Reinecke and Hoedemakers (2006) differentiate upper and lower anterolateral teeth on the basis of the shape of the mesial coronal margin; in upper teeth the margin is undulating, whereas in lower teeth it is clearly concave and produces a vertically directed coronal apex.

Stratigraphic and Geographic Ranges. This species is rarely collected from Calvert Cliffs, although the rarity may be confounded by the small size and comparative delicacy of the teeth. The largest tooth is 5.1 mm high and 7.7 mm wide, which is near the maximum size for this species (Reinecke and Hoedemakers, 2006; Reinecke et al., 2011). *Physogaleus hemmooriensis* teeth have been collected only as two beach specimens from the extreme northern end of Calvert Cliffs and are presumably derived from the Calvert Formation. This species is reliably known from the early to middle Miocene of Belgium, Germany, and the Netherlands and possibly from the Calvert Formation of Delaware and Pungo River Formation of North Carolina (Reinecke and Hoedemakers, 2006; Reinecke et al., 2011; Bor et al., 2012; Everaert, 2014).

Genus ***Carcharhinus*** **Blainville, 1816**



Gray Sharks – *Carcharhinus*

The gray sharks of the genus *Carcharhinus* are spectacularly successful in Holocene faunas, occupying a broad range of lifestyles. Most species (e.g., *C. brachyurus, C. perezii*, and *C. plumbeus*) are littoral and mesotrophic active coastal sharks that are generalized predators of moderate-sized fishes and lightly armored invertebrates. Others, such as *C. leucas*, are larger sharks of littoral habitats that are more eurytrophic, capable of consuming larger prey than the mesotrophic sharks. The gray sharks have also diversified into pelagic habitats, including the macroceanic *C. falciformis* and *C. longimanus* (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998). Most *Carcharhinus* species have a cutting-clutching-type dentition based on dignathic heterodonty with compressed, triangular cutting teeth in the upper jaw and slender clutching teeth in the lower jaw (Cappetta, 1987).

The explosive expansion of the carcharhiniforms during the late Oligocene and Miocene created a number of taxonomic difficulties, and these problems are particularly evident when identifying species of *Carcharhinus*. Extant *Carcharhinus* are characterized by exceptionally high diversity and a high degree of structural similarity (Garrick, 1982; Compagno, 1984; Chiaramonte, 1998; Compagno and Niem, 1998). This is readily apparent in the teeth of extant species, which can be reliably identified to species only with the use of morphometric and cladistic techniques (Naylor and Marcus, 1994). At present, our understanding of how this remarkable genus diversified during the Neogene to produce such a successful group is particularly meager. The earliest *Carcharhinus* are found in the middle to late Eocene of Antarctica (Kriwet, 2005). Eocene and Oligocene *Carcharhinus* are comparatively homogeneous, with upper teeth having unserrated or weakly serrated crowns that are separated from the enameloid shoulders by a distinct notch, although a few teeth with a more modern morphology are known (Adnet et al., 2007; Underwood et al., 2011: fig. 4N). On the basis of molecular data, the genus underwent extensive diversification between the late Oligocene and late Miocene, 23–9 MYA (A. P. Martin, 1995), including the elaboration of serrated coronal cutting edges on many species (Adnet et al., 2007). During the Miocene diversification, teeth of this genus have broadly overlapping morphologies and can be difficult to assign to individual species. Sarao (2005) used the Procrustes method with principle component analysis to evaluate 500 Neogene *Carcharhinus* teeth. Despite the utility of this technique for identifying individual species on the basis of their teeth (e.g., Nyberg et al., 2006; Whitenack and Gottfried, 2010), Sarao was unable to unequivocally identify separate species in this genus because of high morphological overlap and phyletic evolution. In studies with negative evidence there is always the possibility that the most relevant characters were not identified and a larger suite of characters might produce more resolution (Naylor and Marcus, 1994). This does not appear to be the case in Sarao's study, in which 10 lingual and 9 labial characters were employed. However, serrations are a critical factor for identifying Holocene *Carcharhinus* teeth, so an analytical approach capable of quantifying serration size and disposition (e.g., Chandler et al., 2006) might provide additional clarity. This possibility has yet to be demonstrated for *Carcharhinus* teeth, so for the present, some Miocene teeth can be reliably assigned to a species but many cannot. This problem is particularly true for lower teeth, which appear to be morphologically more conservative than upper teeth (Purdy et al., 2001). With the exception of the distinctive lower teeth of *C. leucas*, the assignment of *Carcharhinus* lower teeth from Calvert Cliffs is more provisional than assignments of the upper teeth and must be viewed with appropriate caution.

By the Pliocene, fossil teeth closely resembling those of extant *Carcharhinus* species are present (Purdy et al., 2001; Marsili, 2007b), although their antecedents in the Miocene are still somewhat murky and contentious.

Traditionally, Neogene (especially Miocene) *Carcharhinus* have been assigned to two rather broadly defined species, *C. egertoni* and *C. priscus* (Gillette, 1984; Muizon and DeVries, 1985; Cappetta, 1987; Kent, 1994; Yabumoto and Uyeno, 1994; Laurito Mora and Valerio-Zamora, 2008). Purdy et al. (2001) made the first serious attempt to sort out Neogene *Carcharhinus* species in the Pungo River and Yorktown Formations of Lee Creek Mine, North Carolina, by comparing them with extant species. Bourdon (2009) followed this basic framework but provided a more comprehensive review of Lee Creek Mine *Carcharhinus*. Marsili (2007b) largely followed Purdy et al. in classifying Pliocene *Carcharhinus* from Italy. These three publications represent a substantial improvement over older studies, although they do not resolve all taxonomic issues. Unfortunately, Miocene *Carcharhinus* from Calvert Cliffs reside within the 23–9 MYA interval of rapid diversification of this genus (A. P. Martin, 1995) and, as suggested by Sarao (2005), reflect a complex, low-relief morphospace of rapidly evolving species. Such an adaptive radiation would likely be composed of many relatively localized species with many overlapping and few unique characters. The more recognizable Pliocene and subsequent Holocene species almost certainly arose from this swarm of Miocene *Carcharhinus* by a winnowing of some species and phyletic evolution in others.

The Miocene *Carcharhinus* teeth from Calvert Cliffs are surprisingly diverse and undoubtedly represent multiple species, although the exact number is unclear. Seven tooth forms can be assigned to identifiable species with a reasonable degree of certainty, although many teeth are of intermediate morphologies and combine characters of different tooth forms. Species assignments have been based on comparisons with extant dentitions and published figures and descriptions (Garrick, 1982; Compagno and Niem, 1998; Bourdon, 2009; Voigt and Weber, 2011).

Carcharhinus cf. *C. altimus* (Springer, 1950)

FIGURE 2.22A,B

1950 *Eulamia altima* Springer – Springer, pp. 9–10.

DESCRIPTION. These uncommon teeth are typically small, with a height of about 10 mm, although an exceptionally large specimen (Figure 2.22A,B) with a height of 13 mm is known. Upper teeth have moderately narrow, tapered crowns. The mesial and distal heels are weakly to moderately convex, and the

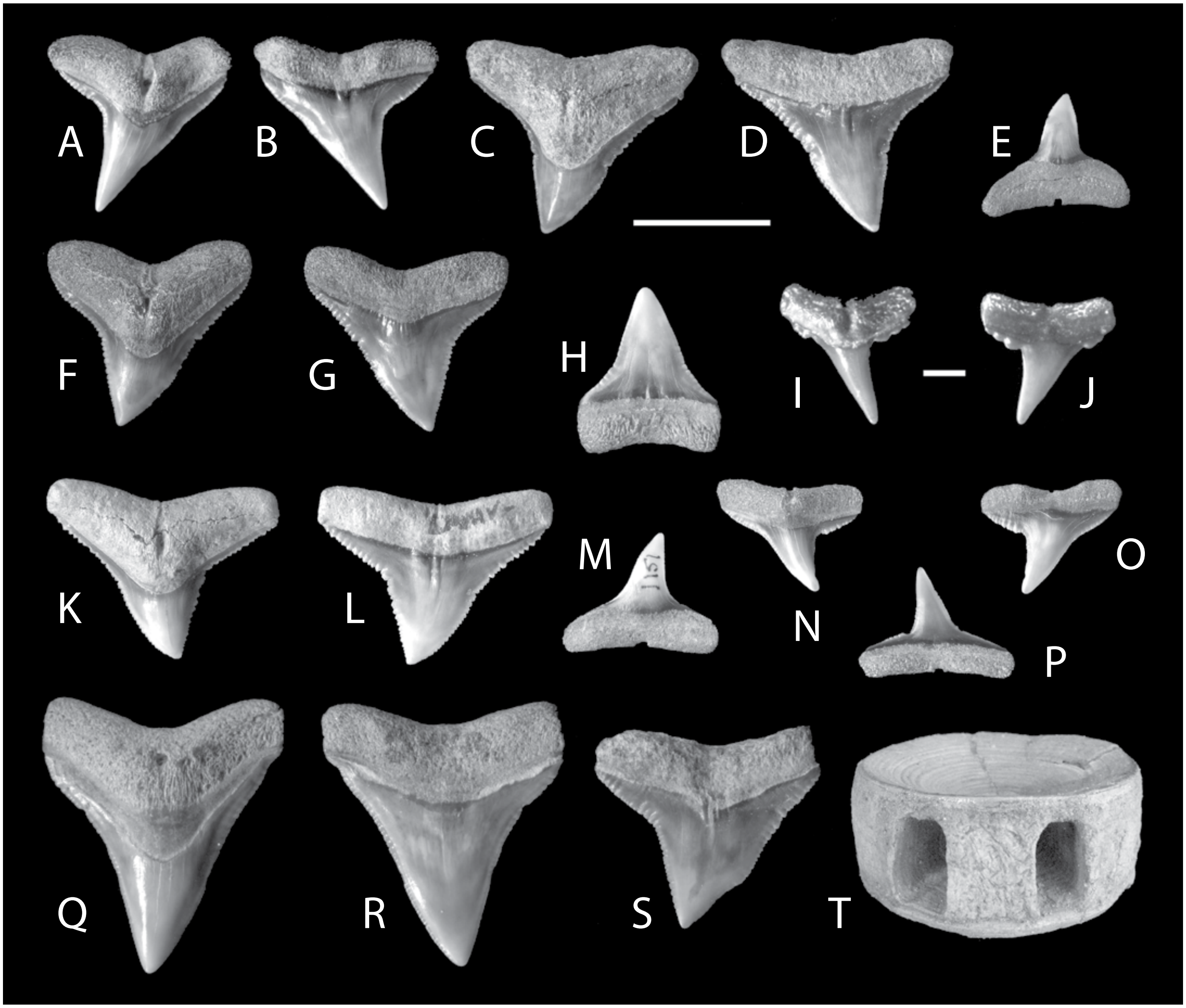


FIGURE 2.22. *Carcharhinus* fossils (1 cm scale bar for A–H, K–T; 1 mm scale bar for I, J). (A) *Carcharhinus* cf. *C. altimus* upper lateral tooth; lingual view (CMM-V-3348; Windmill Point, Maryland). (B) *Carcharhinus* cf. *C. altimus* upper lateral tooth; labial view (CMM-V-3348; Windmill Point, Md.). (C) *Carcharhinus falciformis* upper lateral tooth; lingual view (CMM-V-587; bed 12, Parkers Creek, Md.). (D) *C. falciformis* upper lateral tooth; labial view (CMM-V-587; bed 12, Parkers Creek, Md.). (E) *C. falciformis* lower lateral tooth; labial view (UMCP 980; Matoaka Cottages, Md.). (F) *Carcharhinus leucas* upper lateral tooth; lingual view (CMM-V-2106; Governor Run, Md.). (G) *C. leucas* upper lateral tooth; labial view (CMM-V-2106; Governor Run, Md.). (H) *C. leucas* lower lateral tooth; labial view (UMCP 985; Matoaka Cottages, Md.). (I) *Carcharhinus macloti* upper lateral tooth; lingual view (CMM-V-2945; Bayfront Park, Md.). (J) *C. macloti* upper lateral tooth; labial view (CMM-V-2945; Bayfront Park, Md.). (K) *Carcharhinus perezii* upper lateral tooth; lingual view (CMM-V-659; bed 10, Plum Point, Md.). (L) *C. perezii* upper lateral tooth; labial view (CMM-V-659; bed 10, Plum Point, Md.). (M) *C. perezii* lower lateral tooth; labial view (UMCP 987; Matoaka Cottages, Md.). (N) *Carcharhinus priscus* upper lateral tooth; lingual view (UMCP 981; Matoaka Cottages, Md.). (O) *C. priscus* upper lateral tooth; labial view (UMCP 981; Matoaka Cottages, Md.). (P) *C. priscus* lower lateral tooth; labial view (UMCP 2186; Matoaka Cottages, Md.). (Q) *Carcharhinus plumbeus* upper lateral tooth; lingual view (CMM-V-2951; Flag Ponds, Md.). (R) *C. plumbeus* upper lateral tooth; labial view (CMM-V-2951; Flag Ponds, Md.). (S) Pathological *C. leucas* upper lateral tooth; labial view (CMM-V-2095; bed 12, Scientists Cliff–Parkers Creek, Md.). (T) *C. leucas*? vertebral centrum; dorsal perspective (CMM-V-1652; Parkers Creek, Md.).

distal heel may be separated from distal cutting edge by a notch. The cutting edges have fine serrations that are slightly larger near the junctions between the crown and heels and may become obsolete near the coronal apex. The labial face of the crown is flat, whereas that of the lingual face is weakly convex. A distinct neck is present. There is a moderate to deep nutrient groove on the lingual face of the root, and a basal notch may be present on the weakly arched basal margin of the root. Lower teeth of *C.* cf. *C. altimus* have not been reliably identified from Calvert Cliffs.

Discussion. These teeth have been allied with the extant bignose shark (*C. altimus*) on the basis of a similarities of the fossil specimens with the extant species. In his original description, Springer noted that the teeth of *C. altimus* have heights about 150% of the width. The tallest teeth of *C.* cf. *altimus* had heights only about 115% of the tooth width. Unfortunately, published dentitions of *C. altimus* (Heim, 2000; Voigt and Weber, 2011: pl. 3) are from large adults, rather than juveniles of a size comparable to the typically small teeth from Calvert Cliffs. So although a relationship with *C. altimus* seems likely, the upper teeth of the two species do show some consistent differences, and other associations are possible.

The teeth most closely resemble those of the *C. remotus* (Duméril) specimen illustrated by Bigelow and Schroeder (1948: fig. 76). However, this name is considered invalid and has been placed in synonymy with the blacknose shark, *C. acronotus* (Poey) (Garrick, 1982; Compagno, 1984; Voigt and Weber, 2011). The teeth of *C.* cf. *C. altimus* do share some similarities with those of *C. acronotus*. Both have upper teeth with narrow, tapered, finely serrated cusps and weakly convex, finely serrated heels (Compagno, 1984, 2002; Compagno and Niem, 1998; Voight and Weber, 2011). But although the teeth of *C. acronotus* have a distinctly angular notch between the distal cutting edge and heel, this notch is much less pronounced and more obtuse in *C.* cf. *C. altimus*.

The teeth of *C.* cf. *C. altimus* also have some similarity to those of the extant sandbar shark, *C. plumbeus* (Nardo). Heim and Bourdon (1998–2009b: fig. 8) make the strongest case for placing the teeth identified here as *C.* cf. *C. altimus* in synonymy with *C. plumbeus* by reconstructing an artificial tooth set and comparing it with the dentition of an extant female *C. plumbeus* with an estimated body length of 1.8 m. Their reconstructed dentition does bear a strong resemblance to the extant *C. plumbeus* dentition, but there are two difficulties with this interpretation. First, the extant dentition has crowns that appear to be somewhat narrower than many other *C. plumbeus* dentitions (Bigelow and Schroeder, 1948; Garrick, 1982; Heim, 2001). Second, the reconstructed dentition represents a nonrandom subset of the teeth available for reconstructing the dentition and likely underestimates the total variability within the fossil tooth sample. To test the validity of this assertion, four samples of upper teeth were analyzed. The first sample consists of 11 *C.* cf. *C. altimus* from Calvert Cliffs. The second sample is of five teeth from Calvert Cliffs identified as *C. plumbeus* (see below). The third sample is of the anteriormost eight teeth (excluding symphyseals) of the extant *C. plumbeus* dentition illustrated by Heim and Bourdon (1998–2009b: fig. 8, photographically enlarged), and the fourth sample is the same eight tooth positions of a somewhat broader, more typical dentition from a 1.78 m male (Voigt and Weber, 2011: pl. 25, photographically enlarged). The first eight tooth positions were chosen in the two extant dentitions because they were consistent with the range of tooth morphologies present in the fossil teeth of the first two samples. Differences in coronal width between the four samples were quantified by comparing relative coronal widths (i.e., the width of the cusp at the junction with the shoulders divided by the total width of the tooth) with one-way and subsequent pairwise Tukey HSD tests. Highly significant differences were present ($F_{3,27} = 23.58$, $P < 0.0001$), although they were confined to pairwise differences between *C.* cf. *C. altimus* (mean = 0.42; HSD $P < 0.01$) and each of the three *C. plumbeus* samples (means = 0.54, 0.54, and 0.57, respectively). None of the pairwise differences between the *C. plumbeus* samples were significant (HSD $P > 0.05$). The teeth identified here as *C.* cf. *C. altimus* have crowns that are significantly narrower than those of *C. plumbeus*.

In some respects these teeth also resemble those of *C. ackermannii* Silva Santos and Travassos, 1960 from the early Miocene Pirabas Formation of Brazil (Santos and Travassos, 1960). Reis (2005) refers these teeth to the extant species *C. sorrah* (Valenciennes, in Müller and Henle, 1841), although this assignment seems inappropriate, as *C. ackermannii* teeth lack the obliquely inclined crown, deep distal notch, and large, simple serrations of graded sizes that characterize *C. sorrah* (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Voigt and Weber, 2011). Like the teeth from Calvert Cliffs, the teeth of *C. ackermannii* have a tapered, finely serrate crown and convex, serrated mesial and distal heels. The teeth of *C. ackermannii* differ from the teeth identified as *C.* cf. *C. altimus* in having a broader cusp with more strongly convex cutting edges. Too few specimens of either *C. ackermannii* or *C.* cf. *C. altimus* are available to determine if they are conspecific.

Stratigraphic and Geographic Ranges. *Carcharhinus* cf. *C. altimus* teeth are infrequently collected from Calvert Cliffs, with fewer than 20 known specimens. Teeth are known from all three formations in the cliffs but, as yet, have been collected in situ only from beds 8 and 14. *Carcharhinus* cf. *C. altimus* has previously been reported in the fossil state from the early to middle Miocene (Burdigalian to Serravallian) of Maryland (Kent, 1994; as *Carcharhinus* sp. A) and the late Miocene to early Pliocene of Baja California (Applegate, 1978: tbl. 1; González-Barba and Thies, 2000).

Extant *C. altimus* is an offshore, littoral shark of tropical and warm temperate oceans. It is principally piscivorous, feeding on a variety of teleosts, sharks, and rays, and has been known to eat cuttlefishes. Adults are found primarily in outer shelf habitats at depths of 90 to 500 m, although they are known to make nocturnal migrations into somewhat shallower water. Juvenile individuals are found in water as shallow 25 m (Compagno, 1984, 2002; Anderson and Stevens, 1996; Compagno and Niem, 1998;

Compagno et al., 2005; Castro, 2011; Voight and Weber, 2011). This habitat segregation between adults and juveniles may explain the overwhelming prevalence of smaller teeth in Calvert Cliffs.

Carcharhinus falciformis (Bibron in Müller and Henle, 1839)

FIGURE 2.22C–E

Synonymy follows Purdy et al. (2001) and Marsili (2007b).

Description. The upper teeth (Figure 2.22C,D) have moderately broad, triangular, distally inclined crowns with serrated cutting edges. At roughly the midpoint of both margins the coronal edges are separated from the heels by a notch or gap between serrations. These notches are most easily observed on the labial face, with lighting at a low angle of incidence. Apical to these notches the cutting edges have moderately fine serrations. Basal to the notches the mesial and distal heels have more coarsely serrate edges. The mesial edge is straight or very nearly so, whereas the distal cutting edge is roughly perpendicular to the basal root margin. The labial face of the crown is flat, and the lingual face is clearly convex. There is an indistinct neck between the crown and high root. The nutrient groove is moderately deep, usually forming a shallow notch in the middle of the weakly arched basal margin.

The lower teeth (Figure 2.22E) have very narrow, erect to weakly inclined crowns. Both the mesial and distal edges are convex apically, producing a narrow, spade-like tip, and flare basally onto a steeply angled shoulder. The cutting edges are smooth or weakly serrated, primarily on the coronal apex. There is a concave transition between the cusp and shoulders, and transverse roots with a moderately deep nutrient groove are present.

Discussion. Teeth of the silky shark are comparatively large, with a maximum height of about 15 mm. The upper teeth of *C. falciformis* are distinctive in having moderately broad crowns separated from the mesial and distal shoulders by a distinct notch or gape in the serrations. The condition of the cutting edges on lower teeth is variable and may represent differences between populations (S. Kato, pers. comm. in Applegate, 1967). Some authors describe the cutting edges as smooth (Garrick, 1982; Bass et al., 1973; Compagno, 1984), and some describe them as finely serrate (Compagno and Niem, 1998; Heim and Bourdon, 1998–2009a) and occasionally as smooth or finely serrate (Voigt and Weber, 2011). The length of the cutting edges on lower teeth also vary by position, being restricted to the apical portion of the crown in more anterior teeth and becoming complete on teeth nearer the jaw commissure (Heim and Bourdon, 1998–2009a).

Stratigraphic and Geographic Ranges. The teeth of *C. falciformis* are found all along Calvert Cliffs, but although they are common in the Calvert and Choptank Formations, they are rarer in the St. Marys Formation. They have been collected in situ from beds 3–5, 8, 10–12, 14, and 17 or 19 in Calvert Cliffs and bed 2 in inland sites. Nearly 90 teeth of this species were examined for this study.

Fossils of *C. falciformis* (frequently listed as *C. egertoni*) have previously been reported from the Miocene of North America (Maryland and North Carolina), Lesser Antilles, Italy, Malta, and Panama (Leriche, 1942; Menesini, 1974; Kent, 1994, as *Carcharhinus* sp. A; Purdy et al., 2001; Portell et al., 2008, as C. obscurus; Pimiento et al., 2013a). As discussed below, one of the syntypes of *C. similis* (Probst, 1878: text-fig. 21d–f) from the Miocene of southern Germany is likely attributable to *C. falciformis*. Teeth from *C. falciformis* have also been reported from the Pliocene of California, South Carolina, and Italy (Applegate, 1978; Marsili, 2007b; Cicimurri and Knight, 2009a).

The silky shark is a macropelagic, tropical species that reaches maximum lengths of 3.3–3.5 m. Young individuals are chiefly found over continental shelves, whereas adults venture well out into the open ocean. The species is primarily piscivorous but is also known to feed on squid and crustaceans (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Castro, 2011; Voigt and Weber, 2011). The teeth of *C. falciformis* have been found in association with a *Squalodon* skeleton (USNM 183055), although it is unclear whether these sharks were scavenging the carcass itself or feeding on smaller fishes attracted to the carcass.

Carcharhinus leucas (Valenciennes in Müller and Henle, 1839)

FIGURE 2.22F–H,S

Synonymy follows Purdy et al. (2001) and Marsili (2007b).

Description. The upper teeth (Figure 2.22F,G) of the bull shark are large (up to about 18 mm high), broad, and triangular, with a distally inclined cusp. The edges are coarsely serrated, with the serrations becoming somewhat finer near the tip of the crown. The distal heel is separated from the crown by a very shallow notch on some teeth. The mesial edge is relatively straight and sometimes weakly convex near the tip, whereas the distal edge is concave. The labial face of the crown is flat, and the lingual face is weakly convex. There are an obvious neck and a high root. There is a short, weak nutrient groove with the nutrient foramen displaced basally. The basal margin of the root is arched or angled (Garrick, 1982; Purdy et al., 2001; Marsili, 2007b).

The distinctive lower teeth (Figure 2.22H) have a relatively broad, erect cusp with serrated edges and shoulders. The margins of the apical portion of the crown are ogival, becoming parallel on the basal portion before merging with the steeply angled shoulders. The root has a moderately deep nutrient groove and a noticeably arched or angled basal margin.

Discussion. Reinecke et al. (2011: text-fig. 21) illustrated the syntypes of *C. similis* (Probst, 1878), a Miocene species with broad, triangular crowns and serrated cutting edges, noting its resemblance to the extant species *C. leucas* and *C. amboinensis* (Müller and Henle, 1839). The lower teeth (Reinecke et al., 2011: text-fig. 21k–p) do resemble those of *C. leucas*, but other teeth are probably more properly allied to other species, including *C. falciformis* (text-fig. 21d–f) and *C. plumbeus* (text-fig. 21a–c,g–i). The smaller teeth in Probst's syntypes could be *C. leucas*, one an upper in the posterior half of the jaw (Reinecke et al., 2011: text-fig. 21q,r) and the other a lower (text-fig. 21s,t), but cannot be assigned with certainty.

A few *C. leucas* upper teeth have a peculiar, presumably pathological, condition where the apical portion of the mesial cutting edge is weakly concave and separated from the basal portion by a distinct angularity (Figure 2.22S). This condition is not unique to *C. leucas* and has also been found less commonly in Calvert Cliffs specimens of *C. falciformis* and *C. perezii*, as well as in the angel shark, *Squatina* sp., and the thresher, *A.* cf. *A. superciliosus* (BWK, pers. obs.).

The *C. leucas* teeth from Calvert Cliffs reach a maximum height of about 18 mm. This size is comparable to those of the contemporaneous Pungo River Formation of North Carolina (Purdy et al., 2001). This size is considerably smaller than either Pliocene teeth (Purdy et al., 2001) or those of extant individuals, which reach a height of about 27 mm (BWK, pers. obs.).

Stratigraphic and Geographic Ranges. *Carcharhinus leucas* teeth are common fossils, and more than 70 were examined. This species occurs in all three Calvert Cliffs formations and has been collected in place from beds 4, 8, 10–12, 14, and 17 and at inland sites from bed 1. Other locality data, as with *C. falciformis*, can be difficult to interpret, as the fossil teeth of *C. leucas* are frequently listed as *C. egertoni*. Miocene records of *C. leucas* include Maryland, North Carolina, Ecuador, Germany (discussed above), Malta, and Portugal (Agassiz, 1843; Leriche, 1942; Menesini, 1974; Longbottom, 1979; Antunes et al., 1999a; Purdy et al., 2001; Antunes and Balbino, 2004). Other records include those from the late Miocene/early Pliocene of the Azores (Ávila et al., 2012); the Pliocene of California, North Carolina, South Carolina, Angola, Italy, Panama, and Peru (Antunes, 1963; Applegate, 1978; Purdy et al., 2001; Marsili, 2007b; Cicimurri and Knight, 2009a, as *C. longimanus*; Pimiento et al., 2013a; Landini et al., 2017); and the early Pleistocene of Florida (Scudder et al., 1995).

Bull sharks are large (up to 3.5 m) eurytrophic littoral sharks found in nearshore tropical to warm temperate habitats. They also occur in estuaries and are one of the few sharks to penetrate into freshwater rivers. The large, robust teeth of *C. leucas* are suitable for an exceptionally broad range of prey, including numerous species of teleosts and elasmobranchs, as well as sea turtles, dolphins, terrestrial mammals, sea birds, crustaceans, mollusks, and echinoderms (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Castro, 2011; Voigt and Weber, 2011).

***Carcharhinus macloti* (Müller and Henle, 1838)**

FIGURE 2.22I,J

Synonymy follows Purdy et al. (2001).

Description. The upper teeth (Figure 2.22I,J) have narrow, tapered crowns with smooth cutting edges that are slightly oblique anteriorly and increasingly inclined toward the commissure. The mesial margin of the cusp is straight to weakly convex, whereas the distal margin is straight to somewhat concave. The shoulders bear enlarged, cusplet-like serrations, particularly on the distal shoulder, which is separated from the distal cutting edge by a notch. Serrations on the mesial shoulder are less prominent and may be absent on some teeth. The root lobes are rounded and meet at a broadly obtuse angle. On the lingual face is a narrow nutrient groove that ends basally at a notch.

Discussion. The upper teeth of *C. macloti* are rare from Calvert Cliffs, and only seven specimens were available for study. They are consistent with teeth of similar morphology that were identified as belonging to juvenile or subadult *C. priscus* by Reinecke et al. (2011:66, pl. 77, figs. 6–10).

Lower teeth have not been unambiguously identified from Calvert Cliffs. In extant *C. macloti* the lower teeth have narrow, erect to slightly inclined crowns with smooth cutting edges and smooth, unserrated shoulders. The cutting edges and shoulders meet at a slightly obtuse angle, although the junction is narrowly rounded, rather than notched. The roots are transverse or very widely angled. The nutrient groove resembles that on upper teeth and ends in a deep basal notch (Garrick, 1985; Compagno and Niem, 1998; Voigt and Weber, 2011).

Stratigraphic and Geographic Ranges. *Carcharhinus macloti* teeth are rarely reported as fossils, probably because of their small size and delicate construction, and only nine were available for study. From Calvert Cliffs they are reliably known only from the Calvert Formation and have been collected directly from beds 3, 8, and possibly 14. They have previously been identified from the early Miocene of Brazil (Costa et al., 2009), the Miocene of Maryland (Kent, 1994), the Miocene and possibly early Pliocene of North Carolina (Purdy et al., 2001).

The living hardnose shark is a small, slender shark (maximum length of about 1 m) of tropical inshore habitats in the Indo-West Pacific region. The dentition exhibits gradient monognathic and dignathic heterodonty and is technically of the cutting-clutching type (Cappetta, 1987). However, the crowns of the upper teeth are so narrow that they probably function with the lower teeth as clutching dentition for grasping and restraining small prey. *Carcharhinus macloti* is believed to be primarily piscivorous, feeding chiefly on small teleosts, although it is known to also consume cephalopods and lightly armored crustaceans (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Voigt and Weber, 2011).

Carcharhinus perezii (Poey, 1876)

FIGURE 2.22K–M

Synonymy follows Purdy et al. (2001) and Marsili (2007b); as C. *perezi.*

Description. The upper teeth (Figure 2.22K,L) have moderately narrow, distally inclined crowns. Both the mesial and distal edges have moderately fine serrations that become slightly coarser on the mesial and distal heels. The transition between the cusp and heels is generally gradual, although the distal heel may be separated from the distal cutting edge by an inconspicuous notch. The mesial edge can be convex or nearly straight and in some teeth appears truncated. The distal cutting edge is vertical or concave. There are a flat labial crown face and a convex lingual face. A distinct neck is present. The root of the lingual face is high, with a moderately wide, sometimes shallow, nutrient groove. The basal margin is arched or obtusely angled.

The lower teeth (Figure 2.22M) have erect to semierect, moderately narrow, and smoothly tapered crowns, with fine serrations. In some teeth the crown is separated from the shoulders by an angular transition. The roots are transverse or may have a gently arched basal margin.

Discussion. The Caribbean reef shark has teeth that can be confused with those of *C. falciformis* and, in smaller sizes, *C. priscus*. The teeth of *C. falciformis* differ from those of *C. perezii* in having slightly broader crowns and notches separating both the mesial and distal coronal cutting edges from the shoulders. *Carcharhinus priscus* teeth typically have more angular junctions between the cutting edges than those of *C. perezii* and a tendency for the serrations to become obsolete apically. *Carcharhinus perezii* uppers are among the largest *Carcharhinus* teeth from Calvert Cliffs and can reach maximum heights of about 18 mm and widths of 22 mm.

Lower *C. perezii* teeth resemble those of *C. falciformis*, except that the crowns tend to be more uniformly tapered than the ogival coronal apex of the latter species. Although lower *C. perezii* teeth are usually described as completely serrated (Compagno, 1984; Compagno and Niem, 1998; Voigt and Weber, 2011), Bourdon and Heim (2008–2009) report serrations are restricted to the apical portion of the crown on anterior teeth.

Stratigraphic and Geographic Ranges. More than 60 teeth of *C. perezii* were examined in this study. They are commonly found in the Calvert, Choptank, and St. Marys Formations of Calvert Cliffs. In situ specimens have been collected from beds 3, 4, 8, 10, 12, 14, and 17 or 19, as well as beds 1 and 2 at inland sites. Fossil teeth of *C. perezii* have been documented from the Miocene of Delaware (Purdy, 1998a), Maryland (Kent, 1994; as *Carcharhinus* sp. B), North Carolina (Purdy et al., 2001), Panama (Pimiento et al., 2013a), Portugal (Antunes et al., 1999a; Sánchez-Villagra et al., 2000; Antunes and Balbino, 2004), along with the Pliocene of North Carolina and Italy (Purdy et al., 2001; Marsili, 2007b).

The Caribbean reef shark is a large (3 m long) mesotrophic littoral species and is the most common shark associated with coral reefs in the Caribbean and southern Brazil. It is primarily piscivorous (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Castro, 2011; Voigt and Weber, 2011).

Carcharhinus priscus (Agassiz, 1843)

FIGURE 2.22N–P

Synonymy follows Reinecke et al. (2011).

Description. These teeth are small and relatively delicate (Figure 2.22N,O), with a maximum height of about 10 mm. The upper teeth have a narrow, distally inclined crown. The cutting edges are finely serrated, becoming apically obsolete on some teeth. The mesial edge is weakly convex and is separated from the mesial heel by a weak notch. The distal cutting edge is almost vertical and is separated from the slightly coarser serrations of the distal heel by a notch. The labial face is flat or weakly convex, whereas the lingual face is more strongly convex. There is a distinct neck between the crown and a low root. A moderately deep nutrient groove and a weakly arched basal margin are present.

The lower teeth (Figure 2.22P) are similar to uppers but have narrower, semierect cusps with finely serrated edges, although in some anterior teeth these may be limited to the coronal apex. They have a moderately deep nutrient groove, a basal notch, and transverse roots.

Discussion. Purdy et al. (2001) and Marsili (2007b) placed *C. priscus* as a junior synonym of *C. brachyurus* (Günther). Garrick (1982) was the first to note that on upper *C. brachyurus* teeth the apical portion of the mesial cutting edge is markedly arched and angled distally. This “truncated” crown morphology was used by both Purdy et al. (2001) and Marsili (2007b) in assigning these teeth to *C. brachyurus*.

Reinecke et al. (2011) reexamined the type specimens of *C. priscus*, noting that synonymy with *C. brachyurus* was based on a morphologically constrained subset of these teeth that most closely resembled the extant species. Further, they found that all of the tooth morphologies in the type specimens were present in a large sample of teeth from the Lower Mica Fine Sand Formation (early Miocene) of Germany. This sample included teeth with morphologies that are similar to, but not entirely consistent with, those of the extant species *C. brachyurus*, *C. limbatus*, and *C. perezii*. Reinecke et al. (2011) concluded that these teeth were morphologically distinct and represented a separate species, *C. priscus*. Teeth from Calvert Cliffs are fully comparable with the illustrated specimens of *C. priscus* in Reinecke et al. (2011: pls. 71–77, figs. 6–13). The coronal margins on their early Miocene specimens are somewhat variable, ranging from weakly crenulate to finely and regularly serrate. Teeth from Calvert Cliffs are more typically serrate, although teeth where the serrations disappear apically are still found with some regularity. Further, the truncated crowns used to ally these teeth with *C. brachyurus* are comparatively uncommon.

Of the three extant species Reinecke et al. (2011) found to be similar to *C. priscus*, only one (*C. brachyurus*) has gynandric heterodonty; mature males have teeth with narrower, more oblique crowns with finer serrations (Garrick, 1982). Reinecke et al. (2011) do not discuss gynandric heterodonty, but there are *C. priscus* upper teeth from Calvert Cliffs that have somewhat finer serrations. The crown morphology of these teeth is no more oblique than those of other teeth, so it is unclear whether this represents an incipient heterodonty or simply natural variation in a species with comparatively variable tooth morphology.

The biology of this extinct species is unknown, although the similarities of its teeth to those of *C. brachyurus*, *C. limbatus*, and small *C. perezii* would suggest a piscivorous diet. *Carcharhinus priscus* teeth were found in association with a *Squalodon* skeleton (USNM 183055), although it is unclear whether these sharks were actively scavenging or opportunistically feeding on smaller fishes attracted to the carcass.

Stratigraphic and Geographic Ranges. *Carcharhinus priscus* is abundant and widely distributed along the full length of Calvert Cliffs, although specimens in place are known only from beds 3–5, 8, 10, and 12. Teeth have also been collected at inland sites from beds 1 and 2 of the Calvert Formation. More than 150 teeth were evaluated for this study.

The geographic range of *C. priscus* is difficult to determine since the name has been applied to a range of tooth morphologies.

Carcharhinus plumbeus **Nardo, 1827**

FIGURE 2.22Q,R

Synonymy follows Purdy et al. (2001) and Marsili (2007b).

Description. The upper teeth (Figure 2.22Q,R) have a triangular, highly compressed crown. The mesial coronal margin is weakly sigmoidal, with a steeply angled shoulder. The distal margin is concave and continues out onto the angled shoulder. The cutting edges are finely serrate, becoming slightly coarser on the shoulders. On a few teeth the serrations on the crown and shoulders are separated from the finer serrations near the coronal tip by a gap at roughly the midpoint of both the mesial and distal cutting edges. The labial face of the crown is flat, and the lingual face is very weakly convex. There are a distinct neck and a high root, with a straight or slightly arched basal margin. The nutrient groove is weak and forms a shallow basal notch.

Discussion. Some upper teeth have coarser shoulder serrations separated from the finer serrations of the cusp by a *falciformis*-like gap, and the apex is labially arched. These teeth are thin and compressed and have similarities to those of *C. albimarginata*. Unlike the teeth of this species, the transition between fine and coarse serrations is more apically displaced. Too few teeth of this morphology are available for detailed study and are listed here as a form of *C. plumbeus*. Similar teeth are also known from Lee Creek Mine in North Carolina (USNM 476293; Purdy et al., 2001: fig. 56e). As yet, the lower teeth of *C. plumbeus* have not been reported from Calvert Cliffs.

Stratigraphic and Geographic Ranges. *Carcharhinus plumbeus* teeth are relatively uncommon along Calvert Cliffs (eight known specimens) but occur in all three formations. Teeth collected in context have been obtained only from beds 12 and 14. The teeth of *C. plumbeus* have also been found in the fossil state in the Miocene of North Carolina, Libya, Panama, and Portugal (D'Erasmo, 1951; Antunes et al., 1999a; Purdy et al., 2001; Antunes and Balbino, 2007; Pimiento et al., 2013a); the Pliocene of North Carolina, South Carolina, and Italy (Purdy et al., 2001; Marsili, 2007a, 2007b; Cicimurri and Knight, 2009a); and the Pleistocene of Florida (Scudder et al., 1995).

The sandbar shark is a large (3 m long) coastal to pelagic shark of temperate and tropical oceans between the shoreline and depths of 280 m. The diverse diet consists of many species of teleosts, sharks, skates, rays, bivalves, gastropods, cephalopods, and crustaceans (Compagno, 1984, 1988, 1990b, 2002; Compagno and Niem, 1998; Castro, 2011; Voigt and Weber, 2011).

Carcharhinus **Vertebral Centra**

FIGURE 2.22T

Vertebral centra attributable to *Carcharhinus* are collected with some regularity along Calvert Cliffs. *Carcharhinus* vertebral centra are short, aseptate, and cylindrical. The walls are straight to slightly convex. Foramina are rectilinear to ovate. Diagonal lamellae are present deep within the foramina. Pores tend to be tiny and inconspicuous and can be scattered over the surface or can outline the foramina and rims. Unfortunately, these characters are fairly conservative and vary by region along the vertebral column, making the identification of isolated centra to species particularly difficult (Kozuch and Fitzgerald, 1989; Burris, 2004).

CMM-V-1652 is a set of 11 associated centra (10 complete and 1 partial) from bed 14 with diameters of 35.5–36.1 mm and lengths of 14.0–14.9 mm (Figure 2.22T). Associated with the centra was an upper lateral *C. leucas* tooth with a height of 13.4 mm and a width of 16.4 mm.

With seven identified *Carcharhinus* tooth morphologies from Calvert Cliffs, the diversity of this genus is comparable to that of the contemporaneous Pungo River Formation of North Carolina (six species; Purdy et al., 2001) but considerably larger than the Lower Mica Fine Sand Formation of Germany (two species; Reinecke et al., 2011).

Genus ***Negaprion*** **Whitley, 1940**

Lemon sharks in the genus *Negaprion* are mesotrophic littoral sharks of tropical and temperate coastal waters. They are primarily found in shallow waters, to depths of at least 90 m, and are known to occur in estuarine and lower river habitats.

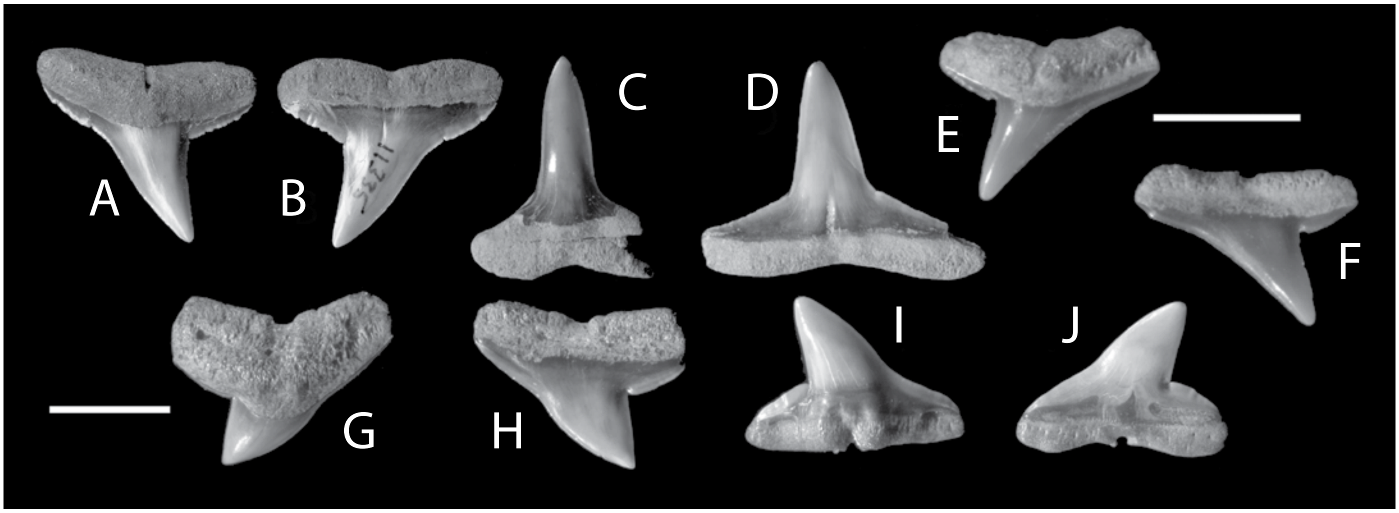


FIGURE 2.23. *Negaprion*, *Rhizoprionodon*, and *Sphyrna* teeth (1 cm scale bar for A–D and G–J; 5 mm scale bar for E, F). (A) *Negaprion eurybathrodon* upper lateral tooth; lingual view (UMCP 11335; Matoaka Cottages, Maryland). (B) *N. eurybathrodon* upper lateral tooth; labial view (UMCP 11335; Matoaka Cottages, Md.). (C) *N. eurybathrodon* lower anterior tooth; labial view (CMM-V-2104; Governor Run/Parkers Creek, Md.). (D) *N. eurybathrodon* lower lateral tooth; labial view (CMM-V-643; Parkers Creek, Md.). (E) *Rhizoprionodon* sp. lateral tooth; lingual view (CMM-V-2946; Bayfront Park, Md.). (F) *Rhizoprionodon* sp. lateral tooth; labial view (CMM-V-2946; Bayfront Park, Md.). (G) *Sphyrna laevissima* upper lateral tooth; lingual view (CMM-V-2947; Bayfront Park, Md.). (H) *S. laevissima* upper lateral tooth; labial view (CMM-V-2947; Bayfront Park, Md.). (I) *S. laevissima* lower lateral tooth; lingual view (CMM-V-2947; Bayfront Park, Md.). (J) *S. laevissima* lower lateral tooth; labial view (CMM-V-2947; Bayfront Park, Md.).

Lemon sharks are of moderately large size, reaching maximum lengths of more than 3 m. Although relatively sluggish, lemon sharks are capable of capturing a variety of teleosts and elasmobranchs, along with seabirds, mollusks, and crustaceans (Compagno, 1984, 2002; Compagno et al., 2005; Castro, 2011).

The dentition is characterized by gradient monognathic heterodonty, and there is little differentiation between upper and lower teeth (Compagno, 1987).

Negaprion eurybathrodon (Blake, 1862)

FIGURE 2.23A–D

Synonymy follows Purdy et al. (2001), Marsili et al. (2007), and Reinecke et al. (2011).

Description. The largest carcharhinid teeth from Calvert Cliffs are from this uncommon species, reaching maximum heights of at least 20 mm. The upper teeth (Figure 2.23A,B) have a narrow, slightly distally inclined crown with smooth cutting edges. The mesial edge is weakly sigmoidal to convex, whereas the distal edge is weakly sigmoidal to nearly straight, collectively producing a smoothly tapered cusp with a mildly ogival apex. The crown is compressed, with a flat labial face and weakly convex lingual face. The elongate enameloid shoulders are weakly serrate. The root is modestly compressed, with a poorly defined nutrient groove. The root lobes are relatively narrow, meeting at a broadly obtuse angle. Upper anterior teeth are taller than wide, whereas the larger lateral teeth have more elongate root lobes and teeth are wider than they are tall.

The lower teeth have narrower, less compressed, and more erect crowns (Figure 2.23C,D). The cutting edges are smooth and may be waisted on the basal half of the cusp of lower anterior teeth (Figure 2.23C). The mesial and distal coronal margins are convex apically, producing an abruptly pointed coronal apex. The shoulders are usually smooth, although they can be very weakly serrate in some specimens. The root is somewhat thicker than on upper teeth, and the lobes are transverse. Root lobes become more elongate on lateral teeth, so that these teeth are broader than they are high.

Discussion. Eastman (1904) reported these kinds of teeth from the Maryland Miocene as two different species, *Carcharias magna* and *C. collata*. White (1955) later placed both of these tooth forms in a single species, with the former as the upper teeth and the latter as the lowers.

Purdy et al. (2001) consider *N. eurybathrodon* the senior synonym of the extant *N. brevirostris*. The largest teeth from Calvert Cliffs (>20 mm) are similar to those examined by Purdy et al. and, on the basis of their comparisons with extant *N. brevirostris*, indicate a maximum body length of about 3 m. This size is identical to that of *N. brevirostris* but less than the reported maximum body length of 3.8 m for the Indo-Pacific species *N. acutidens* (Fischer et al., 1990).

Stratigraphic and Geographic Ranges. More than 30 teeth of this species from Calvert Cliffs were available for study. Beach specimens of *N. eurybathrodon* are known from the Calvert, Choptank, and St. Marys Formations. Teeth collected in situ have been found in beds 3, 4, 8, 10, 12–14, 17, and 19, as well as in bed 1 of inland sites in the Mid-Atlantic region. *Negaprion eurybathrodon* teeth have also been reported from the early Miocene through early Pleistocene of the eastern United States (Maryland, Florida, North Carolina), Australia, Cuba, Ecuador, France, Italy, Malta, Panama, Peru, Poland, and Venezuela (Radwański, 1965; Antunes and Jonet, 1970; Cappetta, 1970; Longbottom, 1979; Cappetta, 1987; Kent, 1994; Scudder et al., 1995; Iturralde-Vinent et al., 1996; Müller, 1999; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Apolín et al., 2004; Marsili et al., 2007; Pimiento et al., 2013a, 2013b; Landini et al., 2017). If Purdy et al. (2001) are correct in considering *N. eurybathrodon* the senior synonym of the extant *N. brevirostris*, the stratigraphic range of this species would extend to the present.

Genus *Rhizoprionodon* Whitley, 1929

The sharpnose sharks (*Rhizoprionodon*) are represented by seven extant species found in tropical and temperate oceans. Although primarily coastal, they have been reported to depths of 500 m on continental slopes. They are small in size, with a maximum length of 1.8 m, a slender body, and a long snout. They are primarily piscivorous, although they are also known to feed on a wide range of primarily benthic invertebrates, such as cephalopods, decapods, crustaceans, polychaetes, and gastropods (Compagno, 1984, 2002; Gallo et al., 2010; Castro, 2011).

The dentition of *Rhizoprionodon* is sexually dimorphic (Springer, 1964; Cappetta, 1987). Females have relatively broad, compressed teeth in both jaws, with smooth cutting edges and a convex distal heel. Male upper teeth are similar to female teeth. Male lower teeth are more distinctive, with a slender, more erect cusp and a more robust root with a prominent lingual protuberance (Cappetta, 1987).

The identification of isolated *Rhizoprionodon* teeth is exceptionally difficult. Garry (2003, 2004) examined the teeth of extant species of *Rhizoprionodon* and *Sphyrna* using morphometric analysis. Although she was able to unambiguously separate the two genera, she was unable to distinguish between individual *Rhizoprionodon* species. Further, *Rhizoprionodon* teeth are regarded by many researchers as virtually impossible to distinguish from those of the extant genera *Loxodon* and *Scoliodon* (Springer, 1964; Cappetta, 1987; Purdy et al., 2001, Ward and Bonavia, 2001). Reinecke et al. (2011) reviewed the tooth morphology in these genera and noted some general differences, although they have yet to be quantitatively evaluated. Because of these difficulties, assignment of the teeth from Calvert Cliffs to *Rhizoprionodon* must be considered provisional.

Rhizoprionodon has a long fossil record, with the earliest species (*R. ganntourensis*) present in the early through late Eocene of Morocco and France (Cappetta and Nolf, 1981; Noubhani and Cappetta, 1997). A number of specific names, including those of several extant species, have been applied to fossil teeth from formations dating as far back as the Eocene (Leriche, 1927; Antunes and Jonet, 1970; Case, 1980, 1981; Applegate, 1986; Bhalla and Dev, 1988; Cappetta, 1987; Naylor and Marcus, 1994; Mustafa and Zalmout, 2000; Wallet, 2006). Species-level identifications are particularly difficult since *Rhizoprionodon* teeth have few diagnostic characters and are morphologically very conservative. The situation is further complicated because *Rhizoprionodon* teeth are also similar in form to those of a number of other sharks, such as *Loxodon*, *Scoliodon*, and *Sphyrna* (Springer, 1964; Cappetta, 1987; Purdy et al., 2001; Ward and Bonavia, 2001; Garry, 2003, 2004; Adnet et al., 2011).

Rhizoprionodon sp.

FIGURE 2.23E,F

Description. The teeth from Calvert Cliffs assigned to *Rhizoprionodon* are small (maximum dimension of about 6 mm), with an oblique crown, a long, weakly to moderately concave mesial margin, and a convex distal heel (Figure 23E,F). The root has a marked lingual protuberance, bearing a deep nutrient groove and a basal notch on the relatively flat basal root edge.

Discussion. Kent (1994) assigned Calvert Cliffs specimens to the European species, *R. ficheuri*. But given the difficulties of assigning isolated teeth of this complex to a specific taxon and the relatively restricted geographic ranges of extant members of this genus (Gallo et al., 2010), it seems prudent to use *Rhizoprionodon* sp., as advocated by Purdy et al. (2001). Unlike the teeth described from Lee Creek Mine, where some teeth are weakly serrate, all of the specimens examined from Calvert Cliffs have entirely smooth cutting edges.

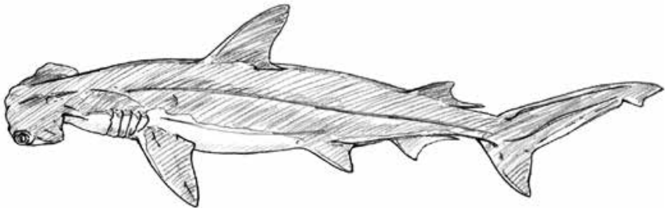
Among Calvert Cliffs fossils, the teeth of *Rhizoprionodon* sp. most closely resemble those of the hammerhead shark, *Sphyrna laevissima*. The teeth of the former are generally smaller, with a maximum dimension of about 6 mm, compared to 18 mm for the latter. Further, the mesial cutting edge of the crown in *Rhizoprionodon* sp. is concave, whereas that of *S. laevissima* is convex or weakly sigmoidal. Some lower *S. laevissima* teeth can also have weakly serrate mesial cutting edges but are nonetheless distinct from *Rhizoprionodon* sp. Compared to lower teeth of *S. laevissima*, the teeth of *Rhizoprionodon* sp. have a more strongly hooked (i.e., mesially directed) coronal apex and a much longer mesial cutting edge extending out onto a noticeably prolonged mesial root lobe.

Stratigraphic and Geographic Ranges. *Rhizoprionodon* teeth are widely distributed in all three formations from Calvert Cliffs, but they are infrequently collected because of their small size, and only about 30 were examined. In situ specimens have been collected from beds 4, 8–10, and 12 in the cliffs and in beds 1 and 2 at inland sites.

Rhizoprionodon teeth have been widely reported in Miocene formations of Austria, France, Germany, Italy, Malta, Portugal, and Switzerland in Europe (Antunes and Jonet, 1970; Cappetta, 1970; Bolliger et al., 1995; Hiden, 1995; Antunes et al., 1999a; Ward and Bonavia, 2001; Antunes and Balbino, 2004; Cappetta and Cavallo, 2006; Reinecke et al., 2011; Vialle et al., 2011) and in the eastern United States (Kent, 1994; Purdy, 1998a; Müller, 1999; Purdy et al., 2001).

FAMILY SPHYRNIDAE GILL, 1872

Genus *Sphyrna* Rafinesque, 1810



Hammerhead Sharks – Sphyrnidae

The hammerhead sharks are characterized by a broad, flattened cephalofoil, forming the distinctive hammer-shaped head that gives the group its name. There are eight Holocene species of hammerheads, and they are widely distributed in tropical to warm temperate coastal waters. They are primarily benthopelagic, although at least one species, *S. lewini*, seasonally ranges farther offshore. Although most species have relatively localized distributions, the three largest species, *S. lewini*, *S. mokarran*, and *S. zygaena*, occur circumglobally (Compagno, 1984, 1988, 1990b, 2002; Castro, 2011).

A number of functions have been hypothesized for the iconic hammerhead cephalofoil, including improved prey localization with vision, olfaction, or electroreception; hydrodynamic lift; and enhanced maneuverability (Springer and Gold, 1989; A. P. Martin, 1993). Experimental studies on possible cephalofoil functions have demonstrated that at the very least, this structure broadens the sensory field of hammerheads, allowing them to search more efficiently. Other functions, such as improved sensory localization and hydrodynamic proficiency have either not been conclusively demonstrated or remain untested (Kajiura, 2001; Kajiura and Holland, 2002; Kajiura et al., 2003, 2005).

Sphyrnids have teeth of moderate size that are organized into dentitions that exhibit dignathic and gradient monognathic heterodonty. Upper teeth typically have broad, distally inclined crowns and a weak to strong distal heel. The lower teeth are similar, except that the crown is somewhat narrower and more erect. The cutting edges can be smooth to finely serrate (Cappetta, 1987; Purdy et al., 2001). Hammerheads are primarily piscivorous, feeding on a variety of teleosts and elasmobranchs, although some smaller species, such as the bonnethead (*S. tiburo*), are typically durophagous, consuming primarily crustaceans and mollusks (Compagno, 1984, 1988, 2002; Castro, 2011).

Extant sphyrnids are represented by two genera, *Sphyrna* (seven species) and *Eusphyra* (one species). The taxonomy of living sphyrnids has yet to be fully determined since studies have produced markedly different phylogenies (Gilbert, 1967; Compagno, 1988; Lavery, 1992; Naylor, 1992; A. P. Martin, 1993). A recent supertree analysis of these earlier studies settles some of these issues while leaving others (e.g., whether *Eusphyra* is embedded within a paraphyletic *Sphyrna*) incompletely resolved (Cavalcanti, 2007).

Undoubted sphyrnids are known from the early Miocene and may be derived from a *Rhizoprionodon*-like ancestral form (Compagno, 1988; Naylor, 1992; Musick et al., 2004). An earlier origin in the Oligocene is plausible (Dutheil, 1991; Génault, 1993; Adnet et al., 2007; Cicimurri and Knight, 2009b), and an even earlier origin in the late Eocene is possible (Adnet et al., 2011). The fundamental difficulty is that early *Sphyrna* and *Rhizoprionodon* teeth both have short, distally angled crowns, a conspicuous distal heel, and a root with a deep nutrient groove and horizontal lobes. Further, purported late Eocene and early Oligocene *Sphyrna* teeth are typically comparable in size to the small teeth of *Rhizoprionodon*, making definitive identifications difficult. Finally, early teeth of the two genera appear to grade into each other (Underwood et al., 2011; Adnet et al., 2011), and small sample sizes prevent quantitative assessments of the degree of overlap. Garry (2003, 2004) has shown it is possible to separate teeth of these two genera with morphometric analysis, but these techniques have not been employed on fossil *Sphyrna* older than the Miocene.

Sphyrna laevissima (Cope, 1867)

FIGURE 2.23G–J

Synonymy follows Reinecke et al. (2011).

DESCRIPTION. The upper teeth of *S. laevissima* have broad, distally inclined crowns and a weakly convex to straight distal heel separated from the distal cutting edge by a distinct notch (Figure 2.23G,H). The mesial margin of the crown is arched, although in some anterolateral teeth there may be a very shallow indentation separating the weak mesial shoulder from the mesial cutting edge. The cutting edges are smooth, although a few teeth have weak, irregular crenulations on the distal heel. The crowns become lower and more distally inclined in posterior-lateral teeth. The root lobes are moderately elongated and bear a deep medial nutrient groove ending in a conspicuous basal notch.

Lower teeth (Figure 2.23I,J) are similar, although the crowns are narrower and generally more erect. As with upper teeth, the crowns become shorter and more inclined near the jaw commissure.

Discussion. Purdy et al. (2001) regarded *S. laevissima* as a junior synonym of *S. zygaena* on the basis of similarities in tooth morphology. Although similarities do exist, the teeth of the two species are morphologically distinct. A morphometric analysis of the teeth of these two species (Reinecke et al., 2011) found several consistent differences. In particular, the upper teeth of *S. laevissima* have broader crowns that are more erect and have a shorter distal cutting edge, whereas the lower teeth have shorter, more triangular crowns. Reinecke et al. (2011) also note that a morphological gradient in late Miocene to early Pliocene teeth suggests that *S. zygaena* may have been derived from *S. laevissima*.

Stratigraphic and Geographic Ranges. Along Calvert Cliffs, *S. laevissima* has been associated as beach specimens with the Calvert and Choptank Formations (Kent, 1994; Müller, 1999) and has been collected from beds 3–5, 8, 10–13, and 19. This species is only infrequently collected, and only 22 teeth were examined.

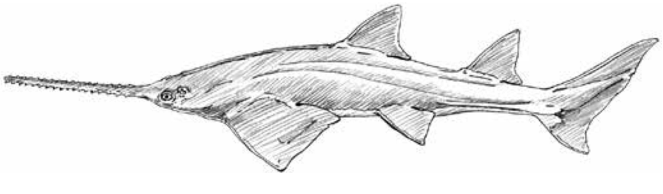
Teeth attributable to *S. laevissima* are known from the late Oligocene through the middle (or perhaps late) Miocene of the eastern United States (Maryland, Virginia, North Carolina, and South Carolina), as well as Barbados, France, Germany, Hungary, the Netherlands, Peru, Poland, Portugal, and Switzerland (Casier, 1958; Antunes and Jonet, 1970; Cappetta, 1970; Antunes et al., 1981; Kent, 1994; Müller, 1999; Purdy et al., 2001; Kocsis, 2007; Cicimurri and Knight, 2009b; Reinecke et al., 2011; Bor et al., 2012; Landini et al., 2017).

Superorder Batomorphii Cappetta, 1980

Order Pristiformes Compagno, 1973

Family Pristidae Bonaparte, 1838

Genus *Pristis* Linck, 1790



Sawfishes – Pristidae

The sawfishes of the genus *Pristis* are elongated rays with a long, dorsoventrally compressed rostrum bearing large, laterally directed rostral teeth. The rostral teeth are unusual in that they grow continuously and are embedded within alveoli along the lateral margins of the rostrum. On the basis of their mode of development, they may not actually represent true teeth (Miller, 1974). The rostral teeth can be quite large, reaching maximum lengths of at least 80 mm (Kent, 1999b; pers. obs.). The number of rostral teeth is variable (16–32 pairs in extant species) and is sexually dimorphic (Thorson, 1973). Oral teeth in *Pristis* (like those of other elasmobranchs) have terminal growth and are attached to the surface of the jaws by proteinaceous fibers. These teeth are quite small (<3 mm) and rarely collected (Cappetta, 1987).

Sawfishes have a surprisingly sharklike body, although they can be readily distinguished from the similar saw sharks (*Pristiophorus*) by the presence of dorsally positioned eyes, ventral gill slits, and pectoral fins with proximal margins that are attached to the head. They use the toothed rostrum to probe soft sediments for buried prey and to stun free-swimming prey. The diet consists primarily of small benthic invertebrates and teleosts, although sawfishes are also capable of consuming smaller nektonic fishes. Extant *Pristis* spp. occur primarily in marine and estuarine habitats, although they can infrequently occur in freshwater (Bigelow and Schroeder, 1953; Whitehead et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

Pristis sp.

FIGURE 2.24A,B

Description. The rostral teeth are large, elongate, and dorsoventrally compressed, with the crowns covered with smooth enameloid. The mesial margin of the crown is broadly convex, whereas the distal margin is nearly straight to weakly convex near the apex. The mesial cutting edge of the crown is rounded, whereas the distal is flat or weakly concave because of the presence of a longitudinal groove running along the distal margin of the crown. The tooth base is wider than the crown, is not covered with enameloid, and has similar, if somewhat less pronounced, mesial and distal profiles. The small oral teeth of this species have not been reported from Calvert Cliffs.

Discussion. Ontogenetic changes may also complicate identifications; extant *Pristis* adult teeth have a grooved distal margin, whereas this characteristic is absent in juvenile teeth (Purdy et al., 2001). Both of the *Pristis* teeth from Calvert Cliffs are of similar size (lengths of 37.0 and 35.3 mm) and are intermediate in size between the smaller, ungrooved teeth (lengths of 23.5–25.5 mm) and larger tooth (length of 52.7 mm) described by Purdy et al. (2001). The larger of the two Calvert Cliffs *Pristis* teeth has a flat distal margin, and the smaller has a very shallow, incipient groove.

Stratigraphic and Geographic Ranges. Only two *Pristis* rostral teeth were available for study, CMM-V-1297 and CMM-V-2113. They were collected in situ from beds 3 and 14, respectively.

A number of *Pristis* spp. have been named from the Miocene of the North Atlantic, including *P. aquitanicus* Delfortrie, *P. atlanticus* Zbyszewsky, and *P. caheni* Dartevelle and Casier (Cappetta, 1987, 2006). Little research has examined the range of variability in these species to assess their validity or even if they are morphologically distinct from extant species.

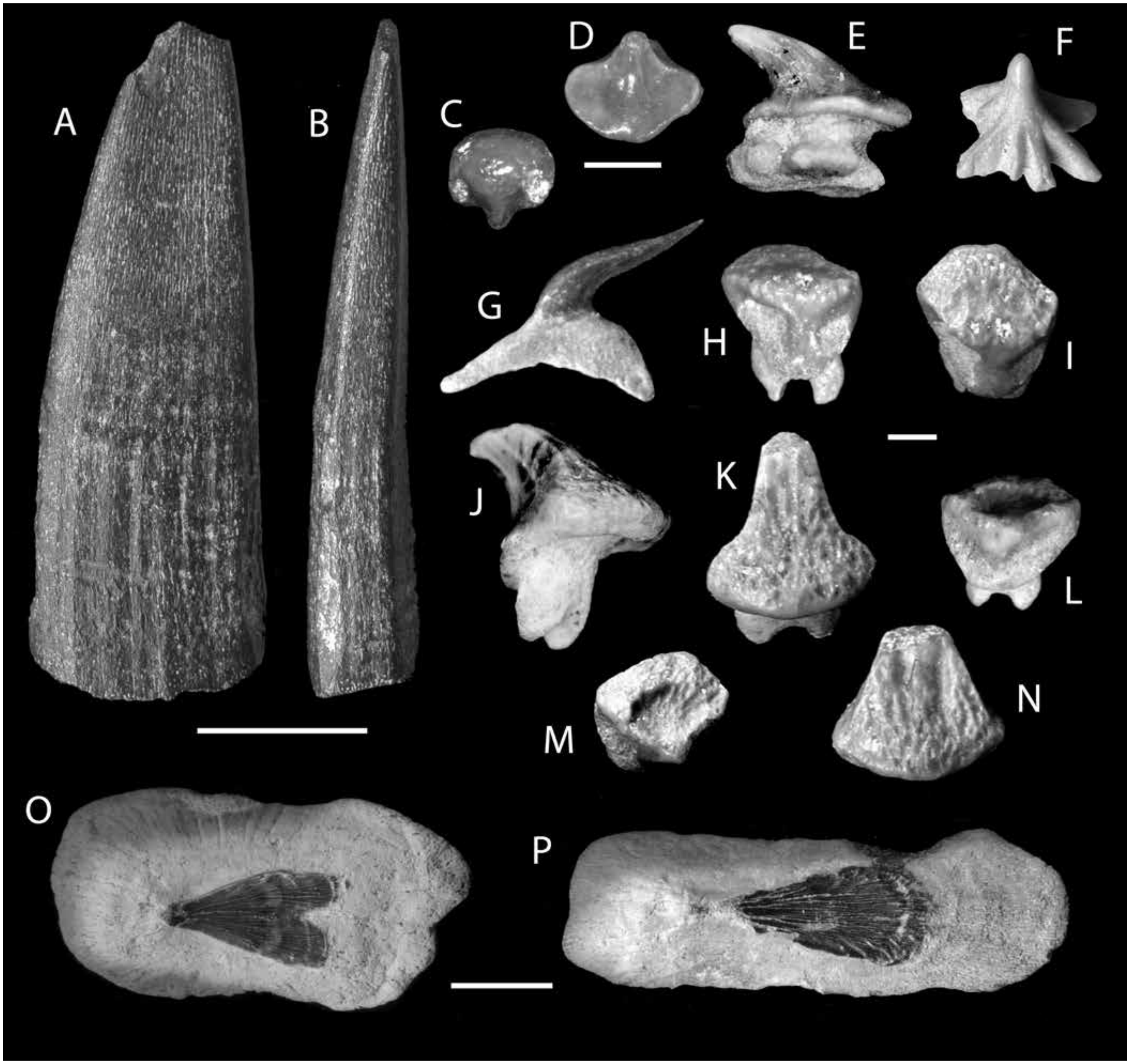
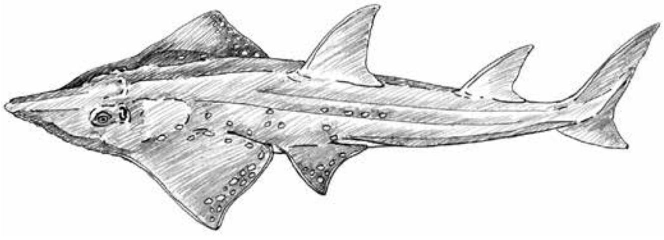


FIGURE 2.24. *Pristis*, *Rhynchobatus*, *Raja*, and *Dasyatis* fossils (separate 1 cm scale bars for A+B and O+P; separate 1 mm scale bars for C+D and E–N). (A) *Pristis* sp. rostral tooth; dorsal view (CMM-V-2113; bed 14, Governor Run–Parkers Creek, Maryland). (B) *Pristis* sp. rostral tooth; distal view (CMM-V-2113; bed 14, Governor Run–Parkers Creek, Md.). (C) *Rhynchobatus* sp. tooth; occlusal view (CMM-V-7737; Bayfront Park, Md.). (D) *Raja* sp. female tooth, occlusal view (CMM-V-7723; bed 3B, New Kent County, Virginia). (E) *Raja* sp. male tooth; lateral view (CMM-V-7730; bed 3B, New Kent County, Va.). (F) *Raja* dorsal thorn; apicolateral view (CMM-V-7695; bed 3, Pamunkey River, Va.). (G) *Raja* alar(?) thorn; lateral view (CMM-V-3775; bed 24, Windmill Point, Md.). (H) *Dasyatis rugosa* female tooth; lingual view (CMM-V-7727; bed 3B, New Kent County, Va.). (I) *D. rugosa* female tooth; occlusal view (CMM-V-7727; bed 3B, New Kent Co., Va.). (J) *D. rugosa* male tooth; lateral view (CMM-V-7726; bed 3B, New Kent Co., Va.). (K) *D. rugosa* male tooth; labial view (CMM-V-7726; bed 3B, New Kent Co., Va.). (L) *D. probsti* female tooth; lingual view (CMM-V-7733; bed 3B, New Kent Co., Va.). (M) *D. probsti* female tooth; occlusal view (CMM-V-7733; bed 3B, New Kent Co., Va.). (N) *D. probsti* male tooth; labial view (CMM-V-7733; bed 3B, New Kent Co., Va.). (O) *Dasyatis* dermal thorn; dorsal view (CMM-V-4572; Bayfront Park, Md.). (P) *Dasyatis* dermal thorn; dorsal view (CMM-V-4542; Plum Point, Md.).

ORDER RAJIFORMES BERG, 1940

FAMILY RHYNCHOBATIDAE GARMAN, 1913

Genus *Rhynchobatus* Müller and Henle, 1837



Wedgefishes – Rhynchobatidae

The wedgefishes of the genus *Rhynchobatus* are the sole representatives of the family Rhynchobatidae. The biology of Holocene *Rhynchobatus* is poorly known, at least in part because of the current rarity of many species due to human activities. They occur in nearshore slope habitats (from the surf zone down to about 70 m) in tropical and subtropical oceans, principally in the Indo-Pacific. Wedgefishes belong to the rhinobenthic ecomorphotype and have a sharklike body with a dorsoventrally compressed head that is contiguous with a triangular snout and the pectoral fins. They reach lengths of about 3.1 m, have a comparatively small mouth and teeth, and feed on benthic prey, such as crustaceans, mollusks, and teleosts (Grant, 1978; van der Elst 1993; Compagno et al., 1989; Compagno, 1990b; Compagno and Last, 1999; Cavanagh et al., 2003).

Rhynchobatus sp.

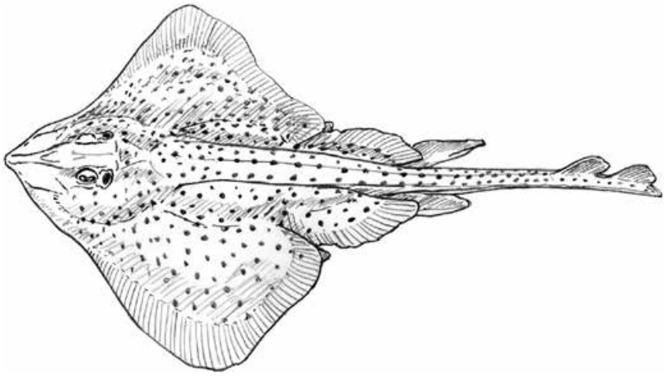
FIGURE 2.24C

DESCRIPTION. These teeth are small and inconspicuous (≤2 mm) and have rarely been collected (six specimens) from the northern end of Calvert Cliffs. The crown is low and globular, is covered with faintly sculptured enameloid, and has a weakly differentiated transverse crest. The most conspicuous feature is a short, moderately broad uvula extending over the medial portion of the lingual root surface. Unlike the similar teeth of *Rhinobatos*, no secondary uvulas extend from the lateral margins of the crown. Instead, the coronal margins angle from the lateral surfaces to the base of the uvula.

DISCUSSION. Teeth from Calvert Cliffs are typically worn and usually lack intact roots. Generalized features include roots that are narrower than the crown, displaced lingually, and separated into two lobes by a broad, deep groove bearing one or two nutrient foramina (Cappetta, 1987; Antunes and Balbino, 2007).

STRATIGRAPHIC AND GEOGRAPHIC RANGES. Neogene *Rhynchobatus* teeth, usually listed as *R. pristinus*, have been widely reported from Europe (Cappetta, 1970; Ward and Bonavia, 2001; Antunes and Balbino, 2007; Reinecke et al., 2011) and somewhat less frequently from Florida and North Carolina (Stoutamire, 1975; Case, 1980; Purdy et al., 2001, as *Rhinobatos* sp.). Unfortunately, there are relatively few species-specific diagnostic characters on *Rhynchobatus* teeth, and they can be easily obliterated by either feeding activities or postmortem wear. As a result, it is unclear whether all of these records represent a single relatively ubiquitous Atlantic species or multiple species. There is some evidence that cryptic species are present in Holocene *Rhynchobatus*; for example, *R. djiddensis* may represent at least four separate species (Compagno, in Cavanagh et al., 2003). Although it is certainly possible that more than one *Rhynchobatus* species existed during the Neogene of the North Atlantic, the possibility is difficult to demonstrate on the basis of the meager evidence currently available.

FAMILY RAJIDAE BONAPARTE, 1831



Skates – Rajidae

The skates of the family Rajidae (=suborder Rajoidei) are an exceptionally diverse component of Holocene faunas, with 27 genera, 245 named species, and perhaps 50–100 unnamed species. Despite their diversity, skates are a very conservative group largely restricted to soft-substrate bottoms in cold antitropical and deepwater environments (McEachran and Miyake, 1990; Ebert and Compagno, 2007; Ebert et al., 2008). The major portion of the disklike body is dorsoventrally compressed, with large triangular pectoral fins fused to the head that produce a roughly rhomboidal body shape. The distal ends of these enlarged pectoral fins produce a metachronal wave that provides the propulsive force for swimming. Unlike the superficially similar dasyatid stingrays, there is no venomous sting on the elongated caudal portion of the body. The mouth and gill slits are ventrally positioned, and they frequently have enlarged thorny denticles on the dorsal surface. They are benthic durophages (rajobenthic ecomorphotype) that feed on crustaceans, mollusks, and small fishes (Feduccia and Slaughter, 1973; Compagno, 1990b; Smale and Cowley, 1992; Orlov, 1998; Scenna et al., 2006). The dentitions of many extant rajids exhibit both gynandric and gradient monognathic heterodonty. Female teeth are low and globular, roughly comparable to those of other rajiforms, such as *Rhinobatos* and *Rhynchobatus*, whereas male teeth have a tall to very tall, lingually angled crown (Cappetta, 1987). This sexual dimorphism is presumed to allow diet partitioning, although the elevated male teeth may be more critical for reproductive behavior (Feduccia and Slaughter, 1973; Smale and Cowley, 1992; Orlov, 1998; Scenna et al., 2006). There is fossil evidence that rajids also use their teeth to scavenge cetacean carcasses (van Netten and Reumer, 2009).

The earliest *Raja*-like fossils are known from the Late Cretaceous, and their teeth are widely distributed in fossil beds during the Cenozoic (Cappetta, 1987; Prasad and Cappetta, 1993). There are numerous fossil species assigned to this genus, although in most cases these species are based on isolated teeth. Identification of rajids on the basis of individual teeth is particularly difficult. Tooth morphology is conservative (Herman et al., 1995), and distantly related genera can have nearly indistinguishable teeth (e.g., *Raja* and *Bathyraja*; Long, 1994). Further, a substantial number of individuals can have dental anomalies that can complicate identifications (Delpiani et al., 2012).

Genus *Raja* Linnaeus, 1758

Raja sp.

FIGURE 2.24D,E

Description. Female teeth (Figure 2.24D) have a low, lingually directed crown. The labial face of the crown is convex and lacks a labial cutting edge. Labial and distal cutting edges are present. In occlusal view, the coronal base is cordate to rhomboidal, with shallow depression between the crown, the cutting edges, and the labiolateral margins of the crown base. The root is small and does not extend beyond the lateral margins of the crown base. In profile, the root is weakly displaced lingually. The flat basal surface of the root is bisected by a conspicuous nutrient groove.

Male teeth (Figure 2.24E) are similar but have a taller, more lingually displaced crown. In profile, the labial margin is convex between the coronal apex and a thick, rounded labial hood, whereas the lingual margin is concave.

Discussion. As is true of most fossil rajid teeth, the specimens from Calvert Cliffs are assigned to the nominate genus, *Raja*. But with numerous rajid genera having conservative dentitions, this generic assignment is, at best, provisional.

Müller (1999) lists six species of fossil *Raja* from the eastern United States. Only one of them is listed from the Calvert and St. Marys Formations of Maryland (*Raja* sp. 2; Müller, 1999:57, text-fig. 18/14–17; pl. 12, figs. 4–5; tbl. 4), and the teeth are comparable to those described above. Curiously, Müller (1999) also lists two additional species (*Raja* sp. 3 and *Raja* sp. 4) from the Little Cove Point Member of the St. Marys Formation in the legends to plate 12 (figs. 7, 9–11) and plate 13 (figs. 3–5). Neither of these species is listed from this formation in the text (p. 57), instead being listed as occurring in the Rushmere Member of the early Pliocene Yorktown Formation of North Carolina. The reason for this discrepancy is unclear, and no specimens matching these specimens are currently known from Calvert Cliffs. Additional species could certainly be present, and ongoing research at the University of Maryland is investigating this possibility.

These teeth resemble *R. ceciliae* (Steurbaut and Herman) in having a small root and mesial and distal cutting edges but lack the distinctive labial cutting edge present on that species (Reinecke et al., 2011). The teeth of *R. gentili* have smooth crowns lacking cutting edges (Cappetta, 1970; Ward and Bonavia, 2001).

Stratigraphic and Geographic Ranges. *Raja* teeth are rarely reported from the Calvert Cliffs, and only 14 specimens are presently known. The teeth of fossil rajids (usually as the nominate genus *Raja*) are widely reported during the Neogene, occurring in virtually all temperate paleofaunas in which microteeth have been examined (Radwański, 1965; Cappetta, 1970, 1987, 2012; Long, 1994; Antunes et al., 1999a; Müller, 1999; Aguilera and Rodriguez de Aguilera, 2001; Purdy et al., 2001; Ward and Bonavia, 2001; Valsecchi et al., 2005; Antunes, 2007; Antunes and Balbino, 2007; Marsili, 2008; Reinecke et al., 2008, 2011; Wijnker et al., 2008; Schultz et al., 2010; Boessenecker, 2011; Vialle et al., 2011; Bor et al., 2012).

Raja Dermal Thorns

FIGURE 2.24F,G

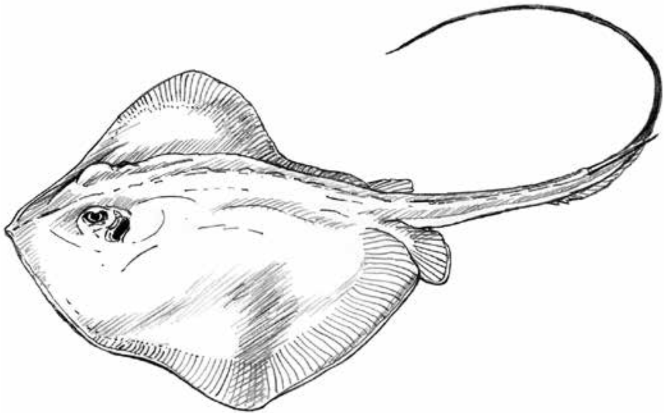
Rajids have dermal denticles enlarged into three different types of dermal thorns: (1) generalized thorns along the dorsal midline, (2) alar thorns on the distal surfaces of the pectoral fins of males, and (3) malar thorns lateral to the orbits and spiracles of males (McEachran and Konstantinou, 1996). Thorn morphology is quite variable and has not been rigorously studied in fossil rajids.

Dorsal thorns are relatively large and robust, with stellate bases (Figure 2.24F). Alar and malar thorns are somewhat smaller and more delicate than dorsal thorns and are rarely collected. Alar thorns generally have simple, linear bases, whereas malar thorns can have linear bases like alar thorns or delicate, stellate bases similar to that of dorsal thorns. The thorn shown in Figure 2.24G has a narrow, elongate base and a slender, sigmoidal spine that is covered by enameloid and closely resembles one of the fossil alar thorns illustrated by Bor et al. (2012: pl. 54, fig. 3a–c). This spine morphology is comparable to that of the alar spines belonging to the extant species *Bathyraja kincaidii* and *R. eglanteria* in McEachran and Konstantinou (1996: figs. 10a,11b, respectively).

ORDER MYLIOBATIFORMES COMPAGNO, 1973

FAMILY DASYATIDAE JORDON, 1888

Dasyatis Rafinesque, 1810



Whiptail Stingrays – Dasyatidae

The widely distributed whiptail stingrays (Dasyatidae) have a dorsoventrally compressed, ovate to rhomboidal body, lacking both dorsal and caudal fins and possessing a long whiplike tail, usually armed with one or more venomous spines. Dasyatids are well adapted for a benthic lifestyle, with dorsal-placed eyes, ventral gill slits, and large winglike pectoral fins. They are found primarily in warm temperate to tropical inshore marine habitats, where they prey on small benthic animals (Bigelow and Schroeder, 1953; Whitehead et al., 1984; Smith and Heemstra, 1986; Lythgoe and Lythgoe, 1992).

The taxonomy of fossil *Dasyatis* is currently in a state of flux. A number of names have been applied to Neogene *Dasyatis* fossils, including extinct species (Cappetta, 1970, 1987; Schultz, 1977; Reinecke et al., 2011), as well as Holocene species (Purdy et al., 2001; Cappetta and Cavallo, 2006). Further, there is evidence that the dasyatids are not a monophyletic group (Carvalho et al., 2004; Claeson et al., 2010; Maisey, 2012).

Like the rajids, *Dasyatis* teeth exist is both cuspidate and molariform morphologies. In the extant Atlantic stingray, *D. sabina* (Lesueur, 1824), Kajiura and Tricas (1996) found that these two tooth forms were not due to a simple sexual dimorphism. Immature individuals and mature females had molariform teeth. The teeth of mature males varied seasonally, with taller cuspidate teeth during the breeding season and molariform teeth the remainder of the year. Such seasonal gynandric heterodonty was likely also present in Calvert Cliffs *Dasyatis*, given the comparative rarity of cuspidate teeth.

Two species are presently recognized from Calvert Cliffs, which may underestimate the number of species actually present. Sculpturing on the occlusal surface of the teeth is critical for correctly identifying species, yet these structures are rapidly degraded by the durophagous lifestyle of dasyatids. A high proportion of fossil dasyatid teeth from Calvert Cliffs have polished occlusal surfaces from use and cannot be reliably identified to species. This high incidence of tooth wear complicates the recognition of rarer species without access to large numbers of specimens.

Dasyatis rugosa (Probst, 1877)

FIGURE 2.24H–K

Synonymy follows Cappetta (1970) and Reinecke et al. (2011).

DESCRIPTION. The molariform teeth (Figure 2.24H,I) have a crown that is moderately high and stout and labial and lingual surfaces that are similar in size. The labial face is moderately to strongly convex, with densely packed ridges and grooves. The lingual face is smooth or ornamented with a few pits and strongly to weakly concave in profile. In occlusal view the labial visor is angular in anterior and lateral teeth, although it may become progressively rounded in posterior teeth. The lingual visor is parabolic or a truncated parabola in occlusal view. The transverse ridge separating the labial and lingual faces is rounded, arched lingually, and irregularly ornamented with ridges and grooves. The root is lingually displaced and has two lobes separated by a deep nutrient groove.

Cuspidate teeth (Figure 2.24J,K) are generally similar to the more common molariform teeth, but the crowns are taller and narrower. They are acutely pointed and triangular in anterior files, becoming lower, less pointed, and asymmetrical in lateral files. The crown base is pentagonal or hexagonal in occlusal view.

DISCUSSION. Müller (1999) lists two *Dasyatis* species from Calvert Cliffs: *D. cavernosa* from the Choptank Formation (p. 60; taf. 14, figs. 1–10; abbildungs 19/5–6) and *Dasyatis* sp. 1 from all three Calvert Cliffs Formations (pp. 60–61; taf. 13, figs. 6–8, 10–11). The illustrated specimens appear to be primarily *D. rugosa*, although some (e.g., abb. 19/6) are referable to *D. probsti.*

The teeth of *D. delfortrieri* Cappetta are generally similar to those of *D. rugosa* in having a completely wrinkled lingual surface. Despite a superficial resemblance, the teeth of the former species differ from those of the latter in having a more regular, honeycomb-like pattern of ridges and pits (Reinecke et al., 2005, 2008). There is also some evidence that *D. delfortrieri* was extinct by the latter part of the early Miocene (Reinecke et al., 2011).

STRATIGRAPHIC AND GEOGRAPHIC RANGES. This species is known from all three formations along Calvert Cliffs, and teeth have been collected in situ from bed 3 of the Calvert Formation in Virginia. Because of their globular shape and small size they are rarely collected, and only 18 specimens were available for study.

Dasyatis rugosa has previously been found from the late Oligocene through the early late Miocene of Austria, Belgium, northern and southern Germany, the Netherlands, Portugal, Switzerland, and North Carolina in the United States (Barthelt et al., 1991; Daxner-Höck et al., 2004; Balbino and Antunes, 2006; Haye et al., 2008; Reinecke and Wienrich, 2009; Reinecke et al., 2011; Bor et al., 2012).

Dasyatis probsti Cappetta, 1970

FIGURE 2.24L–N

Synonymy follows Reinecke et al. (2011).

Description. The molariform teeth of this species (Figure 2.24L,M) have moderately high and comparatively stout crowns. The labial face has two distinct regions. Apically, there is an ovoid concavity that is smooth or has only a few weak ridges. Between this depression and the labial visor the enameloid is ornamented with irregular grooves and ridges. The transverse ridge is strongly arched lingually, sharp, and irregularly ornamented with ridges and pits. The lingual face of the crown is smooth and strongly concave in profile. In occlusal view, the labial visor is angular, whereas the lingual visor is in the form of a parabola or a truncated parabola. The root is small and lingually displaced. Two lobes are present, separated by a deep nutrient groove.

The cuspidate male teeth (Figure 2.24N) resemble the molariform teeth, except that they have a tall, lingually directed crown. The crown is acute and triangular in anterior files, becoming lower and asymmetrical in lateral files; the labial face has a deep depression covered with fine, vertical ridges, whereas the lingual face is smooth. In occlusal aspect, the crown base is hexagonal in shape.

Discussion. The teeth of *D. probsti* are similar in some respects to those of *Taeniura cavernosa* (Probst). Both species have an apical concave depression on the labial coronal face, although it is subcircular in the former species and more triangular in the latter species. The ornamentation on the labial face of *T. cavernosa* consists of closely packed pits (rather than wrinkles), and the edge of the visor is smooth and unornamented. In occlusal view, the labial visor of *T. cavernosa* is arched, whereas that of *D. probsti* is angular (Reinecke et al., 2011).

Stratigraphic and Geographic Ranges. The distribution of *D. probsti* along Calvert Cliffs is poorly documented because of the small size and worn occlusal surfaces of the teeth. Beach specimens occur primarily on the northern half of Calvert Cliffs and are probably associated with the Calvert and Choptank Formations. Teeth of this species are also known from bed 3 of the Calvert Formation at inland sites in the Chesapeake Bay area. Only seven Calvert Cliffs specimens were identifiable to this species.

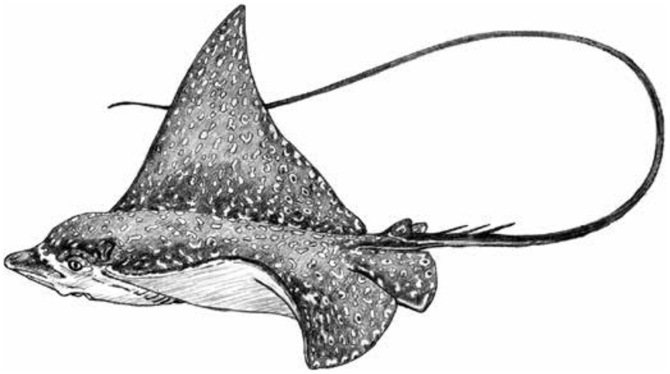
Dasyatis probsti teeth have been previously reported from the middle Miocene of Europe, including Austria, Belgium, southern France, Germany, and the Netherlands (Cappetta, 1970; Schultz, 1977; Bolliger et al., 1995; Reinecke et al., 2011; Bor et al., 2012).

Dasyatis Dermal Thorns

FIGURE 2.24O,P

Large dorsal thorns are commonly collected from Calvert Cliffs and can be quite variable in form. These thorns have a roughly circular to ovoid (sometimes quite elongate) outline. The most elevated portion of each thorn has one to several raised points, each associated with a lobed or lanceolate enameloid cap. The enameloid-free portion of the thorn surface can be striated (Figure 2.24O) or smooth (Figure 242.P). Thorns with striated surfaces are associated with the caudal region, whereas those with smooth surfaces occur on the trunk portion of the body (Bigelow and Schroeder, 1953; Purdy et al., 2001).

FAMILY MYLIOBATIDAE BONAPARTE, 1838



Eagle Rays – Myliobatidae

The myliobatid, or eagle, rays are large, aquilopelagic species. They are powerful swimmers using tapered, high-aspect-ratio pectoral fins for lift-based underwater flight. Eagle rays are durophagous predators of benthic crustacean and mollusks, with strong jaws bearing a dentition of broad, interlocking teeth modified into grinding plates (Bigelow and Schroeder, 1953; Cappetta, 1987; Compagno, 1990b; Herman et al., 2000).

Two genera of myliobatids are known from Calvert Cliffs. The most abundant myliobatid teeth from the Maryland Miocene have traditionally been placed in the genus *Myliobatis* Cuvier, 1817, with Eastman (1904) assigning these teeth to three different species, *M. frangans* Eastman, *M. pachyodon* Cope, and *M. gigas* Cope. Purdy et al. (2001), in discussing comparable Miocene teeth from the Pungo River Formation of North Carolina, argued that they should be more appropriately placed in the genus *Pteromylaeus*. *Myliobatis* teeth can be differentiated from those of *Pteromylaeus* by the lateral elongation of the crown; the width to depth ratio in *Myliobatis* teeth tends to be 4–5:1, whereas in *Pteromylaeus* it is closer to 7–8:1. In addition, *Pteromylaeus* roots tend to be more lingually extended (Herman et al., 2000; Bourdon, 2000–2007; Reinecke et al., 2011). The teeth from Calvert Cliffs are consistent with those of *Pteromylaeus* and, following Purdy et al. (2001), are transferred to this genus.

The less common myliobatid teeth from Calvert Cliffs are very distinctive and can be reliably assigned to the genus *Aetobatus*.

Genus *Pteromylaeus* Garman, 1913

The bull rays of the genus *Pteromylaeus* are widely distributed in warm temperate and tropical nearshore and brackish habitats. The body is broadly rhombohedral, with the enlarged, alate pectoral fins used for locomotion. The head is broad and rounded, whereas the tail is long and slender. Bull rays feed on a variety of invertebrates, such as crustaceans, and mollusks. Large individuals commonly reach lengths of 1.5 m. There are two extant species, one from the Mediterranean, southeastern Europe, and western to southeastern Africa and the other from Ecuador and the Pacific coast of Panama (Compagno et al., 1989; Compagno, 1990b; Schneider, 1990; Brito, 1991; McEachran and Notarbartolo di Sciara, 1995; Seck et al., 2002).

The *Pteromylaeus* tooth plate contains one medial row group and one to three lateral row groups, which may be either labiolingually or laterally elongated on each side (Compagno et al., 1989; Herman et al., 2000; Reinecke et al., 2011).

Pteromylaeus sp.

FIGURE 2.25

Description. Medial teeth are elongated hexagons with acutely angled ends. The occlusal surface is flat to weakly convex and weakly arched, with the ends bent lingually (Figure 2.25A). The basal surface of the root has numerous, parallel, labiolingually directed laminae (Figure 2.25B). The labial and lingual crown faces are ornamented basally with vertical wrinkles that interdigitate between adjacent teeth (Figure 2.25C). A narrow basal ledge on the lingual face supports the basal edge of the crown on the next tooth in the file. In either labial or lingual view there is a weak to moderately strong notch separating the crown from the root at the lateral margins. The roots are slightly thickened medially and in profile are lingually displaced. Foramina run along the labial face above the laminae; the occlusal face shows foramina near the juncture of the laminae, and the lingual face generally bears foramina between the laminae just below the crown.

Lateral teeth are smaller and rhomboidal but otherwise have a structure similar to that of the medial teeth.

Discussion. The medial teeth of *Pteromylaeus* can easily be confused with those of either *Myliobatis* or *Aetomylaeus*. *Pteromylaeus* and *Myliobatis* medial teeth are very similar but differ in shape in occlusal view, being arched in *Pteromylaeus* and relatively straight in *Myliobatis* (Cappetta, 2012:453). *Aetomylaeus* medial teeth differ from both of these genera in having crowns that are noticeably thicker medially than laterally (Cappetta, 2012:446).

The range of variability in extant *Pteromylaeus* teeth is poorly documented. Herman et al. (2000) examined five specimens from *P. bovinus* and found that both ontogenetic and gynandric heterodonty were present but were unable to examine dentitions of the second species, *P. asperrimus*. A number of names have been applied to Neogene species, apart from the three Maryland species listed in Eastman (1904), including *P. apenninus* (Costa), *P. crassus* (Gervais,), *P. gemmellaroi* (Salinas), and *P. meridionalis* (Gervais). Most of these species are based on fragmentary material, and their validity and possible relationships with extant species are unknown. At present, it is unclear whether one or more *Pteromylaeus* species are present in the Maryland Miocene or which name(s) should be used. Purdy et al. (2001) and Bourdon (2000–2007) proposed listing the Miocene teeth from North Carolina as *Pteromylaeus* sp. pending more detailed analyses. That practical approach is followed here.

Stratigraphic and Geographic Ranges. Teeth attributable to *Pteromylaeus* are very commonly collected along Calvert Cliffs, and more than 120 specimens (mostly as fragments) were used in this study. They have been found in place in beds 3–5, 9–12, 14, 17, 19, and 21–23. The geographic range of Miocene *Pteromylaeus* is difficult to determine because of confusion of this genus with *Myliobatis* and possibly *Aetomylaeus* and the fragmentary nature of many specimens. The *Pteromylaeus* illustrated by Cappetta (1970) from southern France and those shown by Purdy et al. (2001) from North Carolina are similar to those from Calvert Cliffs.

Genus *Aetobatus* Blainville, 1816

Spotted eagle rays are nearshore, neritic batoids that are known to occur in lagoonal, estuarine, and coral reef habitats. They have a grinding dentition and are durophagous predators of a variety of benthic species, including polychaetes, mollusks, crustaceans, and teleost fishes (Michael, 1993; Homma and Ishihara, 1994; Compagno and Last, 1999; McEachran and de Carvalho, 2002; Schluessel et al., 2010).

The dentition of *Aetobatus* is unusual among myliobatids in that the teeth are not hexagonal in the occlusal perspective. The lateral margins are convexly arched and lingually directed. Further, there are no lateral tooth rows, and the medial teeth are greatly elongated laterally. The upper and lower teeth are morphologically distinct and easily distinguished. The upper teeth are broadly arched, whereas the lowers are in the form of an acute to weakly obtuse chevron.

Aetobatus arcuatus Agassiz, 1843

FIGURE 2.26

Synonymy follows Reinecke et al. (2011).

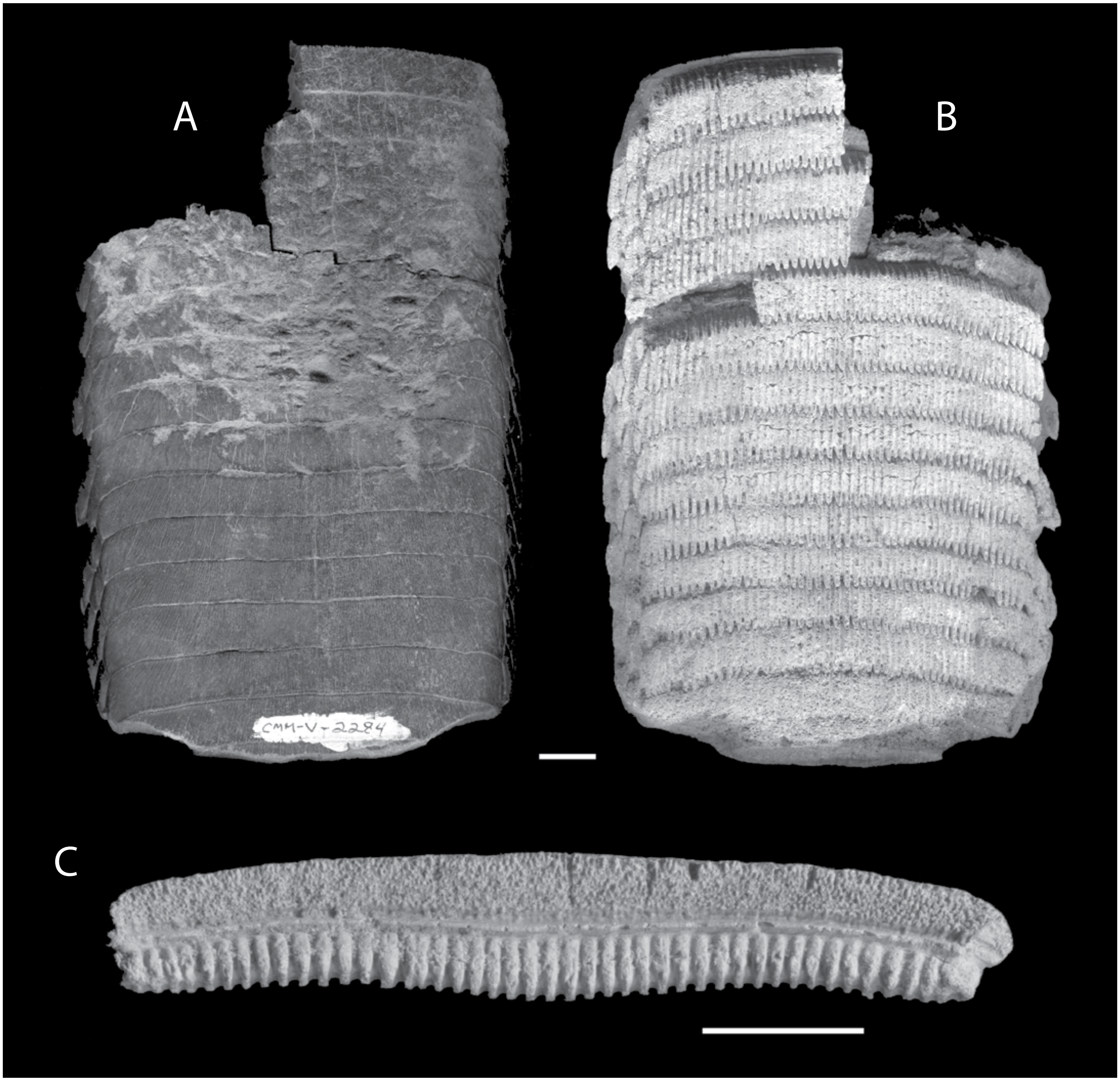


FIGURE 2.25. *Pteromylaeus* sp. fossils (1 cm scale bar). (A) Dental plate; occlusal view (CMM-V-2284; Parkers Creek, Maryland). (B) Dental plate; basal view (CMM-V-2284; Parkers Creek, Md.). (C) Medial tooth; lingual view (CMM-V-1219; bed 14, Governor Run, Md.).

DESCRIPTION. The crescent-shaped upper teeth have flat occlusal surfaces and rounded ends (Figure 2.26A,B). The labial and lingual faces of the crown are vertical and have numerous irregular ridges and grooves that interlock with adjoining teeth. A narrow ridge along the lingual crown face fits into a groove that runs the length of the labial crown face of the next tooth. The roots are very strongly displaced lingually when viewed in profile. As with *Pteromylaeus* teeth, the basal surface of the root has numerous parallel laminae. Because of this strong displacement, the laminae on the lingual surface of the root are readily apparent in occlusal view.

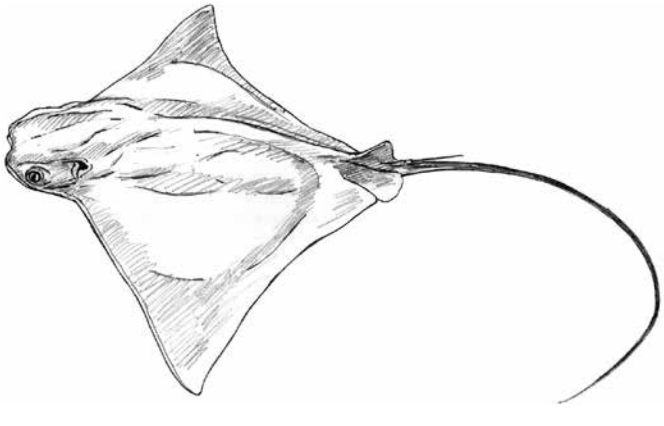
The lower teeth are similar in structure to the uppers, except for the angular, chevron-like shape of the crown and root in occlusal and basal views (Figure 2.26C,D).

DISCUSSION. Two different names have been used for Maryland Miocene *Aetobatus* (Hay, 1902:321), *A. arcuatus* Agassiz and *A. profundus* (Cope). The differences between these two has not been critically evaluated, and Cappetta (2006) considers *profundus* to be a junior synonym of *arcuatus*. Even this attribution is, at best, somewhat tentative, as the range of variation in extinct and extant *Aetobatus* is poorly known. Claeson et al. (2010) compared *A. arcuatus* teeth with the similarly shaped teeth of the extant *A. narinari* and found that they differed in coronal thickness. In *A. narinari* the crown is uniformly thick, whereas in *A. arcuatus* the crown is thicker medially because of a basal expansion of the crown onto the root face. But this character has not been examined in other extant *Aetobatus*, and its usefulness for unambiguously identifying *A. arcuatus* teeth is untested. For the present, *A. arcuatus* is retained as a valid species name.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. Beach specimens of *A. arcuatus* teeth are known from the entire length of Calvert Cliffs and have been reported in situ from beds 4, 5, 10–15, 17, and 19. The species is also known from bed 1 of the Calvert Formation and bed 24 of the St. Marys Formation in river and inland sites of the Mid-Atlantic region. Teeth are somewhat less abundant than those of *Pteromylaeus*, and almost 90 were examined.

Aetobatus arcuatus has previously been reported from early to late Miocene formations of Europe (Leriche, 1926, 1927; Radwa-ski, 1965; Cappetta, 1970; van den Bosch et al., 1975; Holec et al., 1995; Reinecke et al., 2011; Bor et al., 2012), Costa Rica (Mora, 2004), Panama (Gillett, 1984), Saudi Arabia (Thomas et al., 1982), and the eastern United States (Leriche, 1942; Müller, 1999; Purdy et al., 2001).

FAMILY RHINOPTERIDAE JORDAN AND EVERMANN, 1896



Cow-Nosed Rays – Rhinopteridae

The cow-nosed rays, like the related eagle rays, are large, aquilopelagic durophages. They are globally distributed in warm temperate and tropical nearshore and brackish habitats. The body has large triangular pectoral fins used for locomotion, a weakly bilobed head, and a long, flexible tail. Cow-nosed rays have strong jaws and a grinding dentition comparable to that of the myliobatids and have a similar diet of a variety of mollusks and crustaceans. The dental plates typically consist of a medial row of broader teeth, flanked on each side by three or four lateral rows of narrower teeth. Large individuals reach a width of about 200 cm (Bigelow and Schroeder, 1953; Cappetta, 1987; Compagno, 1990b; Herman et al., 2000).

Genus Rhinoptera van Hasselt, 1824

Rhinoptera cf. *R. studeri* (Agassiz, 1843)

FIGURE 2.27A–C

Synonymy follows Cappetta (1970), with the following additions:

1999 *R.* aff. *brasiliensis* Müller – Müller, pp. 64–65, taf. 15, figs. 4, 5.

1999 *R.* aff. *bonasus* (Mitchell) – Müller, p. 65, taf. 15, fig. 7.

2009b *Rhinoptera* cf. *R. studeri* (Agassiz) – Cicimurri and Knight, p. 641, fig. 6G.

DESCRIPTION. Medial teeth are moderately broad hexagons with acutely angled ends. The occlusal surface is flat and symmetrical, with crowns of uniform thickness. The labial and lingual crown faces are only weakly ornamented with fine wrinkles. A weak basal ledge on the lingual face of the crown supports the rounded basal edge of the labial crown face of the adjacent tooth in the file. In profile, the roots are lingually displaced, so that the lingual surface projects slightly beyond the crown. The basal surface of the root has numerous, parallel, labiolingually directed laminae.

The lateral teeth in the files on either side of the medial file are hexagonal and slightly narrower than those of the medial file. They are slightly asymmetrical and have crowns that become thinner distally. Teeth in the marginal files are also hexagonal or pentagonal but have length and breadth that are more nearly equal.

DISCUSSION. The assignment of Miocene *Rhinoptera* to species suffers from many of the same difficulties as myliobatids, such as *Pteromylaeus*. Tooth morphology of extant species is highly variable, and because of the weak interconnection between teeth, fossil species are known almost entirely from isolated teeth. The teeth from Calvert Cliffs most strongly resemble those of *R. studeri*, although without intact dentitions, it is difficult to discern their identity with absolute certainty. Teeth from the medial and adjacent files of *R.* cf. *R. studeri* can most often be confused with the medial teeth of *Pteromylaeus* sp. Teeth of *R.* cf. *R. studeri* have a lower breadth-to-length ratio (about 7:1) compared to that of *Pteromylaeus* sp. (about 12:1). Lateral teeth are more difficult to separate, although the relatively fine ornamentation on the labial

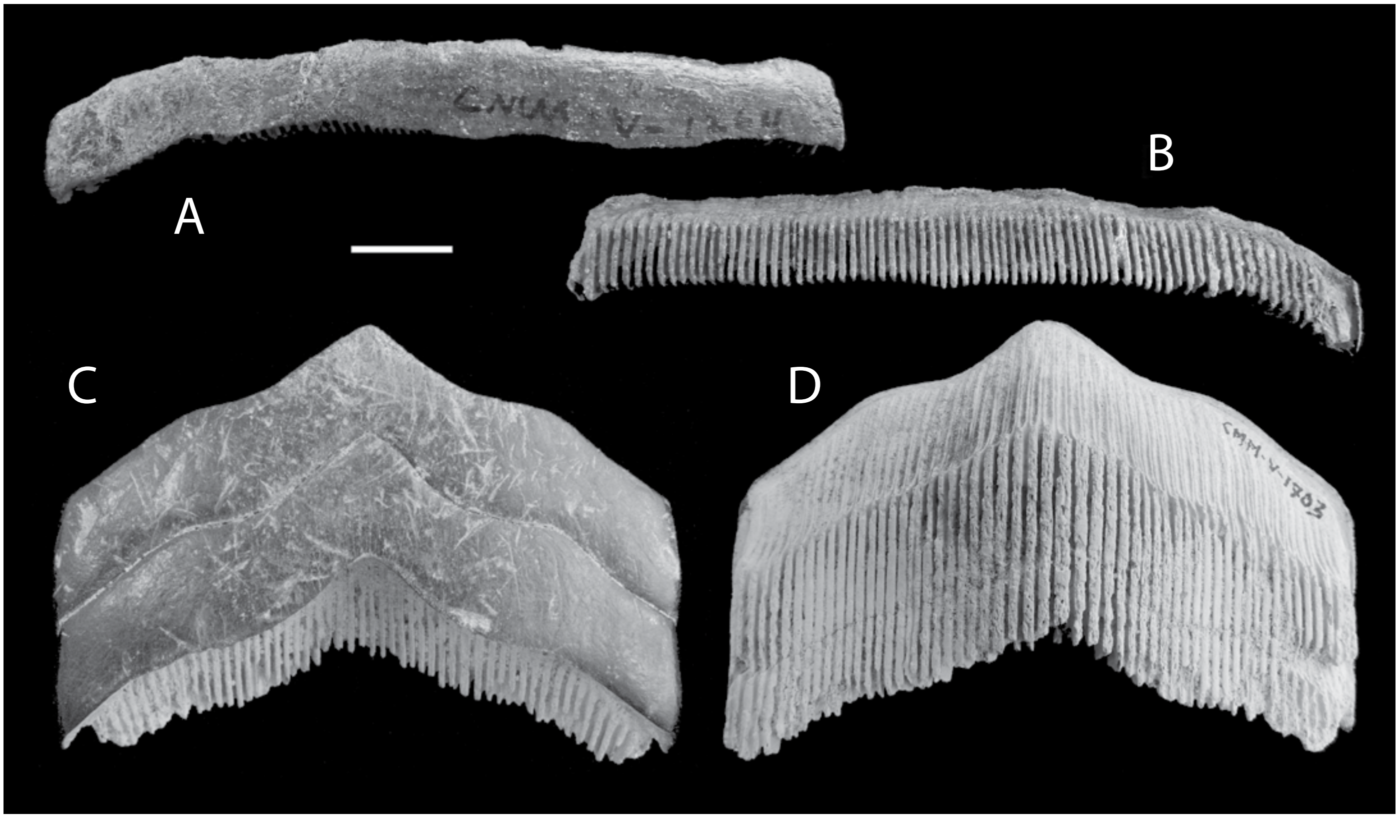


FIGURE 2.26. *Aetobatus arcuatus* teeth (1 cm scale bar). (A) Upper tooth; occlusal view (CMM-V-1264; Western Shores Estates, Maryland). (B) Upper teeth; basal view (CMM-V-1264; Western Shores Estates, Md.). (C) Lower teeth; occlusal view (CMM-V-1703; bed 14, Parkers Creek, Md.). (D) Lower teeth; basal view (CMM-V-1703; bed 14, Parkers Creek, Md.).

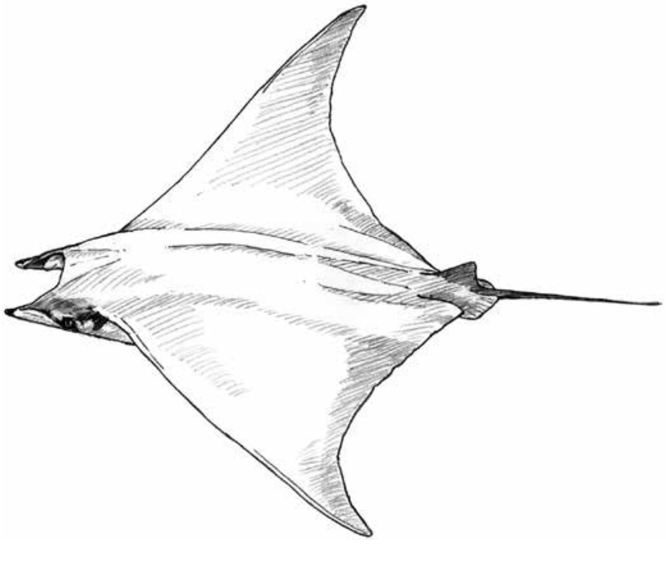
and lingual coronal faces is recognizably different from the coarse ornamentation of *Pteromylaeus* sp. Finally, the root in *R.* cf. *R. studeri* is less strongly displaced lingually than in *Pteromylaeus* sp. and so is less conspicuous in occlusal view.

Müller (1999:64–65) listed four species of *Rhinoptera* from Calvert Cliffs, *R.* aff. *brasiliensis* (taf. 15, figs. 4, 5), *R.* aff. *bonasus* (taf. 15, fig. 7), *Rhinoptera* sp. 1, and *Rhinoptera* sp. 2. Although four species could have co-occurred, a more likely interpretation is that these represent positional variants of a single species (Cicimurri and Knight, 2009b).

Stratigraphic and Geographic Ranges. Along Calvert Cliffs, *Rhinoptera* teeth are typically collected as beach specimens along the northern two-thirds of the cliffs associated with the Calvert and Choptank Formations. Teeth have been collected in situ from beds 2, 3, 10, 12, 14, 17, and 19. This species is less common than either *Pteromylaeus* or *Aetobatus*, and only 14 teeth were studied.

Teeth resembling *R. studeri* have previously been reported from the late Oligocene (Chattian) to middle Miocene (Serravallian) of Europe and eastern North America (Leriche, 1927; Cappetta, 1970, 1987, 2012; Müller, 1999; Cicimurri and Knight, 2009b).

FAMILY MOBULIDAE GILL, 1893



Devil Rays – Mobulidae

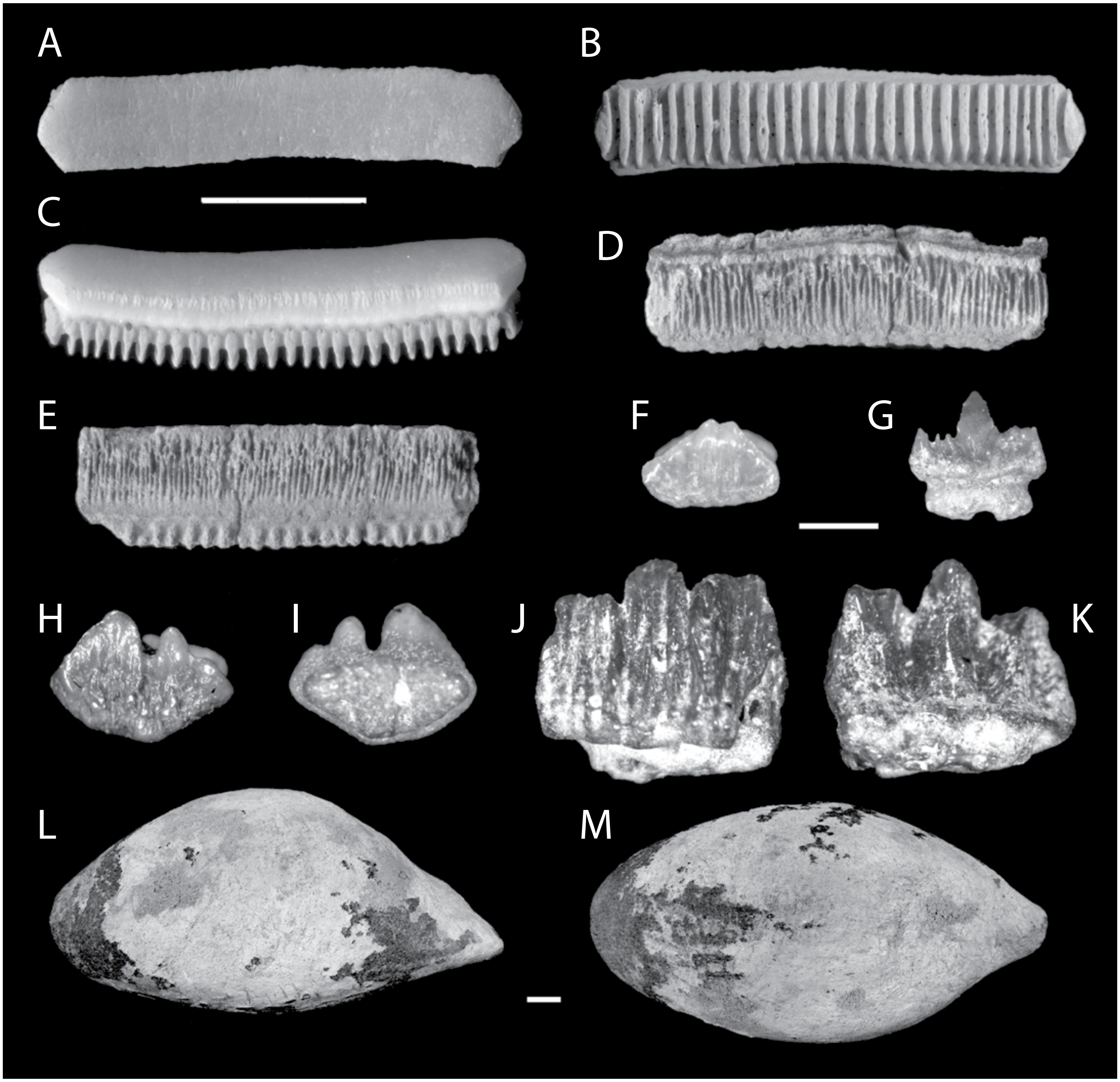


FIGURE 2.27. *Rhinoptera*, *Plinthicus,* and *Mobula* fossils (separate 1 cm scale bars for A–E and L–M; 1 mm scale bar for F–K). (A) *Rhinoptera* cf. *studeri* medial tooth; occlusal view (CMM-V-2780; bed 24, Windmill Point, Maryland). (B) *R.* cf. *studeri* medial tooth; basal view (CMM-V-2780; bed 24, Windmill Point, Md.). (C) *R.* cf. *studeri* medial tooth; lingual view (CMM-V-2780; bed 24, Windmill Point, Md.). (D) *Plinthicus stenodon* medial tooth; labial view (CMM-V-1188; bed 12, Parkers Creek, Md.). (E) *P. stenodon* medial tooth; lingual view (CMM-V-1188; bed 12, Parkers Creek, Md.). (F) *Mobula loupianensis* female tooth; occlusal view (CMM-V-7736; bed 3B, New Kent County, Virginia). (G) *M. loupianensis* male tooth; labial view (CMM-V-7736; bed 3B, New Kent Co., Va.). (H) *M. pectinata* female tooth; occlusal view (CMM-V-7740; Bayfront Park, Md.). (I) *M. pectinata* female tooth; basal view (CMM-V-7740; Bayfront Park, Md.). (J) *M. fragilis* tooth; labial view (CMM-V-7739; Bayfront Park, Md.). (K) *M. fragilis* tooth; lingual view (CMM-V-7739; Bayfront Park, Md.). (L) Mobulid caudal spine base; lateral view (CMM-V-4263; Warrior's Rest, Md.). (M) Mobulid caudal spine base; dorsal view (CMM-V-4263; Warrior's Rest, Md.).

The devil rays of the family Mobulidae are epipelagic and planktivorous, with an aquilopelagic body morphology. The body in the dorsal or ventral perspective is rhomboidal because of the presence of enlarged triangular, winglike pectoral fins. The pectoral fins flap like wings to generate hydrodynamic lift for propulsion. The preorbital portions of the pectoral fins are modified into paired cephalic lobes. They are unique in being the only microphagous batoids; zooplankton is directed into the mouth by expanded cephalic lobes, where it is captured on specialized surfaces of the internal gill openings. Devil rays reach very large sizes, with a span across the pectoral fins of up to 5.2 m and a mass of perhaps 1 ton. Only the *Manta* rays, also in the Mobulidae, attain larger sizes at 7.6 m and 2.4 tons (Notarbartolo-di-Sciara, 1988; Compagno, 1990b; Dean et al., 2007; Sampson et al., 2010).

Mobulids appear to have evolved from ancestral durophagous myliobatiforms with a grinding dentition. The evolution of planktivory in mobulids was accompanied by the loss of the more robust tooth morphologies necessary for crushing armored invertebrate prey and an overall reduction in tooth size. This reduction has been most extensive in *Mobula* and *Manta* and less so in the older *Plinthicus* (Cappetta, 1987; Adnet et al., 2012). Mobulid rays are continuous ram-feeders (Sanderson and Wassersug, 1993). At least some extant species are specialized euphausid feeders (Sampson et al., 2010).

Genus *Plinthicus* Cope, 1869

The teeth of *Plinthicus* are less derived than those of *Manta* and *Mobula* and in morphology more closely resemble the grinding dentition of durophagous myliobatiforms, such as *Rhinoptera*. The dentition consists of multiple files, broadest in medial positions and narrowing laterally. The teeth show few signs of wear, indicative of a diet of soft-bodied prey, prompting Cappetta (1987) to place this genus in the Mobulidae. Manning (2004: fig. 21.6) speculates on a likely evolutionary scenario for the evolution of *Plinthicus*. Manning envisions the origins of *Plinthicus* from the early to middle Eocene *Burnhamia daviesi* (Woodward, 1889), a mobulid with *Rhinoptera*-like teeth. Unlike those of *Rhinoptera*, the teeth of *Burnhamia* have a conspicuous transverse groove on the occlusal surface of the crown and exhibit little premortem wear. In *Burnhamia*, the crown is relatively low and positioned almost directly over the root. The intermediate stage is represented by an unnamed *Plinthicus* sp. from the late Eocene–early Oligocene Byram Formation of Mississippi. Bor (1990) named a new *Plinthicus* species (*P. kruibekensis*) from the early Oligocene Boom Clay Formation of Belgium, but it is unclear if it is conspecific with this contemporaneous unnamed *Plinthicus* sp. from Mississippi. Both have crowns that are taller and thinner, with a reduced root. But *P. kruibekensis* have a smooth occlusal face, whereas the Mississippi *Plinthicus* has a transverse occlusal groove. The terminal species, the middle Miocene *P. stenodon*, has a crown that is taller and strongly angled lingually.

Plinthicus stenodon Cope, 1869

FIGURE 2.27D,E

1869 *Plinthicus stenodon* Cope – Cope, p. 316.
2001 *Plinthicus stenodon* Cope – Purdy et al., pp. 95–96, fig. 12f–j.
2011 *Plinthicus stenodon* Cope – Reinecke et al., pl. 99, fig. 4.

DESCRIPTION. The teeth are distinctive but fragile and rarely collected intact. The crown is very high, labiolingually compressed, and inclined lingually. The occlusal surface is typically flat and may have a few low, flat ridges oriented perpendicular to the long axis of the tooth. Some teeth also have a narrow groove running across the occlusal surface immediately adjacent to the lingual edge. The labial face of the crown is high and concave in profile. The surface is covered by shallow, vertical grooves. The lingual face of the crown is convex in profile and has many narrow, subparallel ridges running from the occlusal surface toward the root. The root is short and narrower than the occlusal surface. The basal surface of the root consists of alternating laminae and deep, foramina-bearing grooves.

DISCUSSION. Purdy et al. (2001) reconstructed the *P. stenodon* dentition as having seven rows, a broad medial row, flanked on each side by somewhat narrower lateral rows, and a pair of much narrower lateral rows along each margin of the dental plate. In the medial and immediately adjacent lateral rows the crown is symmetrical and has a constant coronal height along the width of the tooth.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Plinthicus stenodon* teeth have been collected as beach specimens from the Calvert and Choptank Formations and in situ from beds 3–5, 8, 10, and 12. Specimens are usually badly broken, and largely intact teeth are rare. During this study six large fragments and more than 30 small pieces were examined.

This species has previously been reported from the late Oligocene (Chattian) of South Carolina (Cicimurri and Knight, 2009b) and the early to middle Miocene (Aquitanian–Serravallian) of Maryland, New Jersey, North Carolina, France, Panama, and Venezuela (Leriche, 1942; Cappetta, 1979, 1987; Tedford and Hunter, 1984; Müller, 1999; Purdy et al., 2001; Aguilera and Rodriguez de Aguilera, 2004). *Plinthicus* teeth from the early Miocene of Germany (Reinecke et al., 2011) and Panama (Pimiento et al., 2013b) are not identified to species but have a tall, lingually angled coronal morphology that is consistent with *P. stenodon*.

Genus *Mobula* Rafinesque, 1810

Mobula teeth are much smaller (≤3.5 mm) and morphologically more derived than those of *Plinthicus*. Fossil *Mobula* are known only from isolated teeth and first appear in the early Oligocene (Rupelian; Adnet et al., 2012; Cappetta, 2012). By the Miocene, Cappetta (1970) recognized three *Mobula* species from the south of France, *M. loupianensis*, *M. pectinata*, and *M. fragilis*.

However, the teeth of *Mobula* are highly variable within individual species, exhibiting ontogenetic, gynandric, monognathic, and dignathic heterodonty (Notarbartolo-di-Sciara, 1987), and it is difficult to determine whether the first two represent distinct species or not. Cicimurri and Knight (2009b) in assessing late Oligocene (Chattian) *Mobula* from the Chandler Bridge Formation of South Carolina placed *M. loupianensis* and *M. pectinata* in synonymy, with the specific name *M. loupianensis* having priority. Adnet et al. (2012) performed a more extensive analysis of mobulids and concluded that *M. loupianensis* and *M. pectinata* represented separate species. They noted that differences were most obvious in female teeth; *M. loupianensis* female teeth were characterized by an indistinctly cuspletted transverse ridge, whereas those of *M. pectinata* had more conspicuous cusplets on the transverse ridge. *Mobula fragilis* teeth have a very different morphology and are not easily confused with those of *M. loupianensis* and *M. pectinata*.

Mobula teeth are very rarely collected from Calvert Cliffs, although Purdy et al. (2001) note that *Mobula* teeth were common throughout the Pungo River Formation. It is unclear if the comparative rarity of *Mobula* from Maryland is due to the somewhat cooler waters of this area or a collecting bias arising from the small size and irregular shape of these teeth. Despite the rarity of *Mobula* teeth from Calvert Cliffs, all three of Cappetta's species appear to be present.

Mobula loupianensis **Cappetta, 1970**

FIGURE 2.27F,G

1970 *Mobula loupianensis* Cappetta – Cappetta, pp. 108–110, fig. 20, pl. 26, figs. 1–6.
1976 *Mobula loupianensis* Cappetta – Jonet, pp. 54–56, figs. 1–13.
2001 *Mobula* sp. – Purdy et al., pp. 96, fig. 15a–i,m–o.

DESCRIPTION. These rare teeth are small and delicate, with two distinctive morphologies. Female teeth (Figure 2.27F) have relatively broad, ovoid to rectilinear, lingually inclined crowns that have indistinctly cuspidate transverse ridges. The labial and lingual faces of the crown have undulating surfaces of low, vertical folds that end apically in low, inconspicuous cusplets. The roots are low and in width are equal to or slightly narrower than the crown. The basal surface of the root is divided by one or more shallow grooves, forming two or more lobes. In profile, the root is lingually displaced.

Unicuspidate male teeth (Figure 2.27G) have a prominent central cusp typically flanked by multiple small, but distinct, lateral cusplets on each shoulder. The labial surface of the crown has a broad medial concavity that is most pronounced basally and fades apically. The root is similar to that of female teeth but is noticeably narrower than the crown.

DISCUSSION. The tooth morphology of *M. loupianensis* superficially resembles that of the extant *M. hypostoma*, although *M. loupianensis* teeth consistently have smoother crowns than the sculptured occlusal surfaces of the extant species (Adnet et al., 2012).

The male tooth shown here is tentatively allied with *M. loupianensis* as this is the only *Mobula* species currently known from the horizon where this tooth was collected.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Mobula loupianensis* teeth are rarely collected in this area, having been reported only from four beach specimens from the extreme northern ends of Calvert Cliffs and in situ from bed 3 of the Calvert Formation in Virginia.

Mobula loupianensis has previously been reported from the middle Miocene (Langhian–Serravallian) of France (Cappetta, 1970), Portugal (Jonet, 1976), and North Carolina (Purdy et al. (2001).

Mobula pectinata **Cappetta, 1970**

FIGURE 2.27H,I

1970 *Mobula pectinata* Cappetta – Cappetta, pp. 111–112, fig. 21, pl. 26, figs. 7–9.
1976 *Mobula pectinata* Cappetta – Jonet, pp. 57–58, figs. 14–16.
2001 Mobula sp. – Purdy et al., pp. 96–97, fig. 14a–p.

DESCRIPTION. This rare species is known from a single, well-preserved female tooth. This tooth is small and delicate. The crown is relatively broad, rectilinear, and lingually inclined, with two distinct cusps of different sizes and a smaller, low cusp on the transverse ridge. The labial face of the crown has numerous irregular wrinkles that extend out onto the cusps. The roots are low and slightly narrower than the crown. The basal surface of the root is divided by a single shallow nutrient groove, forming two lobes of unequal sizes.

DISCUSSION. The tooth morphology of *M. pectinata* is similar to that of the extant species *M. thurstoni*. Despite these similarities to the extant form, both Cicimurri and Knight (2009b) and Adnet et al. (2012) found that *M. pectinata* teeth have smoother crowns than the heavily wrinkled occlusal surfaces of *M. thurstoni*.

STRATIGRAPHIC AND GEOGRAPHIC RANGES. *Mobula pectinata* is exceptionally rare and is presently known on the basis of only a single beach specimen from Bayfront Park, Maryland.

Mobula pectinata has previously been reported from the middle Miocene (Langhian) of France (Cappetta, 1970) and Serravallian of Portugal (Jonet, 1976).

Mobula fragilis **(Cappetta, 1970)**

FIGURE 2.27J,K

1970 *Manta fragilis* Cappetta – Cappetta, p. 112, pl. 26, figs. 10, 11.
1976 *Mobula fragilis* Cappetta – Jonet, pp. 57–58, figs. 14–16.
1976 *Mobula cappettai* Jonet – Jonet, pp. 57–58, figs. 14–16.
1981 *Paramobula fragilis* (Cappetta) – Pfeil, p. 366.
2001 *Mobula* sp. – Purdy et al., p. 96, fig. 14j–l.
2102 *Mobula fragilis* (Cappetta) – Bor et al., pp. 84–85, pl. 52, figs. 5–8.

Description. These teeth are very rare and at present are known only from fragments. The teeth are compressed and mesiodistally broader than those of either *M. loupianensis* or *M. pectinata*. The crown is tall, very broad, and lingually inclined. The labial face is concave and thrown into large, vertical ridges and grooves that end as an undulating transverse crest. The roots are low and narrower than the crown. The basal surface of the root is divided by numerous shallow labiolingual grooves, dividing the root into parallel lamellae.

Discussion. The teeth of *M. fragilis* are noticeably larger and of a different morphology than those of *M. loupianensis* and *M. pectinata*. On the basis of this distinctive morphology, Pfeil (1981) erected the genus *Paramobula* for these teeth. But these teeth are within the rather wide range of variation known for extant *Mobula*, and they should be assigned to this genus (Adnet et al., 2012; Cappetta, 2012).

Stratigraphic and Geographic Ranges. *Mobula fragilis* teeth are rarely collected in this area, having been reported only as five beach specimens from the extreme northern end of Calvert Cliffs. *Mobula fragilis* has previously been reported from the late Oligocene of South Carolina (Cicimurri and Knight, 2009b), the middle Miocene (Langhian–Serravallian) of France (Cappetta, 1970), the Netherlands (Bor et al., 2012), Portugal (Jonet, 1976), and the eastern United States (Müller, 1999; Purdy et al., 2001).

Other Elasmobranch Fossils

A number of elasmobranch fossils from Calvert Cliffs cannot be attributed to a specific genus or, in many cases, family. There are also a number of intrusive elasmobranch fossils that have been reworked from underlying Paleogene beds that can be encountered while collecting along the cliffs but do not represent species resident during the Miocene.

Skeletal Fragments

FIGURE 2.28A,B

Elasmobranch skeletal fragments other than vertebral centra are rarely collected from Calvert Cliffs. Elasmobranchs are characterized by the presence of tesserate mineralization of the cartilaginous endoskeleton (Grogan and Lund, 2004; Maisey, 2012). Individual tesserae are prisms of hydroxyapatite-mineralized cartilage and are visible on the surface of skeletal elements as tightly packed, roughly hexagonal plates (Kemp and Westrin, 1979).

Description. Well-preserved skeletal fragments are easily recognized by the presence of a uniformly pebbled surface composed of closely spaced tesserae (Figure 2.28A). Individual tesserae are typically less than 2 mm across and hexagonal in end view. When intact, tesserae have a low, weakly domed outer cap, collectively producing the characteristically textured surface of elasmobranch cartilage. The outer caps of tesserae are frequently lost, exposing the narrow walls and homogeneous interior of the prisms and giving the cartilage a distinctive alveolation, or honeycombed, appearance (Figure 2.28B).

Discussion. The outer tesserate layer of elasmobranch cartilage is frequently badly degraded on beach specimens, revealing the inner core of hyaline cartilage. Such specimens are difficult to distinguish from worn fragments of teleost skeletal elements because the few remaining tesserae can be easily overlooked.

Coprolites

FIGURE 2.28C–E

Coprolites represent permineralized fecal masses of animals. In many cases, coprolites from marine habitats have a whorled or coiled appearance, and they have frequently been attributed to sharks (e.g., Milàn, 2010). But such identifications, particularly in older Paleozoic and Mesozoic sediments, are conjectural as such fecal morphologies are known from other groups (Northwood, 2005; Hunt et al., 2007; Dentzien-Dias et al., 2012). By the Cenozoic, most of the other groups producing such coprolites were extinct or exceptionally rare, so attribution to elasmobranchs is more plausible.

Description. The best-preserved specimens have a cylindrical to ellipsoidal, heteropolar morphology with overlapping whorls restricted to one end. The outer surface is smooth, pitted (Figure 2.28C) or weakly pebbled (Figure 2.28D). The material is generally uniform in composition and in cross section consists of a layer several millimeters thick wrapped over earlier whorls. In many specimens, the ends are damaged or eroded and can be recognized as a coprolite by the outer layer broadly overlapping the core (Figure 2.28E). In other specimens, the coprolite has been fractured, revealing the internal whorls (Figure 2.28D).

Discussion. Spirally coiled coprolites occur in two broad morphologies; amphipolar coprolites have external coiling visible as a spiral groove extending evenly over the entire surface, and heteropolar coprolites have external coiling restricted to a portion of the surface. Amphipolar coprolites are attributed to primitive fishes with simple intestinal valve morphologies, whereas heteropolar coprolites are believed to have been produced by the more complex intestinal valves of elasmobranchs (Northwood, 2005; Hunt et al., 2007; Dentzien-Dias et al., 2012). Elasmobranch heteropolar coprolites can be classified on the basis of the distribution of the external spiral groove on the surface; macrospiral coprolites (=spiral coprolites of Kent, 1994) have a groove over a substantial portion of the surface, whereas microspiral coprolites (=scroll coprolites of Kent, 1994) have the groove restricted to a small area at one end (Hunt et al., 2007). In older Cenozoic sediments, both morphologies are commonly present (Kent, 1999a, pers. obs.; King, 2011), but in Calvert Cliffs the majority are of the microspiral scroll morphology.

The classification of elasmobranch coprolites to more specific taxa (e.g., orders, families, or genera) is generally accepted as being impossible because of broad similarities between elasmobranch taxa and high variability within individual species (McAllister, 1985).

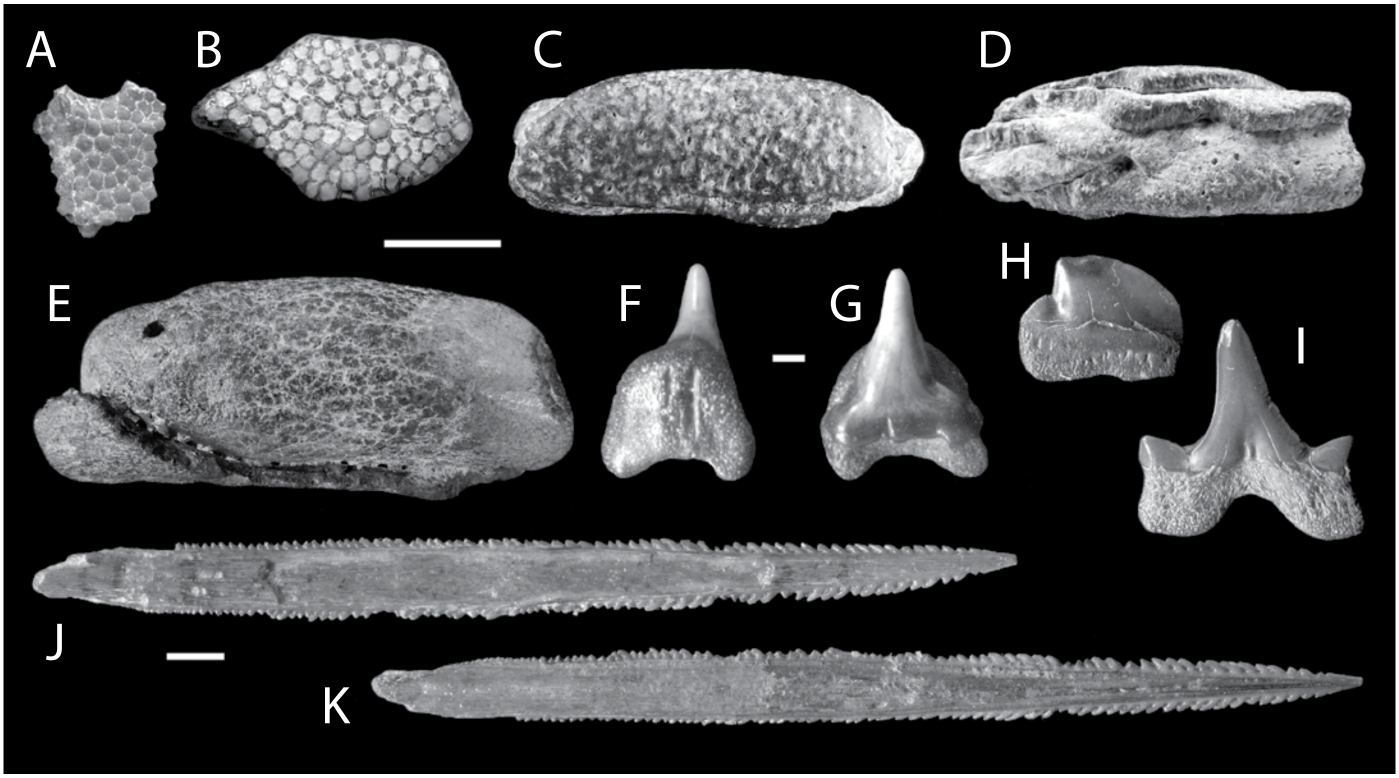


FIGURE 2.28. Other elasmobranch fossils (1 cm scale bar for A–E, H, I; 1 mm scale bar for F, G; 1 cm scale bar for J, K). (A) Elasmobranch tesserate cartilage (CMM-V-7722, Bayfront Park, Maryland). (B) Elasmobranch tesserate cartilage (CMM-V-7453, Scientists Cliffs, Md.). Photo by Stephen Godfrey. (C) Microspiral coprolite; pitted upper surface (UMCP 11475; Matoaka Cottages, Md.). (D) Microspiral coprolite; fractured lower surface revealing whorled interior (UMCP 11475; Matoaka Cottages, Md.). (E) Microspiral coprolite with overlapping outer whorl; lateral view (UMCP 11474; Matoaka Cottages, Md.). (F) Carcharhinid symphyseal tooth; lingual view (CMM-V-7720; Chesapeake Beach, Md.). (G) Carcharhinid symphyseal tooth; labial view (CMM-V-7720; Chesapeake Beach, Md.). (H) *Squalicorax kaupi* tooth; labial view (CMM-V-7738; Bayfront Park, Md.). (I) *Cretolamna appendiculata* tooth; labial view (CMM-V-7721; Bayfront Park, Md.). (J) Myliobatiform caudal spine; dorsal view (CMM-V-2326; Flag Ponds, Md.). (K) Myliobatiform caudal spine; ventral view (CMM-V-2326; Flag Ponds, Md.).

Carcharhinid Symphyseal Teeth

FIGURE 2.28F,G

Description. These teeth are small, with a crown that is very strongly inclined lingually. The cutting edges are smooth, unserrated to weakly serrate. A low, broad ridge may be present on each shoulder of the tooth. The root has short to moderately long lobes and a prominent lingual protuberance that together form a rectilinear or triangular base. A weak nutrient groove is present on the lingual protuberance of some teeth.

Discussion. These teeth are relatively common along the cliffs, although they are easily overlooked because of their small size (typically, <7 mm) and globular shape. There are three similar forms of teeth with this general morphology: (1) one like those in Figure 2.28F,G, with a short crown, very weak cutting edges, broad, rounded shoulders, and a weakly bilobed root with a flat lingual face, (2) similar teeth, but typically with weakly serrate cutting edges and a flat, rectilinear lingual root face, and (3) teeth with slightly taller, weakly distally inclined crowns almost always with serrate edges and a weakly bilobed, less flattened root. The last form has a morphology that grades into that of symphyseal *P. contortus* teeth (Figure 2.21H). All three tooth morphologies could reasonably be interpreted as positional variants of carcharhinid symphyseal teeth, although they cannot be easily assigned to particular species or genera.

Reworked Paleogene Teeth

FIGURE 2.28H,I

At the extreme northern end of Calvert Cliffs the Calvert Formation unconformably overlies older Paleogene sediments (Shattuck, 1904). Although these older horizons are below beach level, teeth from these horizons can be reworked into the lower Calvert Formation. Two Paleogene species occasionally collected from the northern end of Calvert Cliffs are *Cretolamna appendiculata* (Figure 2.28i) and *Squalicorax kaupi* (Figure 2.28H). Identification of the former species is complicated by the description of a new lamniform species with large, cuspletted teeth from the early Miocene (*Megalolamna paradoxodon*; Shimada et al., 2016). Since *M. paradoxodon* has been reported from the Miocene of North Carolina, this species could be present in Calvert Cliffs as well. As noted above (see *Carcharodon*), *Palaeocarcharodon orientalis* may also be present as reworked specimens.

Reworked Paleogene *Carcharias* teeth are a more complex issue, as they can be difficult to definitively separate from those of Miocene species. The identification of *Carcharias* species is based largely on the size, shape, and number of cusplets and on the extent of the striations on the lingual face of the crown. Unfortunately, all of these characters are quickly degraded on beach-worn specimens, making them essentially unidentifiable to individual species. The large, durable teeth of Paleogene myliobatids and rhinopterids are almost certainly reworked as well, but as yet, none have been definitively identified from Calvert Cliffs.

Myliobatiform Caudal Spines

FIGURE 2.28J,K

Description. These spines are elongate and tapered and have a roughly ovoid cross section and coarsely serrated margins. The spine is composed primarily of dentine, although the dorsal surface and ventrolateral margins are covered with enameloid. The enameloid on the dorsal surface of the spine is covered with reticulated longitudinal ridges that are strongest basally and tend to become obsolete distally. The distal portion of the spine is typically more flattened than the base and has a broad, shallow longitudinal groove of variable length. The marginal enameloid serrations are numerous and triangular, with the apices directed basally. There is an elongate to globular base of variable size that anchors the spine in the soft tissues of the body, although it is missing in many specimens.

Discussion. The myliobatiforms are characterized by the presence of one or more caudal spines at the base of the tail. But despite being a distinctive synapomorphy of this order, morphological differences in caudal spines have been largely ignored until relatively recently.

Schwartz (2005, 2007, 2008a,b) documented morphological variation in extant species on the basis of spine length, the number and distribution of serrations, the relative size of the exposed portion of the spine, and the relative length of the dorsal groove. Individual extant species were generally discernible by suites of these characters, and spine morphology was correlated with habitat or lifestyle. Unfortunately, intraspecific variation was also exceptionally high, and there was broad morphological overlap between species, genera, and families in these characters (Schwartz, 2008a:48–49, tbl. 1; 2008b:29–33, tbl. 1). Further, correlations between spine morphology and habitat or lifestyle may not be as definitive as originally proposed (Cuny and Piyapong, 2007). Consequently, isolated spines and spine fragments of fossil myliobatiforms cannot be reliably assigned to specific ray taxa or ecomorphotypes (Marmi et al., 2010). The one apparent exception is the large, distinctive spine base in the mobulids (Figure 2.27L,M), which can be easily identified at least to family.

THE CALVERT CLIFFS CHONDRICHTHYAN FAUNA

Completeness of the Calvert Cliffs Fauna

Calvert Cliffs provides a unique window into the changes occurring in chondrichthyans during the early and middle stages of the Neogene. These changes were based on new groups that arose in the Paleocene or Eocene and then underwent extensive diversification during the late Oligocene and Miocene. Calvert Cliffs captures a detailed record of these changes for an approximately 10 MY interval from the late early Miocene (late Burdigalian) through the early late Miocene (early Tortonian). This fossil record of sharks and rays is extensive (Foote and Sepkoski, 1999; Cappetta, 2012; Maisey, 2012) but unfortunately biased. The primary problem is that the fossil record of these groups is represented almost entirely by teeth, which is not unexpected since teeth are the hardest and most durable tissues produced by cartilaginous fishes (Garrick, 1982). But the completeness of the skeleton has been shown to be correlated with estimates of diversity of fossil groups (Benton et al., 2013; Brocklehurst and Fröbisch, 2014), and the identification of sharks and rays based almost entirely on isolated teeth complicates any comparisons of shark and ray diversity for fossil and Holocene faunas. Additionally, a number of other factors can further confound estimates of fossil diversity and produce unexpected biases (Cooper et al., 2006; Benton et al., 2013; Brocklehurst and Fröbisch, 2014; Huang et al., 2015).

There have been relatively few studies that have examined diversity patterns in fossil elasmobranchs (Foote and Sepkoski, 1999; Kriwet and Benton, 2004; Underwood, 2006; Guinot et al., 2012; Sorenson et al., 2014). Although not all of these studies are directly related to diversity in the Neogene, they all provide an evolutionary context for the appearance of modern shark faunas. The earliest of these studies (Foote and Sepkoski, 1999) found that 95% of extant elasmobranch genera were represented in the fossil record. Further, it found that the probability of an elasmobranch genus being detected within a 5 MY time interval was 10%–15% for Paleozoic genera and 25%–40% for Mesozoic genera. The authors attribute the difference between the Paleozoic and Mesozoic to differences in the available fossil material; Paleozoic forms are known mainly from whole-body fossils, whereas Mesozoic forms are identified primarily from isolated teeth from unconsolidated sediments (see also Cappetta, 2012:30–31; Maisey, 2012). They provide no data for Cenozoic forms but argue that it should be comparable to those from the Mesozoic since both are based on teeth. This supposition is plausible and is consistent with other data on the relative completeness of the fossil record in the Mesozoic and Cenozoic (Benton et al., 2000).

More recently, Guinot et al. (2012) provided a rigorous reevaluation of elasmobranch diversity over the past 300 MY. They found that elasmobranch diversity was essentially constant for orders, families, and genera during the late Cenozoic and that virtually all Holocene elasmobranch taxa above the species level are represented as fossils during the Neogene (Guinot et al., 2012: fig. 3A). These estimates are roughly comparable to those of Foote and Sepkoski (1999) indicating that 95% of extant chondrichthyan genera were represented in the fossil record. But the estimates from both of these studies are global and are not directly applicable to a temporally and regionally restricted locality, such as Calvert Cliffs. Further, these studies do not address the problem of species-level diversity within elasmobranchs.

In overall diversity, the Calvert Cliffs elasmobranch fauna, with 51 species in 32 genera, is roughly comparable to the Holocene fauna from the Mid-Atlantic region of the eastern United States (the Chesapeake Bay and the continental shelves of Delaware, Maryland, and Virginia), with 46 species in 29 genera (Tables 2.1, 2.2). Not included in these tables are the three chimaera species in three separate genera, which raises the totals for the Calvert Cliffs chondrichthyan faunas to 54 species in 35 genera. Of the 29 Holocene genera along the Mid-Atlantic coast, 19 (66%) are present in Calvert Cliffs. Eight additional genera found in Calvert Cliffs (i.e., *Chimaera*, *Hexanchus*, *Notorynchus*, *Hemipristis*, *Negaprion*, *Rhynchobatus*, *Aetobatus*, and *Pteromylaeus*) are extant but not currently resident in Mid-Atlantic waters. Taken as a whole, this number suggests that the Calvert Cliffs fossil beds contain a relatively complete assemblage of chondrichthyans, although studies on other groups (Cooper et al., 2006; Benton et al., 2013; Brocklehurst and Fröbisch, 2014; Huang et al., 2015) have suggested additional, as yet undetected, taxa were very likely present.

Although direct comparisons between the Calvert Cliffs and Holocene faunas are easily interpreted, their validity is difficult to assess. The Calvert Cliffs data are time averaged and represent a range of habitats over a span of approximately 10 MY. Conversely, the Holocene data are cross sectional and represent a geologically brief snapshot in time. Further, taxa missing from the described Calvert Cliffs fauna of fossil cartilaginous fishes will not be randomly distributed among the taxa originally present. The missing taxa will be dominated by forms that are small and rare and have poorly mineralized hard parts. This bias will be exacerbated by collecting techniques typically used along the cliffs that favor larger, more conspicuous teeth over smaller specimens (Raup, 1977; Smith, 1994:108–117; Cooper et al., 2006; Benton et al., 2013; Brocklehurst and Fröbisch, 2014; Huang et al., 2015).

Unfortunately, more precise estimates of the number of species of chondrichthyans in Calvert Cliffs are more difficult to obtain. Extant species of chondrichthyans are described using whole-body morphology and would seem to be well-documented for most groups. But as conservation researchers on extant elasmobranchs have discovered, molecular techniques used to identify body parts have produced ample evidence for cryptic species that were difficult, or even impossible, to separate solely on the basis of morphological criteria. A broad range of chondrichthyans, including cow sharks (*Hexanchus*; Daly-Engel et al., 2018), angel sharks (*Squatina*; Sole-Cava and Levy, 1987), thresher sharks (*Alopias*; Eitner, 1995; see Trejo, 2004, for an opposing view), hound sharks (*Mustelus*; Heemstra, 1997; Gardner and Ward, 2002), guitarfishes (*Rhinobatos*; Sandoval-Castillo et al., 2004), requiem sharks (*Carcharhinus*; Barnstetter, 1982; Pank et al., 2001; Keeney and Heist, 2006; Boomer et al., 2010), hammerhead sharks (*Sphyrna*; Quattro et al., 2006), cat sharks (*Galeus*; Castilho et al., 2007), and wobbegong sharks (*Orectolobus*; Corrigan et al., 2008), all have cryptic sibling species. There is every reason to believe that extinct species based only on tooth morphology would be even more likely to underestimate the number of species present within a genus. This issue is already a concern for some genera (e.g., *Squatina*, Ward and Bonavia, 2001; *Rhizoprionodon*, Garry, 2003, 2004; *Carcharhinus*, Sarao, 2005) in which species cannot be reliably separated by dental characters alone. The validity of these concerns is unclear and remains to be resolved with more detailed morphometric analyses.

Disparity of Calvert Cliffs Chondrichthyans

Although the total number of species and genera is similar between Calvert Cliffs and Holocene elasmobranch faunas, the prevalence of different higher taxa can vary widely (Table 2.1). The Calvert Cliffs selachian fauna of 39 species is dominated by two orders, the lamniforms (16 species) and the carcharhiniforms (16 species), which collectively account for 82% of the shark species (Table 2.1). The Holocene fauna retains a broad range of carcharhiniforms (16 species) but has a dramatically reduced number of lamniforms (7 species), or a total of 82% of selachians.

What is particularly striking in the selachian fauna is the incidence of gigantism (i.e., largest species in a genus); 10 such

TABLE 2.1. Number of species per genus of sharks in Calvert Cliffs and the Holocene epoch of the Mid-Atlantic states of Delaware, Maryland, and Virginia. The number of giant shark species with teeth greater than 3 cm in maximum height or width are shown in parentheses; a dash (–) indicates none are present. Extinct genera are indicated with a dagger (†). Four additional extant species (*Echinorhinus brucus*, *Ginglymostoma cirratum*, *Lamna nasus*, and *Negaprion brevirostris*) may rarely occur as stray individuals. Holocene distributions are based on Bigelow and Schroeder (1948), Compagno (1984, 2002), Whitehead et al. (1984), Smith and Heemstra (1986), Lythgoe and Lythgoe (1992), Michael (1993), Schwartz (2003), Compagno et al. (2005), and Murdy et al. (2013).

Sharks	Calvert Cliffs	Holocene Mid-Atlantic
Order Hexanchiformes		
Notorynchus	1 (1)	–
Hexanchus	1 (1)	–
Order Echinorhiniformes		
Echinorhinus	1 (–)	–
Order Squaliformes		
Centroscyllium	–	1 (–)
Etmopterus	–	1 (–)
Squalus	2 (–)	1 (–)
Order Squatiniformes		
Squatina	1 (–)	1 (–)
Order Orectolobiformes		
Rhincodon	1 (–)	1 (–)
Order Lamniformes		
Carcharias	3 (1)	1 (1)
Carcharoides†	1 (–)	–
Isurus	2 (2)	2 (2)
Carcharodon	2 (2)	1 (1)
Carcharocles†	2 (2)	–
Parotodus†	1 (1)	–
Alopias	4 (2)	2 (–)
Cetorhinus	1 (–)	1 (–)
Order Carcharhiniformes		
Scyliorhinid sp.	1 (–)	1 (–)
Mustelus	1 (–)	1 (–)
Hemipristis	1 (1)	–
Galeocerdo	1 (–)	1 (1)
Physogaleus†	2 (–)	–
Carcharhinus	7 (–)	8 (–)
Prionace	–	1 (–)
Negaprion	1 (–)	–
Rhizoprionodon	1 (–)	1 (–)
Sphyrna	1 (–)	3 (–)
Total	39 (13)	28 (5)

TABLE 2.2. Number of species per genus of batoids in Calvert Cliffs and the Holocene epoch of the Mid-Atlantic states of Delaware, Maryland, and Virginia. Extinct genera are indicated with a dagger (†); a dash (–) indicates none are present. Three additional species (*Aetobatus narinari*, *Manta birostris*, and *Rhinobatos lentiginosus*) may rarely occur as stray individuals. Holocene distributions are based on Bigelow and Schroeder (1953), Whitehead et al. (1984), Smith and Heemstra (1986), Lythgoe and Lythgoe (1992), Michael (1993), Schwartz (2003), and Murdy et al. (2013).

Sharks	Calvert Cliffs	Holocene Mid-Atlantic
Order Pristiformes		
Pristis	1	1
Order Rajiformes		
Amblyraja	–	1
Breviraja	–	1
Dipturus	–	1
Leucoraja	–	3
Raja	1	1
Rhynchobatus	1	–
Order Torpediniformes		
Torpedo	–	1
Order Myliobatiformes		
Dasyatis	2	4
Gymnura	–	2
Aetobatus	1	–
Myliobatis	–	1
Pteromylaeus	1	–
Rhinoptera	1	1
Mobula	3	1
Plinthicus†	1	–
Total	**12**	**18**

species are present in Calvert Cliffs in the genera *Notorynchus*, *Hexanchus*, *Carcharias*, *Isurus*, *Carcharodon*, *Carcharocles*, *Parotodus*, *Alopias*, *Hemipristis*, and *Physogaleus*, but only 6 occur in the Holocene fauna of the Middle Atlantic states (*Carcharias*, *Isurus*, *Carcharodon*, *Galeocerdo*, *Carcharhinus*, and *Sphyrna*). This discrepancy in the number of giant species is even more pronounced because of the puzzling co-occurrence of pairs of species of very similar size within a genus. A reexamination of the Calvert Cliffs shark fauna revealed indications that this pairing is particularly true for larger macrophagous species with teeth of at least 3 cm in maximum dimension (Table 2.1). Two such genera (*Isurus* and *Alopias*) have a pair of species of essentially identical size, making it impossible to determine whether one species is actually larger than its congener (e.g., Figure 2.3A). Two other genera (*Carcharodon* and *Carcharocles*) each have two giant species with the second-largest species only slightly smaller than the largest species. Finally, the genus *Carcharias* is represented by only a single giant species (*C. cuspidatus*) in Calvert Cliffs, although a second giant species is a possibility. *Carcharias taurus* is known to have teeth comparable in size to *C. cuspidatus* (Purdy et al., 2001) but is known from only nine teeth in Calvert Cliffs. Whether larger Calvert Cliffs *C. taurus* teeth are present, making it yet another giant species, will require additional research. In contrast, reevaluating the Holocene fauna for species with teeth more than 3 cm in any dimension adds only a single giant species, a second species in *Isurus*. Taking into account all large macrophagous sharks, there are 13, or possibly 14, species in Calvert Cliffs compared to 5 in the Holocene fauna (Table 2.1).

The Calvert Cliffs batoid fauna (Table 2.2) has a very different diversity pattern from that of the selachians, with two-thirds the number of species (12) of the Holocene fauna (18).

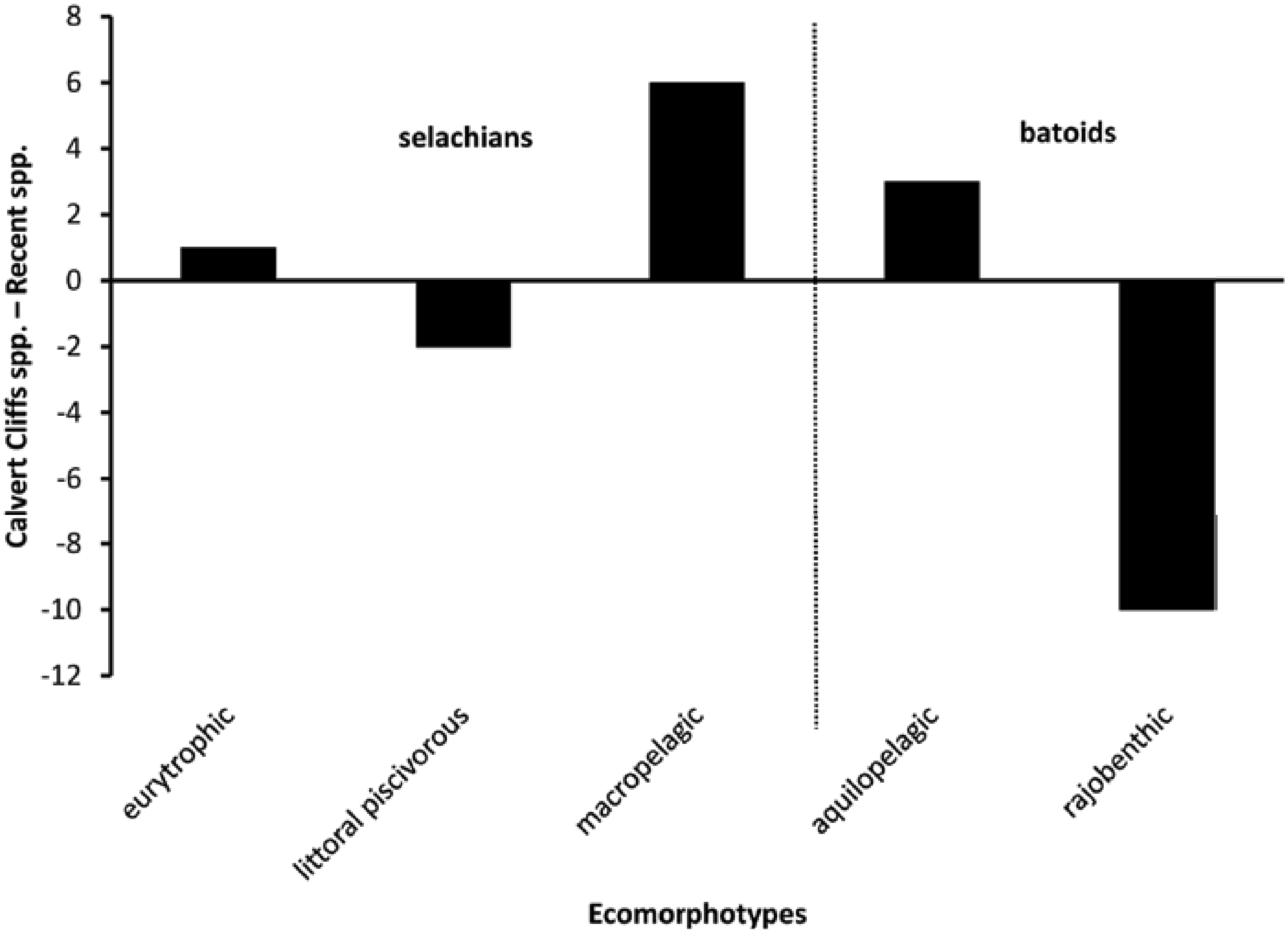


FIGURE 2.29. Comparison of common ecomorphotypes in Calvert Cliffs and the Holocene fauna of the Mid-Atlantic states of the eastern United States. See text for descriptions of ecomorphotypes.

The discrepancy is greatest for three families, the Rajidae (1 Calvert Cliffs species versus 6 Holocene species), the Gymnuridae (0 versus 2 species), and the Dasyatidae (2 versus 5 species). These three families account for 72% of Holocene batoids but only 25% of those from Calvert Cliffs.

Differences in Calvert Cliffs and Holocene faunas are even more striking when species are sorted by their ecological roles within the elasmobranch community. Figure 2.29 depicts the frequency of the five most common elasmobranch ecomorphotypes for Calvert Cliffs compared with the Holocene Mid-Atlantic shark fauna (Compagno, 1990b, with some modifications). Three selachian ecomorphotypes are listed. Eurytrophic sharks are large, active sharks capable of feeding on a broad range of large prey. The littoral piscivorous ecomorphotype is a generalized group of sharks that feed primarily on a variety of fishes. It includes Compagno's littoral and sphyrnid ecomorphotypes but excludes sharks with more specialized diets of the teuthitrophic (=squid-feeding) and cancritrophic (crustacean-feeding) ecomorphotypes. Three of Compagno's ecomorphotypes, archipelagic, macroceanic, and tachypelagic, are difficult to unambiguously distinguish in fossil sharks on the basis of teeth and are combined in Figure 2.29 as a composite macropelagic ecomorphotype. The macropelagic sharks are strongly overrepresented in Calvert Cliffs, almost entirely because of the presence of the giant sharks (e.g., *Carcharodon*, *Carcharocles*, *Parotodus*, and *Alopias*). So the loss of the giant sharks was not simply a loss of lamniforms but more broadly the decimation of sharks with a specific lifestyle.

Two batoid ecomorphotypes are listed in Figure 2.29. Aquilopelagic batoids are large myliobatiform rays adapted for underwater flight using large, triangular pectoral fins. This ecomorphotype is moderately overrepresented in Calvert Cliffs because of the presence of four mobulids (one *Plinthicus* and three *Mobula* species), along with two myliobatids (*Pteromylaeus* and *Aetobatus*) not present in Holocene faunas of the Middle Atlantic region. The rajobenthic ecomorphotype (i.e., rajids, gymnurids, and dasyatids; Compagno, 1990b) is the most diverse group of living batoids but is seriously underrepresented in the Calvert Cliffs fauna. Three factors could plausibly contribute to the paucity of Calvert Cliffs rajobenthic species. First, rajobenthic batoids generally have very small teeth sizes of 3 mm or less. In addition, the teeth have a nondescript, generally globular shape and, taking into account their small size, are easily overlooked during collecting. Second, these batoids use their teeth to crush benthic prey. Such feeding quickly abrades the occlusal surface of the crown, obliterating many of the diagnostic characters used for identifying individual species. Finally, these groups may have been undergoing evolutionary diversification during the Neogene and were not as diverse in the middle Miocene as in Holocene faunas. Good molecular data indicate that this was occurring in the rajids, which had rapid speciation from the late Miocene to Pleistocene (Valsecchi et al., 2005; Pasolini et al., 2011). What is unclear is whether this speciation dramatically increased rajid diversity or reflected species turnover while maintaining relatively constant species richness. In the former, few species of rajids would be present in the middle Miocene, whereas if the latter condition occurred, a number of rajid species are yet to be identified from Calvert Cliffs. Comparable molecular data are not available for gymnurids or dasyatids, so the impact of comparatively recent speciation events is unknown.

Future Research on Calvert Cliffs Chondrichthyans

Despite the extensive history of research on the chondrichthyans of Calvert Cliffs, a number of questions are currently unresolved. The most basic concerns the total number of species actually present along the cliffs. The diversity of the Calvert Cliffs chondrichthyan fauna is certainly comparable to two other well-studied and roughly contemporaneous faunas from the North Atlantic; the Pungo River Formation of Lee Creek Mine, North Carolina (Purdy et al., 2001: tbl. 1), has 46 species in 33 genera, and the Lower Mica Fine Sand Formation in Werder-Uesen, Lower Saxony, Germany (Reinecke et al., 2011), contains 49 species in 38 genera. But these comparisons also suggest that although the known Calvert Cliffs fauna is extensive, it is almost certainly incomplete. Several genera (e.g., *Ginglymostoma, Isistius, Megachasma, Megalolamna, Paragaleus, Pseudocarcharias, Gymnura*) are not presently reported from Calvert Cliffs, although their presence would not be unexpected. The diversity of a number of other genera, such as the rajobenthic *Raja* and *Dasyatis*, are probably underestimated. Neogene representatives of all of these genera have been relatively extensively studied, and new additions to the Calvert Cliffs fauna will probably represent range extensions of known species, rather than new, unnamed species.

At finer levels of resolution, the distribution of species among different horizons is known only at the most basic level, that of presence-absence data. Each horizon represents a specific environment, and along Calvert Cliffs these environments range from open ocean to marginal marine habitats (Visaggi and Godfrey, 2010). Understanding the organization of elasmobranch communities in different habitats requires not only a list of the species present but also the relative abundance of different species and ecomorphotypes.

There is accumulating evidence that tooth morphology in many lineages arises by phyletic evolution. Although this may not reflect the actual evolutionary mechanism producing individual species, documenting stratum-specific changes in morphology will facilitate our understanding of how tooth morphology within a lineage changes over time. For example, *Carcharhinus priscus* has cutting edges with variable morphology (Reinecke et al., 2011). Late Oligocene (Chattian) specimens have cutting edges that can be weakly crenulate to finely serrate. *Carcharhinus priscus* occurs along the length of Calvert Cliffs, and although the teeth are commonly finely serrate, on many specimens the serrations become obsolete apically. What is less clear is whether there are any stratigraphic trends in the condition of the serrations or if they are simply characteristic of a variable morphospecies. Resolving these issues will require both the use of increasingly sophisticated research technologies to provide new types of information and increased participation by the public in the research process.

Since the last major reviews of Calvert Cliffs chondrichthyans (Kent, 1994; Müller, 1999), research on fossil sharks, rays, and chimeras has relied increasingly on statistical methodologies for quantifying and evaluating teeth (Naylor and Marcus, 1994; Adnet, 2006; Chandler et al., 2006; Nyberg et al., 2006; Shin, 2010; Whitenack and Gottfried, 2010). These techniques can provide rigorous assessments of morphology but rely on large samples of carefully collected, well-documented teeth to be of value. For common species, obtaining adequate sample sizes is not particularly difficult, but with species that either are rare or preserve poorly, it requires far more effort. Fortunately, research on fossil chondrichthyans has long benefitted from the active participation by the public. Many individuals are amateur or recreational collectors, although some are so knowledgeable that they are more appropriately considered avocational or independent paleontologists (Cozart, 1997). The importance of all of these individuals cannot be overestimated; numerous individuals routinely make their private collections available for study, and this generosity is reflecteded by the high proportion of museum specimens that were obtained from nonprofessionals.

As already discussed, the only ecomorphological group seriously underrepresented in the Calvert Cliffs beds is the rajobenthic ecomorphotype (Figure 2.29). Further complicating the detection and identification of batoids in these three families is that they all have similar tooth morphologies, with most of the diagnostic characters being the occlusal surface of the crown.

Unfortunately, rajobenthic batoids use their teeth to crush benthic invertebrates, effectively obliterating the diagnostic characters before the teeth are shed and replaced. Even in large samples of these teeth, most cannot be reliably identified to species, and many cannot be identified to genus. This sampling deficiency is currently being addressed with a very large scale citizen science project in cooperation with the Paleo Quest, in which high school students sort screened sediment samples and extract microteeth for more detailed analysis by the Fossil Shark Research Group at the University of Maryland, College Park. The project has the capacity to process large volumes of screened material in order to find and identify overlooked species of batoids and selachians. Preliminary results from this synergistic relationship include evidence for additional scyliorhinid, hemigaleid, and rajid species, as well as the first ginglymostomatid and parascylliid species from Calvert Formation sediments. As yet, none of these species have been fully documented and are the subject of ongoing research.

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ADDENDUM: A NEW SPECIES OF GIANT THRESHER SHARK (FAMILY ALOPIIDAE) WITH SERRATED TEETH

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The Neogene has a remarkably complex array of large macrophagous sharks (BWK, this chapter) that is well represented along the eastern United States. Despite extensive research on fossil elasmobranchs in this area, one species of large thresher shark (family Alopiidae) with distinctively serrated teeth has not been previously named.

Systematic Paleontology

Subclass Elasmobranchii Bonaparte, 1838

Superorder Selachimorpha Nelson, 1984

Order Lamniformes Berg, 1958

Family Alopiidae Bonaparte, 1838

Genus *Alopias* Rafinesque, 1810

Alopias palatasi, new species

FIGURE 2.A1

Holotype. An anterior tooth at the Calvert Marine Museum (CMM-V-385).

Type Locality. Parkers Creek, Maryland.

Horizon. Calvert Formation (bed 12).

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Paratypes. Calvert Marine Museum: CMM-V-3876 (beach-collected tooth, Flag Ponds, Maryland), CMM-V-3981 (beach-collected tooth, Parkers Creek, Maryland), CMM-V-4242 (beach-collected tooth, Calvert County, Maryland), and CMM-V-5823 (river-collected tooth, south end of Buck Island, Calibogue Sound downstream of the mouth of the May River, South Carolina). U.S. National Museum of Natural History: USNM 411148 (bed 12, Calvert Formation, Parkers Creek, Maryland) and USNM 639783 (beach-collected tooth, Parkers Creek, Maryland).

Additional Material. Kent's reference collection, University of Maryland, College Park: UMCP 12147 (beach-collected tooth, Chesapeake Beach, Maryland), UMCP 12155 (river-collected tooth, Morgan River, South Carolina), UMCP 12158 (river-collected tooth, Westmoreland/Stratford Hall, Virginia), and UMCP 12166 (beach-collected tooth, northern Calvert Cliffs, Maryland). Mike Elwood collection: two teeth (bed 12, Calvert Formation, north of Scientists Cliffs, Maryland). Harriet Ertman collection: one river-collected tooth (Stratford Hall, Virginia). Walt Johns collection: one beach-collected tooth (Governor Run, Maryland), one beach-collected tooth (Plum Point, Maryland), and three beach-collected teeth (one whole tooth and two tooth fragments; Stratford Hall, Virginia). Jason Osborne collection: scuba-collected tooth (Newport News unit, Calvert Formation, New Kent County, Virginia).

Etymology. Named for Mark Palatas, who provided one of the original specimens (CMM-V-5823; Figure 2.A1G,H) for study.

Diagnosis. The holotype (CMM-V-385; Figure 2.A1A,B) is an upper anterior (A3?) tooth. The crown is broad and compressed, with cutting edges that are coarsely serrated. The serrations are irregular in size on the basal portions of the crown, becoming somewhat finer and more regular apically. The mesial cutting edge is convex, whereas the distal edge is markedly concave. The lingual coronal face is relatively flat, whereas the labial face is weakly convex. The root is compressed with substantially shortened and relatively deep root lobes that do not extend beyond the lateral shoulders of the crown. The basal root margin is strongly arched.

Anterior teeth closer to the jaw symphysis (Figure 2.A1C,D) are less strongly arched distally than the holotype and have somewhat broader crowns. The root lobes on these teeth may extend slightly beyond the lateral margins of the crown.

Upper lateral teeth (Figure 2.A1E,F) are more triangular, with the height and width being nearly identical. The mesial cutting edge is less convex than in anterior teeth and may become weakly sigmoidal in some specimens. The distal edge is only weakly concave. The root is compressed, with a broadly arched to slightly obtuse basal margin. The root is typically slightly broader than the base of the crown.

Lower lateral teeth (Figure 2.A1G,H) have crowns weakly inclined distally and a strongly arched basal root margin. The root is slightly thicker than in upper lateral teeth, although this character is somewhat variable.

Lateral teeth located nearer the commissure have crowns that become lower and more distally arched. In some cases the coronal apex is positioned distal to the distal margin of the root. The distal cutting edge becomes progressively more strongly concave, and the basal root margin becomes more weakly arched.

Remarks. *Alopias palatasi* resembles the more widely known *A. grandis* but has coarsely serrated cutting edges. These serrations are substantially larger and more distinctive than those of the weakly crenulated specimens of *A. grandis* (Kent, this chapter). The teeth of *A. palatasi* can also be quite large, with the largest specimens more than 40 mm in height (P. Picard, Germany, personal communication, 2015).

The teeth of *A. grandis* and *A. palatasi* are similar in a number of respects, including large teeth with tall, broad, compressed crowns and shortened root lobes. In addition to coarsely serrate cutting edges *A. palatasi* also differs from the unserrated species in having more extensive monognathic heterodonty; the broadly triangular lateral teeth of *A. palatasi* are only occasionally present in *A. grandis*.

A number of embayments occur along the Neogene paleocoastline of the eastern United States (Ward and Powars, 2004: fig. 1), and teeth of *A. palatasi* have been found in three of these, the Salisbury Embayment (Maryland and Virginia), the Albemarle Embayment (North Carolina), and the Charleston Embayment (South Carolina). From north to south localities where *A. palatasi* teeth have been found include the following.

Maryland. The distribution of *A. palatasi* along Calvert Cliffs is restricted to the northern portion of the cliffs (Flag Ponds to Chesapeake Beach), a region of the cliffs associated with the Calvert and Choptank Formations (Ward and Andrews, 2008: fig. 5; Visaggi and Godfrey, 2010: fig. 3). The Calvert Formation within this region of the cliffs includes a small exposure of the Fairhaven Member (bed 3B, middle Burdigalian) and a much more extensive exposure of the Plum Point Member (beds 4–16A, late Burdigalian to late Langhian). The entire sequence of Choptank Formation sediments (beds 17–20, Serravallian) is present in this region.

Virginia. *Alopias palatasi* teeth have been found as beach specimens along the Potomac River at Wakefield, Horseshoe Cliffs, Stratford Cliffs, and Nomini Cliffs. The stratigraphy along this portion of the Potomac River is moderately complex (Ward and Andrews, 2008: fig. 7); the principal horizons in these localities are extensive exposures of the Calvert Formation (Plum Point Member, beds 14, 15; late Langhian) and the Eastover Formation (Claremont Manor Member [late Tortonian] and Cobham Bay Member [Messinian]). Between the Calvert and Eastover sediments are smaller, more variable exposures of the Choptank Formation (Boston Cliffs Member, bed 19; middle Serravallian) and the St. Marys Formation (late Serravallian). The St. Marys sediments have been reliably assigned to a specific horizon (Ward and Andrews, 2008:49, fig. 7); possible assignments include the Little Cove Point Member (beds 21–23, Tortonian) and the Windmill Point Member (bed 24). The cliffs in this area are capped with a layer of sediments questionably assigned to

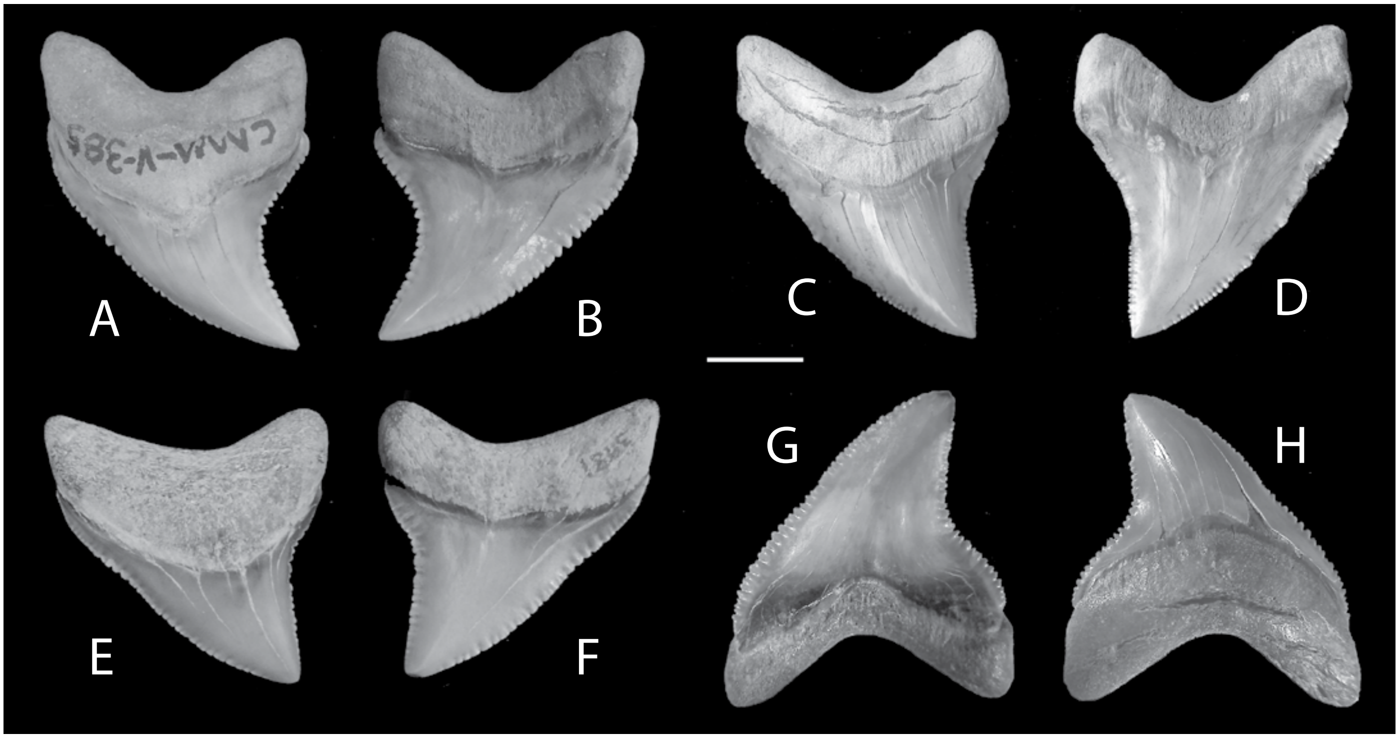

FIGURE 2.A1. *Alopias palatasi* (new species) teeth. Scale bar = 1 cm. (A) Right upper anterior tooth (holotype; CMM-V-385; lingual view). (B) Right upper anterior tooth (holotype; CMM-V-385; labial view). (C) Right upper anterior tooth (CMM-V-7735; lingual view). (D) Right upper anterior tooth (CMM-V-7735; labial view). (E) Right upper lateral tooth (paratype; CMM-V-3981; lingual view). (F) Right upper lateral tooth (paratype; CMM-V-3981; labial view). (G) Left lower lateral tooth (paratype; CMM-V-5823; labial view). (H) Left lower lateral tooth (paratype; CMM-V-5823; lingual view).

the middle Pliocene Yorktown Formation (late Zanclean to early Piacenzian). A single specimen has also been collected in situ from the Pamunkey River, New Kent County (J. Osborne, Paleo Quest, pers. comm., 2015), in the Newport News unit (basal Calvert Formation, early Burdigalian; Edwards et al., 2005).

North Carolina. *Alopias palatasi* is poorly documented from North Carolina. This species is not listed in the extensive review of sharks and rays from Lee Creek Mine, North Carolina (Purdy et al., 2001). Teeth have been collected as river specimens from the Meherrin River, Hertford County, North Carolina (M. Palatas, Sharks Underground, pers. comm., 2014; S. Alter, pers. comm., 2015). The fossil beds in this area represent the early to middle Miocene Pungo River Formation (Burdigalian to Langhian), late Miocene Eastover Formation (Cobham Bay Member, Messinian), and the Middle Pliocene Yorktown Formation (Sunken Meadow, Rushmere and Morgarts Beach Members, late Zanclean to early Piacenzian; Miller, 1982; Gibson, 1983; Geisler et al., 2012). Although the Pungo River Formation is generally accepted as being of Burdigalian to Langhian age (Gibson, 1987; Purdy et al., 2001), the beds in this area may extend into the early Serravallian (Gibson, 1983).

South Carolina. Teeth of *A. palatasi* are occasionally collected as river or scuba specimens from the coastal area of southwestern South Carolina in southern Beaufort County, including the Broad and May River areas (M. Palatas, pers. comm., 2014; S. Alter, pers. comm., 2015). The stratigraphy of Beaufort County consists largely of undifferentiated early Miocene (Aquitanian and Burdigalian) sediments typically overlain with Quaternary marine terraces (Doar and Clendenin, 2002). *Alopias palatasi* specimens from this area are almost certainly derived from these early Miocene sediments. Seaward a thin stratum of the younger Coosawhatchie Formation intrudes between the undifferentiated Miocene formations and the cap of marine terraces (Doar and Clendenin, 2002). The Coosawhatchie Formation is middle Miocene in age (Langhian to Serravallian; Popenoe, 1990), and *A. palatasi* teeth collected in tidal portions of the South Carolina coastline (such as the Mark Palatas specimen; CMM-V-5823) could be from this formation rather than the underlying early Miocene beds.

Outside of the eastern United States, partially and fully serrated teeth of *A. palatasi* are occasionally found in the Upper Globigerina Limestone above the C2 phosphorite on the Mediterranean island of Malta (middle Miocene, Langhian; Ward and Bonavia, 2001), indicating that it had a wider distribution than the western Atlantic (D. Ward, personal observation). As yet there is no evidence of *A. palatasi* in mainland Europe. Recent monographs on the elasmobranchs of Germany (Reinecke et al., 2011) and the Netherlands (Bor et al., 2012) include no teeth attributable to *A. palatasi*. The sister species, *A. grandis,* is known from Belgium, but no *A. palatasi* have been found to date (Pieter De Schutter, pers. comm., 2012; Everaert, 2014).

The rarity of *A. palatasi* precludes a definitive assessment of its stratigraphic range, although across all three Neogene embayments *A. palatasi* is, with one possible exception, always found in localities with Burdigalian or Langhian fossil beds. Certainly, both older and younger sedimentary horizons occur in all of the localities, so a broader stratigraphic range is possible, but the Burdigalian-Langhian interval appears to be the primary distribution. Further, in all three embayments *A. palatasi* teeth are typically found comingled with the teeth of the giant otodontid *Carcharocles chubutensis*, a species well represented in the Burdigalian to Langhian and possibly into the Serravallian (BWK, this chapter). The distribution of *A. palatasi* teeth in the Langhian of Malta is consistent with Burdigalian-Langhian distribution observed in the western North Atlantic.

The one exception to this general Burdigalian-Langhian pattern of distribution is a single *A. palatasi* tooth from Flag Ponds (CMM-V-3876). This is a heavily worn beach specimen, so it is unclear whether it was derived from the Choptank Formation (Serravallian) or the upper Plum Point Member (late Langhian) located slightly more than 2 km upstream of Flag Ponds at Calvert Beach. This distance is likely too far for water transport of the tooth given the weak alongshore currents in this area, but it could have been rafted downstream attached to beach ice during the spring thaw.

The three known in situ specimens of *A. palatasi* provide a somewhat clearer estimate of stratigraphic range. The oldest specimen was collected from the Newport News beds, an informal basal unit of the Calvert Formation on the Pamunkey River, Virginia. There is some controversy about the exact age of this bed, ranging from late Aquitanian (on the basis of the age of bed 1; Vogt et al., this volume) to earliest Burdigalian (Edwards et al., 2005). The other two *A. palatasi* specimens were both collected from bed 12 of the Plum Pont Member (Calvert Formation, middle Langhian).

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3

Miocene Bony Fishes of the Calvert, Choptank, St. Marys, and Eastover Formations, Chesapeake Group, Maryland and Virginia

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Stephen J. Godfrey[2]

ABSTRACT. Bony fishes are relatively common in the Miocene deposits of the Chesapeake Group. In the past three decades, intensive collecting has resulted in the accumulation of a large number of bony fish remains. Thirty-eight actinopterygian taxa, based on fossil bones, are now known from the Chesapeake Group. A diverse otolith assemblage of at least 55 taxa has also been reported. The reduced size of many of the otoliths is probably related to their juvenile nature. Such an abundance of juveniles suggests that the Salisbury Embayment represented a nursery ground for most of the Miocene. The fish taxa recognized in the deposits of the Chesapeake Group show a clear general affinity for well-oxygenated muddy and sandy substrates. The assemblages are dominated primarily by shallow-water fishes characteristic of the inner shelf and secondarily by epipelagic taxa. Benthopelagic fishes characteristic of the outer shelf and upper slope are nearly absent in the Calvert Formation (exceptions are *Brotula* sp. and *Lopholatilus ereborensis*). The common occurrence of open-ocean taxa (billfishes, tunas, wahoos) in the Calvert, Choptank, and Eastover Formations suggests that deposition took place in the distal portions of the inner shelf. Overall, the ichthyofaunal composition is consistent with the sedimentary and paleontological record, which evidences a general regressive trend from the Calvert to the St. Marys Formations, representing a gradual shallowing within the Salisbury Embayment. The fish assemblages of the Chesapeake Group exhibit a modern aspect, with most of the taxa belonging to genera or higher categories that currently occur in the northwestern Atlantic, including along the coasts of Maryland and Virginia.

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INTRODUCTION

Miocene deposits of the Middle Atlantic Coastal Plain include a series of remarkably fossiliferous interbedded siliciclastic deposits that extensively crop out with spectacular exposures in the Chesapeake Bay area in Maryland and Virginia. These richly fossiliferous deposits have attracted the attention of North American paleontologists since the nineteenth century (e.g., Conrad, 1830, 1842; Darton, 1891; Harris, 1893), providing the basis for stratigraphic subdivision and correlation of the Neogene Chesapeake Group (see Shattuck, 1904). Multiple systems of stratigraphic subdivision have been used to define the sedimentary units of the Miocene deposits of the Chesapeake Group, including the zones (Harris, 1893; Shattuck, 1904), members (Gernant, 1970), depositional sequences (e.g., Kidwell, 1984, 1988, 1989, 1997), depositional events (e.g., Ward, 1992), and beds (Ward and Andrews, 2008). Kidwell (1988) pointed out that the Miocene siliciclastic deposits of the Chesapeake Group provide rare, direct evidence for coastal sediment sinks during marine transgression. Stratigraphic and taphonomic evidence suggests that fossil concentrations in these Miocene units can be interpreted as stratigraphically condensed records of a suite of transgressive shallow marine to paralic environments (Kidwell, 1989). In the Maryland-Virginia area, the Neogene deposits of the Chesapeake Group directly overlie Paleogene units. The Miocene sedimentary units of the Chesapeake Group include the Calvert, Choptank, St. Marys, and Eastover Formations separated from each other by relatively short temporal gaps, spanning the Aquitanian, Burdigalian, Langhian, Serravallian, and Tortonian stages (see Vogt et al., this volume). Overall, the Miocene deposits of the Chesapeake Group record the gradual shallowing within the Salisbury Embayment, a landward extension of the Baltimore Canyon Trough bounded by the Norfolk High on the south and by the South Jersey High on the north (Poag, 1979). Within the Salisbury Embayment, maximum water depth and fully marine inner to middle shelf conditions occurred during deposition of the Calvert, Choptank, and Eastover Formations, whereas deposition of the St. Marys Formation took place during the transition from open marine shelf conditions to tidally influenced low-salinity muddy coastal environments (e.g., Ward and Blackwelder, 1980; Kidwell, 1989).

Bony fishes are relatively abundant in the Miocene deposits of the Chesapeake Group. However, these remains have not been properly investigated, resulting in a largely incomplete and underestimated diversity (see Kimmel and Purdy, 1984). Fossil bony fish remains were first documented from the deposits of the Chesapeake Group by Cope (1867), who cursorily reported the presence of isolated sphyraenid teeth in the Maryland Miocene. Two years later, he described (Cope, 1869) the sciaenid *Pogonias multidentatus* on the basis of a single upper pharyngeal plate from the Miocene deposits of Nomini Cliffs, Westmoreland County, Virginia. Subsequently, Leidy (1873a,b,c) described the sturgeon *Acipenser ornatus* and the wrasse *Protautoga conidens* from the Miocene of Virginia. Eastman (1904) produced the first systematic account of the fish remains of the Miocene of Maryland, describing teeth of the barracuda *Sphyraena speciosa* from the Calvert Formation, as well as of gadid and sciaenid saccular otoliths from the St. Marys Formation. Hussakof (1908) discussed and illustrated the type specimen of *Pogonias multidentatus* in his catalog of types and illustrated fossil fishes housed in the American Museum of Natural History. Smith (1909) presented new material of this species from the Miocene of Maryland, providing additional morphological evidence to support its separate specific status. In 1917, Berry described the sailfish *Istiophorus calvertensis* on the basis of an incomplete rostrum collected from Tar Bay, Virginia, in the argillaceous beds assigned to the Calvert Formation and more recently referred to the Eastover Formation (Kimmel and Purdy, 1984; Fierstine, 1998). Berry (1932) documented the presence of isolated teeth belonging to the sparid genus *Lagodon* from the St. Marys Formation, and Lynn and Melland (1939) presented a well-preserved neurocranium with associated otolith from the Calvert Formation that they assigned to *Felichthys stauroforus*. Blake (1940) described the albuloid *Paralbula dorisiae* on the basis of an eroded dental plate collected at Plum Point from deposits of the Calvert Formation. In his monographic review of the Tertiary fish faunas of the eastern and central United States, Leriche (1942) listed seven taxa from the Miocene deposits of the Chesapeake Group (*Acipenser ornatus*, *Arius* sp., *Sphyraena speciosa*, *Pogonias multidentatus*, *Protautoga conidens*, Gadidae indet., and Sciaenidae indet.). Dante (1953) reviewed the sciaenid otolith previously illustrated by Eastman (1904), together with additional material from the Calvert Formation, and described *Sciaenops eastmani*. Kimmel and Purdy (1984) provided a brief overview of the fish faunas of the Calvert and Eastover Formations, listing at least 12 taxa. Weems (1985) analyzed the ocean sunfish genera *Mola* and *Ranzania* from the Calvert and Choptank Formations. More recently, Müller (1999) presented a broad analysis of the otolith assemblages of the whole Chesapeake Group. Moreover, a number of new species were described from the St. Marys Formation, including the stargazer *Astroscopus countermani* by Carnevale et al. (2011), the channel catfish *Ictalurus countermani* by Lundberg and Luckenbill (2012), and the needlefish *Belone countermani* by de Sant'Anna et al. (2013). Finally, Carnevale and Godfrey (2014) described the skeletal remains and possible trace fossils of the tilefish *Lopholatilus ereborensis* from the Calvert Formation.

Extensive geological and paleontological explorations of the Miocene deposits of the Chesapeake Group in the last three decades have resulted in the accumulation of a vast collection of bony fish remains primarily housed in the Calvert Marine Museum (CMM), Solomons, Maryland, and the Department of Paleobiology of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. This chapter briefly describes and illustrates the diversity of Miocene bony fishes of the marine and paralic siliciclastic deposits of the Chesapeake Group and discusses their paleoenvironmental significance. The taxonomic classification and nomenclature used, unless otherwise noted, follow Nelson (2006). Many of the taxa described herein would benefit from a more detailed examination. Furthermore, it is our hope that this chapter will prompt collectors to show their fish finds to qualified researchers and that this will stimulate additional research into this remarkable ichthyofauna.

SYSTEMATIC DESCRIPTIONS

CLASS OSTEICHTHYES HUXLEY, 1880

SUBCLASS ACTINOPTERYGII COPE, 1887

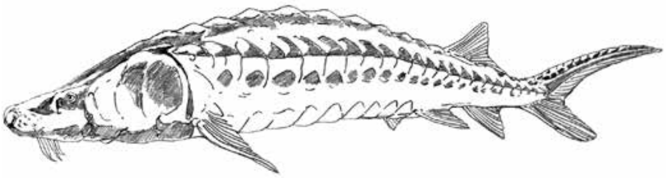
SERIES CHONDROSTEI MÜLLER, 1844

ORDER ACIPENSERIFORMES BERG, 1940

FAMILY ACIPENSERIDAE BONAPARTE, 1831

Gen. et sp. indet.

FIGURE 3.1A,B



Sturgeon – Acipenseridae

Referred Material. CMM-V-98, partially complete lateral scute; CMM-V-99, partially complete right posttemporal and fragments of skull roofing bones; CMM-V-100, dorsal dermal bony scute (Figure 3.1A); CMM-V-265, partially complete lateral scute; CMM-V-279, fragments of skull roofing bones; CMM-V-289, lateral scute; CMM-V-1417 (Figure 3.1B), lateral scute; CMM-V-1907, dorsal scute; CMM-V-1997, partially complete left cleithrum and two isolated lateral scutes and fragments of dermal scutes; CMM-V-2068, partially complete dermal scute; CMM-V-2140, partially complete dermal scute; CMM-V-2439, partially complete dermal scute; CMM-V-2577, partially complete dermal scute; CMM-V-2597, partially complete dermal scute; CMM-V-2612, partially complete ventral scute; CMM-V-2767, partially complete lateral scute; CMM-V-2913, extensively fragmented skull roofing bones; CMM-V-3785, eight isolated dermal scutes; CMM-V-3938, two isolated partially preserved dermal scutes; CMM-V-3953, partially complete dermal scute; CMM-V-3985, partially complete lateral scute; CMM-V-4104, partially complete left supracleithrum; CMM-V-4126, two isolated partially complete dermal scutes; CMM-V-4234, partially complete dermal scute; CMM-V-4250, partially complete left clavicle and three isolated dermal scutes; CMM-V-4299, partially complete right opercle; CMM-V-4312, four isolated dermal scutes; CMM-V-4423, dorsal scute; CMM-V-4530, partially complete dermal scute; USNM 25880, fragments of dermal bones; USNM 438665, partially complete lateral scute; USNM uncataloged, fragmentary skull roofing bones and two isolated dermal scutes and five isolated partially complete lateral scutes.

Horizon. Calvert, Choptank, St. Marys, and Eastover Formations.

Remarks. The material consists of isolated, thick, and often fragmented dermal bones, including skull roofing and pectoral girdle elements and, more frequently, dermal bony scutes (Figure 3.1A,B). These dermal bones exhibit a strongly ornamented outer surface and a nearly smooth inner surface.

Overall, the available Miocene acipenserid material from the Chesapeake Group has not revealed any genus- or species-level diagnostic feature, thereby precluding a detailed taxonomic identification. Leidy (1873b) described the species *Acipenser ornatus* on the basis of a lateral scute from the Calvert Formation, Virginia (see also Leriche, 1942); the type specimen described and illustrated by Leidy is now considered lost (Purdy et al., 2001). In a recent revision of the North American fossil record of the Acipenseridae, Hilton and Grande (2006) demonstrated that there are no diagnostic characters that differentiate the type material of this fossil species from other acipenserids, thereby rendering *Acipenser ornatus* a nomen dubium.

Sturgeons are anadromous and occur in the shallow waters of the continental shelf, commonly near the mouth of rivers. They are bottom feeders, mostly on benthic invertebrates and small fishes.

SERIES NEOPTERYGII REGAN, 1923

DIVISION GINGLYMODI COPE, 1872

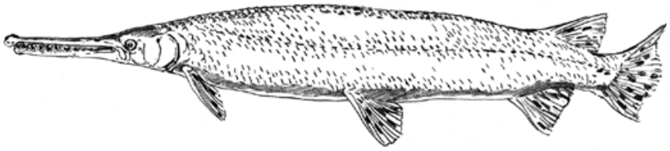
ORDER LEPISOSTEIFORMES HAY, 1929

FAMILY LEPISOSTEIDAE CUVIER, 1825

Genus *Lepisosteus* Linnaeus, 1758

Lepisosteus sp.

FIGURE 3.1C–E



Gar – *Lepisosteus* sp.

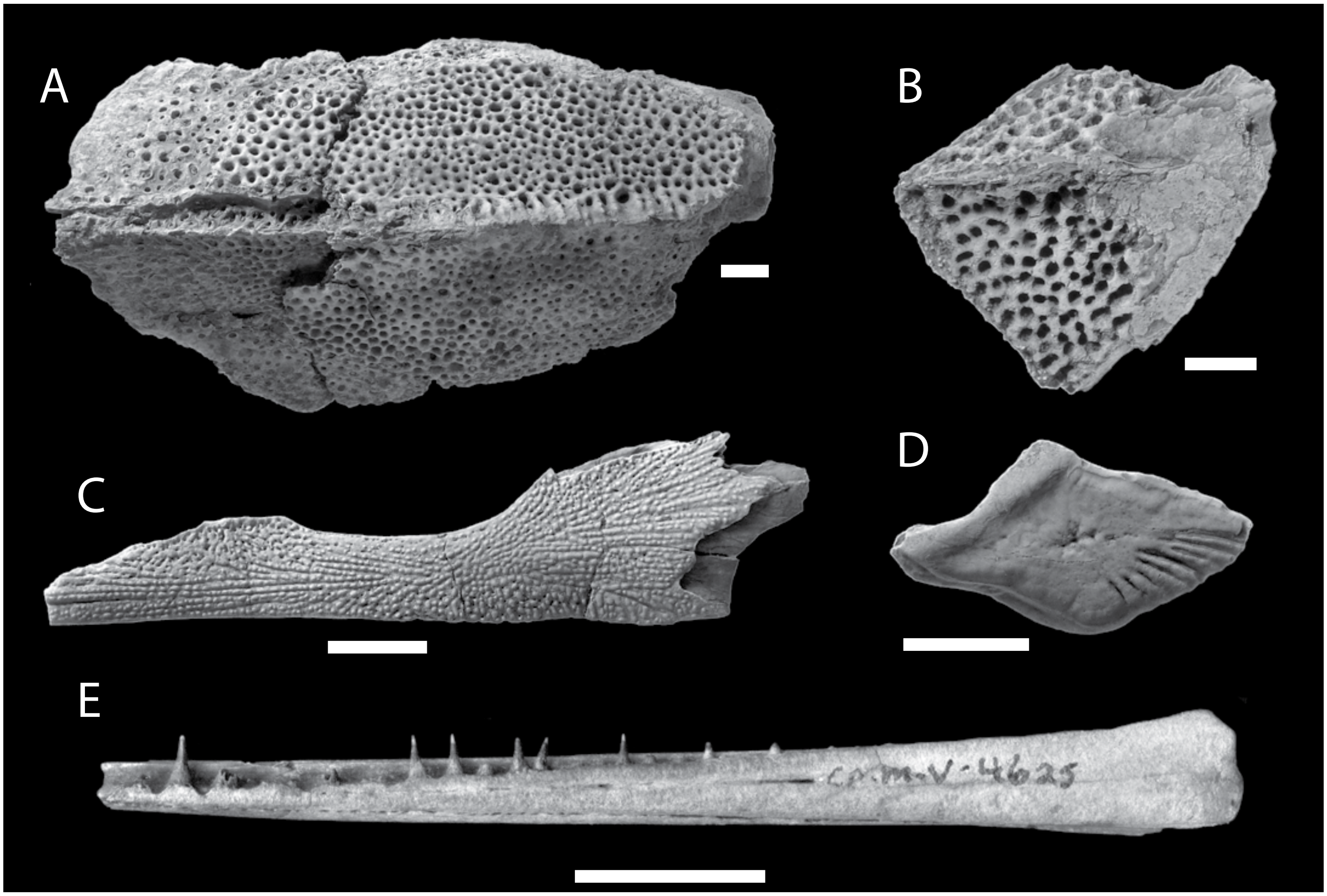


FIGURE 3.1. (A) CMM-V-100, Acipenseridae gen. et sp. indet., dorsal dermal bony scute in dorsal view. (B) CMM-V-1417, Acipenseridae gen. et sp. indet., right lateral dermal bony scute in lateral view. Anterior to right. (C) CMM-V-3137, *Lepisosteus* sp., right frontal in dorsal view. Anterior to left. (D) CMM-V-3992, *Lepisosteus* sp., ganoid scale, external view. Anterior to left. (E) CMM-V-4625, *Lepisosteus* sp., right dentary in medial view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

Referred Material. CMM-V-3137, partially complete right frontal (Figure 3.1C); isolated scales CMM-V-97, CMM-V-362, CMM-V-3079, CMM-V-3135, CMM-V-3278, CMM-V-3575, CMM-V-3992 (Figure 3.1D), CMM-V-4625, partial left dentary (Figure 3.1E); USNM uncataloged, isolated scales.

Horizon. St. Marys Formation.

Remarks. An incomplete, narrow (measurable frontal width to length ratio = 0.24), and finely sculptured right frontal (Figure 3.1C), an incomplete extremely slender right dentary (Figure 3.1E), and 10 isolated rhomboid ganoid scales (Figure 3.1D) possibly belonging to a single individual are referred to the family Lepisosteidae. Within Lepisosteidae, the genus *Lepisosteus* is characterized by the lowest values of the ratio between frontal width to length (0.21–0.28; Grande, 2010); because of the incompleteness of the available frontal, it is reasonable to hypothesize that the calculated value was certainly originally lower than 0.24, thereby suggesting that the fossil remains from the St. Marys Formation pertain to the genus *Lepisosteus*.

Gars are freshwater and estuarine ambush predators that feed primarily on smaller fishes.

Division Halecostomi Regan, 1923

Subdivision Halecomorphi Cope, 1872

Order Amiiformes Hay, 1929

Family Amiidae Bonaparte, 1838

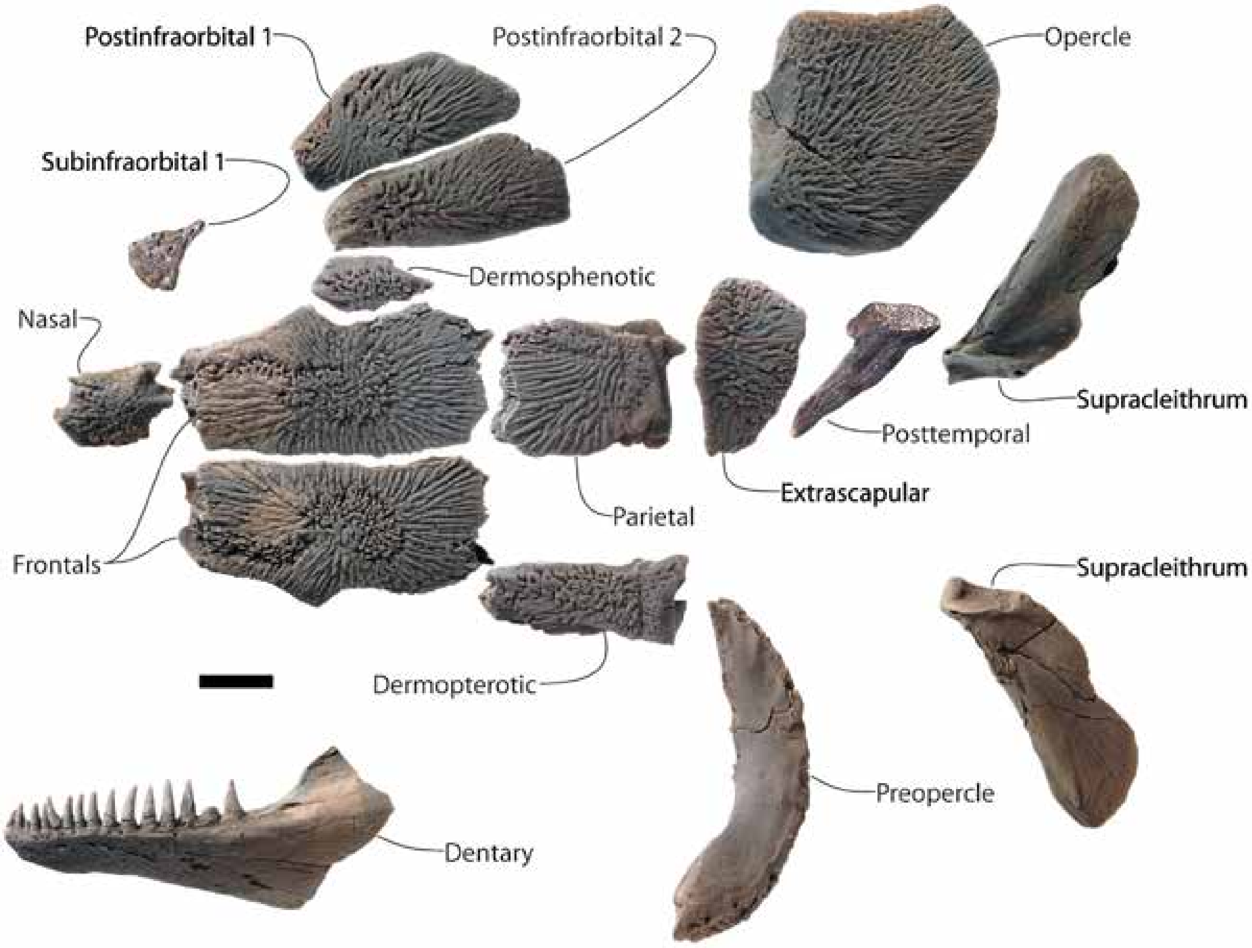
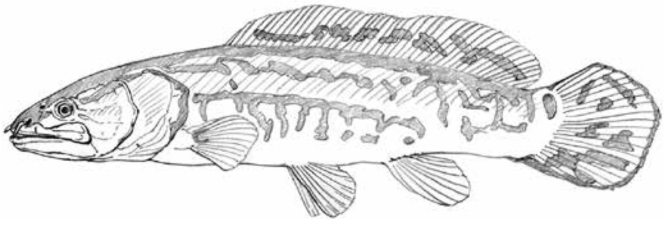


FIGURE 3.2. CMM-V-3134, *Amia* cf. *calva* disarticulated partial skull (flattened into the dorsoventral plane; elements variously shown in dorsal or lateral view). Anterior to left. Not all cranial bones preserved are included here. Specimen lightly coated with sublimed ammonium chloride. Scale bar equals 10 mm.

Genus *Amia* Linnaeus, 1766

Amia cf. *calva* Linnaeus, 1766

FIGURE 3.2



Bowfin – *Amia* cf. *calva*

Referred Material. CMM-V-3134 (Figure 3.2), well-preserved isolated bones from a single individual, including left and right frontals, right parietal, right dermosphenotic, right dermopterotic, right extrascapular, right posttemporal, left lachrymal, left antorbital, left nasal, a single left postinfraorbital (io4), two right postinfraorbitals (io4 + io5), right subinfraorbital, left preopercle, right opercle, right hyomandibula, right metapterygoid, left branchiopercle, left branchiostegal ray, left and right supracleithra, partially complete left cleithrum, a single abdominal centrum, and a single scale.

Horizon. St. Marys Formation.

Remarks. The available material consists of 25 bones belonging to a single individual (Figure 3.2). Most of the bones are extensively sculptured on their outer surfaces and are nearly identical to the corresponding ones of the extant bowfin *Amia*

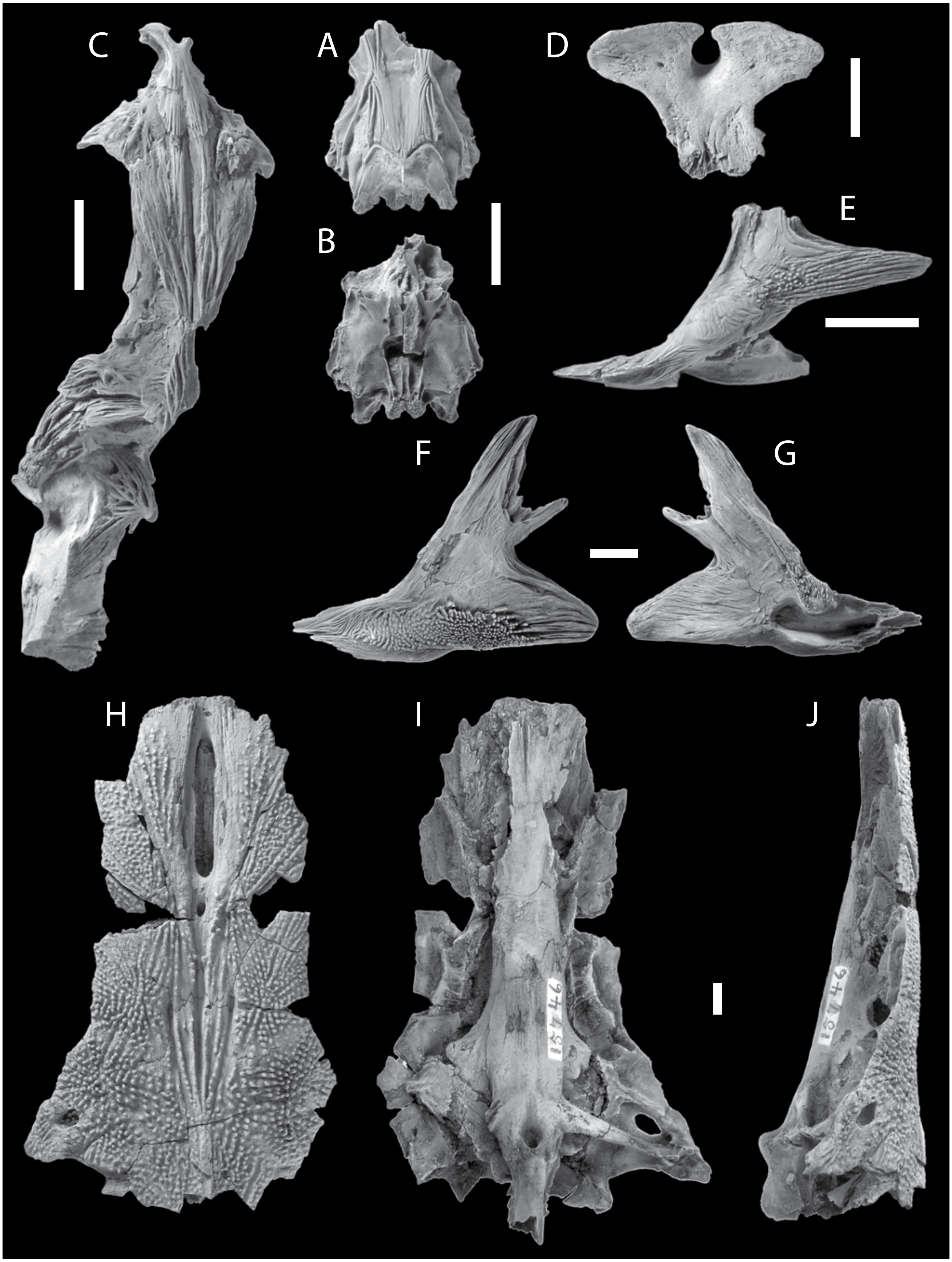

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FIGURE 3.3. (*Facing page*) (A, B) CMM-V-3070, *Alosa* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to top of page. (C) CMM-V-3282, *Ictalurus countermani*, holotype, nearly complete neurocranium in dorsal view. Anterior to top of page. (D) CMM-V-3318, *Ictalurus countermani*, paratype, partial mesethmoid. Anterior to top of page. (E) CMM-V-3282, *Ictalurus countermani*, holotype, left cleithrum and coracoid bones in lateral view. (F, G) CMM-V-3207, *Ictalurus countermani*, paratype, left cleithrum in lateral and medial views, respectively. (H–J) USNM 15746, *Ariopsis stauroforus*, holotype, neurocranium in dorsal, ventral, and left lateral views, respectively. Anterior to top of page. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

calva. Unfortunately, because the skull is not complete, we could not confirm generic-level diagnostic characters (i.e., pointed teeth on coronoids and vomers, parasphenoid tooth patch being long and narrow, and possession of 75–82 preural centra; Grande and Bemis, 1998). Nevertheless, the great similarity of the fossil bones illustrated herein to those of the bowfin suggests a similar generic assignment. As far as the attribution at the species level is concerned, considering that the material from the St. Marys Formation includes two right postinfraorbital bones, of which the upper is evidently larger than the lower, which is in accordance with the species diagnosis provided by Grande and Bemis (1998), it is possible to tentatively refer CMM-V-3134 to the living species of bowfin.

Bowfins inhabit swampy, vegetated lakes and rivers of eastern North America. They are voracious and opportunist feeders subsisting on insects, crustaceans, fishes, and amphibians.

SUBDIVISION TELEOSTEI MÜLLER, 1846

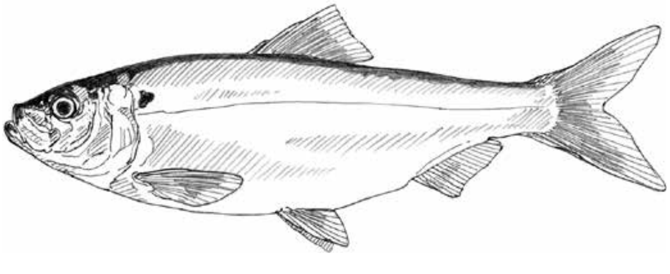
ORDER CLUPEIFORMES BLEEKER, 1859

FAMILY CLUPEIDAE CUVIER, 1817

Genus *Alosa* Linck, 1790

Alosa sp.

FIGURE 3.3A,B



Shad – *Alosa* sp.

REFERRED MATERIAL. CMM-V-3070 (Figure 3.3A,B), partially complete neurocranium; CMM-V-3405, partially complete neurocranium.

HORIZON. St. Marys Formation.

REMARKS. The available material consists of two incomplete neurocrania lacking most of the orbital and ethmoid portions (Figure 3.3A,B). The general external outline of the neurocrania, particularly the relative development and mutual position of the epioccipitals; the broad and perpendicularly oriented transverse processes of the sphenotics; ornamentation of the frontals; and the morphology of pterotics, prootics, and intercalars are consistent with those of certain species of the clupeid genus *Alosa* (see Svetovidov, 1964). Despite a close similarity to the extant *Alosa sapidissima*, the fragmentary nature of the material does not allow for a more detailed taxonomic attribution.

Shad of the genus *Alosa* are anadromous planktivores that feed primarily on small arthropods, fish eggs, and algae. They are very common in nearshore waters but also occur in depths of more than 200 m.

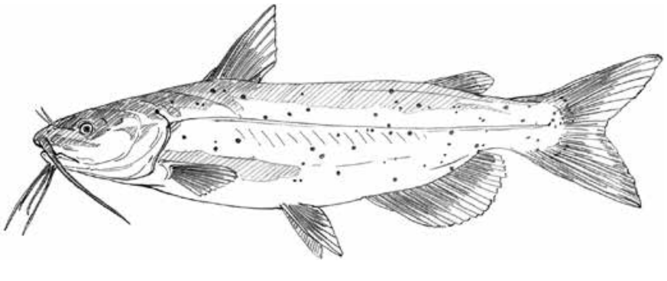
ORDER SILURIFORMES CUVIER, 1817

FAMILY ICTALURIDAE GILL, 1861

Genus *Ictalurus* Rafinesque, 1820

Ictalurus countermani Lundberg & Luckenbill, 2012

FIGURE 3.3C–G



Catfish – *Ictalurus countermani*

HOLOTYPE. CMM-V-3282, nearly complete neurocranium with articulated Weberian complex (Figure 3.3C), left supracleithrum, left pectoral girdle (Figure 3.3E), pectoral-fin spine, and two abdominal vertebrae.

PARATYPES. CMM-V-3207, left cleithrum (Figure 3.3F,G); CMM-V-3316, right premaxilla; CMM-V-3318, mesethmoid (Figure 3.3D).

REFERRED MATERIAL. CMM-V-3319, dorsal-fin spine.

HORIZON. St. Marys Formation.

REMARKS. A few isolated bones and a nearly complete neurocranium belonging to a single individual are assigned to the extant genus *Ictalurus*. Placement within the family Ictaluridae is justified by the presence of three of the four putative synapomorphies of this family as proposed by Lundberg (1970) and subsequently discussed by Grande and Lundberg (1988). The synapomorphies include (1) the possession of a large and smooth temporal fossa bounded by the adductor muscle scar that develops from the lateral edge of the frontal to the occipital region involving the sphenotic, pterotic, supraoccipital, and posttemporo-supracleithrum; (2) a posttemporo-supracleithrum with an anterior process (=subpterotic process of Lundberg, 1970, 1982) that articulates with the ventral surface of the outer pterotic wing; (3) the position of the exit of the infraorbital canal from the frontal located well anterior to the frontal-sphenotic joint; and (4) the lack of vomerine teeth. The outline of the neurocranial bones, cleithrum, and pectoral-fin spine cannot be distinguished in the fossil and extant species of the genus *Ictalurus* (see Lundberg, 1970, 1975). More particularly, the available material shows at least some of the synapomorphies of the genus *Ictalurus* defined by Lundberg (1982): a superficial part of the supraoccipital ornamented with longitudinal grooves and ridges, the absence of the spine located along the lateral margin of the sphenotic, lateral ethmoid wings curved downward, an enlarged optic foramen, and a ventral keel of the coracoid that is elongated, nearly reaching the coracoid symphysis. According to Lundberg and Luckenbill (2012), *Ictalurus countermani* exhibits four synapomorphies of the *I. punctatus* group (channel catfish): the transverse crest of the supraoccipital being tilted obliquely backward and expanded onto the base of the supraoccipital process; the parasagittal crest of the supraoccipital being narrow and rounded; the horizontal shelves of the orbitosphenoid being reduced in width; and the posterior process of the cleithrum being strongly ornamented with at least moderately coarse tubercles.

Ictalurus countermani is unique within the *I. punctatus* group in having a low, obtusely angular sphenotic process developed at midlength along the sphenotic margin; a posterior cleithral process deep at its base, with an exceptionally coarse tuberculate ornamentation; and a pectoral-fin spine shaft that is broad, dorsoventrally depressed, and lenticular in cross section with ridged and dentate anterior and posterior margins, anterior dentations that are evenly spaced and relatively large, and posterior dentations that are relatively small in size (see Lundberg and Luckenbill, 2012).

Catfishes of the genus *Ictalurus* inhabit streams, rivers, creeks, ponds, and lakes and rarely enter brackish waters. They feed on a wide variety of prey items, including worms, mollusks, insects, crustaceans, fishes, and small mammals.

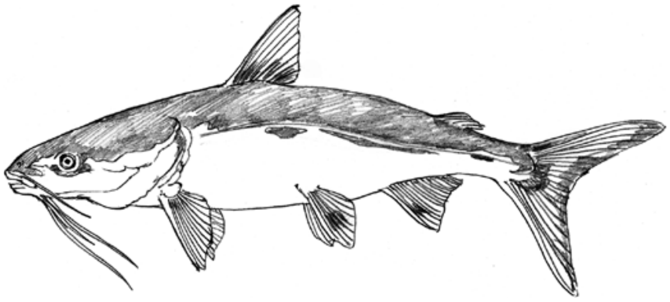
FAMILY ARIIDAE BLEEKER, 1862

Genus *Ariopsis* Gill, 1861

REMARKS. In a recent phylogenetic study of the family Ariidae, Kailola (2004) considered the genus *Ariopsis* as valid, characterized by two distinct geographic components, one American and the other typical of Australia and New Guinea. Marceniuk and Menezes (2007) included the species of this genus within the limits of the genus *Sciades*. Ferraris (2007) interpreted the two geographic components hypothesized by Kailola (2004) as separate genera, with the American species included in *Ariopsis* and those of the Australia–New Guinea region placed in *Neoarius*.

Ariopsis stauroforus (Lynn & Melland, 1939)

FIGURE 3.3H–J



Catfish – *Ariopsis stauroforus*

1939	*Felichthys stauroforus* Lynn & Melland, pp. 14–20, figs. 1–3.
1975	*Arius stauroforus* (Lynn & Melland) – Lundberg, p. 3.
1984	*Arius felichthys* – Kimmel & Purdy, pl. 1, fig. 5.
1999	*Arius stauroforus* (Lynn & Melland) – Muller, p. 77, fig. 27.
2001	*Bagre stauroforus* (Lynn & Melland) – Purdy, Schneider, Applegate, McLellan, Meyer, & Slaughter, p. 165.
2007	*Felichthys stauroforus* Lynn & Melland – Ferraris, p. 32.
2012	cf. *Ariopsis felis* – Lundberg & Luckenbill, p. 8, fig. 23.

HOLOTYPE. USNM 15746, a partially complete neurocranium and a left lapillus (utricular otolith; Figure 3.3H–J).

REFERRED MATERIAL. CMM-V-3317, complete dorsal-fin spine (see Lundberg and Luckenbill, 2012); USNM 336490, partial neurocranium; USNM 336491, partial pectoral-fin spine; USNM 542405, partial neurocranium lacking the anterior portion of the orbital and ethmoid regions.

HORIZON. Calvert Formation.

Remarks. Lynn and Melland (1939) presented a detailed description of the type specimen that was interpreted to be closely related to the extant hardhead catfish *Ariopsis felis*. Subsequently, Kimmel and Purdy (1984) presented a partial neurocranium that they referred to the sea catfish genus *Arius*.

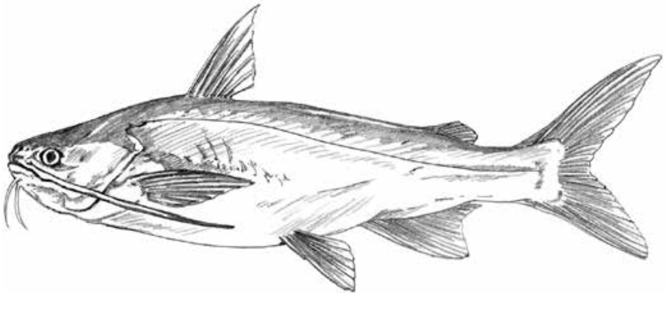
The analysis of the type and other material has evidenced several diagnostic features of the family Ariidae (see Acero and Betancur, 2007), including an extremely developed lapillus, relatively swollen otic capsules, a well-developed ventral process of the basioccipital, and a well-developed foramen (=temporal fossa of Acero and Betancur, 2007) between the posttemporo-supracleithrum, extrascapula, and pterotic. The well-defined aortic canal on the basioccipital and the absence of the anterior nuchal plate clearly support its inclusion within the subfamily Ariinae (see Acero and Betancur, 2007). Among the new-world genera of the subfamily Ariinae, the overall physiognomy of the fossils is consistent with that of certain species of the genus *Ariopsis*. More specifically, the neurocranium exhibits a close similarity to those characteristics of the extant *Ariopsis felis*, from which they differ in having a larger parasphenoid, a wider medial groove of the neurocranium that originates from the center of the supraoccipital, and enlarged anterior and posterior cranial fontanels.

Extant sea catfishes of the genus *Ariopsis* inhabit coastal marine and brackish environments and, to a lesser degree, large and medium rivers, where they are found in turbid waters over muddy bottoms. They feed mainly on invertebrates and small fishes.

Genus *Bagre* Cloquet, 1816

Bagre sp.

FIGURE 3.4A,B



Catfish – *Bagre*

Referred Material. USNM 542406, articulated skeleton consisting of an incomplete neurocranium lacking the ethmoid and most of the orbital regions, and part of the left pectoral girdle (including the pectoral-fin spine), the median nuchal plate, and the dorsal-fin spine (Figure 3.4A,B).

Horizon. Calvert Formation.

Remarks. The outer surface of the cranial bones and cleithrum is extensively sculptured. The morphology of the skull roofing bones, the overall outline of the neurocranium and cleithrum, the relative development of the postcleithral process of the cleithrum, the presence of transverse ridges with one or two peaks along the anterior margin of the dorsal-fin spine (see Purdy et al., 2001), the subrectangular morphology of the supraoccipital bone, the overall morphology of the median nuchal plate, and the size and shape of the foramen (=temporal fossa of Acero and Betancur, 2007) between the posttemporo-supracleithrum, extrascapula, and pterotic are extremely similar to those of the species of the catfish genus *Bagre,* to which the material documented herein is tentatively referred.

Sea catfishes of the genus *Bagre* mainly inhabit marine habitats around the mouths of rivers but also inhabit brackish estuaries with high salinities. They prefer muddy bottoms and feed primarily on benthic invertebrates and small fishes.

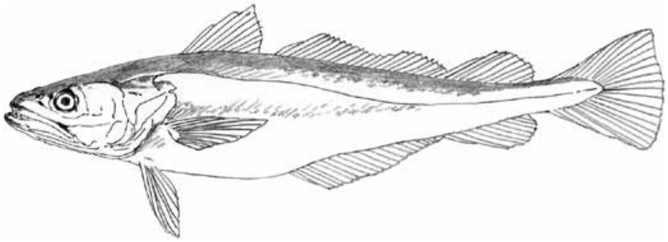
ORDER GADIFORMES GOODRICH, 1909

FAMILY MERLUCCIIDAE GILL, 1884

Genus *Merluccius* Rafinesque, 1810

Merluccius sp.

FIGURE 3.4C–F



Hake – *Merluccius* sp.

Referred Material. CMM-V-3488, nearly complete left mandible (Figure 3.4E,F); CMM-V-4492, partially complete right premaxilla (Figure 3.4C,D); USNM uncataloged, partially complete right dentary.

Horizon. St. Marys Formation.

Remarks. The premaxilla has a short, nearly vertical ascending process and a robust articular process with a rounded dorsal profile (Figure 3.4C). The alveolar process is long and straight, with two rows of large teeth. The dentary is greatly elongate and bears two rows of conical pointed teeth with lingually recurved tips; the teeth of the labial row are more firmly attached to the dentary than those of the lingual row, which are not preserved in the specimen; a deep groove extends for most of the length of the dentary along its ventrolateral surface. The anguloarticular is laminar, with a short and narrow coronoid process (Figure 3.4E,F).

The morphology of the premaxilla and mandibular bones is consistent with that of the genus *Merluccius*. In particular,

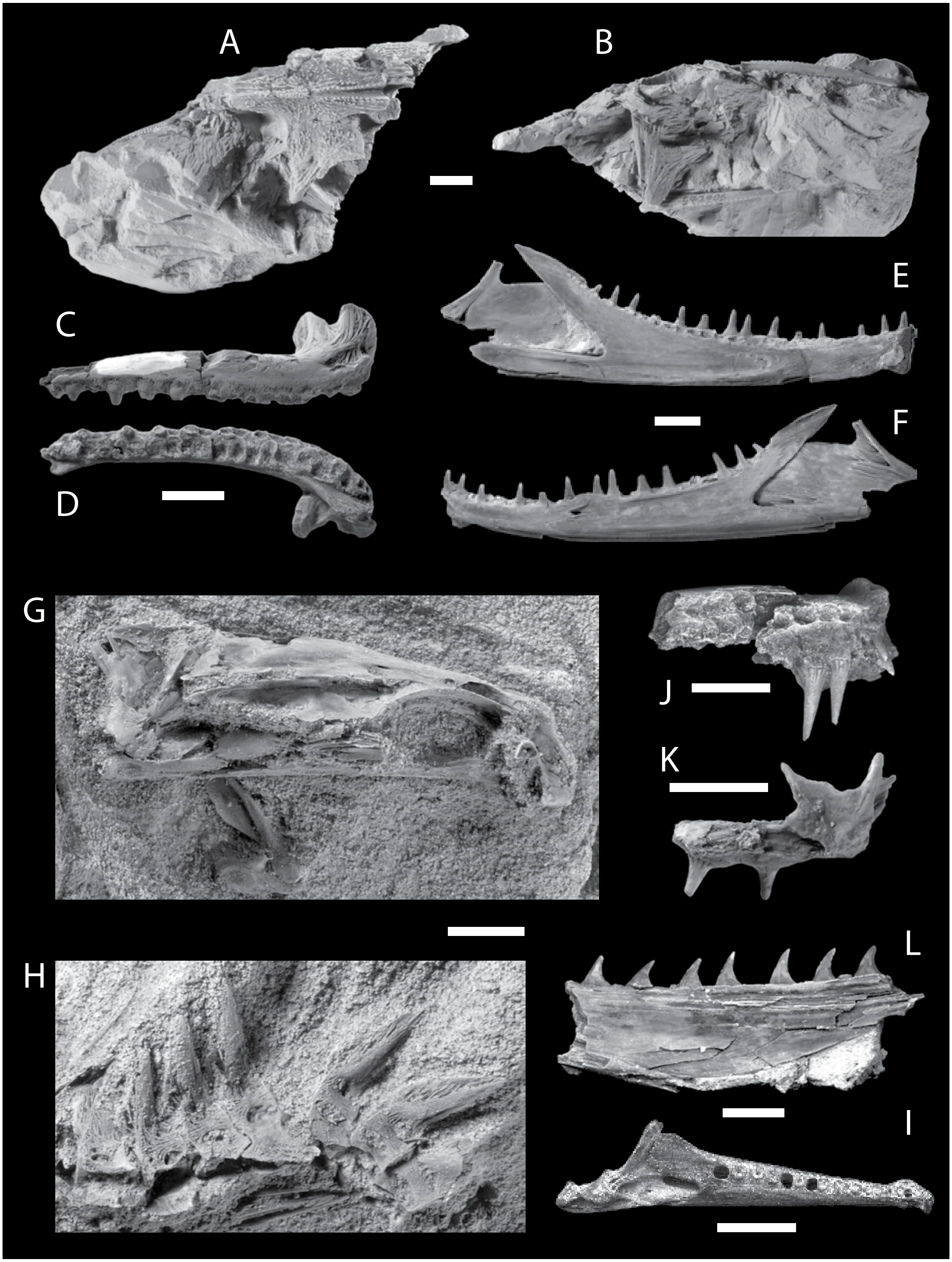

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FIGURE 3.4. (*Facing page*) (A, B) USNM 542406, *Bagre* sp., partial articulated skeleton in dorsal and ventral views, respectively. (A) Anterior to right. (B) Anterior to left. (C, D) CMM-V-4492, *Merluccius* sp., right premaxilla in lateral and ventral views, respectively. (E, F) CMM-V-3488, *Merluccius* sp., left mandible in medial and lateral views, respectively. (G) CMM-V-4637, *Brotula* sp., neurocranium in right lateral view. Anterior to right. (H) CMM-V-4637, *Brotula* sp., abdominal vertebrae in left lateral view. (I) CMM-V-2509, *Opsanus* sp., partial left mandible, medial view. (J) CMM-V-839, *Lophius* sp., partial right premaxilla in medial view. (K) USNM 24865, *Lophius* sp., palatine in lateral view. (L) CMM-V-4628, *Lophius* sp., partial left dentary in lateral view. Anterior to left. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

the arrangement of the premaxillary teeth in two rows is typical of that genus (see Inada, 1981; Howes, 1991). Within the genus *Merluccius*, the identification at the species level is based primarily on the morphology of selected osteological structures (hyomandibula, sagitta, urohyal) that are not observable in the available material.

Hakes are marine demersal fishes recorded at depths of 1 to 400 m. They are often abundant on sandy grounds. Hakes are voracious predators of fishes and crustaceans.

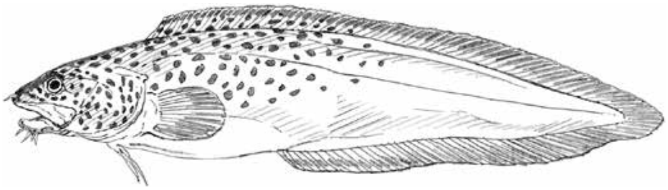
ORDER OPHIDIIFORMES BERG, 1937

FAMILY OPHIDIIDAE RAFINESQUE, 1810

Genus *Brotula* Cuvier, 1829

Brotula sp.

FIGURE 3.4G–H



Brotulas – *Brotula* sp.

REFERRED MATERIAL. CMM-V-4637, partially complete articulated skeleton (Figure 3.4G,H).

HORIZON. Calvert Formation.

REMARKS. The single available specimen consists of a partially complete, articulated skeleton represented by a well-preserved neurocranium and fragmentary skull bones, 11 abdominal vertebrae, and fragments of what appear to be pleural ribs and epineural bones.

The neurocranium is elongate and tubular, its length approximately three times its maximum depth (Figure 3.4G). The ethmoid region is very short. The orbit is oblong. The skull roof is smooth except for a low crest developed in the temporal region of the frontal. The vomer prominently projects ventrally. The mesethmoid consists of a stout, nearly vertical and laterally compressed bony lamina. The lateral ethmoid bears a laterally directed flange. The frontals are the largest bones of the skull roof. The parietal is subtriangular in outline. The supraoccipital extends posteriorly into a very low, laterally compressed crest. The parasphenoid and basioccipital are very robust and thickened.

The vertebral centra are massive and subquadrangular, bearing large bladelike parapophyses (Figure 3.4H). The bases of the neural arches are greatly expanded. The lateral surfaces of the centra, neural arches, and parapophyses are extensively ornamented with small deep pits and delicate ridges.

The morphological features of the neurocranium (general proportions and the structure of the frontals, supraoccipital crest, parasphenoid, and vomer) and the architecture and ornamentation of the abdominal vertebrae are extremely similar to those of the bearded brotula *Brotula barbata* (e.g., Patterson and Rosen, 1989: fig. 8). The specimen is referred herein to an indeterminate species of the genus *Brotula*; because of its incompleteness, it is preferable to use the open nomenclature until more complete articulated skeletons become available.

Brotulas are benthopelagic, inhabiting marine waters to depths of more than 600 m, but are common on the continental shelf on muddy and sandy bottoms. Brotulas feed primarily on fishes and crustaceans, mainly crabs.

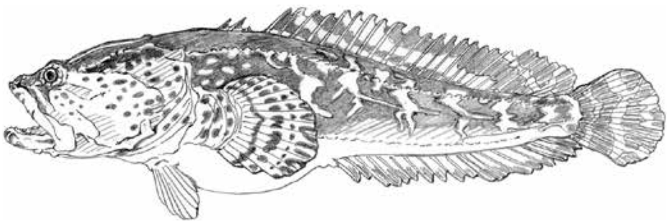
ORDER BATRACHOIDIFORMES GOODRICH, 1909

FAMILY BATRACHOIDIDAE JORDAN & EVERMANN, 1898

Genus *Opsanus* Rafinesque, 1818

Opsanus sp.

FIGURE 3.4I



Toadfish – *Opsanus* sp.

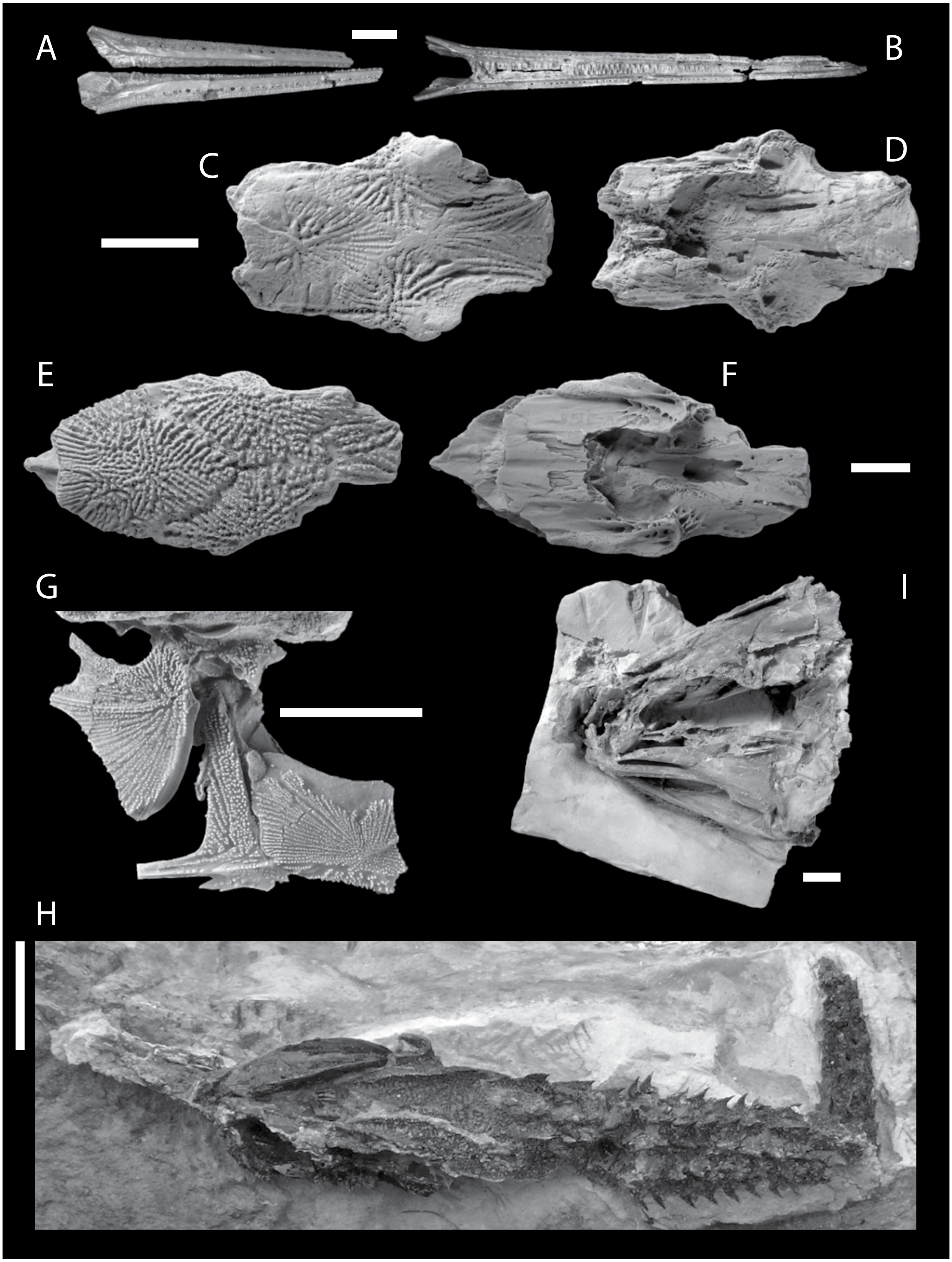

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FIGURE 3.5. (*Facing page*) (A, B) CMM-V-3695, *Belone countermani*, holotype, articulated partial premaxillae and dentaries, respectively, in occlusal views. Anterior to right. (C, D) CMM-V-2006, *Prionotus* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to left. (E, F) CMM-V-2195, *Prionotus* sp., partial neurocranium in dorsal and ventral views, respectively. Anterior to left. (G) CMM-V-4631, *Prionotus* sp., left infraorbitals and preopercle and opercle. Anterior to left. (H) CMM-V-4535, Agonidae gen. et sp. indet.; nearly complete articulated skeleton in ventral view. Anterior to left. (I) USNM 542411, *Morone* sp., partial head skeleton in left lateral view. Anterior to left. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

REFERRED MATERIAL. CMM-V-2509, partially complete left mandible (Figure 3.4i).

HORIZON. Choptank Formation.

REMARKS. A single left mandible documents the presence of the toadfish genus *Opsanus* in the Miocene deposits of the Chesapeake Group. The dentary is elongate and slender, with a single row of rounded sockets that extends for most of its length. In the symphyseal region, some supernumerary teeth are irregularly arranged in an additional row. The anguloarticular is characterized by a thick ridge along its lateral side and a well-developed, obliquely oriented coronoid process. The dorsal margin of the joint between the dentary and the coronoid process of the anguloarticular is characterized by a rounded profile (see Greenfield et al., 2008).

The mandible cannot be distinguished from those of the extant oyster toadfish *Opsanus tau*. However, additional comparative information is necessary for a more detailed identification of the material.

Toadfishes of the genus *Opsanus* occur primarily inshore at depths up to 50 m on rocky bottoms and close to reefs. According to Thomson et al. (1978), some species of this genus migrate offshore during cold weather. Toadfishes are voracious predators that feed primarily on worms, crustaceans, and fishes.

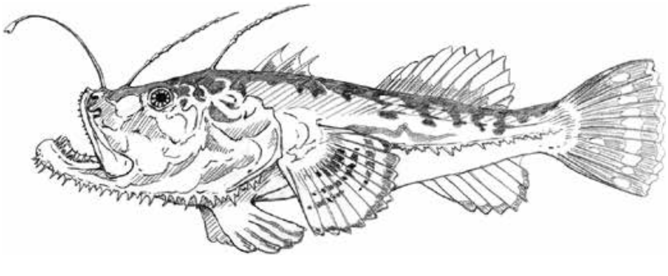
ORDER LOPHIIFORMES GARMAN, 1899

FAMILY LOPHIIDAE RAFINESQUE, 1810

Genus *Lophius* Linnaeus, 1758

Lophius sp.

FIGURE 3.4J–L



Lophiid Anglerfish – *Lophius* sp.

REFERRED MATERIAL. CMM-V-839, partially complete right premaxilla (Figure 3.4J); CMM-V-1363, partially complete right premaxilla and right dentary associated with a vertebral column of *Thunnus* sp.; CMM-V-2777, isolated teeth; CMM-V-4624, partially complete right premaxilla; CMM-V-4628, partially complete left dentary (Figure 3.4L); CMM-V-4629, partially complete left dentary; USNM 24865, left and right dentaries and a right palatine (Figure 3.4K); USNM uncataloged, partially complete right premaxilla.

HORIZON Calvert, St. Marys, and Eastover Formations.

REMARKS. All the available bones are incomplete and only moderately well preserved. The large and robust caniniform teeth with shallow vertical grooves at their bases, as well as the posterior triangular teeth of the outer row of the dentary, exhibit the attachment structure (ankylosis and fibrous hinge) typical of the genus *Lophius* (see Kerebel et al., 1979). The bifid anterior head of the palatine also supports the assignment to the genus *Lophius* (see Carnevale and Pietsch, 2012).

Lophiid anglerfishes of the genus *Lophius* are benthic and inhabit different substrates at depths ranging from the shoreline to greater than 600 m, where they feed on fishes and invertebrates.

ORDER BELONIFORMES BERG, 1937

FAMILY BELONIDAE BONAPARTE, 1837

Genus *Belone* Cuvier, 1816

Belone countermani de Sant'Anna, Collette, & Godfrey, 2013

FIGURE 3.5A,B

Needlefish – *Belone countermani*

HOLOTYPE. CMM-V-3695, articulated partially complete premaxillae and dentaries belonging to a single individual (Figure 3.5A,B).

Horizon. St. Marys Formation.

Remarks. De Sant'Anna et al. (2013) provided a detailed description of this specimen, the only fossil belonid known from the Maryland Miocene. The premaxillae are delicate and elongate (Figure 3.5A). There are two series of premaxillary teeth; the teeth of the inner series are arranged into a single row of relatively large conical elements, whereas those of the outer series consist of a dense band of very small accessory teeth that reach the lateral margin of the bone. The dentaries are slender and elongate, characterized by a thickened symphyseal portion and a moderately thin rostral end. The contralateral dentaries articulate through strong symphyseal interdigitation (Figure 3.5B; de Sant'Anna et al., 2013: fig. 6); however, this interdigitation does not extend up to the anterior tip of the mandible. Sockets document the presence of a single row of teeth of varying sizes in the rostral region; these teeth are associated with a dense series of numerous tiny accessory villiform elements posteriorly and a single outer series of accessory teeth in the symphyseal region (de Sant'Anna et al., 2013: figs. 4, 5).

The dentition of *Belone countermani* most closely resembles that of *B. belone*, an extant needlefish that inhabits the Mediterranean Sea and eastern North Atlantic Ocean (Collette and Parin, 1970; de Sant'Anna et al., 2013). Although they are similar, morphological differences warrant placement in separate species. With so little fossil material known of *B. countermani*, there is a high probability that additional finds will add significantly to our understanding of its morphology.

The garfish *B. belone* inhabits the brackish, shallow marine and oceanic biotopes of the eastern North Atlantic and Mediterranean, where it feeds on small fishes, mostly clupeoids.

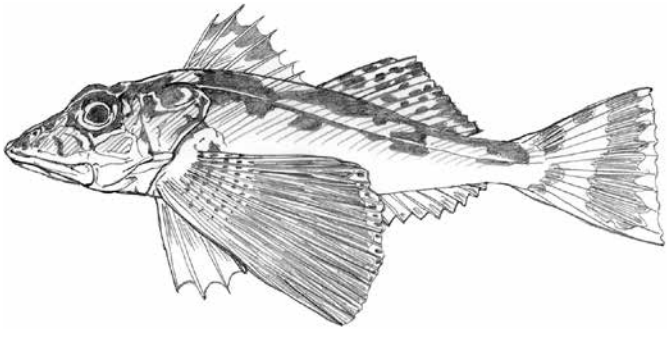
Order Scorpaeniformes Garman, 1899

Family Triglidae Risso, 1926

Genus *Prionotus* Lacépède, 1801

Prionotus sp.

FIGURE 3.5C–G



Sea Robin – *Prionotus* sp.

Referred Material. CMM-V-2006, partially complete neurocranium (Figure 3.5C,D); CMM-V-2195 (Figure 3.5E,F), partially complete neurocranium; CMM-V-3408, partially complete lachrymal; CMM-V-4337, partially complete neurocranium; CMM-V-4338, partially complete neurocranium; CMM-V-4631, left infraorbitals and preopercle and opercle (Figure 3.5G).

Horizon. Calvert and St. Marys Formations.

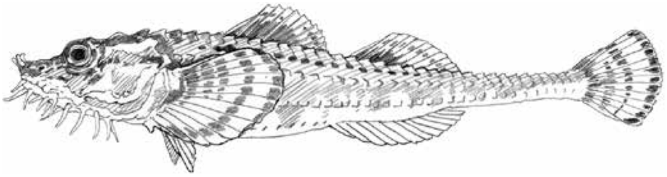
Remarks. The available material consists exclusively of cranial remains (Figure 3.5C–G). The outer sides of the bones exhibit the elaborate sculpturing pattern characteristic of the members of the family Triglidae (e.g., Allis, 1909; Carnevale, 2008). The neurocrania are always represented by the orbital-ethmoid region, which includes the median mesethmoid, paired nasals, lateral ethmoids, and the anterior part of the frontals (Figure 3.5C–F). The neurocranial architecture and the morphological structure of the opercular bones (Figure 3.5G), as well as the external ornamentation pattern of the bones, fit very well with those of the sea robins of the genus *Prionotus*. A more detailed taxonomic identification is not possible without additional and more complete specimens.

Sea robins of the genus *Prionotus* are marine demersal inhabitants of the continental shelf down to about 200 m, where they feed primarily on worms, mollusks, and crustaceans. *Prionotus* species often enter brackish waters.

Family Agonidae Swainson, 1839

Gen. et sp. indet.

FIGURE 3.5H



Poacher – Agonidae

Referred Material. CMM-V-4535, nearly complete articulated skeleton partially embedded in sediment (Figure 3.5H).

Horizon. St. Marys Formation.

Remarks. A recently discovered nearly complete articulated skeleton documents the presence of the family Agonidae in the deposits of the Little Cove Point Member of the St. Marys Formation (Figure 3.5H). The fossil is still partially embedded in sediment, and its detailed anatomical and systematic analysis is currently in progress using computer tomography. The general morphology of the fossil, with a slender body tapering to the caudal peduncle and covered with thick bony plates bearing a strong blunt retrorse spine arising from the center, unambiguously supports its assignment within the family Agonidae (see Kanayama, 1991).

Agonids inhabit the sandy and rocky bottoms of the shallow marine biotopes of the northern Pacific, North Atlantic, North Sea, and the Patagonian region, where they feed on crustaceans and other benthic invertebrates.

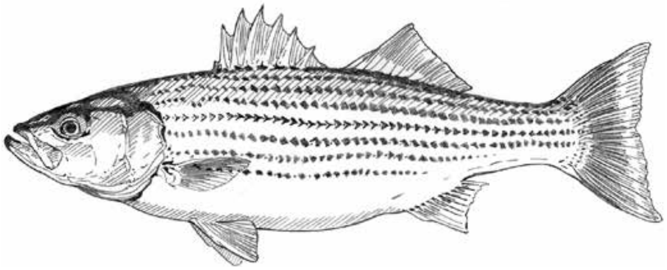
ORDER PERCIFORMES BLEEKER, 1859

FAMILY MORONIDAE FOWLER, 1907

Genus *Morone* Mitchill, 1814

Morone sp.

FIGURE 3.5I



Bass – *Morone* sp.

REFERRED MATERIAL. USNM 542410, partially complete head skeleton; USNM 542411, partial head skeleton (Figure 3.5i).

HORIZON. Calvert Formation.

REMARKS. The available material includes two partial skulls collected from the Calvert Formation. The excellent preservation of these specimens allows for the observation of a number of anatomical features that clearly evidence their affinity with the extant species of the genus *Morone*. In particular, the general outline of the neurocranium, the irregular configuration of the transverse lateral process of the sphenotic, the delicate subtriangular anterior process arising from the anterodorsal margin of the mesethmoid, the morphology of the jaw and suspensorial bones, the large bands of small premaxillary and dentary teeth, and the posterior enlarged laminar flange at the angle formed by the convergence of the horizontal and vertical arms of the preopercle are extremely similar to those of the extant striped bass *Morone saxatilis* (see Woolcott, 1957). However, the complete absence of characters of the axial skeleton, as well as of any morphometric or meristic features, does not allow for an unambiguous taxonomic interpretation at the specific level.

Basses of the genus *Morone* are anadromous and extremely common in shallow coastal waters and brackish biotopes. They enter rivers to spawn mostly during the spring. Fishes of the genus *Morone* are voracious and opportunistic predators that feed on a variety of fishes and invertebrates.

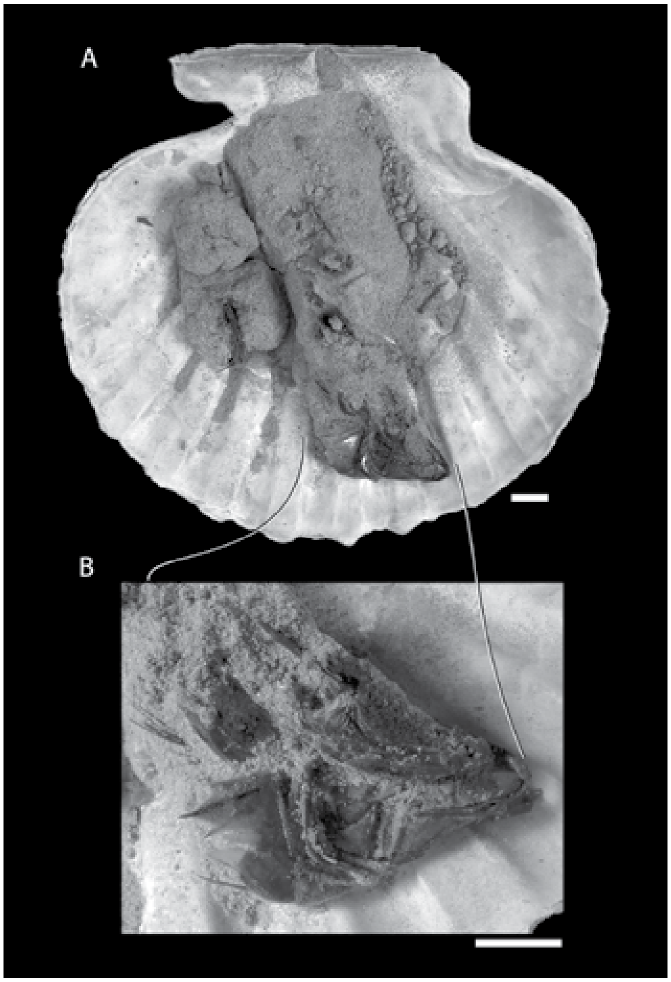


FIGURE 3.6. CMM-V-4622, Serranidae, gen. et sp. indet. (A) Partial articulated skeleton preserved inside joined valves of a Miocene scallop shell, *Chesapecten nefrens*. (B) Enlarged view of skull in right lateral view. Anterior to right. Scale bars equal 10 mm.

FAMILY SERRANIDAE SWAINSON, 1839

Gen. et sp. indet.

FIGURE 3.6

REFERRED MATERIAL. CMM-V-4622, partially complete articulated skeleton preserved inside joined valves of a *Chesapecten* (Figure 3.6).

HORIZON. Choptank Formation.

REMARKS. Although a large part of the skeleton is still embedded in the sediment, it is possible to observe the skull roof, both lower jaws, the right suspensorium, and the opercular complex (Figure 3.6). The preopercle is ornamented

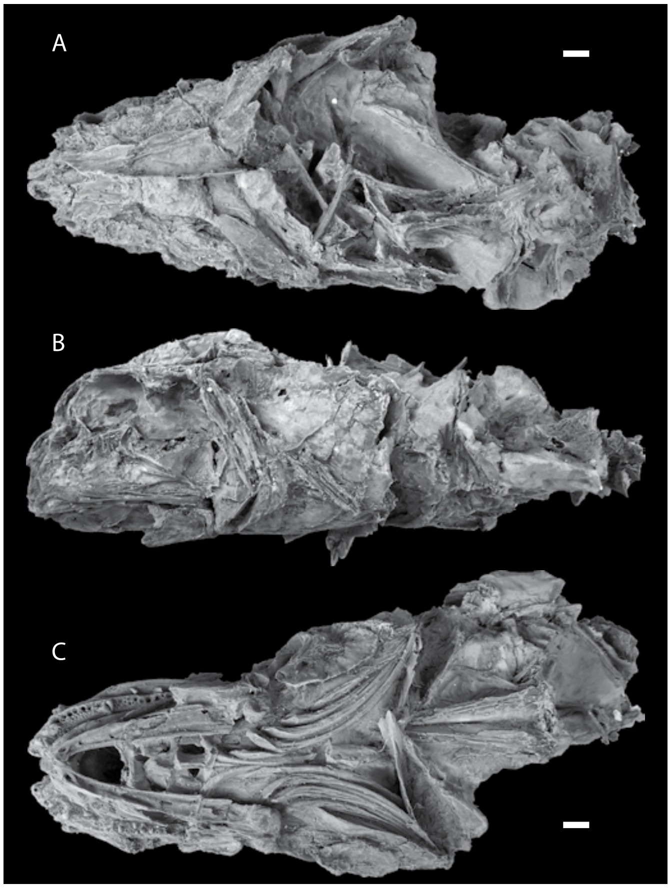


FIGURE 3.7. (A–C) USNM 467782, *Lopholatilus ereborensis*, holotype, nearly complete well-preserved skull and partial axial skeleton in dorsal, left lateral, and ventral views, respectively. Specimen is lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

with fine serrations along the posterior margin of the vertical arm and by short, strong spines along the ventral margin of the horizontal arm and at the corner formed by the confluence of the two arms (Figure 3.6B). The opercle has three spines along its posterior margin, of which the central spine represents the distal end of the median horizontal ridge that originates from the articular surface for the opercular process of the hyomandibula.

The serrated posterior and ventral margins of the preopercle and the presence of three spines along the posterior margin of the opercle are clearly indicative of the family Serranidae (see Johnson, 1983). A more detailed identification of the fossil is not possible because of its inadequate preservation.

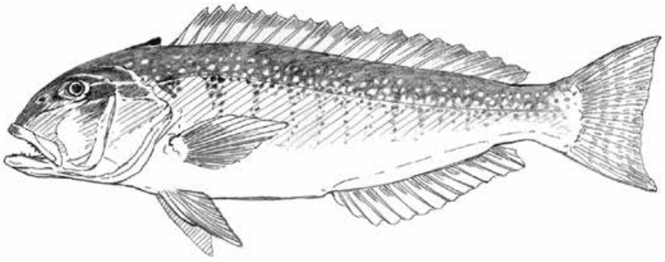
The family Serranidae includes more than 470 species of marine predatory fishes common in tropical and temperate areas of the world.

FAMILY MALACANTHIDAE GÜNTHER, 1861

Genus *Lopholatilus* Goode & Bean, 1880

Lopholatilus ereborensis Carnevale & Godfrey, 2014

FIGURE 3.7



Tilefish – *Lopholatilus ereborensis*

1984 *Lopholatilus* sp. – Kimmel and Purdy, p. 208, fig. 20, pl. 2, figs. 1–2.

HOLOTYPE. USNM 467782, nearly complete well-preserved head skeleton and partial axial skeleton (Figure 3.7).

PARATYPES. CMM-V-4635, partially complete head skeleton; CMM-V-4636, partially complete head skeleton; CMM-V-4638, partially complete head skeleton; CMM-V-4821, partially complete head skeleton plus six articulated abdominal vertebrae; USNM 467776, partially complete head skeleton.

REFERRED MATERIAL. CMM-V-4639, partially complete head skeleton; USNM 467777, partially complete head skeleton; USNM 467779, partially complete head skeleton; USNM 467781, partially complete head skeleton.

HORIZON. Calvert Formation.

REMARKS. All the available material consists of relatively well preserved articulated cranial remains from beds 11 to 14 of the Calvert Formation. USNM 467782 also includes 10 abdominal centra, two caudal centra, some scattered dorsal-fin elements, and large parts of the appendicular girdles.

The head is massive, rather wide, and moderately deep, with its maximum depth contained slightly less than two times in head length. The snout is very short (contained more than four times in head length) and the orbit is moderately large (Figure 3.7). Because of the reduced length of the snout, the anterior profile of the head appears very steep.

The neurocranium is very high and bears a robust, moderately high supraoccipital crest that apparently reaches the anterior margin of the orbit and a less developed temporal crest; two prominent thick anteroventrally directed processes with a nearly ovoid anterior profile arise from the anterodorsal margin of the mesethmoid. The occipital region gently slopes in an oblique direction. The high lachrymal is thickened and extensively ornamented along its lateral surface.

The upper jaw is protrusible and slightly oblique, approximately reaching the posterior margin of the orbit. The premaxilla bears a very short and distally pointed ascending process (length of the ascending process 34–36.5% of the length of the alveolar process) and a laminar articular process with rounded dorsal profile. The alveolar process bears a single outer row of strong conical teeth and an inner dense band of villiform teeth. The dentary bears a single outer row of strong conical teeth similar to those of the premaxilla and villiform teeth restricted to the symphyseal region. A very short, pointed, and vertically directed symphyseal process arises from its anteroventral corner.

The suspensorial bones are relatively well exposed in most of the specimens.

The preopercle has a finely serrated posterior margin; the angle between the vertical and horizontal arms measures about 120°. The vertical arm of the preopercle is considerably shortened, with the horizontal arm measuring between 52.8% and 66.4% of the length of the vertical arm. The opercle is laminar, very thin, and characterized by a strongly thickened anterior margin; a thickened horizontal ridge extends posteriorly from the articular condyle for the hyomandibular process and possibly terminates posteriorly into a spine.

The hyoid bar is very compact, with a medially exposed dorsal hypohyal. There are six saber-like branchiostegal rays.

Except for the atlas and second abdominal vertebra, the vertebral centra are subrectangular, longer than high, with a deep fossa along their lateral sides. Vertebrae 3 through 10 bear relatively large bladelike parapophyses.

The overall morphology of the neurocranium, upper and lower jaws, suspensorial bones, and opercular apparatus is very similar to that of the great northern tilefish *Lopholatilus chamaeleonticeps*. In particular, the specimens examined show some features that are clearly diagnostic of *Lopholatilus*, including the paired prominent curved and anteroventrally directed processes arising from the anterodorsal margin of the mesethmoid, the large thick and extensively sculptured lachrymal, and the oral jaw dentition pattern. Despite their incompleteness, the fossils show a few evident characters that clearly separate them from the extant species of the genus *Lopholatilus* (Carnevale and Godfrey, 2014). Compared to those of extant congenerics, the head of *Lopholatilus ereborensis* is moderately developed vertically; its depth is contained slightly less than two times in head length (~52% versus 72%–100% of head length). As a result of the strong shortening of the ethmoid region of the neurocranium, the snout of *Lopholatilus ereborensis* is broadly shortened relative to that characteristic of both extant species (snout length ~22% versus 27%–51% of head length). The ascending process of the premaxilla is notably reduced in size compared to those of extant species, its length being 34%–36.5% of that of the alveolar process (versus 49%–52% in *Lopholatilus chamaeleonticeps*). The vertical arm of the preopercle is remarkably shortened compared with that of extant members of the genus *Lopholatilus* (the length of the horizontal arm of the preopercle measures between 52.8% and 66.4% of that of the vertical arm versus ~42% in *Lopholatilus chamaeleonticeps*). Finally, the vertical and horizontal arms of the preopercle form an angle (~120°) broader than that of the extant species (105°–110°; see Dooley, 1978). All of these characters appear to be unique to the Miocene fossils, representing a reasonable basis for the creation of a new species. Purdy et al. (2001) described the species *Lopholatilus rayus* on the basis of material from the Pliocene Yorktown Formation, North Carolina. On the basis of their diagnosis, the separate status of that extinct species was supported by a single character, the possession of an inner row of villiform teeth on the dentary that extends backward from the symphyseal region up to the coronoid process. As discussed above, this character is absent in the fossil *Lopholatilus* from the Calvert Formation.

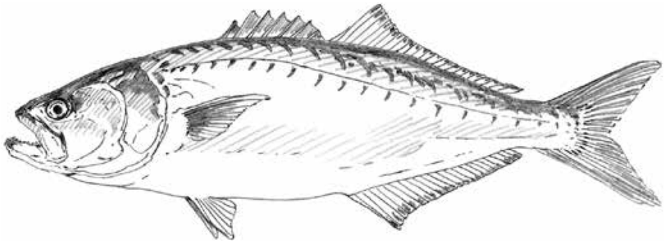
North Atlantic tilefishes of the genus *Lopholatilus* generally occur along the continental slope and the upper reaches of the canyons at depths ranging between 120 and 200 m (Dooley, 1978). *Lopholatilus* has been recorded at depths of more than 500 m. Grimes et al. (1986) recognized two critical habitat requirements for *Lopholatilus*, a temperature range between 9°C and 14°C and shelter; they are known to excavate large vertical and oblique burrows. Carnevale and Godfrey (2014) proposed that certain large (10–25 cm in diameter) cylindrical-shaped trace fossils (dwelling burrows, i.e., domichnia) penetrating the fine-grained sands of the middle part of the Calvert Formation were produced by *Lopholatilus ereborensis*, representing the product of their burrowing activity. Tilefishes of the genus *Lopholatilus* prey on fishes and a variety of invertebrates.

Family Pomatomidae Gill, 1865

Genus *Pomatomus* Lacépède, 1802

***Pomatomus* sp.**

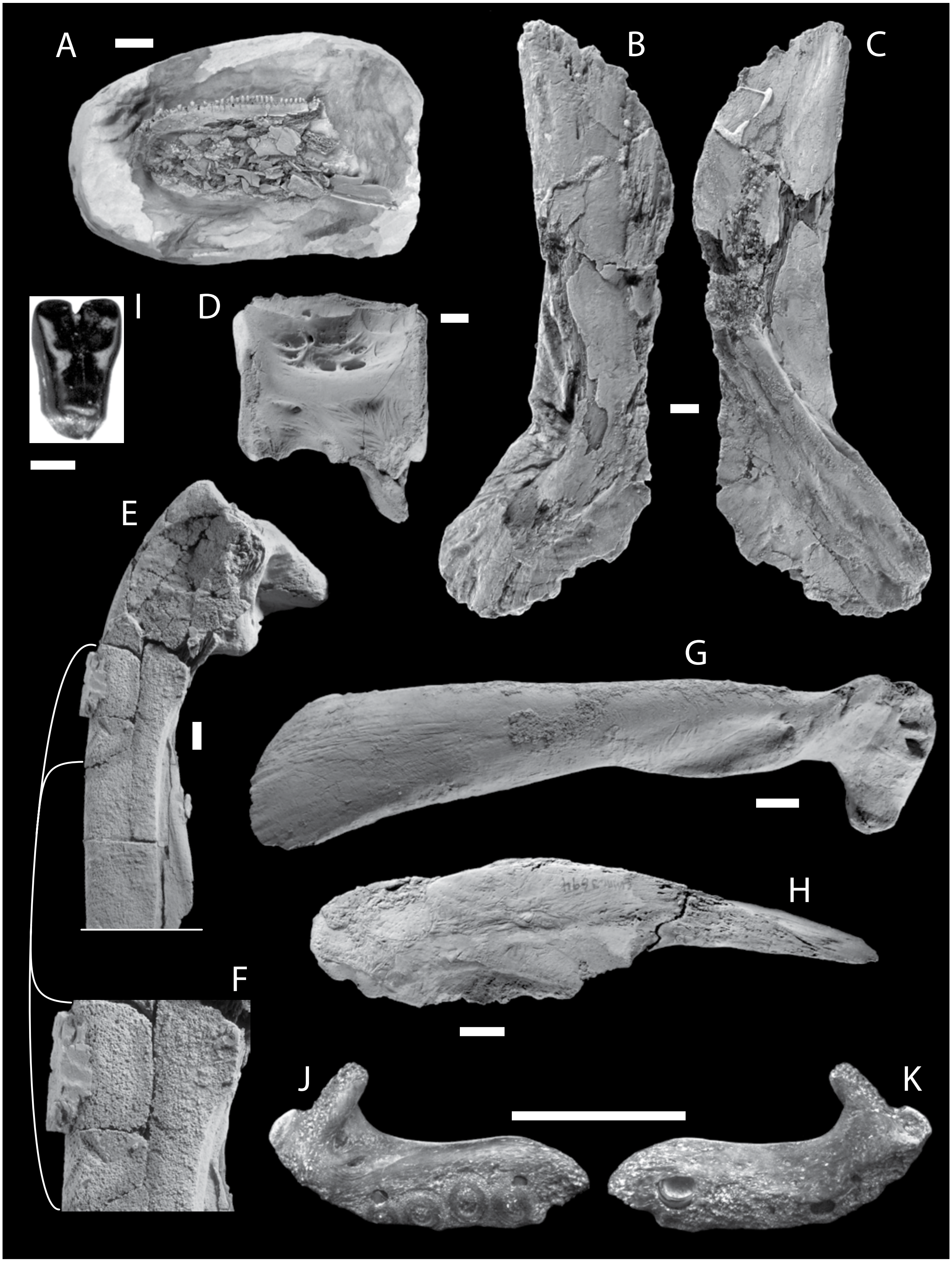
FIGURE 3.8A



Bluefish – *Pomatomus* sp.

Referred Material. CMM-V-1933, partially complete right dentary (Figure 3.8A); CMM-V-3237, isolated tooth.

Horizon. Calvert and St. Marys Formations.


A
B
C
I
D
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K

FIGURE 3.8. (*Facing page*) (A) CMM-V-1933, *Pomatomus* sp., partial right dentary in medial view. Anterior to left. (B, C) CMM-V-3694, *Rachycentron* sp., left preopercle in lateral and medial views, respectively. (D) CMM-V-3694, *Rachycentron* sp., caudal vertebra in lateral view. (E, F) CMM-V-3694, *Rachycentron* sp., premaxilla in ventral view and an enlargement, respectively. Anterior to top. (G) CMM-V-3694, *Rachycentron* sp., left maxilla in medial view. Anterior to right. (H) CMM-V-3694, *Rachycentron* sp., right second pharyngobranchial in ventral view. (I) CMM-V-2023, *Lagodon* sp., isolated tooth. (J, K) CMM-V-3209, *Stenotomus* sp., partial right premaxilla in ventral and dorsal views, respectively. Specimens (except I) are lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm, except for that of (I), the *Lagodon* sp. tooth, which is 1 mm.

REMARKS. The dentary is relatively large, slightly curved, and bears a single row of labiolingually compressed, subtriangular, and deeply socketed teeth along its dorsal margin (Figure 3.8A; Johnson, 1986; Bemis et al., 2005). The symphyseal margin of this bone is strongly thickened and nearly vertical, with a medially curving dorsal portion. A single isolated tooth is also present in the collection of the CMM; it is subtriangular in shape and laterally compressed, identical to those of the extant bluefish *Pomatomus saltatrix*.

The fragmentary nature of the material does not allow for a more detailed taxonomic interpretation, for which much more comparative information would be necessary.

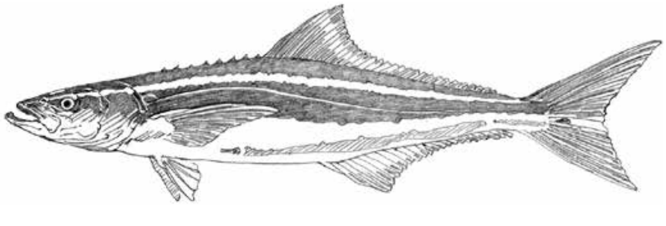
Bluefishes occur in coastal and oceanic tropical and subtropical waters with a circumglobal distribution. Adults often enter estuaries and other brackish-water biotopes. Bluefishes are voracious and aggressive predators that feed on cephalopods, crustaceans, and other fishes.

FAMILY RACHYCENTRIDAE GILL, 1895

Genus *Rachycentron* Kaup, 1826

Rachycentron sp.

FIGURE 3.8B–H



Cobia – *Rachycentron* sp.

REFERRED MATERIAL. CMM-V-3694, several partially articulated bones belonging to a single individual: articulated sclerotic ring, nearly complete right premaxilla (Figure 3.8E,F), nearly complete left maxilla (Figure 3.8G), partially complete left suspensorium, partially complete left preopercle (Figure 3.8B,C), right second pharyngobranchial (Figure 3.8H), nearly complete right posttemporal, and three caudal vertebrae (Figure 3.8D).

HORIZON. Calvert Formation.

REMARKS. The available material consists of a largely incomplete individual collected from bed 11 of the Calvert Formation.

The premaxilla is long and curved, with massive and articular processes; the dentigerous area is extremely expanded, with a large number of tiny alveoli for the insertion of villiform teeth (Figure 3.8E,F). The maxilla is strongly curved and gradually expands posteriorly; the articular head is massive, separated through a deep sulcus from the lateral process; the latter bears a prominent dorsally thickened apophysis anteroventrally connected with the articular head; the posterior margin of the maxilla is nearly vertical, notably expanded, and characterized by a crenulated margin (Figure 3.8G). The suspensorium consists of several bony fragments, among which the anterior palatine articular head for the maxillary facet can be easily recognized. The preopercle is crescent-shaped, with a thickened anterior ridge preceded by a bony shelf (Figure 3.8B,C). What appears to be the second pharyngobranchial is a thick, rodlike bone with a broad anterior articular head and an elongate dentigerous area along its ventral margin (Figure 3.8H). The posttemporal is laterally flattened, elliptical, and elongate, with two anterior processes for neurocranial articulation. The dorsal process is extremely elongate and terminates anteriorly as a dorsoventrally flattened bony lamina; the ventral process is short and round in cross section; a bony lamina is placed between these two processes. The vertebral centra are subrectangular with well-developed dorsolateral fossa and strong ventral prezygapophyses (Figure 3.8D).

None of the available bony elements can be distinguished from those of the extant cobia *Rachycentron canadum*. However, despite this great similarity, the incompleteness of the specimen does not allow for an unambiguous identification at the species level.

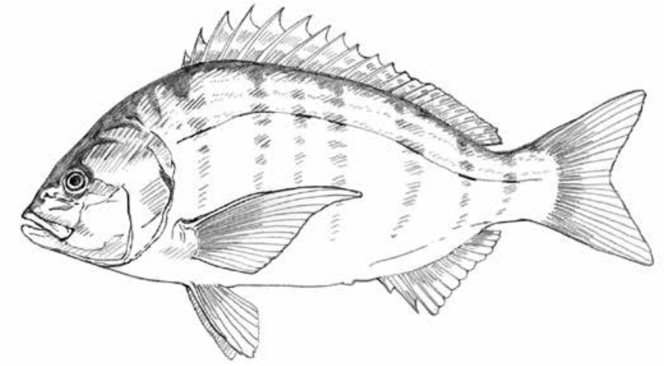
Cobias are marine and occur worldwide in a variety of tropical and subtropical habitats and occasionally enter estuaries and other brackish biotopes, feeding on crustaceans, cephalopods, and other fishes.

FAMILY SPARIDAE BONAPARTE, 1832

Genus *Lagodon* Holbrook, 1855

Lagodon sp.

FIGURE 3.8I



Pinfish – *Lagodon* sp.

Referred Material. CMM-V-2023, isolated tooth (Figure 3.8i); CMM-V-2715, isolated tooth; CMM-V-2778, isolated tooth.

Horizon. Calvert and St. Marys Formations.

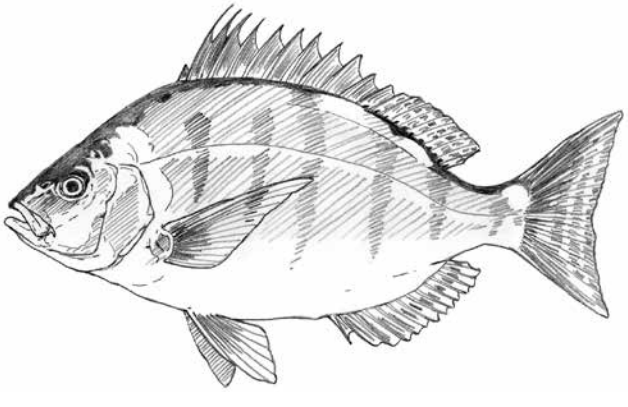
Remarks. The available material consists solely of isolated incisiform teeth with bilobate tips and a base that is rounded in cross section (Figure 3.8i). These teeth are identical to those characteristic of the extant pinfish *Lagodon rhomboides*. Isolated teeth belonging to the genus *Lagodon* were described from the deposits of the St. Marys Formation by Berry (1932).

The pinfish is a shallow marine sparid commonly found to depths of about 70 m on vegetated or rocky bottoms. It commonly enters brackish and freshwater environments. Pinfishes feed primarily on crustaceans and other invertebrates.

Genus *Stenotomus* Gill, 1865

Stenotomus sp.

FIGURE 3.8J,K



Scup – *Stenotomus*

Referred Material. CMM-V-3209, partially complete right premaxilla (Figure 3.8J,K); USNM 559398, partially complete right premaxilla.

Horizon. St. Marys Formation.

Remarks. Both available specimens are represented by right premaxillae characterized by largely incomplete ascending processes. The alveolar process is distally spatulate and bears sockets of rounded, possibly molariform teeth that become gradually larger distally.

Despite their incompleteness, the overall morphology of the premaxillae and the gradual distal enlargement of the teeth are very similar to those found exclusively within the extant Atlantic scup *Stenotomus chrysops*.

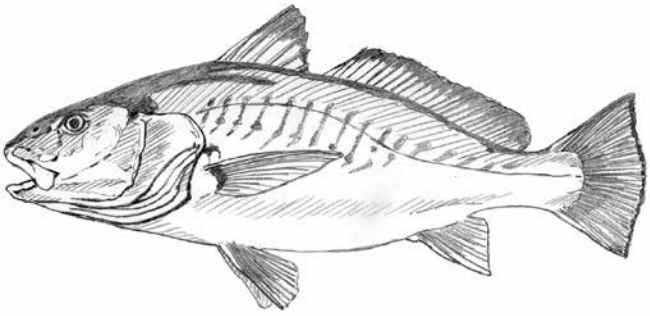
Scups of the genus *Stenotomus* are shallow marine demersal fishes that often enter brackish waters. They feed on a variety of invertebrates, including worms, crustaceans, cephalopods, and echinoderms.

Family Sciaenidae Cuvier, 1829

Genus *Micropogonias* Bonaparte, 1831

Micropogonias sp.

FIGURE 3.9A



Croaker – *Micropogonias* sp.

Referred Material. CMM-V-1688, partially complete left preopercle (Figure 3.9A).

Horizon. Calvert Formation.

Remarks. The available material consists of an incomplete left preopercle. The preopercle is crescent shaped, with a strong thickening along its anterior margin. The posterior margin is serrated, with three short spines and a strong robust spine located at the level of the angle formed by the convergence of the horizontal and vertical arms. A broad shallow laterosensory canal is overlaid by narrow struts that run longitudinally behind the anterior thickening of the bone.

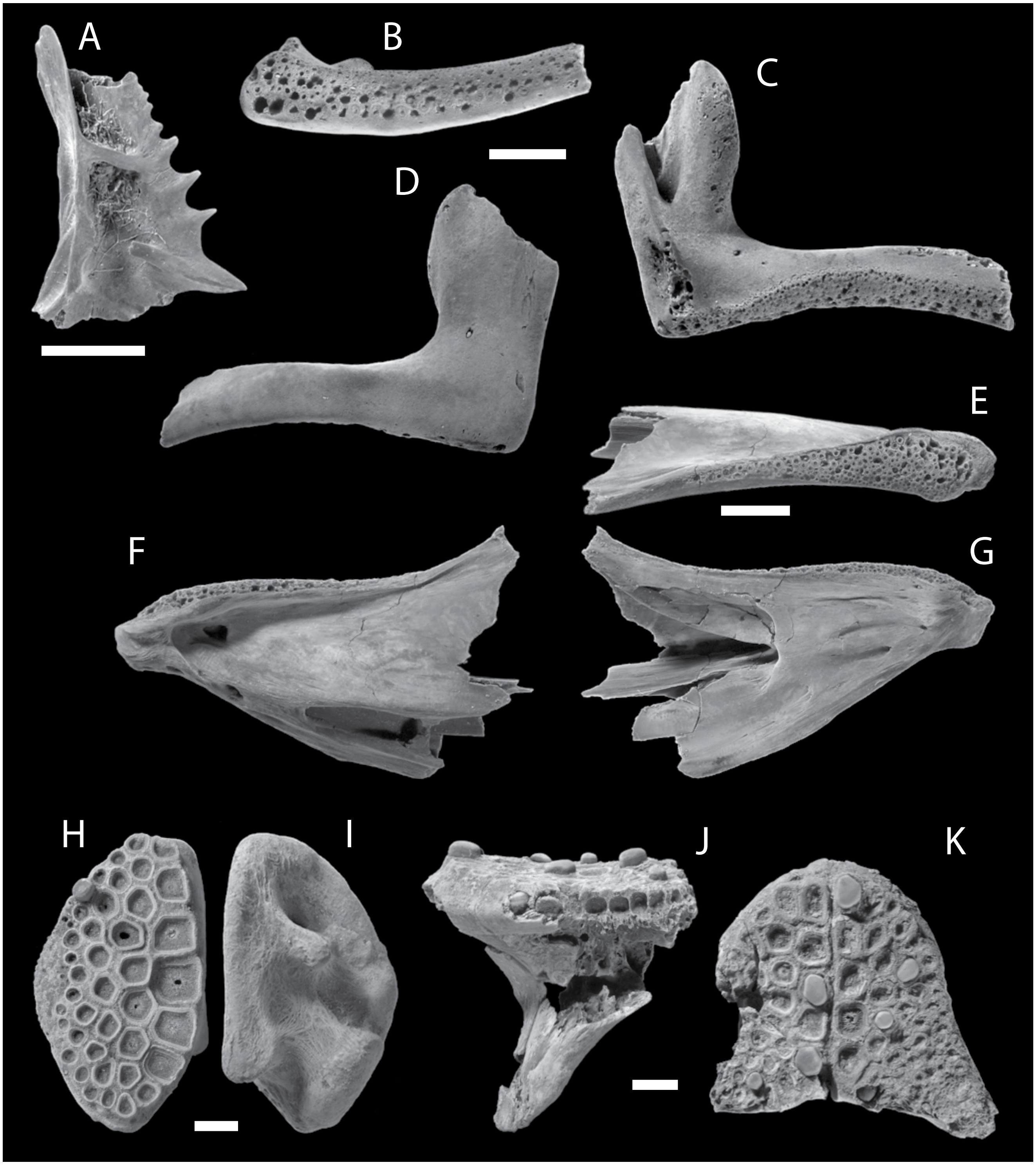


FIGURE 3.9. (A) CMM-V-1688, *Micropogonias* sp., partial left preopercle in lateral view. (B–D) CMM-V-3982, *Pogonias* sp., premaxilla in occlusal, medial, and lateral views, respectively. (E–G) CMM-V-4627, *Pogonias* sp., left dentary in occlusal, lateral, and medial views, respectively. (H, I) CMM-V-2341, *Pogonias* sp., third pharyngobranchial in occlusal and dorsal views, respectively. (J, K) USNM 336494, *Pogonias* sp., partial fifth ceratobranchial in right lateral and occlusal views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

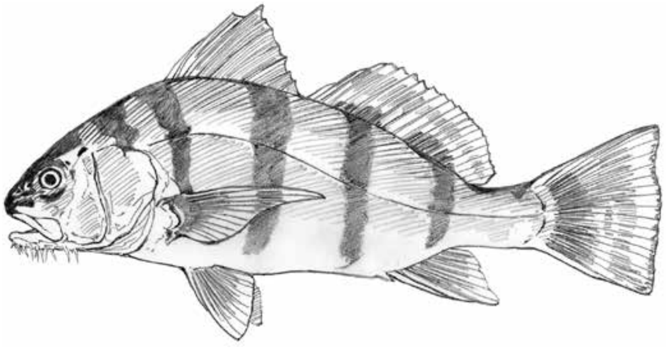
The general morphology of the bone and, in particular, the relative development and position of the spines along its posterior margin are extremely similar to those of the preopercle of the extant species of the genus *Micropogonias*, more specifically to those of the preopercle of the Atlantic croaker *Micropogonias undulatus*.

Croakers of the genus *Micropogonias* are demersal and usually occur in coastal marine or brackish waters over soft bottoms, where they feed on worms, crustaceans, and fishes.

Genus *Pogonias* Lacépède, 1801

Pogonias sp.

FIGURES 3.9B–K, 10



Black Drum – *Pogonias* sp.

Referred Material. CMM-V-173, isolated pharyngeal tooth; CMM-V-201, isolated pharyngeal tooth; CMM-V-272, 23 isolated pharyngeal teeth and partial maxilla; CMM-V-280, nearly complete dentary; CMM-V-328, two isolated pharyngeal teeth; CMM-V-951, partial third pharyngobranchial; CMM-V-1045, isolated pharyngeal tooth; CMM-V-1067, two isolated pharyngeal teeth; CMM-V-1093, isolated pharyngeal tooth; CMM-V-1168, isolated pharyngeal tooth; CMM-V-1375, isolated pharyngeal tooth; CMM-V-1394, isolated pharyngeal tooth; CMM-V-1778, isolated pharyngeal tooth; CMM-V-2142, isolated pharyngeal teeth; CMM-V-2258, isolated pharyngeal tooth; CMM-V-2341, four partial third pharyngobranchials (Figure 3.9H,I) and a single partial fifth ceratobranchial; CMM-V-2372, isolated pharyngeal tooth; CMM-V-2377, six isolated pharyngeal teeth; CMM-V-2584, two isolated pharyngeal teeth; CMM-V-2655, isolated pharyngeal teeth; CMM-V-2779, nine isolated pharyngeal teeth; CMM-V-2793, two isolated pharyngeal teeth; CMM-V-3071, partial third pharyngobranchial; CMM-V-3382, partial third pharyngobranchial; CMM-V-3392, third pharyngobranchial; CMM-V-3566, two complete premaxillae; CMM-V-3794, two third pharyngobranchials; CMM-V-3962, partially complete third pharyngobranchial; CMM-V-3982, premaxilla (Figure 3.9B–D); CMM-V-3999, premaxilla; CMM-V-4100, partially complete third pharyngobranchial; CMM-V-4203, four isolated pharyngeal teeth; CMM-V-4226, partially complete third pharyngobranchial; CMM-V-4254, two isolated pharyngeal teeth; CMM-V-4314, two third pharyngobranchials; CMM-V-4532, two partially complete third pharyngobranchials; CMM-V-4627, dentary (Figure 3.9E–G); USNM 13904, third pharyngobranchial; USNM 16362, partially complete fifth ceratobranchial; USNM 336494, partially complete fifth ceratobranchial (Figure 3.9J,K); USNM 542408, poorly preserved posterior portion of the neurocranium (Figure 3.10A,B); USNM 542409, poorly preserved posterior portion of the neurocranium; USNM uncataloged, extensively fragmented neurocranial remains and a single premaxilla and nine partial third pharyngobranchials.

Horizon. Calvert, Choptank, St. Marys, and Eastover Formations.

Remarks. The available material consists primarily of cranial and branchial bones, dominated by the massive and robust pharyngeal plates (third pharyngobranchials and fifth ceratobranchials), which, presumably because they are so robust, seem predisposed to becoming fossilized. The neurocranial remains, even if scarcely preserved, exhibit the characteristic parasphenoid with a flat semicircular facet encircled by a thin crest-like rim (Figure 3.10A,B), which is functionally associated with the upper pharyngeal jaws (e.g., Stiassny and Jensen, 1987; Sasaki, 1989).

The premaxilla bears an anteroposteriorly flattened elongate ascending process that gradually tapers dorsally and an oblong, well-developed articular process (Figure 3.9B–D). The alveolar process is relatively short, with numerous sockets of varying sizes, of which the anterior ones and those of the labial row are more developed. The dentary is relatively short and subtriangular in outline and tapers conspicuously anteriorly; the symphyseal surface is flattened and obliquely oriented; in dorsal view, the alveolar surface has an elongate teardrop shape, with many small circular alveoli (Figure 3.9E–G). A wide furrow through which the mandibular laterosensory canal passes is clearly exposed along the lateral surface of this bone (Figure 3.9F).

The upper pharyngeal jaw (third pharyngobranchial) is massive, elongate, and roughly ovoid in outline (Figure 3.9H,I); its dorsal surface is characterized by a thick ridge along the medial margin. At about the midpoint in the length of this ridge, a strong rounded process for the articulation of the second epibranchial originates and passes posterolaterally toward the center of the bone. Most of the occlusal surface is occupied by 28 to 45 thick, rounded to polygonal molariform crushing teeth of varying sizes. The lateral portion of the occlusal surface exhibits several alveoli for small conical teeth. The lower pharyngeal jaw is very large and massive and consists of the fully coalesced fifth ceratobranchials forming a single unit characterized by an interdigitating suture between the elements (Figure 3.9J,K; see Chao, 1978; Sasaki, 1989; Grubich, 2003), a unique condition of the genus *Pogonias*. The occlusal surface of the lower pharyngeal jaw bears a varying number of rounded to polygonal molariform crushing teeth.

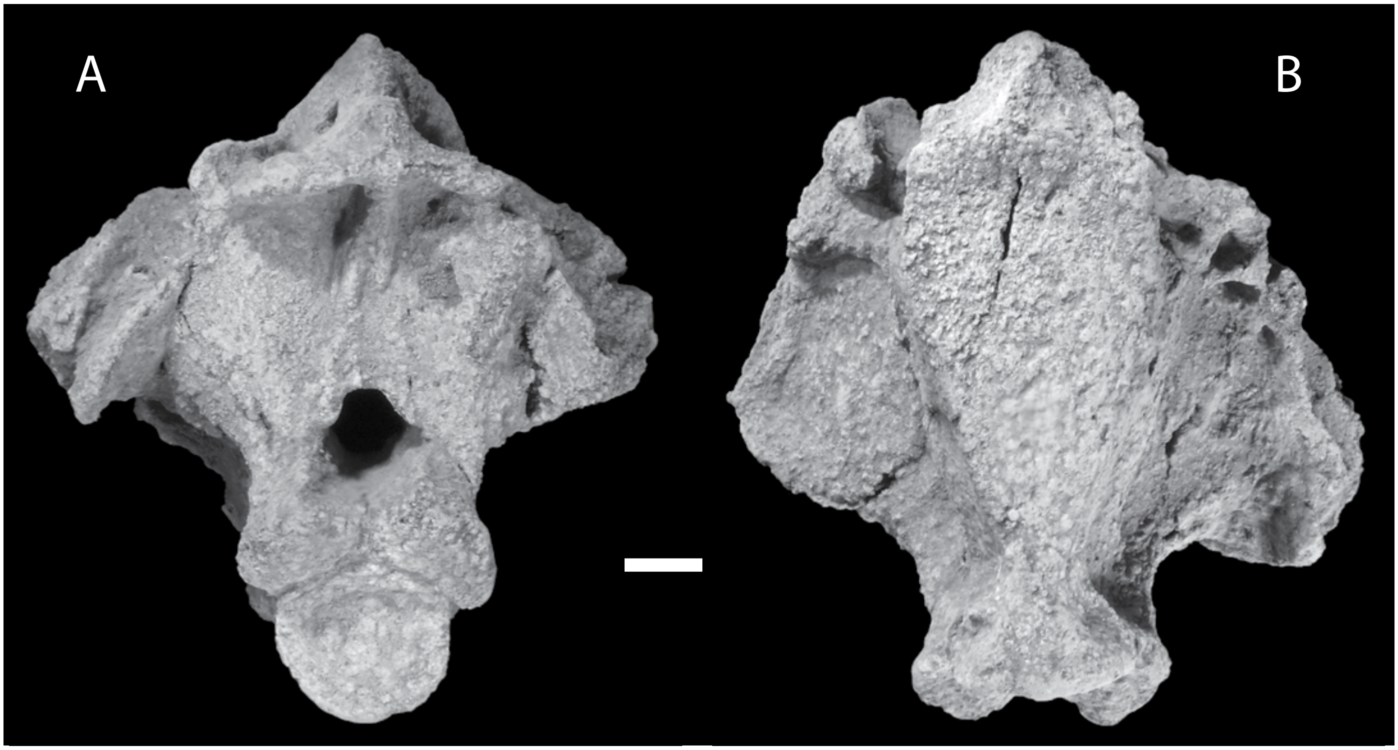


FIGURE 3.10. (A, B) USNM 542408, *Pogonias* sp., poorly preserved posterior portion of the neurocranium in posterior and ventral views, respectively. Specimen is lightly coated with sublimed ammonium chloride. Scale bar equals 10 mm.

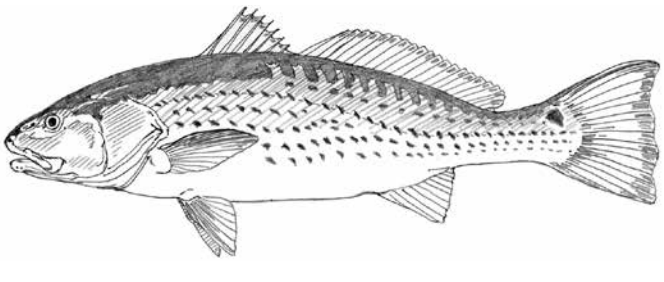
The overall morphology of the upper pharyngeal jaws is extremely similar to that of the extant black drum *Pogonias cromis*; moreover, the number of crushing teeth of each upper pharyngeal element is also within the range of this species. Cope (1869) described the fossil species *Pogonias multidentatus* on the basis of a single upper pharyngeal bone from the Calvert Formation of Westmoreland County, Virginia, characterizing it as having a higher number of molariform teeth on its occlusal surface compared to the extant black drum. Just like the specimen reported by Cope (1869; but see also Smith, 1909; Purdy et al., 2001), some of the upper pharyngeal jaws available to us have 45 molariform teeth, which is more than in the extant species. A cursory comparative analysis of the extant *Pogonias* pharyngeal apparatus reveals broad variability in the number of molariform teeth (22–43) in the occlusal surface of the upper pharyngeal jaws of the black drum, thereby suggesting that the number of molariform teeth in the upper pharyngeal jaw does not represent a valid diagnostic character for the discrimination of the species within the genus *Pogonias*. As a consequence, *Pogonias multidentatus* should be regarded as a nomen dubium.

Black drums occur in brackish and shallow water and are very common over muddy and sandy bottoms, especially in areas with large river runoffs. They feed mostly on mollusks, crustaceans, and fishes.

Genus *Sciaenops* Gill, 1863

Sciaenops sp.

FIGURES 3.11–13



Red Drum – *Sciaenops* sp.

Referred Material. CMM-V-132, opercle (Figure 3.12G); CMM-V-139, opercle and a single vertebral centrum and several pleural ribs; CMM-V-144, opercle; CMM-V-157, premaxilla; CMM-V-166, premaxilla (Figure 3.11A–C); CMM-V-162, two dentaries; CMM-V-167, premaxilla; CMM-V-271, first abdominal vertebra; CMM-V-276, premaxilla; CMM-V-319, 13 vertebrae belonging to a single individual (Figure

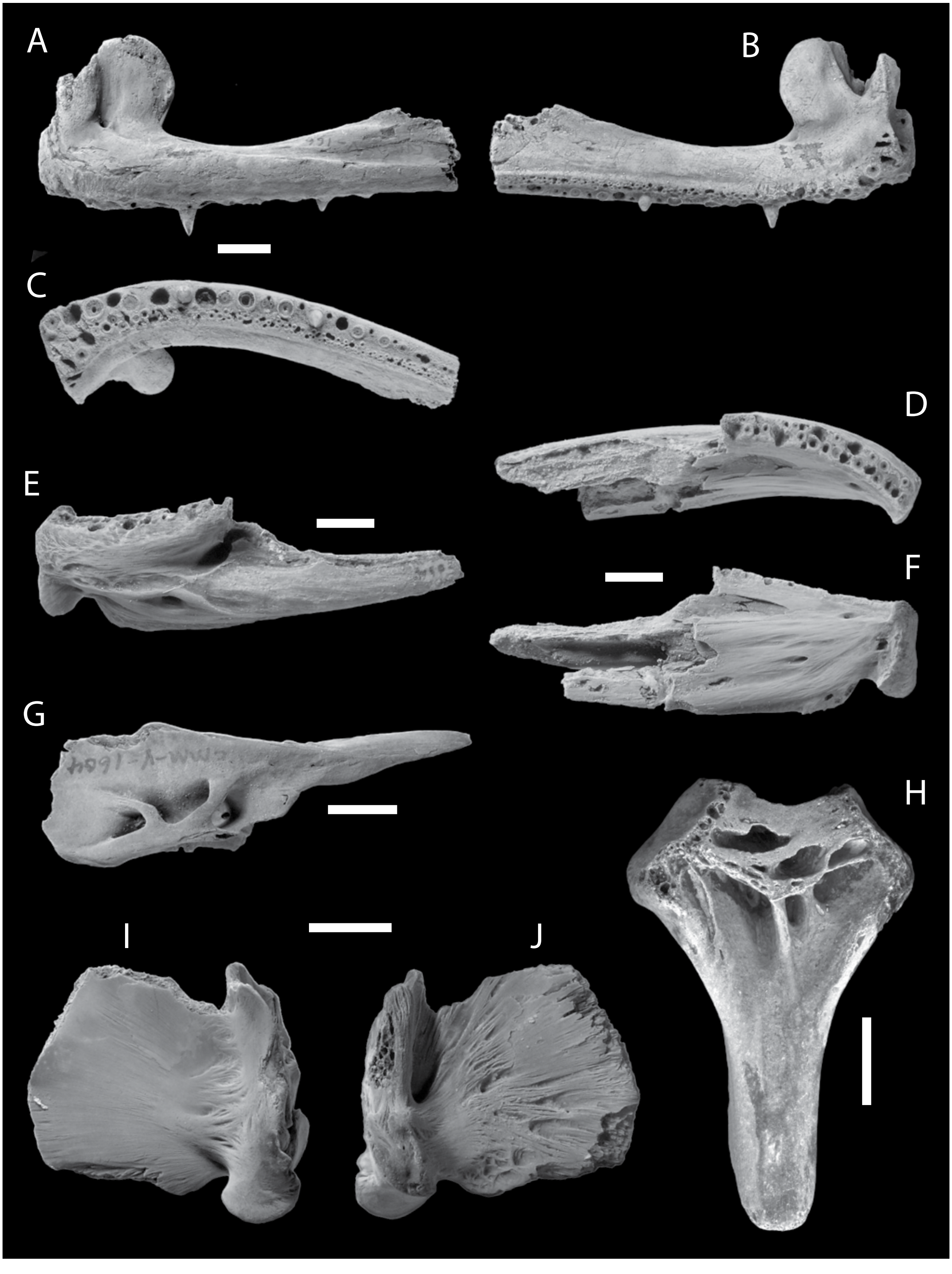

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FIGURE 3.11. (*Facing page*) (A–C) CMM-V-166, *Sciaenops* sp., left premaxilla in lateral, medial, and occlusal views, respectively. (D–F) CMM-V-977, *Sciaenops* sp., left dentary in occlusal, lateral, and medial views, respectively. (G) CMM-V-1604, *Sciaenops* sp., posttemporal in lateral view. (H) CMM-V-3234, *Sciaenops* sp., vomer in ventral view. (I, J) CMM-V-3205, *Sciaenops* sp., right quadrate in lateral and medial views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

3.13A–F); CMM-V-836, premaxilla; CMM-V-896, maxilla; CMM-V-954, lachrymal and opercle; CMM-V-977, dentary (Figure 3.11D–F); CMM-V-1259, premaxilla; CMM-V-1436, articular (Figure 3.12A,B); CMM-V-1600, premaxilla; CMM-V-1604, posttemporal (Figure 3.11G); CMM-V-1721, isolated scale; CMM-V-1781, isolated scale; CMM-V-1868, vomer; CMM-V-1912, premaxilla; CMM-V-2134, premaxilla; CMM-V-2185, premaxilla; CMM-V-2340, premaxilla; CMM-V-2341, three third pharyngobranchials; CMM-V-2356, partial anguloarticular with associated retroarticular (Figure 3.12C,D); CMM-V-2357, dentary; CMM-V-2423, premaxilla; CMM-V-2457, premaxilla; CMM-V-2503, third pharyngobranchial; CMM-V-2786, premaxilla; CMM-V-2954, four premaxillae and two dentaries; CMM-V-2964, first abdominal vertebra; CMM-V-3026, maxilla; CMM-V-3038, opercle; CMM-V-3074, isolated scale; CMM-V-3116, preopercle (Figure 3.12F); CMM-V-3205, quadrate (Figure 3.11 I,J); CMM-V-3234, vomer (Figure 3.11H); CMM-V-3242, palatine; CMM-V-3243, isolated scales; CMM-V-3254, dentary; CMM-V-3395, maxilla; CMM-V-3398, single scale; CMM-V-3460, premaxilla; CMM-V-3462, several scales; CMM-V-3476, palatine; CMM-V-3517, vertebral centrum; CMM-V-3566, three premaxillae and six maxillae, five dentaries, and a single hyomandibula (Figure 3.12E); CMM-V-3567, several vertebral centra; CMM-V-3719, isolated scales and lepidotrichia (Figure 3.13G); CMM-V-3725, two maxillae and four dorsal spines; CMM-V-3735, premaxilla; CMM-V-3798, eight premaxillae and a single dentary; CMM-V-3928, premaxilla; CMM-V-3954, premaxilla; CMM-V-3969, two premaxillae; CMM-V-3974, vomer; CMM-V-4039, opercle; CMM-V-4098, partially complete preopercle; CMM-V-4119, nine opercles and several dorsal-fin spines; CMM-V-4135, opercle; CMM-V-4169, third pharyngobranchial; CMM-V-4249, four opercles; CMM-V-4280, opercle; CMM-V-4294, third pharyngobranchial; CMM-V-4311, 10 premaxillae and two maxillae, a single quadrate, and several isolated vertebrae and dorsal-fin spines; CMM-V-4313, third pharyngobranchial; CMM-V-4493, nearly complete hyoid bar (Figure 3.12I); CMM-V-4529, two maxillae; CMM-V-4554, three opercles and three hypobranchials; CMM-V-4626, third pharyngobranchial (Figure 3.12H); CMM-V-4628, two partial opercles and a single hyoid bar; USNM 387748, premaxilla; USNM uncataloged, four premaxillae, four dentaries, a single anguloarticular with an articulated retroarticular, and a single opercle.

Horizon. Calvert, Choptank, St. Marys, and Eastover Formations.

Remarks. The material referred to the genus *Sciaenops* consists mostly of isolated cranial bones collected throughout the Chesapeake Group.

The vomer is diamond shaped and toothless, with a cavernous ventral surface characterized by thick irregular struts (Figure 3.11H); the vomerine lateral process has broad and flat to slightly convex facets.

The posttemporal is laminar and approximately triangular in outline (Figure 3.11G). It possesses an elongate and dorsoventrally flattened dorsal arm that tapers anteriorly into a blunt spine; the posterior portion of the bone consists of a laterally compressed and flat bony lamina marked by a trough for the laterosensory canal. The infraorbital branch of the laterosensory canal occupies most of the ventral portion of this bone, with two external large fenestrae separated from each other by a large laminar strut.

The premaxilla has a large and anteroposteriorly flattened ascending process nearly perpendicular to the alveolar process and an articular process with a thickened and gently rounded posterior margin and relatively low postmaxillary process (Figure 3.11A–C). The alveolar process is elongate, with an outer row of large conical teeth that increase in size toward the symphysis and a dense inner band of villiform teeth that also increase in size anteriorly, reaching remarkable size in the lingual row (Figure 3.11C). The proximal portion of the maxilla is characterized by a large articular head with slightly concave anterior facets of irregular shapes; the articular head is continuous posteriorly with a laterally compressed shank from which it is separated through a marked notch for the articulation of the palatine. All available dentaries are incomplete; the alveolar surface is occupied by a dense series of closely spaced sockets for strongly pointed teeth (Figure 3.11D–F). The thick symphyseal margin is nearly vertical, and there is a deep notch along the anteroventral margin. A relatively deep furrow that held the mandibular laterosensory canal is clearly visible along the lateral surface of the dentary. The anguloarticular is massive, with a large articular condyle for the quadrate (Figure 3.12C,D); along the lateral surface of the anguloarticular there is a deep trough for the mandibular laterosensory canal, which is partially arched by a relatively narrow, flat laminar strut. The thick retroarticular caps the posteroventral corner of the mandible.

The quadrate is flat and rectangularly shaped, with a nearly vertical anterior edge, an extremely large and thickened transverse articular head, and a large medial recess to accommodate the symplectic (Figure 3.11 I,J). The transverse development of

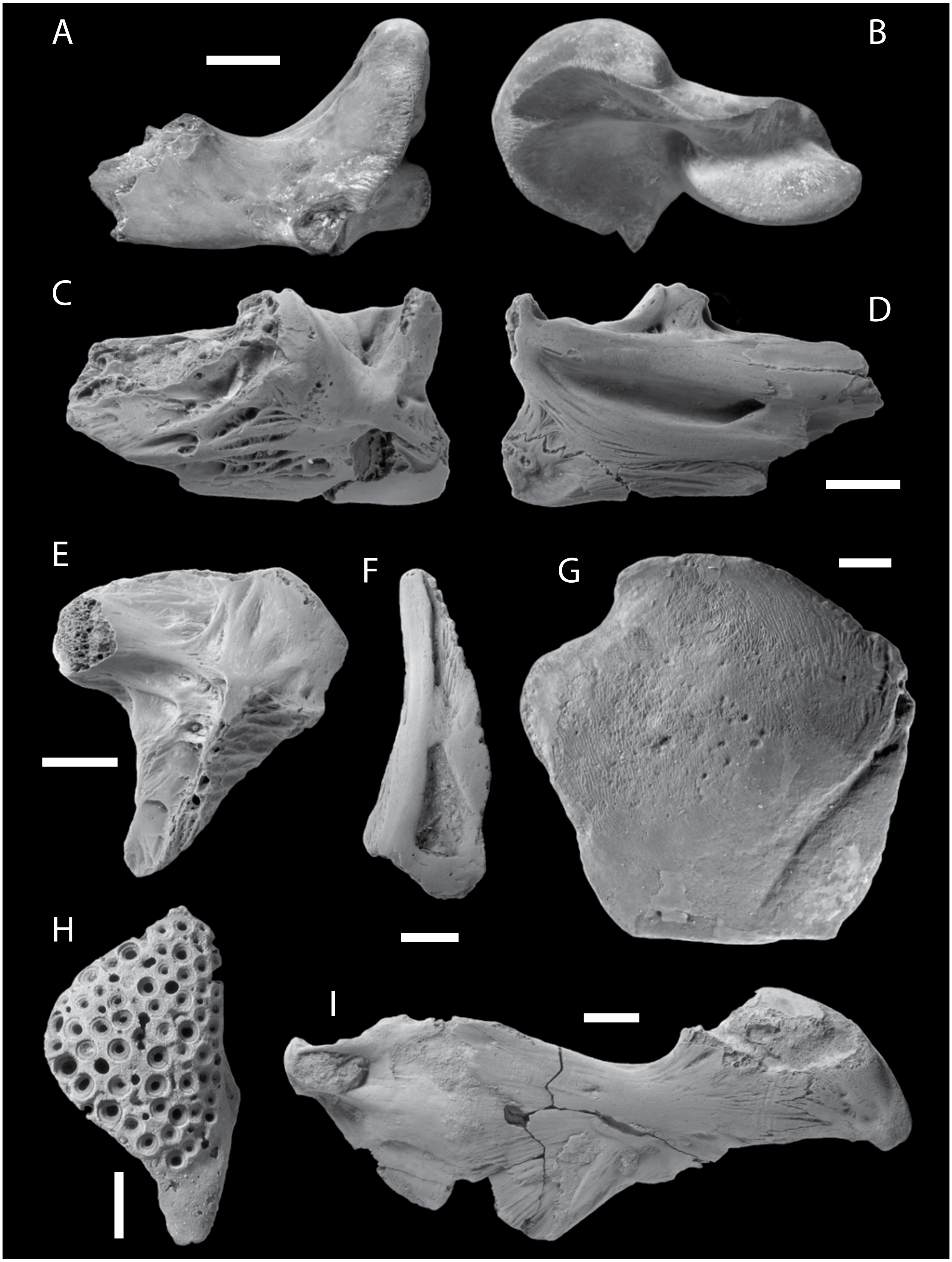
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FIGURE 3.12. (*Facing page*) (A, B) CMM-V-1436, *Sciaenops* sp., anguloarticular. (C, D) CMM-V-2356, *Sciaenops* sp., left partial anguloarticular with associated retroarticular in medial and lateral views, respectively. (E) CMM-V-3566, *Sciaenops* sp., hyomandibula in lateral view. (F) CMM-V-3116, *Sciaenops* sp., preopercle in lateral view. (G) CMM-V-132, *Sciaenops* sp., opercle in lateral view. (H) CMM-V-4626, *Sciaenops* sp., third pharyngobranchial in occlusal view. (I) CMM-V-4493, *Sciaenops* sp., nearly complete hyoid bar. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

the articular head extends to the whole posterior of the bone. The palatine is a toothless bone with a robust thickened anterior ethmoid process. Both the rostropalatine (anterior) and ethmopalatine (posterior) facets for the connection with the lateral ethmoid are well developed. Only a partial left hyomandibula is available for comparative analysis (Figure 3.12E); it bears an anterior articular head and an anterodorsal lens-shaped condyle for articulation with the prootic and sphenotic. A well-developed lateral crest can be observed along the main shaft of the bone; both lateral and medial surfaces are ornamented by a complex cavernous system of irregular ridges, furrows, and pits.

The preopercle is crescent-shaped (Figure 3.12F), with a strongly thickened anterior margin and a finely serrated posterior margin; the configuration of the canal for the laterosensory system is clarified by five external fenestrae separated from each other by relatively large laminar horizontal struts that overlie the canal itself. The opercle is large, massive, and apparently quadrangular in shape (Figure 3.12G), with a convex dorsal margin and a finely sculptured outer surface characterized by delicate and irregular elongate ridges. Its anterior margin is conspicuously thickened, but it terminates at the anterodorsal corner of the bone with a rounded articular facet for the opercular process of the hyomandibula. A shallow furrow that passes vertically parallel to the anterior thickening of the bone represents the trough for the opercular branch of the facial nerve. Additionally, a strong ridge originates from the anterodorsal corner and terminates posteriorly as a blunt spine with a rounded profile; another spine is located ventral to the major one, separated from it by a shallow concavity.

The hyoid bar is relatively large and robust (Figure 3.12I). The dorsal hypohyal is extremely thick and irregular in shape, with a slightly concave recess for the basibranchial articulation along its medial surface. The ventral hypohyal is conical, with a robust anteroventral process. The anterior ceratohyal is the largest bone of the hyoid bar; it is laterally compressed and hourglass shaped, with a low laminar median process emerging along its ventral margin. The posterior ceratohyal is triangular and laterally compressed.

The upper pharyngeal plate (third pharyngobranchial) appears to be approximately quadrangular in outline. The occlusal surface is flattened to gently convex and completely covered with large and thick conical teeth, in many cases represented by their sockets. The third hypobranchial is short and clavate, with a flattened dorsal surface.

The atlas (first abdominal vertebra) has a very short disk-shaped centrum with an autogenous neural spine, two large anterodorsal condylar surfaces, and posteriorly directed lateral apophyses (Figure 3.13A,B). The second abdominal vertebra is short and disk-shaped, with well-developed dorsal prezygapophyses, posteriorly directed lateral apophyses, and a deep fossa for epineural insertion on the laterodorsal surface of the centrum at the base of the neural arch (Figure 3.13C,D). The third vertebra has a short centrum with well-developed dorsal prezygapophyses, reduced lateral apophyses, and dorsolaterally large fossa for the insertion of pleural ribs (Figure 3.13E). The other abdominal vertebrae are subrectangular (longer than high), with short postzygapophyses, parapophyses, and deep and large lateral fossae (Figure 3.13F; mesonephros pits sensu Topp and Cole, 1968). Some abdominal centra possess a thin osseous bridge across the contralateral parapophyses. The caudal vertebrae are rectangular, longer than high, and morphologically uniform, with two deeply ornamented lateral fossae separated from each other by a strengthening ridge.

The scales are large, feebly ctenoid, and subrectangular to ovoid, with a gently rounded posterior margin (Figure 3.13G).

The classification of the taxa of the family Sciaenidae is based primarily on characters that are not observable (otolith, swim bladder, etc.) in the preserved fossils (e.g., Chao, 1978). However, a comparative osteological analysis of the fossils documented herein has revealed a close similarity to the extant red drum *Sciaenops ocellata*. In particular, the dentition pattern and the morphology of the premaxilla, articular head of the maxilla, opercle, and third pharyngobranchial are clearly diagnostic of the genus *Sciaenops* (Sasaki, 1989; Grubich, 2003). The fossil material cannot be confidently accommodated within the variability of *Sciaenops ocellata* because there are some remarkable differences that might support a separate specific status, including the extremely variable size of the dentary teeth of the inner band, most notably the enlarged ones in the symphyseal area, the presence of an osseous bridge across the parapophyses of the posterior abdominal vertebrae, and the disk-shaped morphology and reduced size of the two anteriormost vertebral centra.

The red drum is demersal and typically is found in coastal marine and brackish waters from Massachusetts to northern Mexico. It feeds primarily on mollusks, crustaceans, and fishes.

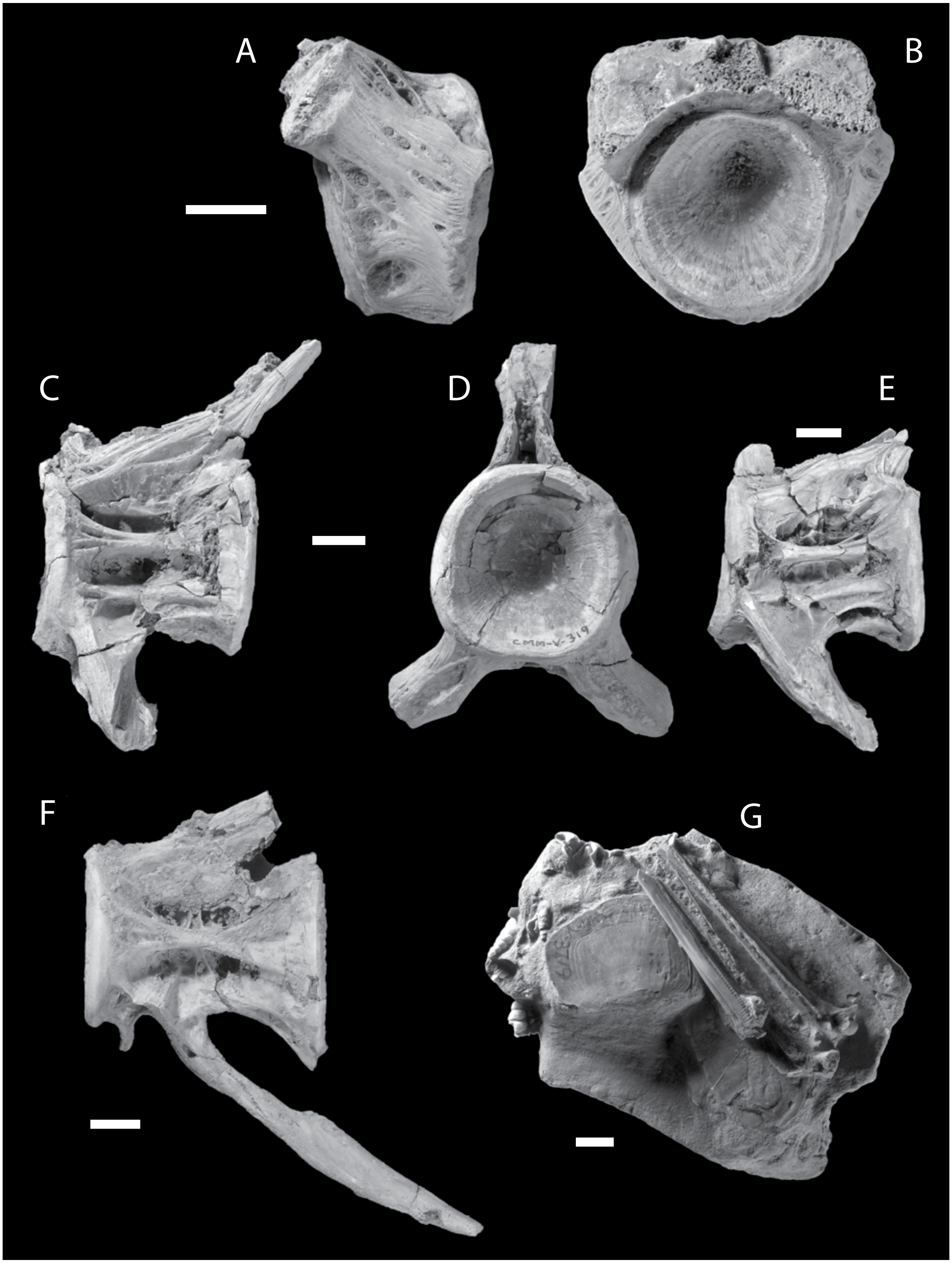
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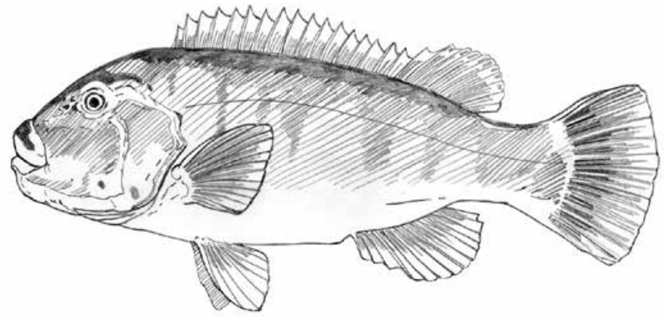
FIGURE 3.13. (*Facing page*) (A, B) CMM-V-319, *Sciaenops* sp., atlas vertebra in left lateral and anterior views, respectively. (C, D) CMM-V-319, *Sciaenops* sp., second abdominal vertebra in left lateral and anterior views, respectively. (E) CMM-V-319, *Sciaenops* sp., third vertebra in left lateral view. (F) CMM-V-319, *Sciaenops* sp., posterior abdominal vertebra in left lateral view. (G) CMM-V-3719, *Sciaenops* sp., isolated scales and lepidotrichia. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

FAMILY LABRIDAE CUVIER, 1817

Genus *Tautoga* Mitchill, 1814

Tautoga sp.

FIGURE 3.14A



Tautog – *Tautoga* sp.

1873 *Protautoga conidens* Leidy – (Leidy, 1873c)
1902 *Tautoga conidens* (Leidy, 1873c) – Hay, p. 401.

Referred Material. CMM-V-327, partially complete right premaxilla; CMM-V-4138, left upper third pharyngobranchial; CMM-V-4160, premaxillary tooth; CMM-V-4395, partially complete right premaxilla and three isolated teeth; CMM-V-4632, partially complete left premaxilla (Figure 3.14A); USNM uncataloged, fragmentary pharyngeal jaw.

Horizon. Calvert, St. Marys, and Eastover Formations.

Remarks. The available premaxillae are incomplete, lacking the ascending (and fused articular) process (Figure 3.14A). The anteriormost tooth of each premaxilla is the largest and is characterized by an elongate pedicel that sustains a massive thick crown of variable morphology, from blunt and rounded to incisiform and paddle shaped to approximately pointed. The teeth are arranged in two rows, the outer characterized by widely separated large elements, whereas the inner consists of small incompletely erupted elements. The upper pharyngeal jaws (third pharyngobranchials) are subtriangular in shape, with teeth characterized by blunt rounded crowns of varying sizes.

The morphology of the premaxillae, pharyngeal jaws, and teeth are very similar to those of the extant tautog *Tautoga onitis*. The fossils are therefore referred to the genus *Tautoga*; however, because of the fragmentary nature of the available material, it is not possible to extend the taxonomic identification to the species level. According to Purdy et al. (2001), the fossil species *Protautoga conidens* established by Leidy (1873a) on the basis of an incomplete premaxilla from the Miocene of Virginia (see also Leriche, 1942) must be considered a junior synonym of *Tautoga onitis*.

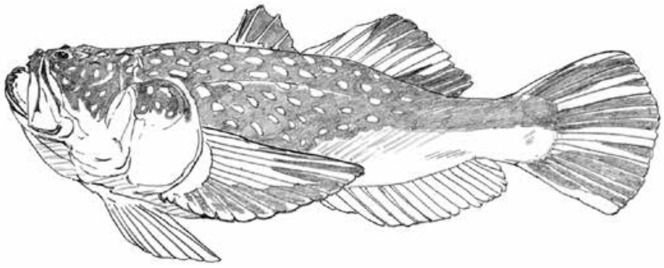
The tautog is a western north Atlantic demersal species typical of hard-bottom habitats at depths up to 75 m. It occasionally enters brackish waters. The tautog diet consists primarily of worms, mollusks, and crustaceans.

FAMILY URANOSCOPIDAE BLEEKER, 1859

Genus *Astroscopus* Brevoort in Gill, 1860

Astroscopus countermani Carnevale, Godfrey, & Pietsch, 2011

FIGURE 3.14B–E



Stargazer – *Astroscopus countermani*

Type Material. CMM-V-4231 (Figure 3.14B–E), holotype, nearly complete neurocranium and a nearly complete right hyomandibula; CMM-V-2022, paratype, partially complete neurocranium.

Horizon. St. Marys Formation.

Remarks. The available material was described in detail and illustrated by Carnevale et al. (2011). According to these authors, the fossils exhibit a number of features that strongly support their placement as a new species of the stargazer genus *Astroscopus*. The neurocranium is short, broad, and dorsoventrally depressed, with a rugose or strongly sculptured outer surface (Figure 3.14B–E). The postorbital portion of the neurocranium is longer than the orbital portion and is laterally expanded, with the distance between the lateral tips of the lateral ethmoids representing less than 60% of the measurement taken between the outermost margins of the sphenotics. The neurocranial length represents more than 90% of its width. The interorbital anterolateral processes of the frontals are broad, not constricted at their bases, with the width of the interorbital region representing 27% of the neurocranial width. The posterior region of the frontal has a large anterolateral expansion that results in the nearly complete exclusion of the sphenotic from the cranial roof. The large parietals are rectangular. The anterolateral corner of the sphenotic is prominent and forms a short posterolateral border of the orbit. The hyomandibula is characterized by having a prominent tuberosity arising from its dorsolateral surface, large and elongate articular heads, and a well-developed anteriorly directed spur.

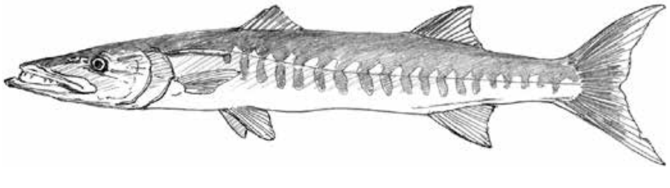
Carnevale et al. (2011) hypothesized that *Astroscopus countermani* was a predatory fish that inhabited the subtropical and warm temperate Atlantic coasts of North America during the Miocene, living in shallow marine and paralic waters nearly totally buried in muddy or sandy substrates.

FAMILY SPHYRAENIDAE RAFINESQUE, 1815

Genus *Sphyraena* Klein, 1778

Sphyraena sp.

FIGURE 3.14F



Barracuda – *Sphyraena* sp.

REFERRED MATERIAL. CMM-V-1063, CMM-V-1098, CMM-V-2376, CMM-V-2776, CMM-V-3198, CMM-V-3335, CMM-V-3580, isolated tooth (Figure 3.14F); USNM uncataloged, 21 isolated teeth.

HORIZON. Calvert, St. Marys, and Eastover Formations.

REMARKS. The presence of barracudas in the Miocene deposits of the Chesapeake Group is evidenced exclusively by isolated teeth (Figure 3.14F). The teeth are lanceolate, labiolingually compressed, in some cases with a slightly sigmoid cutting edge, and ornamented with short and discontinuous vertical striae. Premaxillary teeth appear to be characterized by a postapical barb (Nishimoto and Ohe, 1982), as seen in Figure 3.14F.

Sphyraenid teeth do not show diagnostic characters to differentiate one species from another. Leidy (1873a) described a sphyraenid, *Sphyraena speciosa* on the basis of isolated teeth from the Calvert Formation, Virginia; this species was also reported from the Miocene of Maryland by Cope (1867). On the basis of his description, it is not possible to detect any diagnostic feature to distinguish such a species from other sphyraenids, thereby suggesting that *S. speciosa* should be considered a nomen dubium.

Barracudas occupy a wide range of marine and brackish habitats, where they live predominantly near the surface. They are voracious predators that feed primarily on fishes and cephalopods and occasionally on crustaceans.

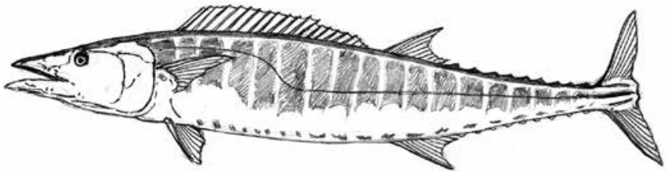
FAMILY SCOMBRIDAE RAFINESQUE, 1815

REMARKS. Kimmel and Purdy (1984) illustrated some scombrid bones that they referred to an indeterminate species of the genus *Katsuwonus*. A morphological analysis of that material has not revealed any diagnostic character of *Katsuwonus,* and it is therefore interpreted as belonging to an indeterminate scombrid taxon. Indeterminate scombrid remains from the Calvert Formation were previously reported by Leriche (1942).

Genus *Acanthocybium* Gill, 1862

Acanthocybium cf. *solandri* (Cuvier, 1832 in Cuvier & Valenciennes, 1831)

FIGURE 3.15



Wahoo – *Acanthocybium* cf. *solandri*

REFERRED MATERIAL. CMM-V-137, hypural complex; CMM-V-158, dentary fragment; CMM-V-159, partial right dentary; CMM-V-160, left premaxilla (Figure 3.15A,B); CMM-V-284, partially complete left dentary; CMM-V-322, dentary fragment; CMM-V-357, premaxillary fragment; CMM-V-1598, partially complete right dentary; CMM-V-1812, partially complete right dentary (Figure 3.15C,D); CMM-V-2010, dentary fragment; CMM-V-2332, partially complete left dentary

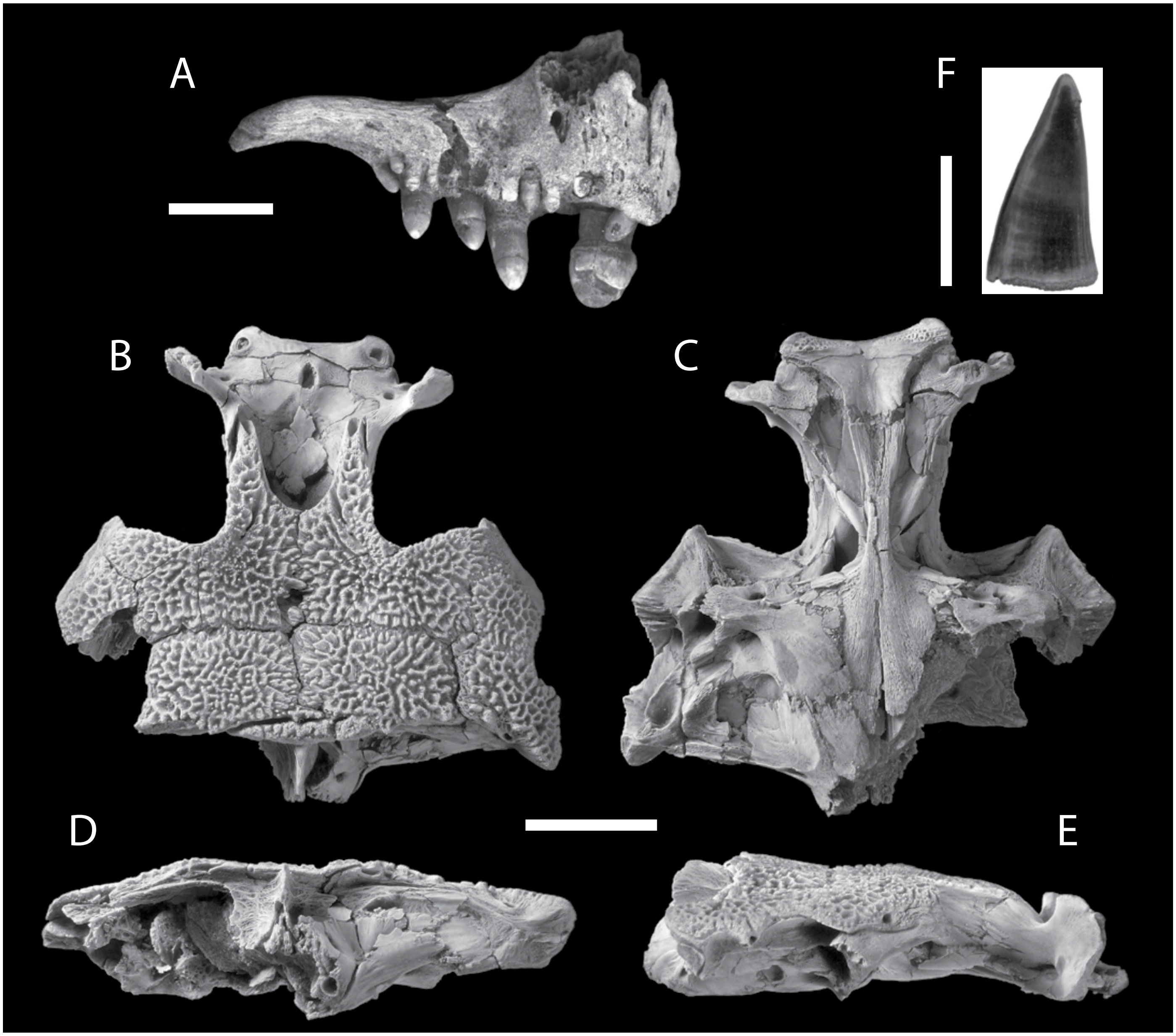


FIGURE 3.14. (A) CMM-V-4632, *Tautoga* sp., partial left premaxilla in medial view. (B–E) CMM-V-4231, *Astroscopus countermani*, holotype, nearly complete neurocranium in dorsal, ventral, posterior, and right lateral views, respectively. (F) CMM-V-3580, *Sphyraena* sp., isolated tooth. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

(Figure 3.15E,F); CMM-V-2629, partially complete right dentary; CMM-V-3710, dentary fragment; CMM-V-4426, dentary fragment; CMM-V-4432, complete hypural complex (Figure 3.15G); USNM 559394, dentary fragment; USNM 20108, complete right premaxilla; USNM 20109, partially complete left dentary; USNM 135183, premaxillary fragment; USNM 135184, dentary fragment; USNM 135186, dentary fragment; USNM 204217, partially complete left dentary; USNM 214428, partially complete right dentary; USNM 265236, dentary fragment; USNM uncataloged, partially complete left premaxilla, right premaxilla, left dentary, and dentary fragment.

Horizon. Calvert and Choptank Formations.

Remarks. The premaxilla is long, curved, and anteriorly pointed (Figure 3.15A,B). The ascending process is long and very robust. The anterior and ventral margins form an angle of about 37°. The alveolar process bears a single row of large, tightly packed, and labiolingually compressed subtriangular teeth. The dentary is thick, massive, and laterally compressed, with a nearly straight anteroventral margin, a prominent notch along the anterior margin (see Collette and Russo, 1984), and a dense series of large, closely spaced, and labiolingually compressed subtriangular teeth (Figure 3.15C,F).

The hypural complex is rhomboid in outline, with a median notch along its posterior margin (Figure 3.15G). The complex is characterized by the complete fusion of the parhypural and bears a well-developed laterally emerging parhypurapophysis. A deep fossa is usually developed just behind the fused hemicentrum.

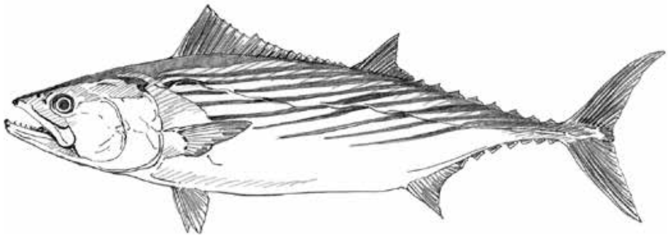
The fossils from the Calvert and Choptank Formations are tentatively referred (see Conrad, 1938; Collette and Russo, 1984) to *Acanthocybium solandri* because of the following characteristics unique to the wahoo. The premaxilla has an arrow-shaped outline, with a relatively low angle between its anterior and ventral margins. The morphology of the dentary is characterized by a prominent notch along its anterior margin. Finally, the structure of the hypural complex has a median posterior indentation, the complete fusion of the parhypural, and the presence of a deep fossa behind the fused hemicentrum.

The wahoo is an oceanic epipelagic piscivorous species distributed worldwide in tropical to warm temperate waters.

Genus *Sarda* Cuvier, 1829

Sarda sp.

FIGURE 3.16A,B



Bonito – *Sarda* sp.

Referred Material. USNM 559305, nearly complete left premaxilla (Figure 3.16A,B).

Horizon. Calvert Formation.

Remarks. The premaxilla is moderately curved, with a stout arrow-shaped anterior portion and a single row of well-developed conical teeth. The angle between the anterior and ventral margins measures 50°. The ascending process has a sharp anterodorsal end. The general outline of the bone, more specifically the anterodorsal end of the ascending process, is clearly diagnostic of the genus *Sarda* (see Collette and Chao, 1975).

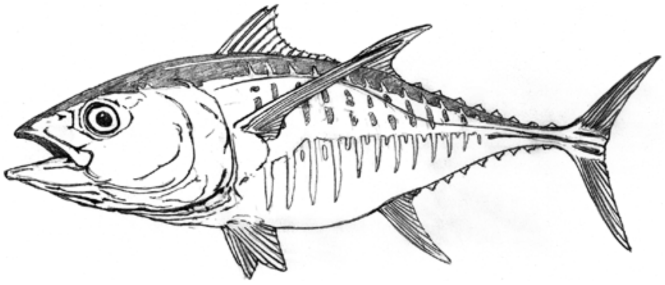
This premaxilla does not present sufficient anatomical information to differentiate or ally it with any extant species within the genus *Sarda*.

Bonitos of the genus *Sarda* are coastal epipelagic fishes that often enter estuaries. They prey on cephalopods and a variety of other fishes.

Genus *Thunnus* South, 1845

Thunnus sp.

FIGURE 3.16C–H



Tuna – *Thunnus* sp.

Referred Material. CMM-V-137, hypural (Figure 3.16F); CMM-V-161, partially complete right dentary (Figure 3.16C,D); CMM-V-932, nearly complete abdominal vertebra; CMM-V-947, partially complete caudal peduncle vertebra; CMM-V-950, partially complete caudal peduncle vertebra; CMM-V-964, three associated nearly complete caudal peduncle vertebrae (Figure 3.16G,H); CMM-V-1363, partially complete articulated vertebral column associated with jaw bones of *Lophius* sp.; CMM-V-1640, partially complete right dentary; CMM-V-2052, numerous partially complete caudal and caudal peduncle vertebrae; CMM-V-4178, nearly complete caudal peduncle vertebra; CMM-V-4388, four partially complete caudal vertebrae and a single nearly complete caudal peduncle vertebra (Figure 3.16E); USNM 24899, extensively fragmented skull bones (premaxillae, dentaries, fragments of opercular bones) and partially complete articulated vertebral column (31 vertebrae); USNM 387790, partially complete abdominal vertebra; USNM, uncataloged specimen consisting of four partially complete isolated caudal vertebrae.

Horizon. Calvert and Choptank Formations.

Remarks. The premaxilla is stout and curved, with a single row of small, widely spaced conical teeth. The dentary is rather thick and characterized medially by a strong crest with a rounded profile that originates from the symphyseal region

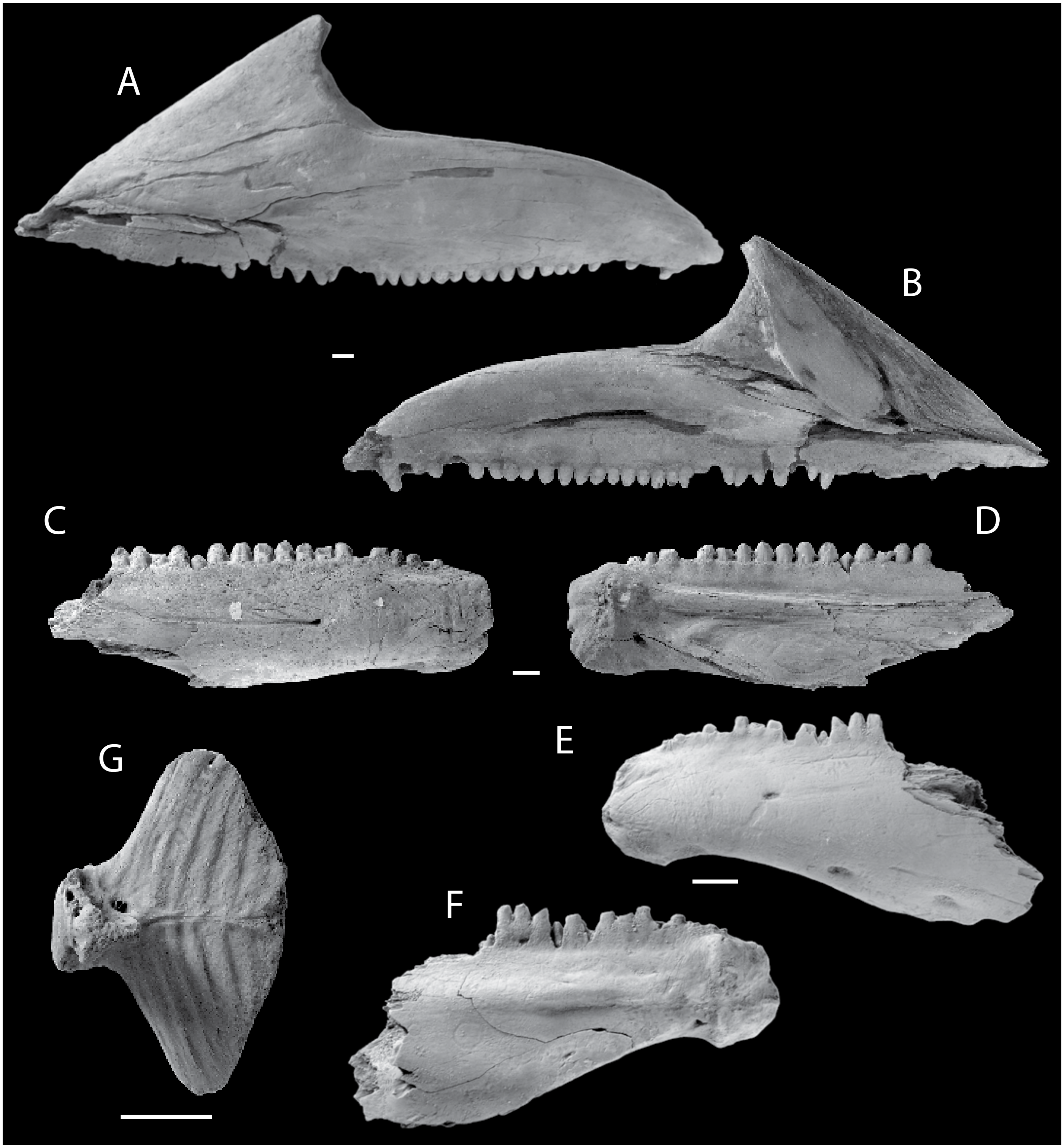


FIGURE 3.15. (A, B) CMM-V-160, *Acanthocybium* cf. *solandri*, left premaxilla in lateral and medial views, respectively. (C, D) CMM-V-1812, *Acanthocybium* cf. *solandri*, partial right dentary in lateral and medial views, respectively. (E, F) CMM-V-2332, *Acanthocybium* cf. *solandri*, partial left dentary in lateral and medial views, respectively. (G) CMM-V-4432, *Acanthocybium* cf. *solandri*, hypural in left lateral view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

(Figure 3.16C,D). The anterior margin of this bone is subvertical, with a shallow concave notch developed labially in the middle of its length. Another well-developed notch is located anteroventrally just behind the symphysis. Small and widely spaced conical teeth arranged in a single row occupy the dorsal margin of the dentary. The opercle and subopercle are approximately polygonal in outline.

The abdominal centra are approximately square (Figure 3.16E), whereas the caudal centra are subrectangular and longer than high (Figure 3.16G,H). The centra are characterized by two deep fossae separated by a strong median ridge along the lateral sides, and an approximately triangular articular surface for ligament attachment is located anteriorly on the median strengthening ridge. The vertebrae of the caudal peduncle are remarkably compressed dorsoventrally and possess a thin, broad keel arising laterally from the median ridge on both sides and flattened, stout neural and haemal spines.

The hypural is rhomboid in outline, with a deep fossa developed just behind the fused hemicentrum and immediately above the small hypurapophyses (Figure 3.16F).

The premaxillae, dentaries, and vertebrae have several morphological features that are clearly diagnostic of the genus *Thunnus* (De Sylva, 1955; Gibbs and Collette, 1967; Collette and Chao, 1975). In particular, the outline of the dentaries, the tooth size and arrangement, and the vertebrae with deep fossae separated by a median horizontal strengthening ridge with an anterior articular surface for the insertion of the epineurals, strongly support this generic attribution. Unfortunately, classification at the specific level is not possible because of the fragmentary nature of the available material. Moreover, as reported by Gibbs and Collette (1967), morphological variability is so great in some skeletal elements of the genus *Thunnus* that it is not possible to distinguish between extant species on the basis of these highly variable bones. Some skeletal characters are useful for the positive identification of species, but these are not preserved in the material available to us.

Tunas are oceanic and migrate seasonally close to shore, often entering brackish-water habitats. Usual prey includes schooling fishes, but they also feed on crustaceans and cephalopods.

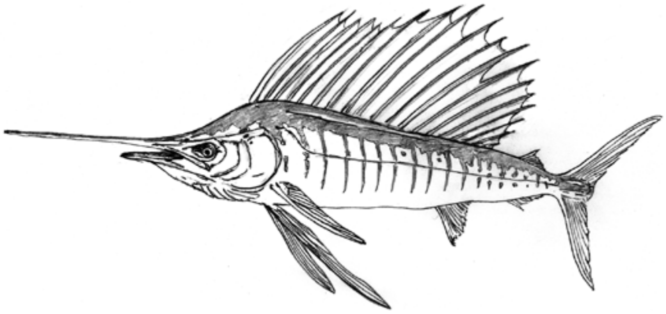
FAMILY ISTIOPHORIDAE LÜTKEN, 1875

REMARKS. Billfish remains are usually found in the Miocene deposits of the Chesapeake Group as isolated fragmented bones (Berry, 1917; Kimmel and Purdy, 1984). The identification of billfish remains to genus or species is extremely problematic, the results of which are usually broadly subjective. In an attempt to reduce ambiguity in the taxonomic analysis of isolated billfish remains, Fierstine and Voigt (1996) and Fierstine (1998, 2001) examined the range of variation in extant skeletal elements and developed a morphometric technique of identification that could be applied to disarticulated bones, whether fossil or extant. This method has been used to analyze billfish remains from the Miocene deposits of the Chesapeake Group of Maryland and Virginia, leading to the recognition of at least two taxa, *Istiophorus* cf. *platypterus* and *Makaira* cf. *nigricans*. According to the method elaborated by Fierstine (1998, 2001), an identification can be made by converting measurements of individual fossil bones into ratios and comparing them to those obtained for extant billfishes (see Carnevale et al., 2002). Some of the fossil ratios are outside the ranges observed for extant material; for this reason, specimens identified at the species level are only tentatively assigned to an extant taxon. In many cases the preservation of the material is inadequate to allow for the morphometric survey and, as a consequence, for a reasonable taxonomic interpretation.

Genus *Istiophorus* Lacépède, 1801

Istiophorus cf. *platypterus* (Shaw & Nodder, 1792)

FIGURE 3.17A–D



Sailfish – *Istiophorus* cf. *platypterus*

1917 *Istiophorus calvertensis* Berry, pp. 461–463, figs. 1–2.

1984 *Istiophorus calvertensis* (Berry) – Kimmel and Purdy, p. 208, pl. 1, fig. 7.

1987 *Pseudohistiophorus calvertensis* (Berry) – Schultz, p. 171.

1998 *Istiophorus* cf. *platypterus* (Shaw & Nodder, 1792) – Fierstine, pp. 40–41, figs. 8B, 9.

2001 *Istiophorus* cf. *platypterus* (Shaw & Nodder, 1792) – Fierstine, pp. 36–37.

REFERRED MATERIAL. CMM-V-270, complete atlas (first abdominal vertebra), (Figure 3.17B,C); CMM-V-1766, articulated partially complete dentaries; USNM 9344, partially complete rostrum (Figure 3.17A); USNM 186813, partially complete rostrum; USNM 542404, hypural complex (Figure 3.17D).

HORIZON. Calvert, Choptank, and Eastover Formations.

REMARKS. The material consists of two partially preserved rostra (Figure 3.17A), a single isolated first abdominal vertebra (Figure 3.17B,C), and a complete hypural complex (Figure 3.17D). One of the rostra, USNM 9344, constitutes the holotype specimen of *Istiophorus calvertensis* described by Berry (1917) from the deposits of the Eastover Formation cropping

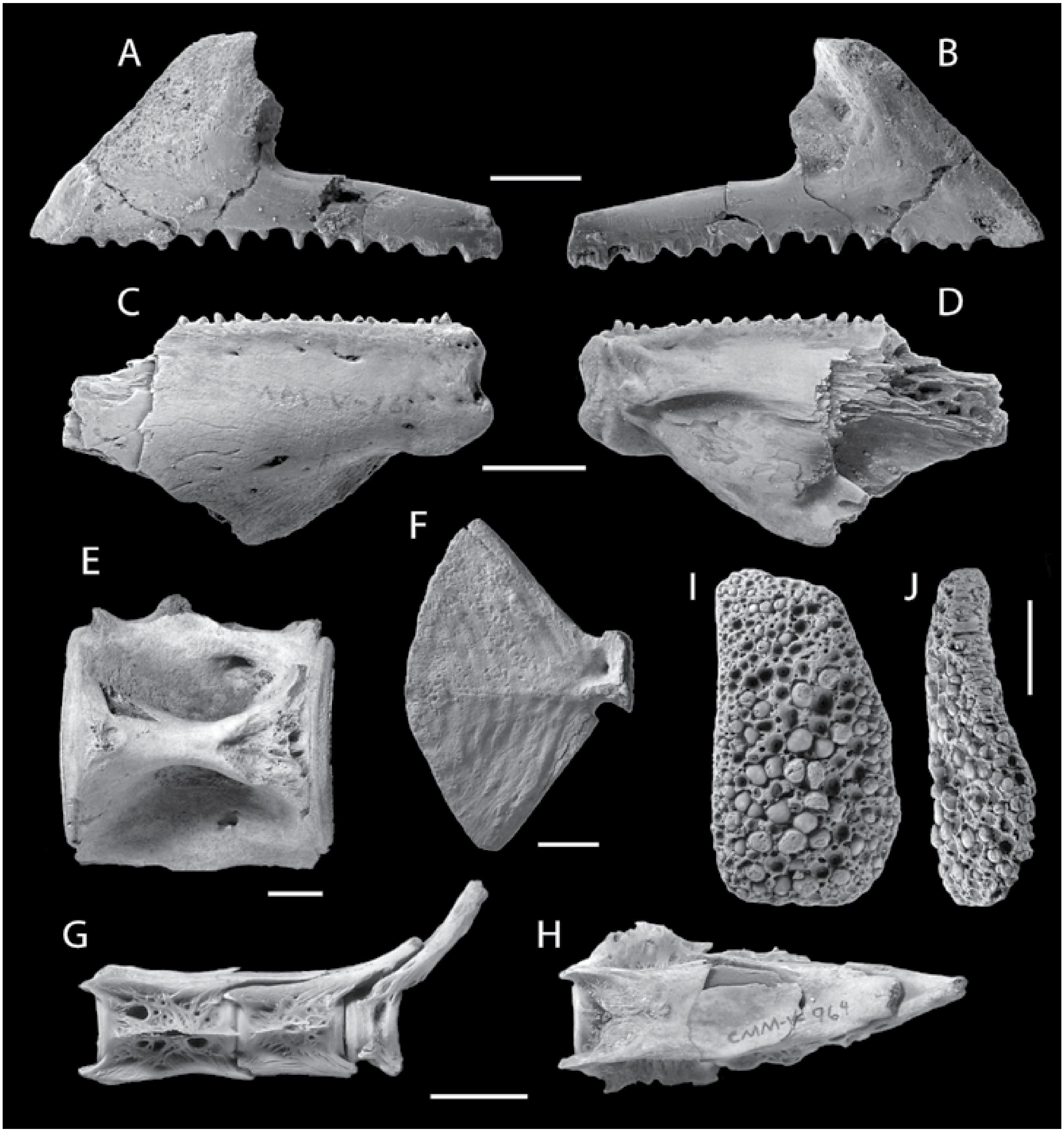


FIGURE 3.16. (A, B) USNM 559305, *Sarda* sp., nearly complete left premaxilla in lateral and medial views, respectively. (C, D) CMM-V-161, *Thunnus* sp., partial right dentary in lateral and medial views, respectively. (E) CMM-V-4388, *Thunnus* sp., abdominal vertebra. (F) CMM-V-137, *Thunnus* sp., hypural in right lateral view. (G, H) CMM-V-964, *Thunnus* sp., three associated caudal peduncle vertebrae. (I, J) CMM-V-2490, "*Paralbula*" *dorisiae*, tooth plate in occlusal and lateral views, respectively. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

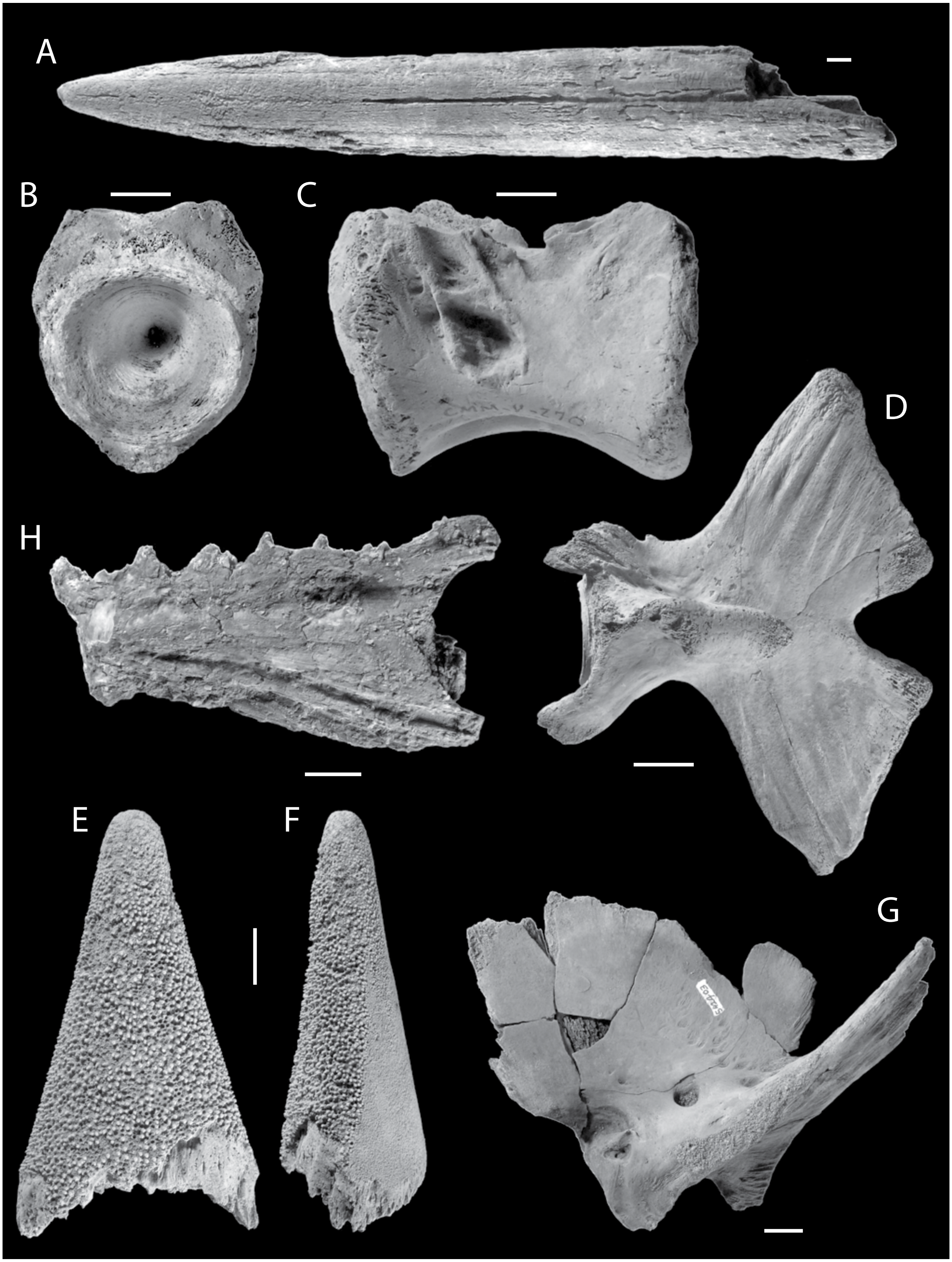

A
B
C
D
H
E
F
G

FIGURE 3.17. (*Facing page*) (A) USNM 9344, *Istiophorus* cf. *platypterus* (holotype of *I. calvertensis*), partial rostrum. (B, C) CMM-V-270, *Istiophorus* cf. *platypterus*, complete atlas in anterior and left lateral views, respectively. (D) USNM 542404, *Istiophorus* cf. *platypterus*, hypural complex in left lateral view. (E, F) USNM 542403, *Makaira* cf. *nigricans*, predentary in occlusal and right lateral views, respectively. (G) USNM 542403, *Makaira* cf. *nigricans*, left quadrate in lateral view. (H) USNM 542407, *Paralichthys* sp., left dentary in lateral view. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

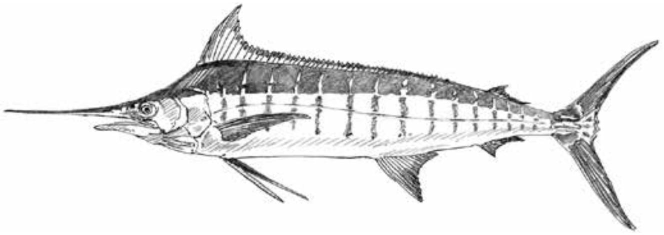
out at Tar Bay, James River, Virginia. Fierstine (1998, 2001) redescribed the specimen in detail and provided morphometric evidence of its affinities with the extant sailfish *I. platypterus*. The ratios of the rostrum formerly referred to *I. calvertensis*, as well as the other material referred herein to *I.* cf. *platypterus*, are presented in Table 3.1.

The sailfish is an oceanic, epipelagic species usually inhabiting the waters above the thermocline. Sailfishes are distributed close to the coasts, where they feed on fishes, cephalopods, and crustaceans.

Genus *Makaira* Lacépède, 1802

Makaira cf. *nigricans* Lacépède, 1802

FIGURE 3.17E–G



Blue Marlin – *Makaira* cf. *nigricans*

1998 *Makaira* cf. *nigricans* Lacépède – Fierstine, pp. 30–40, figs. 4–8A.
2001 *Makaira* cf. *nigricans* Lacépède – Fierstine, p. 37.

Referred Material. CMM-V-128 and CMM-V-129, partially complete rostra; USNM 375733, partially complete neurocranium, basisphenoid, vomer, rostrum, right lateral ethmoid, right ectopterygoid, right metapterygoid, right anguloarticular, right maxilla, right palatine, left prenasal, left dentary, predentary, and right lachrymal; USNM 542403, predentary and left quadrate (Figure 3.17E–G); USNM uncataloged, complete hypural complex.

Horizon. Calvert and Eastover Formations.

Remarks. Fierstine (1998) presented a detailed description of a partially articulated neurocranium, a rostrum, a jaw, and suspensorial bones. The ratios of selected bones described by Fierstine (1998), as well as the other material referred herein to *Makaira* cf. *nigricans,* are presented in Table 3.2.

The blue marlin is an oceanic species that primarily inhabits blue waters down to 200 m, where it feeds mostly on fishes but also on cephalopods.

Family Istiophoridae, gen. et sp. indet.

Referred Material. CMM-V-183, partially complete rostrum; CMM-V-184, partially complete rostrum; CMM-V-220, complete abdominal vertebra; CMM-V-321, partially complete rostrum; CMM-V-337, complete abdominal vertebra; CMM-V-1839, partially complete predentary; CMM-V-1908, partially complete predentary; CMM-V-1915, two partially complete hypural complexes; CMM-V-1998, complete caudal vertebra; CMM-V-1999, partially complete right scapula; CMM-V-2239, partially complete rostrum; CMM-V-2511, partially complete abdominal vertebra; CMM-V-2684, partially complete rostrum; CMM-V-2983, partially complete rostrum; CMM-V-3835, partially complete rostrum; CMM-V-3956, partially complete rostrum; CMM-V-4148, two complete caudal vertebrae; CMM-V-4576, partially complete rostrum; CMM-V-4827, partially complete neurocranium; USNM 186808, partially complete rostrum; USNM 186809, two vertebrae (one abdominal and one caudal); USNM 186810, five abdominal vertebrae and right cleithrum, right coracoid, right postcleithrum, and caudal-fin rays; USNM 186812, partially complete caudal vertebra; USNM 241559, hypural complex and five isolated dorsal-fin spines; USNM 639712, predentary and partial abdominal vertebra; USNM 415609, partially complete rostrum; USNM 559395, partially complete rostrum; USNM 559393, partially complete rostrum; USNM uncataloged, partially complete rostrum and two partially complete caudal vertebrae, a single abdominal vertebra, and a single hypural complex.

Horizon. Calvert, Choptank, St. Marys, and Eastover Formations.

ORDER PLEURONECTIFORMES BLEEKER, 1859

FAMILY PARALICHTHYIDAE REGAN, 1910

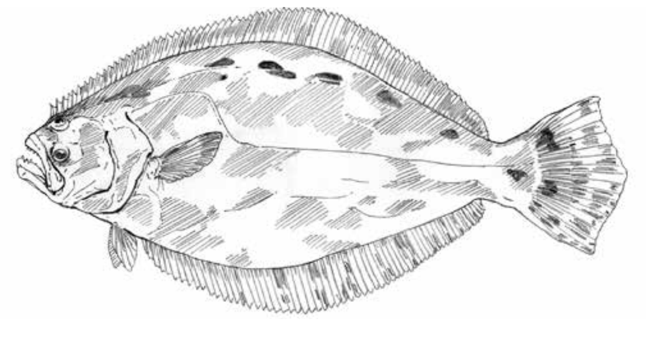
Genus *Paralichthys* Girard, 1858

TABLE 3.1. The ratios of the rostrum formerly referred to *I. calvertensis*, as well of the other material referred herein to *I.* cf. *platypterus*. Abbreviations follow Fierstine and Voigt (1996) and Fierstine (1998, 2001); a dash (–) indicates data are unavailable.

Ratios	USNM 9344	USNM 186813	USNM 542404	CMM-V-270	CMM-V-1766
Rostrum					
D1/W1	0.72	–	–	–	–
H1/D1	0.27	–	–	–	–
DD1/D1	0.43	–	–	–	–
D2/W2	0.69	0.57	–	–	–
H2/D2	0.27	0.27	–	–	–
DZ/P	0.34	–	–	–	–
Dentary					
DAD/DJL	–	–	–	–	0.43
22nd vertebra					
ASW/VAD	–	–	–	0.70	–
VAD/CL	–	–	–	0.83	–
VPD/CL	–	–	–	0.83	–
LAD/LPD	–	–	–	0.86	–
NW/CL	–	–	–	0.57	–
NW/LPD	–	–	–	0.70	–
ASW/CL	–	–	–	0.74	–
VAD/LAD	–	–	–	1.17	–
VPD/LPD	–	–	–	1.01	–
VAD/VPD	–	–	–	1.00	–
LAD/CL	–	–	–	0.70	–
LPD/CL	–	–	–	0.81	–
Hypural					
HDD/HL	–	–	0.56	–	–
HDD/HH	–	–	0.29	–	–
HDD/HW	–	–	0.50	–	–
HL/HH	–	–	0.52	–	–
HW/HL	–	–	0.98	–	–
HW/HH	–	–	0.51	–	–
HNL/HL	–	–	0.30	–	–

***Paralichthys* sp.**

FIGURE 3.17H



Lefteye Flounder – *Paralichthys* sp.

Referred Material. USNM 542407, left and right dentaries belonging to a single individual (Figure 3.17H).

Horizon. Eastover Formation.

Remarks. The dentaries are high and very thick, with a single row of strong caniniform teeth (Figure 3.17H). The anterior margin is nearly straight and obliquely oriented. There is a shallow notch along the anteroventral margin. Two parallel and relatively deep grooves run ventrally from the symphyseal region along the lateral surface. A flat bony flange with a linear dorsal profile is located along the dorsal margin behind the tooth row.

The dentaries from the Eastover Formation documented herein cannot be distinguished from those of the extant flounder *Paralichthys dentatus*.

Lefteye flounders of the genus *Paralichthys* are benthic species that occur primarily on sandy or muddy substrates from the shore to a depth of 200 m. They often enter brackish waters and feed primarily on fishes and crustaceans.

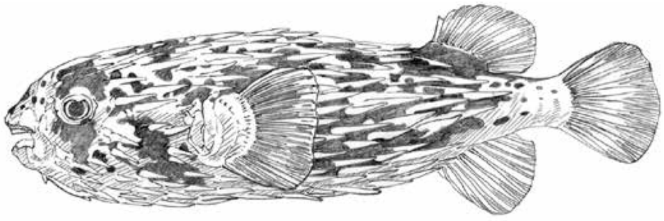
ORDER TETRAODONTIFORMES REGAN, 1929

FAMILY DIODONTIDAE BIBRON, 1855

Genus Chilomycterus Bibron, 1846

Chilomycterus sp.

FIGURE 3.18K,L



Burrfish – *Chilomycterus* sp.

REFERRED MATERIAL. CMM-V-172, fused dentaries; CMM-V-361, fused premaxillae; CMM-V-890, fused premaxillae; CMM-V-891, fused premaxillae; CMM-V-3338, fused dentaries (Figure 3.18K); CMM-V-3770, fused dentaries; CMM-V-4624, isolated dermal spine (Figure 3.18L).

HORIZON. Calvert and Eastover Formations.

REMARKS. Mouth plates are represented by both upper and lower jaws, which in origin consisted of the teeth of the biting edge fused with the dentaries and premaxillae into a solid crushing beak. The trituration teeth internal to the biting edge of both upper and lower jaws form a large plate divided into right and left halves, each formed by a series of large, flattened triturating tooth plates (Tyler, 1980; Figure 3.18K). The number of individual plates in the single series to each side of the midline usually increases with increasing specimen size. Unfortunately, all the jaw specimens are strongly eroded, represented only by fused contralateral tooth plates. Lower jaws can be distinguished from the upper jaws because of their rounded rather than pointed profile when observed in occlusal view (Figure 3.18K). Mouth plates, however, are not taxonomically useful because they are nearly indistinguishable in the genera *Diodon* and *Chilomycterus*. However, these two genera can be easily separated on the morphology of their dermal spines (see Tyler, 1980). CMM-V-4624 (Figure 3.18L) consists of a nonerectile, short, thick, and pointed spine arising from a large triradiate basal plate clearly belonging to the genus *Chilomycterus* (see Tyler, 1980; Leis, 2006). Because spines of *Diodon* have not yet been found, we tentatively suggest that all the diodontid skeletal remains found in the Miocene deposits of the Chesapeake Group should be assigned to *Chilomycterus*. The fragmentary nature of the material does not allow for species-level attribution.

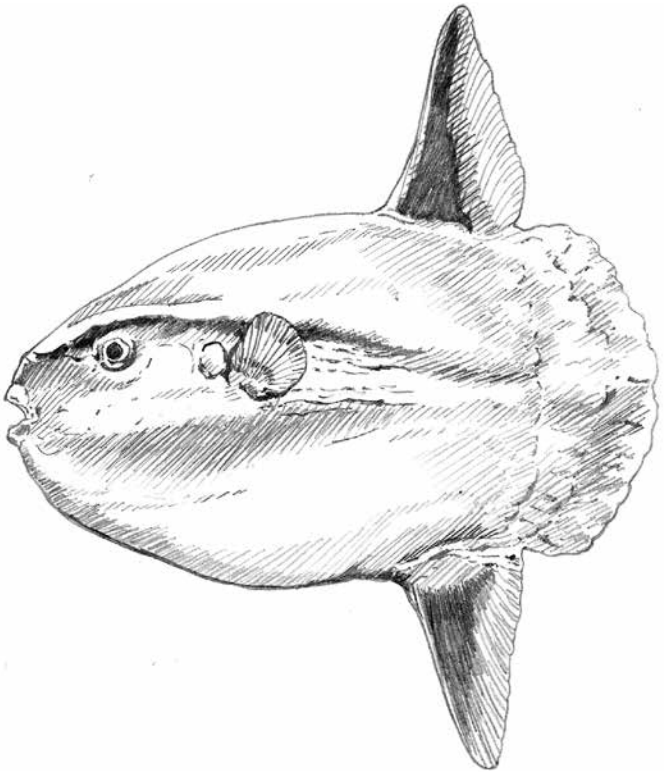
Burrfishes occur primarily in seagrass beds in bays and coastal lagoons, where they feed on crustaceans.

FAMILY MOLIDAE RANZANI, 1837

Genus *Mola* Koelreuter, 1770

Mola pileata (Van Beneden, 1881)

FIGURE 3.18A–C



Ocean sunfish – *Mola pileata*

HOLOTYPE. USNM 186983, premaxillary beak (Figure 3.18A–C).

HORIZON. Choptank Formation.

REMARKS. Weems (1985) referred a toothless premaxillary beak lacking a palatal tooth brace from bed 19 of the Choptank Formation to the molid species *Mola chelonopsis* (Figure 3.18A–C). However, Gregorova et al. (2009) concluded that this same specimen likely belongs to *Mola pileata* or perhaps to a new undescribed species of *Mola*.

Ocean sunfishes of the genus *Mola* are pelagic, with a worldwide distribution in tropical to temperate waters; they feed mainly on jellyfishes and other pelagic soft-bodied invertebrates and fish larvae.

TABLE 3.2. The ratios of selected bones described by Fierstine (1998), as well as of the other material referred herein to *Makaira* cf. *nigricans*. Abbreviations follow Fierstine and Voigt (1996) and Fierstine (1998, 2001); a dash (–) indicates data are unavailable.

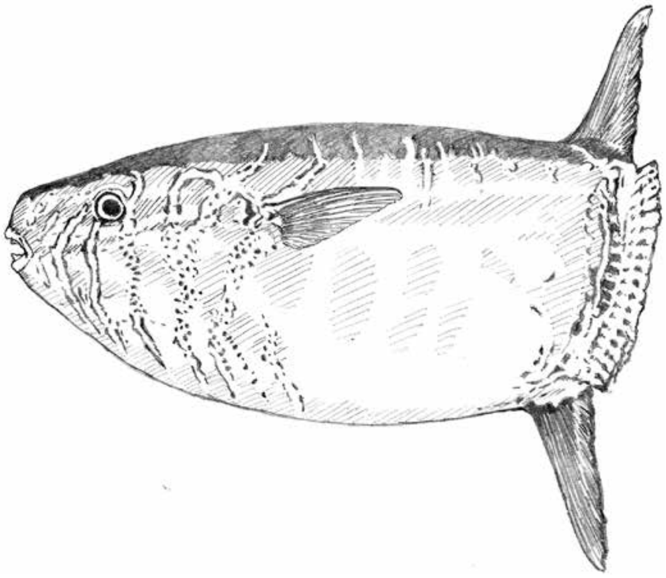
Ratios	USNM 375733	USNM 542403	USNM uncataloged	CMM-V-128+129
Neurocranium				
TD/MBO	0.50	–	–	–
NWB/TD	0.70	–	–	–
PAD/PAFW	0.53	–	–	–
PAW/PAFW	0.70	–	–	–
PAD/PAW	0.76	–	–	–
Predentary				
PW/PL	0.74	0.65	–	–
PD/PL	0.52	0.41	–	–
PD/PW	0.70	0.63	–	–
Rostrum				
D2/W2	0.70	–	–	0.54
H2/D2	0.18	–	–	0.30
DD2/D2	0.47	–	–	0.27
Maxilla				
ML/MOL	0.17	–	–	–
MW/MOL	0.14	–	–	–
MW/ML	0.79	–	–	–
MH/ML	0.64	–	–	–
MVW/MVH	1.3	–	–	–
MVW/ML	0.37	–	–	–
MVW/MW	0.46	–	–	–
MVW/MH	0.57	–	–	–
Articular				
AL/ASM	0.79	–	–	–
AW/AL	0.77	–	–	–
AAL/AL	0.59	–	–	–
ATW/AL	1.2	–	–	–
AW/ATW	0.66	–	–	–
Quadrate				
QAW/QH	–	0.23	–	–
QMW/QAW	–	1.10	–	–
QAW/QHS	–	0.30	–	–
QMW/QHS	–	0.34	–	–
QMW/QHL	–	0.96	–	–
Hypural				
HDD/HL	–	–	0.41	–
HDD/HH	–	–	0.15	–
HL/HH	–	–	0.37	–
HNL/HL	–	–	0.17	–

Genus *Ranzania* Nardo, 1840

Remarks. The genus *Ranzania* includes a single extant species, *Ranzania laevis*, and at least four fossil species (see Carnevale and Santini, 2007), two of which are known exclusively from the Miocene and Pliocene deposits of the Middle Atlantic Coastal Plain (see Weems, 1985). *Ranzania laevis* is an oceanic pelagic species that occurs worldwide in warm and temperate waters, where it feeds primarily on planktonic crustaceans. On the basis of functional considerations, however, Weems (1985) suggested that the fossil species *Ranzania grahami* was characterized by feeding habits similar to those of *Mola*.

Ranzania grahami Weems, 1985

FIGURE 3.18D–I



Ocean sunfish – *Ranzania grahami*

Holotype. USNM 186986, premaxillary and dentary beaks (Figure 3.18D,E) and jugular and nasal dermal plates (not illustrated) and a partially complete articulated dorsal dermal shield (Figure 3.18H,I).

Paratypes. USNM 16364, premaxillary beak; USNM 16668, premaxillary beak; USNM 16743, premaxillary beak; USNM 186982, premaxillary beak; USNM 265391, partial premaxillary beak; USNM 265394, premaxillary beak; USNM 265395, premaxillary beak; USNM 265651, nasal dermal plate; USNM 265653, jugular dermal plate (Figure 3.18F,G).

Referred Material. CMM-V-140, nasal dermal plate; CMM-V-150, dentary beak; CMM-V-186, premaxillary beak; CMM-V-187, premaxillary beak; CMM-V-191, nasal dermal plate; CMM-V-217, premaxillary beak; CMM-V-232, jugular dermal plate; CMM-V-230, nasal dermal plate; CMM-V-233, nasal dermal plate; CMM-V-285, premaxillary beak; CMM-V-286, premaxillary beak; CMM-V-315, dentary beak; CMM-V-888, premaxillary beak; CMM-V-892, a single nasal and two jugular dermal plates; CMM-V-1004, dentary beak; CMM-V-1005, dermal plate; CMM-V-1641, two premaxillary beaks; CMM-V-1719, nasal dermal plate; CMM-V-1854, premaxillary beak; CMM-V-1883, dentary beak; CMM-V-1891, three premaxillary beaks and five jugular and five nasal dermal plates; CMM-V-1984, jugular dermal plate; CMM-V-2044, premaxillary beak; CMM-V-2064, a single dentary and four premaxillary beaks and one jugular and one nasal dermal plates; CMM-V-2137, three premaxillary beaks; CMM-V-2138, three nasal dermal plates; CMM-V-2139, two dermal plates; CMM-V-2143, two jugular plates; CMM-V-2246, jugular dermal plate; CMM-V-2434, premaxillary beak; CMM-V-2501, dentary beak; CMM-V-2508, jugular dermal plate; CMM-V-2510, nasal dermal plate; CMM-V-2553, jugular dermal plate; CMM-V-2561, a single jugular and two nasal dermal plates; CMM-V-2579, jugular dermal plate; CMM-V-2685, premaxillary beak and nasal dermal plate; CMM-V-2788, dermal plates; CMM-V-3029, three nasal plates; CMM-V-3076, jugular dermal plate; CMM-V-3078, jugular dermal plate; CMM-V-3328, premaxillary beak; CMM-V-3800, two premaxillary beaks and six jugular and two nasal dermal plates; CMM-V-4004, premaxillary beak; CMM-V-4092, premaxillary beak; CMM-V-4211, premaxillary beak; CMM-V-4227, jugular dermal plate; CMM-V-4255, premaxillary beak and three nasal dermal plates; CMM-V-4277, nasal dermal plate; CMM-V-4292, nasal dermal plate; CMM-V-4308, jugular dermal plate; CMM-V-4340, nasal dermal plate; CMM-V-4413, two premaxillary beaks; CMM-V-4420, premaxillary beak and nasal dermal plate; CMM-V-4424, dermal plate; CMM-V-4547, jugular dermal plate; CMM-V-4558, jugular dermal plate; CMM-V-4565, nasal dermal plate; CMM-V-4577, nasal dermal plate; CMM-V-4596, jugular dermal plate; USNM 135737, jugular dermal plate; USNM 265649, premaxillary beak; USNM 265652, partial jugular dermal plate; USNM 391878, premaxillary beak; USNM 410274, jugular dermal plate; USNM 639711, premaxillary beak; USNM 2015682, dentary beak.

Horizon. Calvert Formation.

Remarks. Abundant jaw and dermal skeleton remains are referred herein to the species *Ranzania grahami* on the basis of the diagnostic features described by Weems (1985).

The premaxillary beak is massive and does not have a bony shelf on the palatal bracing; it is usually toothless and only rarely has small and irregularly disposed teeth (Figure 3.18D). The dentary beak, with a robust biting edge, is similar to that of the extant *Ranzania laevis*; the teeth appear to be absent or, at least, remarkably reduced (Figure 3.18E).

The massive carapace consists of irregular and extremely thickened plates (Figure 3.18H,I). Of the whole dermal covering, the nasal and jugular plates can be distinguished from the other elements. The nasal plate is approximately ovoid in outline, whereas the jugular plate is greatly elongate, with a rounded external surface and a flat to slightly concave median surface characterized by a thick median ridge (Figure 3.18F,G).

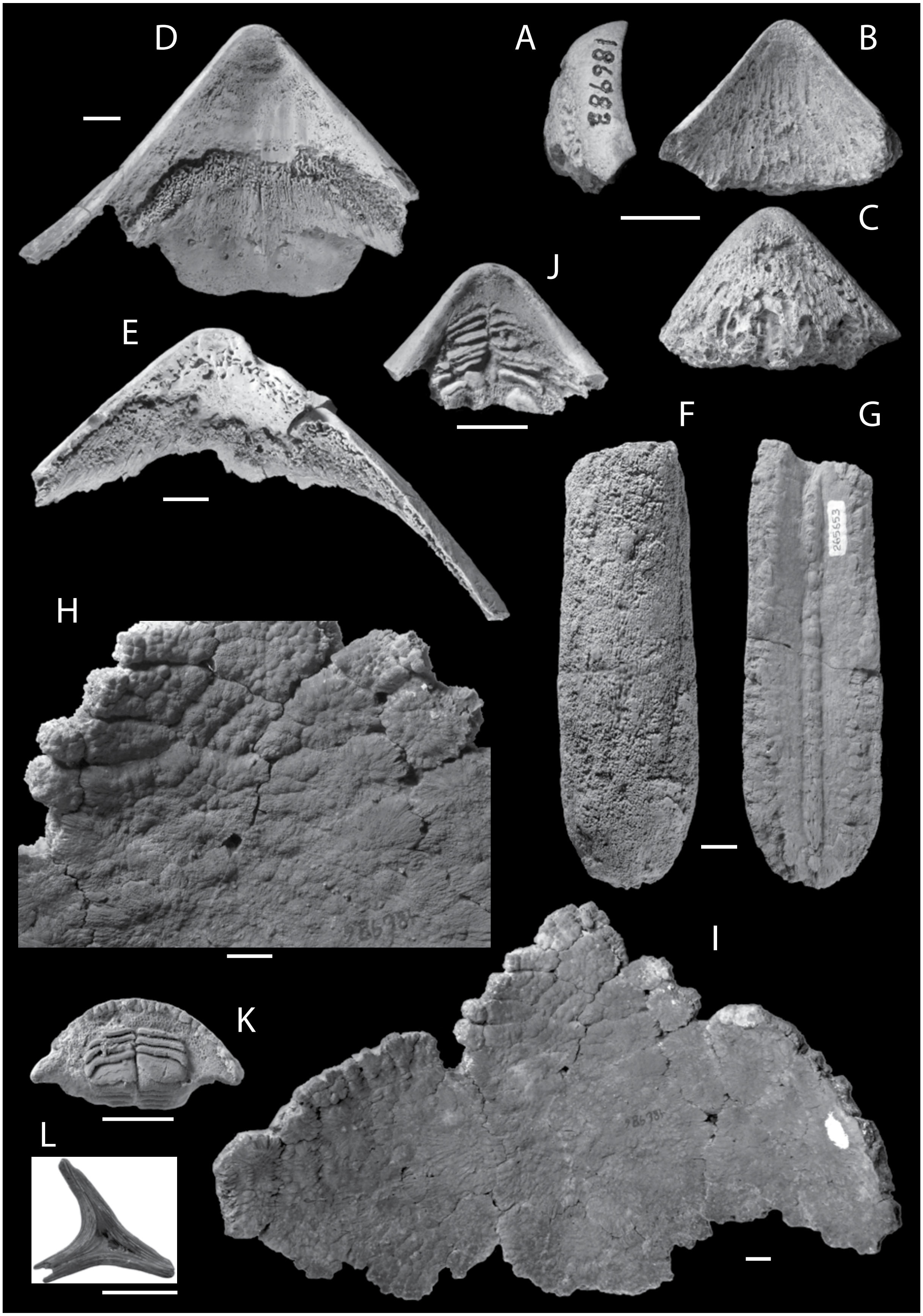
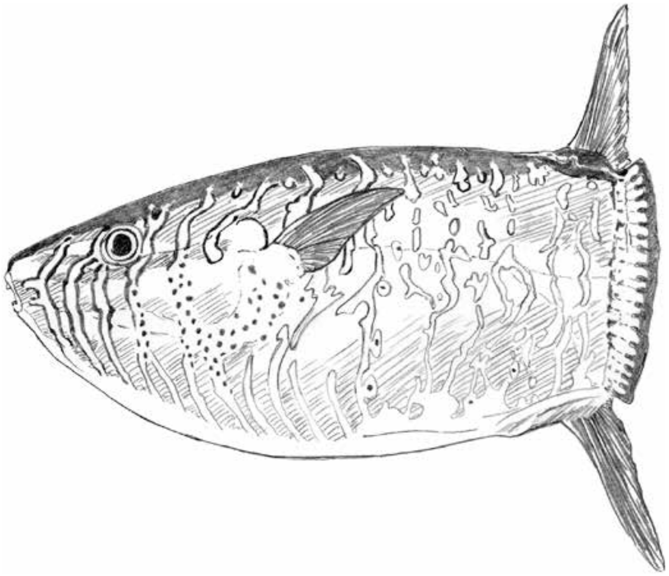

D
A
186983
B
C
J
E
F
G
265653
H
I
K
L

FIGURE 3.18. (*Facing page*) (A–C) USNM 186983, *Mola pileata*, premaxillary beak in right lateral, ventral (occlusal), and dorsal views, respectively. Anterior to top of page. (D) USNM 186986, *Ranzania grahami*, holotype, premaxillary beak in ventral (occlusal view). Anterior to top of page. (E) USNM 186986, *Ranzania grahami*, holotype, dentary beak in dorsal (occlusal view). Anterior to top of page. (F, G) USNM 265653, *Ranzania grahami*, jugular dermal plate in external and internal views, respectively. (H, I) USNM 186986, *Ranzania grahami,* holotype, partial articulated dorsal dermal shield, internal view (H shows an enlarged view of the anterior margin of I). (J) USNM 265392, *Ranzania tenneyorum*, holotype, premaxillary beak in ventral (occlusal view). Anterior to top of page. (K) CMM-V-3338, *Chilomycterus* sp., fused dentaries, occlusal view. Anterior to top of page. (L) CMM-V-4624, *Chilomycterus* sp., isolated dermal spine. Specimens lightly coated with sublimed ammonium chloride. Scale bars equal 10 mm.

***Ranzania tenneyorum* Weems, 1985**

FIGURE 3.18J



Ocean sunfish – *Ranzania tenneyorum*

Holotype. USNM 265392, premaxillary beak (Figure 3.18J).

Referred Material. Six premaxillary beaks: CMM-V-185, CMM-V-931, CMM-V-2137, CMM-V-2441, CMM-V-4464, USNM 336431.

Horizon. Calvert Formation.

Remarks. The available material consists solely of isolated premaxillary beaks. The beaks are characterized by three well-developed pairs of tooth rows located on a bony shelf separated by a vertical sill from the main level of the palatal bracing bone; a notch is clearly exposed behind the tooth rows (Figure 3.18J).

Comments on "*Paralbula*" *dorisiae* Blake, 1940

FIGURE 3.16 I,J

A few thick tooth plates with phyllodont teeth (see Estes, 1969) from the Calvert and St. Marys Formations are present in the collections of the CMM (CMM-V-325, CMM-V-1024, CMM-V-2154, CMM-V-2215, CMM-V-2490; Figure 3.16 I,J) and USNM (USNM 16134, holotype; USNM 559397; USNM uncataloged). The teeth are irregularly arranged, nearly globular or subspherical in outline, and slightly depressed apically (Figure 3.16 I,J). Blake (1940) interpreted these tooth plates as being related to those of the Eocene albuloid *Paralbula marylandica* and created the new species *Paralbula dorisiae* to accommodate them. In a comprehensive study on the evolution and diversity of phyllodont fishes, Estes (1969) excluded the possibility that the Miocene tooth plates from the Chesapeake Group could belong to the genus *Paralbula* and, more generally, to the albuloid family Phyllodontidae. According to Estes (1969), the Miocene phyllodont tooth plates from the Chesapeake Group actually belong to the percomorph *Crommyodus irregularis,* a species created by Cope (1869) on the basis of material from the Miocene of New Jersey. Within percomorphs, phyllodont teeth are known to occur in the Carangidae, Diodontidae, and Labridae (hypsigenines, odacines, scarines) and, possibly, in certain extinct members of the family Sciaenidae (Estes, 1969). However, the fragmentary nature of the available material, as well as the lack of useful characters to interpret its possible affinities within percomorphs, defies taxonomic identification at this time.

Remarks on Otolith Assemblages

FIGURE 3.19

Otoliths, together with isolated teeth, were the first reported actinopterygian remains from the Miocene deposits of the Chesapeake Group (Eastman, 1904; Hay, 1928). In the first synoptic work on the Miocene fishes from Maryland, Eastman (1904) briefly discussed the otolith record of the Chesapeake Group and illustrated gadid and sciaenid sagittas from the St. Marys Formation without any indication of their taxonomic affinities. About half a century later, Dante (1953) described a new species, *Sciaenops eastmani*, on the basis of the material previously illustrated by Eastman (1904) and additional specimens from the Calvert Formation; his diagnosis was based on juvenile features, and for this reason Fitch and Lavenberg (1983) considered it to be a synonym of the extant *Sciaenops ocellata.* Nevertheless, Schwarzhans (1993) included *Sciaenops eastmani* within the fossil genus *Trewasciaena* together with material from the Miocene of Germany. A comprehensive study of the Miocene otoliths of Maryland was being prepared by John E. Fitch (n.d.), but unfortunately, his untimely death precluded full revision of the material. More recently, Müller (1999) made an extensive study of Tertiary ichthyofaunas of the Atlantic Coastal Plain, including the Calvert, Choptank, St. Marys, and Eastover Formations. About 64 taxa were described and illustrated from the Miocene of the Chesapeake Group, and several new otolith-based taxa were created. Many of his generic identifications, however, are not consistent with the analysis of skeletal remains presented herein. Since a complete review of the Miocene otolith assemblages of the Chesapeake Group is beyond the scope of our study, we investigated the relatively large otolith collection housed in the CMM in light of the results of the study of skeletal remains. Therefore, our taxonomic interpretations may appear rather conservative and with a broad use of open nomenclature. The most commonly found taxa are compiled in Figure 3.19. Throughout the Miocene, members of the families Gadidae (*Gadiculus* cf. *argenteus*, *Micromesistius cognatus*, *Trisopterus sculptus*) and Sciaenidae (*Cynoscion* sp., *Genyonemus* sp., *Leiostomus* sp., *Menticirrhus* sp., *Pachyurus* sp., *Pogonias* sp., *Sciaenops* sp.) are by far the dominant components of the assemblages, which also include a subordinate contingent of taxa of the families Ophidiidae (*Lepophidium* aff. *cervinum*, *Otophidium* sp.), Merlucciidae (*Merluccius* sp.), Ammodytidae (*Ammodytes* sp.), Triglidae (*Prionotus* sp.), Uranoscopidae (*Astroscopus* sp.), and Paralichthyidae (*Citharichthys* sp.). Representatives of other families are relatively rare (see Müller, 1999, for a detailed account). In some cases, the otolith and skeletal records are strongly consistent, including relative abundances as, for example, in the case of the red drum *Sciaenops*, which is extremely abundant in both records.

DISCUSSION

The analysis of the bony fish remains from the marine and paralic siliciclastic deposits of the Chesapeake Group presented herein provides a substantial improvement of our knowledge about the evolution of the structure and composition of the Miocene fish communities of the Salisbury Embayment and, more generally, of the middle sector of the eastern Atlantic coast of the North American continent. The investigation carried out on the paleoichthyological material housed in the collections of the CMM and the Department of Paleobiology of the USNM resulted in the identification of at least 38 taxa on the basis of fossil bones collected over more than a century from the Calvert, Choptank, St. Marys, and Eastover Formations. This represents a remarkable increase in the number of recognized taxa with respect to the previous reviews of the paleoichthyological record (e.g., Leriche, 1942; Kimmel and Purdy, 1984), which recognized less than a dozen taxa. An evaluation of the Miocene bony fish diversity from the deposits of the Chesapeake Group, however, should also include the diverse otolith assemblages described by Fitch (n.d.) and more recently by Müller (1999), who recognized at least 55 taxa in the Chesapeake Group. Therefore, a combined census of both the skeletal remains and otoliths of the Chesapeake Group results in the identification of at least 87 fish taxa, of which only a few (e.g., *Ariopsis stauroforus*, *Brotula* sp., *Merluccius* sp., *Pogonias* sp., *Prionotus* sp., *Sciaenops* sp.) are common to both records (Tables 3.3, 3.4).

As previously mentioned, this paleoichthyofaunal survey is based on the study of museum material fortuitously collected over more than a century from the deposits of the Chesapeake Group cropping out in Maryland and Virginia. The complete absence of a quantitative approach in the collection of these fossils makes it very difficult to provide a detailed paleoecological analysis of the fish assemblages. Nevertheless, some general paleoecological considerations can be provided on the basis of the biological and environmental affinities of the recognized taxa.

Within the sedimentary successions of the Chesapeake Group, skeletal remains are much more abundant and diverse in the Calvert and St. Marys Formations, with 26 and 20 taxa respectively, possibly reflecting depositional contexts wherein fossilization was favored. The otolith record shows a similar trend, with highly diverse assemblages in the Calvert and St. Marys Formations and only a few taxa recognized from both the Choptank and Eastover Formations (see Müller, 1999).

The fish assemblages of the Calvert, Choptank, St. Marys, and Eastover Formations exhibit a modern aspect. Although the ichthyofaunal compositions of the various formations are characterized by broad differences, it is interesting to note a persistent abundance of sturgeons (Acipenseridae gen. et sp. indet.), drums (*Pogonias* sp., *Sciaenops* sp.), and billfishes (Istiophoridae gen. et sp. indet.) throughout the sedimentary successions of the Chesapeake Group. The faunistic differences existing between the four formations clearly reflect the physiographic and environmental evolution of the Salisbury Embayment during the Miocene (e.g., Ward and Andrews, 2008; Petuch and Drolshagen, 2010).

The reduced size of many of the otoliths (ammodytids, cynoglossids, gadids, merlucciids, ophidiids, paralichthyids, and sciaenids) from the deposits of the Chesapeake Group is probably related to their juvenile nature. Such an abundance of juveniles suggests that the Salisbury Embayment represented a nursery ground for most of the Miocene.

The Calvert ichthyofauna is dominated by sturgeons (Acipenseridae gen. et sp. indet.), tilefishes (*Lopholatilus ereborensis*), drums (*Pogonias* sp., *Sciaenops* sp.), scombrids (*Acanthocybium* cf. *solandri*, *Thunnus* sp.), billfishes (*Istiophorus* cf. *platypterus*, *Makaira* cf. *nigricans*, Istiophoridae gen. et sp. indet.), burrfishes (*Chilomycterus* sp.), and ocean sunfishes (*Ranzania grahami*). The presence of tunas, billfishes, and other schooling predatory fishes, together with the abundance of large sharks and marine tetrapods, suggests that the Salisbury Embayment was a highly productive feeding ground during the deposition of the Calvert Formation. Overall, the Calvert ichthyofauna consists of a mixture of tropical, subtropical, and

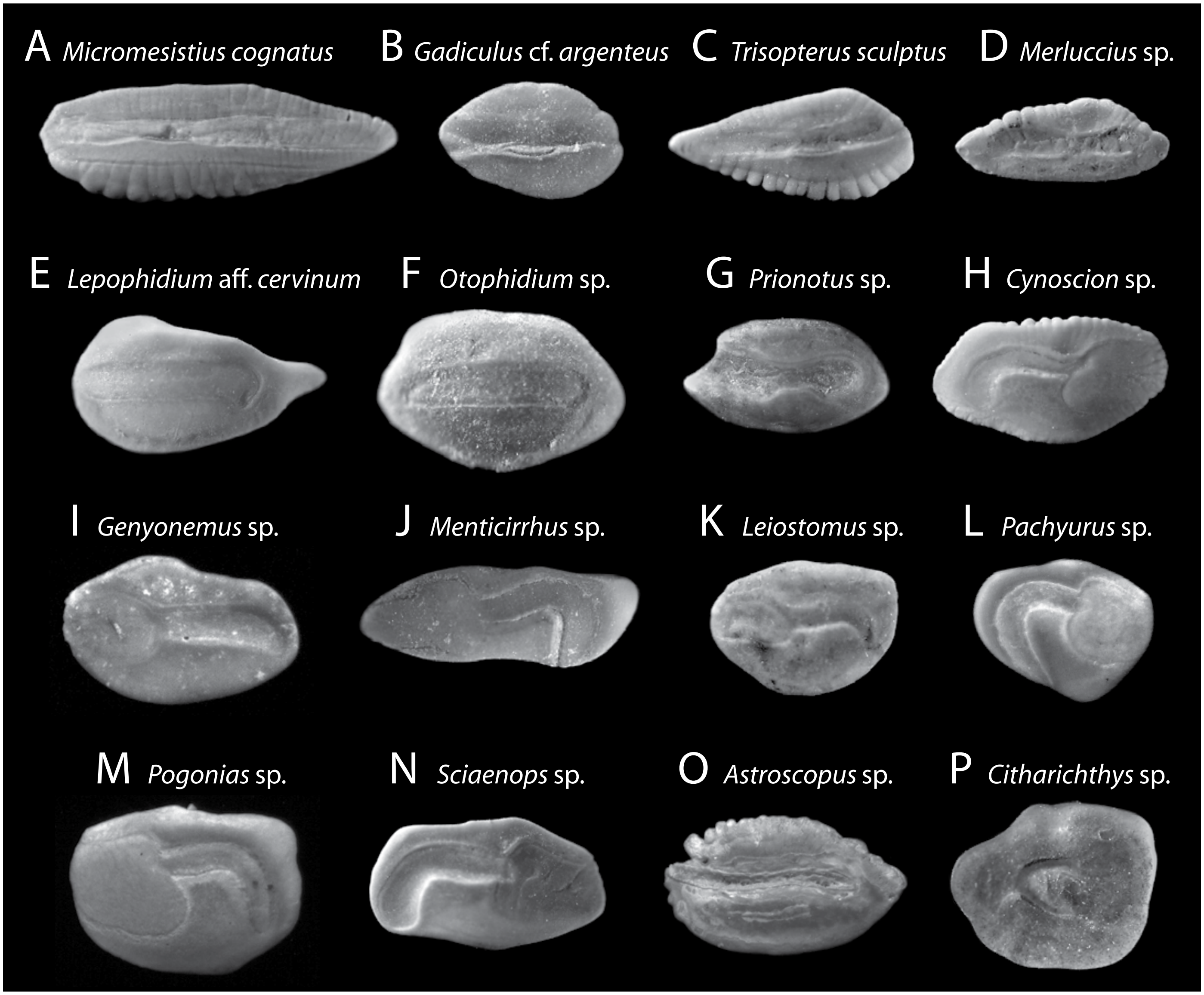


FIGURE 3.19. Otoliths from the Chesapeake Group. (A) *Micromesistius cognatus*. (B) *Gadiculus* cf. *argenteus*. (C) *Trisopterus sculptus*. (D) *Merluccius* sp. (E) *Lepophidium* aff. *cervinum*. (F) *Otophidium* sp. (G) *Prionotus* sp. (H) *Cynoscion* sp. (I) *Genyonemus* sp. (J) *Menticirrhus* sp. (K) *Leiostomus* sp. (L) *Pachyurus* sp. (M) *Pogonias* sp. (N) *Sciaenops* sp. (O) *Astroscopus* sp. (P) *Citharichthys* sp. Not to scale.

warm temperate taxa, with a few taxa of cold temperate affinity (*Lopholatilus ereborensis*). The tropical-subtropical contingent includes the sea catfish *Ariopsis stauroforus*, the wahoo *Acanthocybium* cf. *solandri*, the billfishes *Istiophorus* cf. *platypterus* and *Makaira* cf. *nigricans*, and the barracuda *Sphyraena* sp., which are indicative of temperatures of 27°C or higher (see Purdy et al., 2001). According to Müller (1999), the abundance of gadid otoliths in the deposits of the Calvert Formation is indicative of the presence of cool waters; however, the recognized gadid taxa belong to the thermophilous genera *Gadiculus*, *Micromesistius*, *Phycis*, and *Trisopterus*, which commonly occur in warm temperate waters (see Carnevale et al., 2012).

The Calvert ichthyofauna shares some taxa (*Bagre*, *Chilomycterus*, *Lagodon*, *Pogonias*, *Sarda*, *Sphyraena*, and *Thunnus*) with the partially coeval Burdigalian assemblage of the Pungo River Formation, North Carolina (see Purdy et al., 2001). However, the Pungo River ichthyofauna is characterized by a lower number of taxa, some of which (*Aluterus* sp., *Auxis* sp., *Hemirhabdorhynchus* sp., *Megalops* cf. *atlanticus*) have not been recorded in the Calvert Formation or, more generally, in the whole Chesapeake Group.

Fish remains are relatively uncommon in the Choptank Formation. The Choptank ichthyofauna, however, is similar to that of the Calvert Formation, being dominated by sturgeons (Acipenseridae gen. et sp. indet.), drums (*Pogonias* sp., *Sciaenops* sp.), scombrids (*Acanthocybium* cf. *solandri*, *Thunnus* sp.), and billfishes (*Istiophorus* cf. *platypterus*, Istiophoridae gen. et sp. indet.).

The fish assemblage of the St. Marys Formation seems to document a general cooling, as evidenced by the absence of thermophilous sea catfishes and wahoos and, more specifically, by the presence of *Merluccius* sp. and a member of the family Agonidae, a clade currently exclusive to cold temperate and polar waters of the North Pacific, Arctic Sea, northern North Atlantic, and North Sea and off the Patagonian region of the Southern Hemisphere (Kanayama, 1991). The remarkable cooling trend that occurred during deposition of the St. Marys Formation is also well documented in the otolith record. According to Müller (1999), the presence of otoliths belonging to the larger gadines *Gadus* and *Melanogrammus* in the St. Marys Formation resulted from a transatlantic migration of taxa typical of the North Sea Basin facilitated by a general drop in the temperatures in the North Atlantic. However, despite the abundance of cool-water taxa, remains of a certain number of subtropical and tropical fishes, including barracudas (*Sphyraena* sp.) and billfishes (Istiophoridae gen. et sp. indet.), are relatively common in the St. Marys Formation.

The Eastover ichthyofauna is scarcely diversified and is characterized by rare remains, among which drums (*Pogonias* sp., *Sciaenops* sp.) and billfishes (*Istiophorus* cf. *platypterus*, *Makaira* cf. *nigricans*, Istiophoridae gen. et sp. indet.) are dominant.

In summary, the mixture of thermophilous fishes with taxa of cold temperate and northern affinities characteristic of the assemblages of the Calvert, Choptank, St. Marys, and Eastover Formations could be indicative of the persistent presence of a well-defined climatic latitudinal zonation but also of wide seasonal temperature changes in a general condition similar to that characterizing the Chesapeake Bay area today (see Murdy et al., 1997).

The fish taxa recognized in the deposits of the Chesapeake Group show a clear general affinity for well-oxygenated muddy and sandy substrates. The assemblages are dominated primarily by shallow-water fishes characteristic of the inner shelf and secondarily by epipelagic taxa. Benthopelagic fishes characteristic of the outer shelf and upper slope are nearly absent in the Calvert Formation (exceptions are *Brotula* sp., *Lopholatilus ereborensis*). The common occurrence of open-ocean taxa (billfishes, tunas, wahoos) in the Calvert, Choptank, and Eastover Formations suggests that the deposition took place in the distal portions of the inner shelf. Overall, the ichthyofaunal composition is consistent with the sedimentary and paleontological record, which evidences a general regressive trend from the Calvert to the St. Marys Formation, representing a gradual shallowing within the Salisbury Embayment (e.g., Gernant et al., 1971; Kidwell, 1984, 1988, 1989, 1997; Ward, 1992; Shideler, 1994; Ward and Andrews, 2008).

The depth of deposition of the Calvert Formation is highly variable, with bed 11 having originated in the basinward parts of the shelf, recording the maximum depositional depth of the formation (Kidwell, 1989). Fish remains were collected in large part from beds 11, 12, and 14 of the Plum Point Member. These beds include tilefish remains belonging to the genus *Lopholatilus*, which can provide some indication of the minimum depth of the Calvert depositional environment. Extant species of the genus *Lopholatilus* range in depth between 80 and 540 m but usually occur at depths between 100 and 300 m near the 15°C isotherm (Dooley, 1978; Grimes et al., 1980, 1986); this range suggests that it is unlikely that the depositional depths of beds 11, 12, and 14 were shallower than 80 m, as suggested by micropaleontological studies (Gibson, 1983).

There are no fish taxa that would suggest a precise estimate of the minimum depositional depth for the Choptank Formation. However, toadfishes of the genus *Opsanus* usually occur at depths less than 50 m (Manooch, 1984). Gernant (1970) suggested that depositional environments were less than 60 m deep for the formation as a whole and that the ocean was less than 25 m deep for some beds. On the basis of foraminiferal assemblages, Gibson (1983) suggested that deposition of the Choptank Formation took place in open, shallow marine waters up to 30 m deep.

The presence of brackish and freshwater (e.g., *Amia* cf. *calva*, *Lepisosteus* sp., *Ictalurus countermani*) taxa in the St. Marys Formation and the concurrent abundance of marine euryhaline and stenohaline species could be related to wide seasonal oscillations of salinity that possibly occurred within the Salisbury Embayment because of episodic increase of the freshwater supply, as well as to habitat heterogeneity. Because of the variety of the recognized ecological categories, the evaluation of the depositional depth of the St. Marys Formation is rather problematic; in any case, taking into consideration the presence of the benthopelagic genus *Merluccius* and of indeterminate remains belonging to the billfish family Istiophoridae, it seems reasonable to conclude that the average depositional depth for the St. Marys Formation would have been a few dozen meters.

As far as the Eastover Formation is concerned, sedimentary features and macrobenthic assemblages (see Ward and Blackwelder, 1980) appear to be consistent with the ichthyofaunal composition and are indicative of marine depositional environments located in the inner shelf.

As discussed above, the fish assemblages of the Chesapeake Group exhibit a modern aspect, with most of the taxa belonging to genera or higher categories that currently occur in the northwestern Atlantic, including the coasts of Maryland and Virginia. Two of the taxa recorded in the St. Marys Formation, however, are very interesting from a biogeographic point of view since today they are absent or have been artificially introduced in

TABLE 3.3. Skeletal taxonomy of bony fishes from the Chesapeake Group. An X indicates a taxon is present in a particular formation or habitat; a question mark (?) indicates a taxon may be present; a dash (–) indicates taxon is not present.

Taxonomy		Formation				Habitat			
Family	Taxon	Calvert	Choptank	St. Marys	Eastover	Freshwater	Brackish	Shallow marine	Open marine
Acipenseridae	*Acipenseridae* gen. et sp. indet.	X	X	X	X	X	X	X	–
Lepisosteidae	*Lepisosteus* sp.	–	–	X	–	X	X	–	–
Amiidae	*Amia* cf. *A. calva*	–	–	X	–	X	–	–	–
Clupeidae	*Alosa* sp.	–	–	X	–	X	X	X	X
Ictaluridae	*Ictalurus* sp.	–	–	X	–	X	X	–	–
Ariidae	*Ariopsis stauroforus*	X	–	–	–	X	X	X	–
	Bagre sp.	X	–	–	–	–	X	X	–
Merlucciidae	*Merluccius* sp.	–	–	X	–	–	–	X	X
Ophidiidae	*Brotula* sp.	X	–	–	–	–	–	X	X
Batrachoididae	*Opsanus* sp.	–	X	–	–	–	–	X	–
Lophiidae	*Lophius* sp.	X	–	–	–	–	–	X	X
Belonidae	*Belone* sp.	–	–	X	–	–	X	X	X
Triglidae	*Prionotus* sp.	X	–	X	–	–	X	X	–
Agonidae	Agonidae gen. et sp. indet.	–	–	X	–	–	X	X	–
Perciformes indet.	*“Paralbula” dorisiae*	X	–	X	–	?	?	?	?
Moronidae	*Morone* sp.	X	–	–	–	X	X	X	–
Serranidae	Serranidae gen. et sp. indet.	–	X	–	–	–	X	X	X
Malacanthidae	*Lopholatilus ereborensis*	X	–	–	–	–	–	X	X
Pomatomidae	*Pomatomus* sp.	X	–	X	–	–	X	X	X
Rachycentridae	*Rachycentron* sp.	X	–	–	–	–	X	X	X
Sparidae	*Lagodon* sp.	X	–	X	–	–	X	X	–
	Stenotomus sp.	–	–	X	–	–	X	X	–
Sciaenidae	*Micropogonias* sp.	X	–	–	–	–	X	X	–
	Pogonias sp.	X	X	X	X	–	X	X	–
	Sciaenops sp.	X	X	X	X	–	X	X	–
Labridae	*Tautoga* sp.	X	–	X	X	–	X	X	–
Uranoscopidae	*Astroscopus countermani*	–	–	X	–	–	X	X	–
Sphyraenidae	*Sphyraena* sp.	X	–	X	X	–	X	X	X
Scombridae	*Acanthocybium* cf. *solandri*	X	X	–	–	–	–	X	X
	Sarda sp.	X	–	–	–	–	X	X	X
	Thunnus sp.	X	X	–	–	–	X	X	X
Istiophoridae	*Istiophorus* cf. *platypterus*	X	X	–	X	–	–	X	X
	Makaira cf. *nigricans*	X	–	–	X	–	–	X	X
	Istiophoridae gen. et sp. indet.	X	X	X	X	–	–	X	X
Paralichthyidae	*Paralichthys* sp.	–	–	–	X	–	X	X	–
Diodontidae	*Chilomycterus* sp.	X	–	–	X	–	–	X	–
Molidae	*Mola pileata*	–	X	–	–	–	–	X	X
	Ranzania grahami	X	–	–	–	–	–	X	X
	Ranzania tenneyorum	X	–	–	–	–	–	X	X

TABLE 3.4. Otolith taxonomy of bony fishes from the Chesapeake Group, based primarily on Müller (1999), except for Sciaenops, which is based on Fitch (n.d.). An X indicates a taxon was present in a particular formation; a dash (–) means taxon was not present.

Taxonomy		Formation			
Family	**Taxon**	**Calvert**	**Choptank**	**St. Marys**	**Eastover**
Congridae	*Conger* sp.	X	–	–	–
	Brevoortia aff. *B. tyrannus* (Latrobe, 1802)	–	–	X	–
Ariidae	*Ariopsis* aff. *A. felis* (Linnaeus, 1758)	–	X	–	–
	Ariopsis stauroforus (Lynn & Melland, 1939)	X	–	–	–
Argentinidae	*Argentina* sp.	–	–	X	–
Myctophidae	*Diaphus* sp.	X	–	–	–
Gadidae	*Phycis* spp.	X	–	–	–
	Urophycis aff. *U. tenuis* (Mitchill, 1815)	–	–	X	–
	"gen. aff. *Urophycis*" sp.	–	–	X	–
	Gadiculus argenteus (Guichenot, 1850)	–	–	X	–
	Gadiculus labiatus (Schubert, 1905)	X	–	X	–
	Gadiculus aff. *benedeni* (Leriche, 1926)	–	–	–	X
	Trisopterus sculptus (Koken, 1884)	X	X	X	–
	Gadus marylandicus Müller, 1999	–	–	X	–
	Melanogrammus antecedens Müller, 1999	–	–	X	–
	Micromesistius cognatus (Koken, 1891)	X	X	X	–
Merlucciidae	*Merluccius albidus* (Mitchill, 1817)	X	–	X	–
	Merluccius sp.	X	–	–	–
Ophidiidae	*Brotula* sp.	X	–	–	–
	Lepophidium aff. *cervinum* (Goode & Bean, 1885)	–	–	–	X
	Lepophidium elongatum Müller, 1999	–	–	X	–
	Chilara aff. *C. taylori* (Girard, 1858)	–	–	–	X
	Otophidium nolfi Müller, 1999	–	–	X	–
Triglidae	*Prionotus* spp.	X	X	X	–
	"genus *Triglidarum*" sp.	X	–	–	–
Chandidae	"genus *Chandidarum*" sp.	–	–	X	–
Serranidae	"genus *Serranidarum*" spp.	–	–	X	X
	Epinephelus sp.	–	–	X	–
	"gen. aff. *Epinephelus*" sp.	X	–	–	–
Haemulidae	"genus *Pomadasyidarum*" sp.	–	–	–	X
Carangidae	"genus *Carangidarum*" sp.	–	–	X	–
Sparidae	*Archosargus* sp.	–	–	X	–
	Lagodon aff. *L. rhomboides* (Linnaeus, 1766)	X	–	X	–
	"genus *Sparidarum*" sp.	–	–	X	–
Sciaenidae	*Umbrina* sp.	–	–	X	–
	Pogonias sp.	–	–	X	–
	Sciaenops sp.	X	–	X	–
	Leiostomus compressus Müller, 1999	X	–	–	–
	Leiostomus crassior Müller, 1999	–	–	X	–

TABLE 3.4. (*Continued*)

Taxonomy		Formation			
Family	Taxon	Calvert	Choptank	St. Marys	Eastover
	Genyonemus calvertensis Müller, 1999	X	–	–	–
	"gen. aff. *Genyonemus*" *pertenuis* Müller, 1999	X	–	–	–
	Menticirrhus aff. *M. litoralis* (Holbrook, 1855)	–	–	X	–
	Menticirrhus sp.	–	–	X	–
	"gen. aff. *Pachyurus*" *atavus* Müller, 1999	X	–	–	–
	"gen. aff. *Pachyurus*" *breviformus* Müller, 1999	–	–	X	–
	Cynoscion senior Müller, 1999	X	–	X	X
Uranoscopidae	*Astroscopus* sp.	–	–	X	X
Ammodytidae	*Ammodytes* aff. *hexapterus* Pallas, 1814	–	–	X	X
	Ammodytes sp.	–	–	X	–
	"genus *Percoideorum*" *subcircularis* Müller, 1999	X	–	–	–
	"genus *Percoideorum*" sp.	–	–	X	–
Pleuronectidae	"genus *Pleuronectidarum*" sp.	–	–	X	–
Paralichthyidae	*Citharichthys* spp.	X	–	X	X
Cynoglossidae	*Symphurus* sp.	X	–	–	–
	"genus *Pleuronectiformorum*" spp.	–	–	X	–

the northwestern Atlantic waters. One of these is the needlefish *Belone* that is today restricted to the eastern Atlantic and the Mediterranean Sea; the occurrence of *Belone* in the St. Marys Formation might be in some ways related to the same transatlantic migration that resulted in the arrival of the gadine *Gadus* and *Melanogrammus* in the northwestern Atlantic waters.

Lundberg and Luckenbill (2012) discussed the biogeographic significance of the peculiar distribution of the Miocene catfish *Ictalurus countermani*, which is extralimital to the known range of fossil and extant channel catfish species (*I. punctatus* group) and, more generally, the entire genus *Ictalurus*; the current presence of at least two *Ictalurus* species along the Atlantic coasts of the United States is the result of transplantation that started in the last decades of nineteenth century (Lundberg and Luckenbill, 2012).

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4

Crocodilians of the Calvert Cliffs

Robert E. Weems

ABSTRACT. Crocodilian remains from the Calvert Cliffs are referable to the tomistomine genus *Thecachampsa*. The closest living relative is *Tomistoma schlegelii*, the false gharial of Southeast Asia. Two species are present: *Thecachampsa sericodon* Cope and *Thecachampsa antiquus* (Leidy). The type specimen of the Florida tomistomine *Gavialosuchus americanus* is referable to *T. sericodon*, and some other specimens previously referred to *G. americanus* belong to *T. antiquus*. These tomistomine species are found in shallow marine coastal deposits, indicating that they habitually inhabited coastal marine waters as do the modern saltwater crocodile (*Crocodylus porosus*) and American crocodile (*C. acutus*). Tomistomine remains are fairly common in the Miocene coastal marine deposits of North America, South America, Europe, Africa, and southern Asia. By the Pliocene, however, tomistomines had become restricted to Southeast Asia. Today, *Tomistoma schlegelii*, the sole surviving tomistomine species, is found only in freshwater. A few crocodilian osteoderms from the Calvert Formation in Delaware do not pertain to *Thecachampsa*. They may pertain to *Alligator olseni* White and indicate that a strictly freshwater crocodilian was also present during Calvert time. Its remains should eventually be found along the Calvert Cliffs.

INTRODUCTION AND TAXONOMIC HISTORY

Joseph Leidy (1851a, 1852) described the first Miocene crocodilian from the Atlantic Coastal Plain and named it "*Crocodilus antiquus*." It was based upon two teeth, two vertebrae, a rib fragment, and an ungual phalanx collected from bluffs along the Potomac River at Stratford Hall Plantation, the ancestral home of the Lee family of Virginia (Figure 4.1). These bluffs expose vertebrate-bearing Miocene strata referable to

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FIGURE 4.1. Map of a portion of northeastern Virginia and adjacent Maryland, showing locations where the skulls and postcranial remains of Miocene tomistomine crocodilians described herein were mostly found. (1) Stratford Hall and Wakefield (George Washington Birthplace National Monument), located in Westmoreland County, Virginia, along the south bank of the Potomac River. The holotype of "*Crocodilus*" *antiquus* is from near Stratford Hall. (2) The Popes Creek bluffs, located in Charles County, Maryland, along the east bank of the Potomac River. (3) The Thomas residence, located in Charles County, Maryland, near the west bank of the Patuxent River. (4) The Calvert Cliffs along the western shore of the Chesapeake Bay in Calvert County, Maryland.

TABLE 4.1. Differences and similarities among species of *Thecachampsa.*

Character	*Thecachampsa carolinensis*	*Thecachampsa antiquus*	*Thecachampsa sericodon*
Snout proportions	Relatively wide	Narrow	Very narrow
Premaxillaries	Short	Elongate	Elongate
Nasals	Narrow	Very narrow	Very narrow
Dentition	Homodont	Homodont	Heterodont
Carinas on teeth	Weak to absent	Weak to absent	Usually prominent
Tooth function	Crushing	Crushing	Piercing (anterior), shearing (posterior)
Tooth spacing	Close	Wide	Wide
Premaxillaries indent maxillaries ventrally	Slightly	Deeply	Deeply
Number of teeth in dentary	16	17	18
Femur	Moderately robust	Robust	Moderately robust
Ilium	Iliac blade long	Iliac blade long	Iliac blade short

four formations: the upper part of the Calvert Formation and the Choptank Formation (middle Miocene) and also the St. Marys and Eastover Formations (upper Miocene; Figure 4.2A). Leidy did not specify a specific horizon from which his specimen came, but he did state that it was found in association with "*Pecten jeffersonius*." This name cannot represent a valid modern identification because today that species name is affixed to a Pliocene species (*Chesapecten jeffersonius*) that does not occur in any of the Miocene and Pleistocene units exposed at Stratford. However, it does serve to associate Leidy's crocodile remains with some other species of *Chesapecten*, shells of which are abundant in the Stratford area in the Choptank Formation but not in the Calvert, St. Marys, or Eastover Formations. Therefore, the type specimen almost certainly was found in the Choptank Formation.

In 1867, Edward Drinker Cope described two additional species of Miocene crocodilians from the Maryland Coastal Plain and assigned them to a new genus, *Thecachampsa*. He based one species, *T. contusor*, on a single, short, conical tooth (Figure 4.2B) from southern Maryland. The other species, *T. sericodon*, he based upon elongate, curved teeth of cylindrical form with long, delicate cutting edges (Figure 4.2E) that came from Maryland and also New Jersey (Cope, 1869b). Cope (1869a,b) also described a third species that he named *Thecachampsa sicaria* (Figure 4.2D).

This last species, also from the Miocene of Maryland, was based on a posterior maxillary fragment with teeth that had greatly compressed crowns and very long crenulated cutting edges. In the same year, Othniel C. Marsh (1869) introduced a name for a fourth new species of *Thecachampsa*, *T. squankensis*, on the basis of teeth that came from either the Eocene (Cope, 1882) or the Miocene (Steel, 1973) of New Jersey.

In addition to these Miocene species, Cope also named or assigned several Eocene species to *Thecachampsa*. In 1869, he referred "*Crocodilus*" *fastigiatus* (Leidy, 1851b) to *Thecachampsa,* and in 1871 he also referred "*Crocodilus*" *rugosus* (Emmons, 1858) to *Thecachampsa*. In 1872, he described *Thecachampsa serratus* from the Eocene of New Jersey, possibly the Shark River Formation (Hay, 1930:154). All of these species are of very doubtful validity (i.e., they are nomena dubia), and none of them has any direct bearing on the Miocene species assigned to *Thecachampsa*.

Of the five nominal Miocene species placed within the genus *Thecachampsa* prior to 1870, three proved to be invalid. Several years after he described *T. contusor*, Cope (1871a:64) concluded that the distinctive surface texture characteristics of the type specimen tooth for this species came from "attrition and partial destruction of the enamel." He therefore synonymized this species with "*Crocodilus*" *antiquus*, with which it agreed in all other characteristics, as a new combination, *Thecachampsa antiqua*. This made *Thecachampsa contusor* a junior synonym of "*Crocodilus*" *antiquus*, and later authors have concurred with this designation (for example, Steel, 1973). In the case of *Thecachampsa squankensis,* Marsh published this name in anticipation of describing it as a new species. He never illustrated, described, or designated type material for this species, however, so *T. squankensis* is a name without any type specimen or description and thus is a nomen vanum. Two species of *Thecachampsa* (*T. sericodon* and *T. sicaria*) were considered to be different until Myrick (2001) noted that the two different tooth morphologies characterizing these putative species were present in teeth found in close association with a single skull (USNM 25243). The obvious conclusion was that these two types of teeth represent only one species of heterodont crocodilian, for which the name *Thecachampsa sericodon* has priority. Myrick, however, also

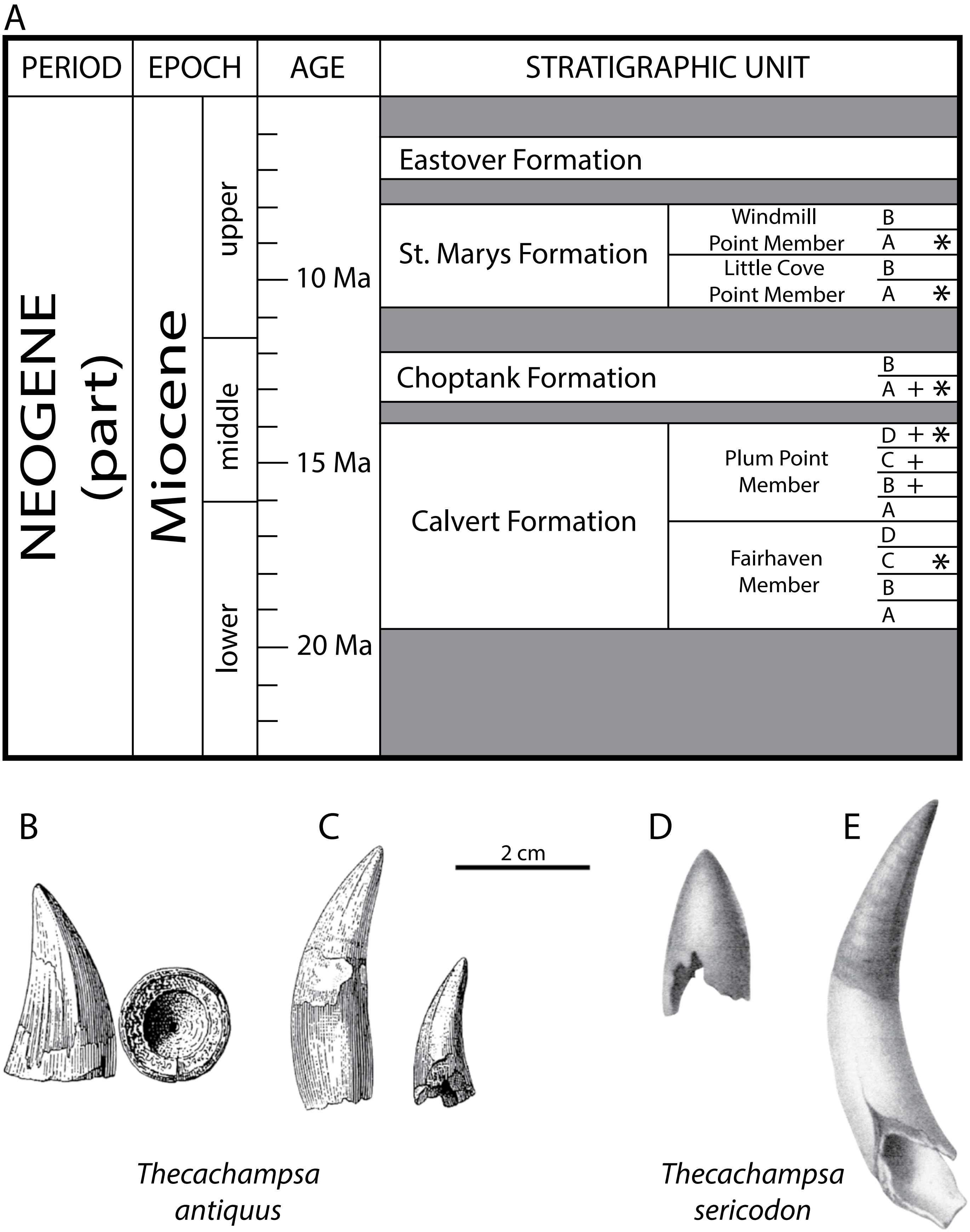
A
PERIOD
EPOCH
AGE
STRATIGRAPHIC UNIT
NEOGENE (part)
Miocene
upper
middle
lower
10 Ma
15 Ma
20 Ma
Eastover Formation
St. Marys Formation
Windmill Point Member
B
A *
Little Cove Point Member
B
A *
Choptank Formation
B
A + *
Calvert Formation
Plum Point Member
D + *
C +
B +
A
Fairhaven Member
D
C *
B
A
B
C
2 cm
D
E
Thecachampsa antiquus
Thecachampsa sericodon

FIGURE 4.2. (*Facing page*) (A) Miocene stratigraphic units present in the coastal plain of Virginia and Maryland. Specimens of *Thecachampsa sericodon* (crosses) have come from the upper Plum Point Member of the Calvert Formation and the lower part of the Choptank Formation. Specimens of *Thecachampsa antiquus* (asterisks) have come from the Calvert, Choptank, and St. Marys Formations. Nearly all of these units were deposited in shallow to mid-shelf marine environments. These units range in age from about 19 to 8 MYA. (B) Holotype posterior tooth of *Thecachampsa contusor* (junior synonym of *Thecachampsa antiquus*), adapted from Case (1904). (C) Holotype anterior teeth of *Thecachampsa antiquus*, adapted from Case (1904). (D) Holotype posterior tooth of *Thecachampsa sicarius* (junior synonym of *Thecachampsa sericodon*), adapted from Cope (1871b). (E) Holotype anterior tooth of *Thecachampsa sericodon*, adapted from Cope (1871b).

concluded that *T. antiquus* was synonymous with *T. sericodon* and *T. sicaria* because he noticed that some of the teeth in the middle region of the tooth row in *T. sericodon* were quite similar to anterior teeth of *T. antiquus*. This observation is true, but in the larger sample available here for study, it is a problem only when trying to identify individual teeth, which may be identifiable to *Thecachampsa* sp. only if they come from the middle region of the tooth row. For anterior and posterior teeth, especially for fairly complete individual dentitions, there is no ambiguity in separating these two taxa. The heterodont dentition of *T. sericodon*, with long and recurved anterior teeth (Figure 4.2E) and bladelike posterior teeth (Figure 4.2D), is distinctive and quite different from the homodont dentition of *T. antiquus*, which consists of shorter and blunter teeth (Figure 4.2B,C). Although the type material of both species is sparse, their differences are distinctive and diagnostic. Unfortunately, the teeth of the type specimen of *T. antiquus* are missing (Spamer et al., 1995:111) and probably lost, but the two most complete holotype teeth were illustrated by Leidy (1852) and later by Case (1904). The holotype tooth of the junior synonym of *T. antiquus*, *T. contusor*, has also been illustrated (Case, 1904), so much of the range of tooth morphology of *T. antiquus* is documented (Figure 4.2). These two Miocene species of *Thecachampsa* clearly had different dietary preferences and feeding strategies (Massare, 1987), *T. sericodon* being adapted to snagging and slicing food (probably fish) and *T. antiquus* being adapted to crushing food (perhaps turtles).

The material described here provides a large number of additional characteristics that further serve to distinguish these two species and also serve to much better characterize the genus *Thecachampsa* relative to other tomistomine crocodilians (Table 4.1). The type material of these two species would not be considered sufficient to erect a new species today, but both species were described long before modern standards became established, both species have been in the literature for more than 140 years, and the genus *Thecachampsa* was validly established by Cope, as discussed below. For all of these reasons, especially with the addition of much more complete material discussed and illustrated here, a meaningfully complete diagnosis is now possible both for the genus *Thecachampsa* and for its two constituent Miocene species.

The proper taxonomic placement of the genus *Thecachampsa* among the Crocodylia long remained enigmatic because the type material was so fragmentary. The type material included distinctive teeth, but a meaningful diagnosis of the genus *Thecachampsa* and its placement among the Crocodylia could not be made from such sparse remains. In 1870, Cope considered *Thecachampsa* to be a gavial and noted that species of *Thecachampsa* had been found in Europe. Yet despite this prescient analysis, Cope later (1882) synonymized *Thecachampsa* with "*Crocodilus*" (i.e., *Crocodylus*). This synonymy of *Thecachampsa* with *Crocodylus* has been accepted by some subsequent workers (Hay, 1902, 1930; Steel, 1973) and rejected by others (Toula and Kail, 1885; Case, 1904). More recently, Myrick (2001) chose to revive the name *Thecachampsa* and correctly associated it with the tomistomine crocodilians.

When Cope (1867) proposed the name *Thecachampsa*, he described two species to go in it (*T. contusor* and *T. sericodon*) but neglected to designate either of these species as the type species of the genus. Cope (1882:984) later corrected this by noting parenthetically that the type of *Thecachampsa* was *T. sericodon*. Much later, Hay (1902:512) designated *T. contusor* as the type species of *Thecachampsa* without explanation, perhaps on the basis of page priority, which is not supported by the International Code of Zoological Nomenclature's Principle of the First Reviser (International Commission on Zoological Nomenclature, 1999: article 24). The International Code of Zoological Nomenclature (article 69.1) explicitly states,

> If an author established a nominal genus or subgenus but did not fix its type species, the first author who subsequently designates one of the originally included nominal species validly designates the type species of that nominal genus or subgenus (type by subsequent designation), and no later designation is valid.

Thus, Cope's designation of *T. sericodon* as the type species of *Thecachampsa* has priority and is binding.

Although Cope suppressed the name *Thecachampsa* in 1882, synonymizing it with *Crocodylus*, the fact that he bothered at the same time to designate *T. sericodon* as the type species suggests that perhaps he held out hope that the genus eventually would prove to be valid. The skull discussed by Myrick (2001) fulfilled that hope by showing that "*sericodon*" teeth are distinctive and can be uniquely associated with a species of Calvert crocodilian that clearly does not belong to *Crocodylus*. Because of this, *Thecachampsa* again became a valid genus with a valid type species.

Myrick (2001) synonymized "*Crocodilus*" *antiquus* with *Thecachampsa sericodon*, but a number of specimens discussed here, not considered in his analysis, do not support this conclusion. During the 160 years since Leidy described "*Crocodilus*" *antiquus*, far more complete remains of both that species and *Thecachampsa sericodon* have been collected in Virginia and Maryland and donated to the collections of the National Museum of Natural History and the Calvert Marine Museum. Another important specimen, discussed and illustrated here, belongs to Stratford Hall Plantation and is kept there. This material shows that although "*Crocodilus*" *antiquus* is similar and rather closely related to *Thecachampsa sericodon*, it is not identical to that species and therefore represents a distinct second species within the genus *Thecachampsa*.

The specimens on which the present analysis is based come from a number of famous vertebrate fossil localities. They are (1) the cliffs along the south shore of the Potomac River estuary in Westmoreland County, from near Wakefield (George Washington Birthplace National Monument) to Stratford Hall Plantation; (2) the Popes Creek bluffs along the Potomac River estuary in Charles County, Maryland; (3) bluffs along and marl pits near the Patuxent River estuary in Charles County, Maryland; and (4) the Calvert Cliffs along the western shore of the Chesapeake Bay in Calvert County, Maryland (Figure 4.1). This area encompasses the geographic region and geologic strata from which the type material of both *Thecachampsa sericodon* and "*Crocodilus*" *antiquus* came.

Museum Abbreviations

AMNH FARB	American Museum of Natural History, fossil amphibian, reptile, and bird collection, New York, New York, USA
ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA
CMM	Calvert Marine Museum, Solomons, Maryland, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
STHA	Stratford Hall paleontological collection, Stratford, Virginia, USA
UF	University of Florida, Florida Museum of Natural History, Gainesville, Florida, USA
USNM	National Museum of Natural History (formerly U.S. National Museum), Smithsonian Institution, Washington, D.C., USA

SYSTEMATIC PALEONTOLOGY

Reptilia Laurent, 1768

Archosauria Cope, 1869a

Crocodylia Gmelin, 1789

Gavialidae Adams, Baikie, and Barron, 1854

Tomistominae Kälin, 1955

Thecachampsa Cope, 1867

Type Species. *Thecachampsa sericodon.*

Crocodile – *Thecachampsa* – Gavialidae

Thecachampsa sericodon Cope, 1867

Thecachampsa sericodon Cope, 1867:143 (original description).

Thecachampsa sicaria Cope, 1869b:8 (original description).

Thecachampsa sicaria Cope, 1869a:63, pl. v, fig. 6.

Thecachampsa sericodon Cope, 1867: Cope, 1869a:64–65, pl. v, figs. 7, 8.

Thecachampsa sericodon Cope, 1867: Cope, 1870:90–91.

Thecachampsa sicaria Cope, 1869: Cope, 1870:90–91.

Crocodylus sericodon (Cope, 1869): Cope, 1882:984.

Crocodylus sicaria (Cope, 1869): Cope, 1882:984.

Crocodylus sericodon (Cope, 1869): Hay, 1902:513.

Crocodylus sicarius (Cope, 1869): Hay, 1902:513.

Tomistoma americana Sellards, 1915:135–138, figs. 1–2.

Crocodylus sericodon (Cope, 1869): Steel, 1973:65.

Crocodylus sicarius (Cope, 1869): Steel, 1973:65.

Megalodelphis magnidens Kellogg, 1944 (holotype only):445, pl. 2, fig. 2; pl. 3, fig. 2.

Gavialosuchus americanus (Sellards, 1915): Morgan, 1986:414–415, fig. 1.

Thecachampsa antiqua (Leidy, 1852) (partem): Myrick, 2001:224, fig. 5.

Holotype. Three anterior teeth, ANSP 9443-9445, possibly (but not certainly) from a single individual (Spamer et al., 1995:150).

Diagnosis. Medium-sized crocodilian with elongate, curved teeth of cylindrical form that bear long, delicate cutting edges (carinas).

Type Locality and Horizon. Found near the residence of James T. Thomas, near the Patuxent River, Charles County, Maryland, USA, in sediments of the upper Plum Point Member (Plum Point D) of the Calvert Formation (middle Miocene; Weems and Edwards, 2007).

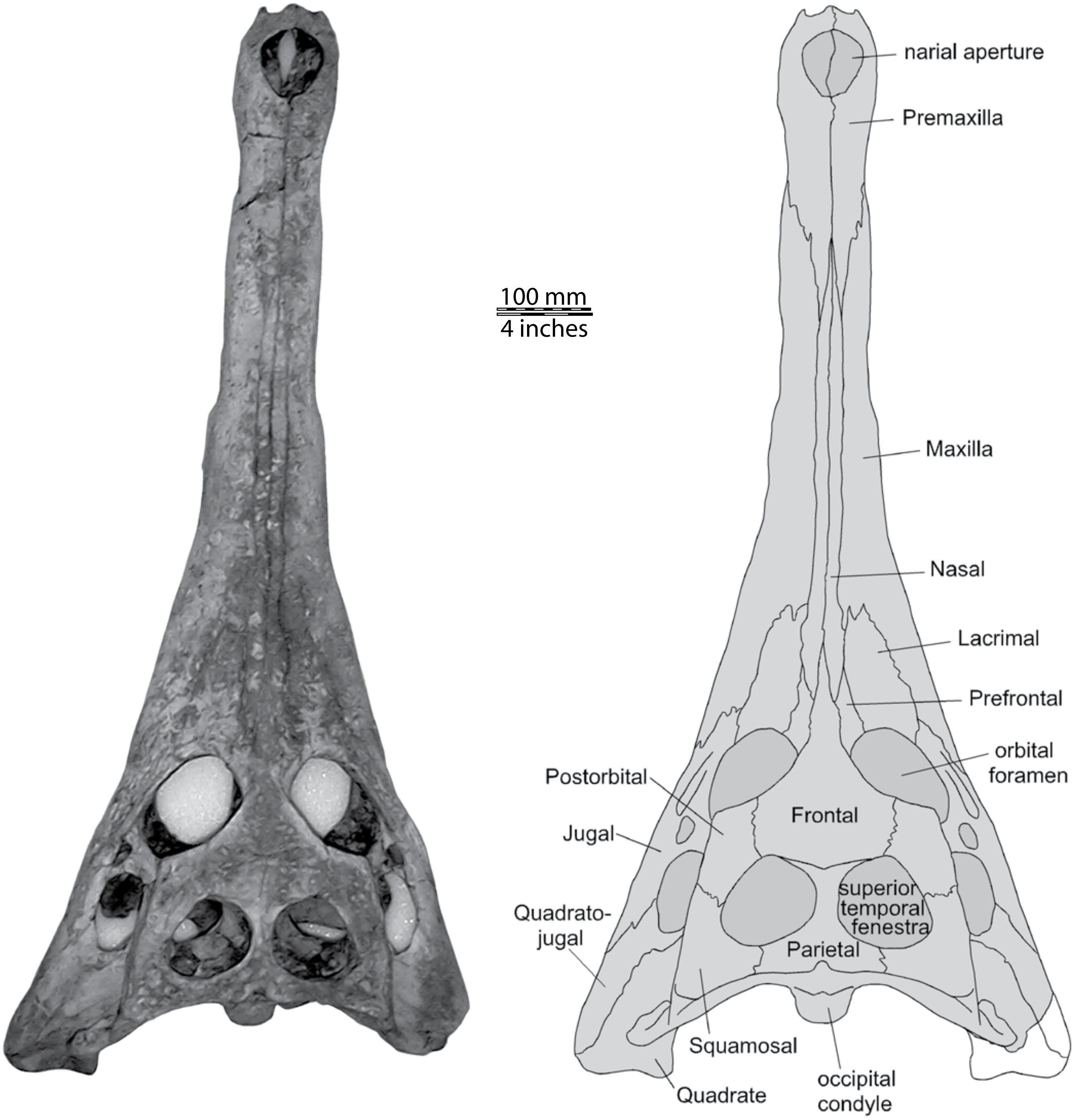

FIGURE 4.3. Photograph (left) and restoration (right) of the Wakefield skull of *Thecachampsa sericodon* Cope (USNM 25243) in dorsal view.

Previously Referred Material. (1) AMNH 1321 (now AMNH FARB 1321), tooth and right maxillary fragment, holotype of *Thecachampsa sicarius*, from Patuxent River, Maryland (Cope, 1869b; a cast of the maxillary fragment is at the USNM, USNM 26186). (2) USNM 25243, nearly complete skull with associated scattered teeth, bones, and armor collected by Albert Myrick in 1968 along bluffs near Wakefield Plantation, Westmoreland County, Virginia. Plum Point Member (Plum

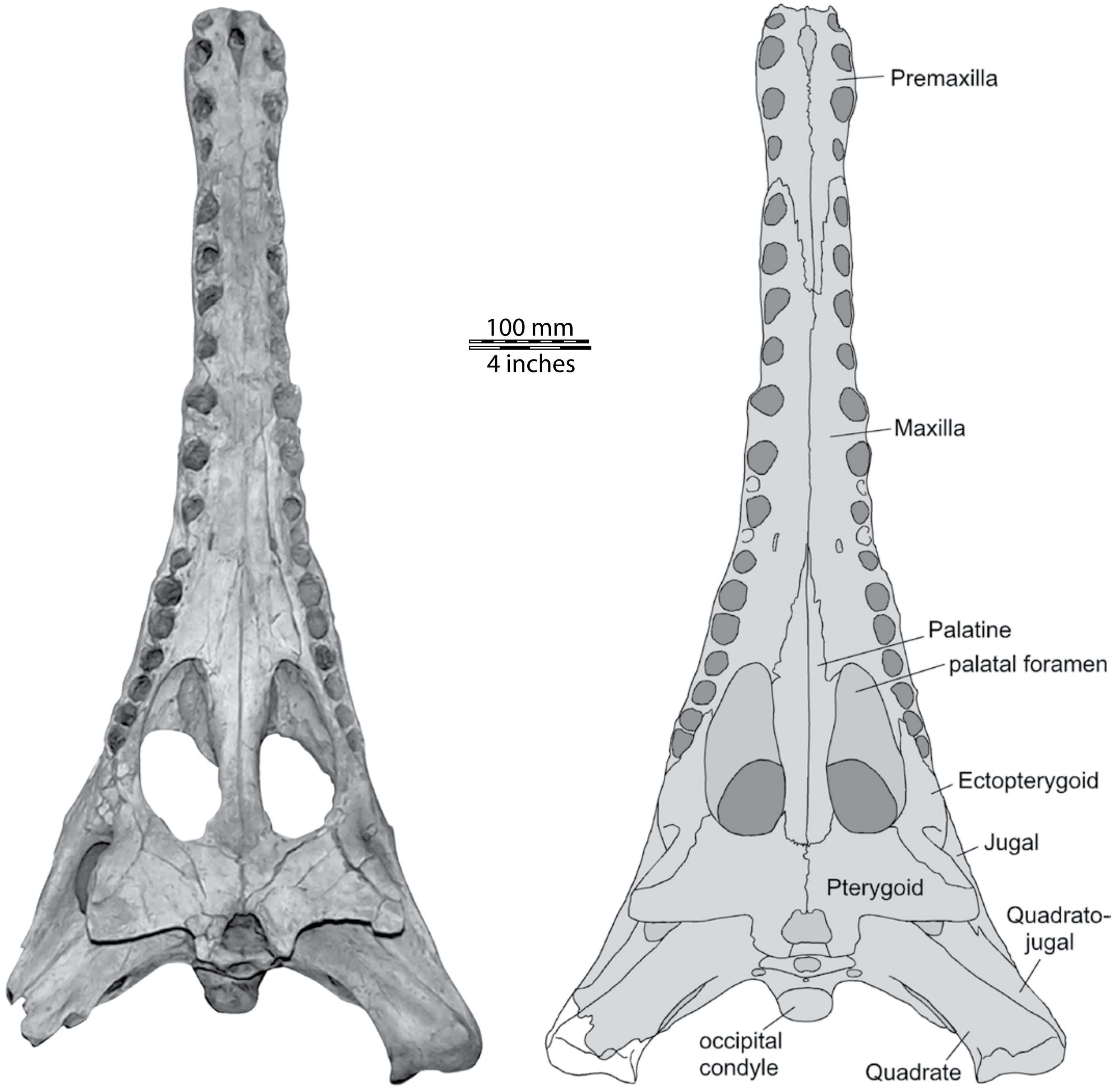

FIGURE 4.4. Photograph (left) and restoration (right) of the Wakefield skull of *Thecachampsa sericodon* Cope (USNM 25243) in ventral view.

Point B), Calvert Formation (middle Miocene). Skull discussed and dorsal view illustrated in Myrick (2001).

Newly Referred Material. (1) STHA1, a large portion of anterior skull including premaxillae, maxillae, nasals, frontals, prefrontals, lacrimals, and portions of the parietals, postorbitals, and right quadrate; lower jaws, including most of the dentaries, portions of the splenials, surangulars, angulars, and the right articular; 22 isolated teeth plus 1 in place in the right dentary and 3 in the maxillaries; 22 presacral vertebrae, both sacral vertebrae, and 3 caudal vertebrae; both ilia, both ischia, both pubes, 1 complete and 1 partial femur, both tibiae and fibulae, left astragalus, left calcaneum; numerous rib fragments;

FIGURE 4.5. The skull of the Stratford Hall Plantation specimen of *Thecachampsa sericodon* Cope (STHA1). (A) Skull in dorsal view, (B) skull in ventral view, and (C) lower jaws in dorsal view.

numerous whole and fragmentary pieces of dermal armor. Collected by Jon Bachman, Dianne Bachman, Su Weems, and Robert Weems in 1997 along bluffs at Stratford Hall Plantation, Westmoreland County, Virginia. Upper Plum Point Member (Plum Point D), Calvert Formation (middle Miocene). (2) USNM 8816, anterior rostrum, type specimen of *Tomistoma americana*, collected by Anton Schneider, Polk County, Florida, Bone Valley Member of Peace River Formation (middle or upper Miocene). (3) MCZ 17883, partial rostrum and portions of right and left mandibles, including symphysis, type specimen of *Megalodelphis magnidens*, Mulberry, Polk County Florida, Bone Valley Member of Peace River Formation (middle or upper Miocene). (4) CMM-V-2074, posterior tooth, found between Scientists Cliffs and Parkers Creek, Calvert County, Calvert Formation, Plum Point Member (Plum Point C, Shattuck zone 12) (Shattuck, 1904). (5) CMM-V-0004, anterior tooth, Harpers' Cliffs just north of Matoaka near St. Leonard, Calvert County, Choptank Formation (Choptank A, Shattuck zone 17). (6) CMM-V-1701, anterior tooth, south of Parkers Creek, Calvert Formation, Plum Point Member (Plum Point D, Shattuck zone 14). (7) CMM-V-3548, anterior tooth, western shore of Chesapeake Bay, Calvert County, Calvert Formation, Plum Point Member (Plum Point D, Shattuck zone 14).

EXPANDED DIAGNOSIS. Medium-size crocodilian, about 4 m [13 ft] in total adult body length (assuming body proportions similar to those of *Tomistoma schlegelii*). Adult skull length approximately 70 cm [2 ft]. Rostrum elongate, narrow anteriorly. Nasals widely separated from the narial opening in external view by the inward and backward extension of the premaxillaries; outer borders of maxillaries extend much farther forward on snout than nasals. Extent of the premaxillaries forward of the maxillaries relatively greater than in other well-known tomistomine species, except for "*Tomistoma*" *calaritanus*. Prefrontals much larger than in "*T.*" *calaritanus*. Dentition heterodont; anterior teeth elongate, conical, recurved, and pointed; posterior teeth low crowned, laterally compressed, upright, and bladelike. Dentaries and splenials fused along an elongate symphysis over a distance of about 40% of the length of the lower jaws. Five premaxillary teeth, 14 maxillary teeth, and 18 dentary teeth, all with prominent carinas. Premaxillary and maxillary teeth are separated both by a distinct diastema and by a pronounced lateral crocodyloid notch. First premaxillary teeth robust and directed forward. Fifth maxillary teeth enlarged and maxilla swollen around its socket. In ventral view, premaxillaries deeply indent maxillaries along the midline of the mouth back to the level of the front of the third maxillary teeth. Pterygoid flanges knob-like and flared strongly outward laterally. Dermal armor mostly unkeeled but some with low, elongate rounded keels.

HORIZON, AGE, AND DEPOSITIONAL SETTING. The type specimen of *T. sericodon* came from the Calvert Formation, and the type specimen of *T. sicarius* probably also came from the same unit. The two fairly complete specimens discussed here were recovered from the middle Miocene Plum Point Member (Plum Point B and D) of the Calvert Formation (Figure 4.2A). The Calvert Formation, like most of the other Neogene stratigraphic units in the Virginia and Maryland Coastal Plain, was deposited in a low-energy, shallow to mid-shelf marine environment (Mixon et al., 1989). In the cliffs at and between Wakefield and Stratford Hall, the Plum Point Member of the Calvert Formation has yielded numerous fossil specimens of whales, porpoises, sea turtles, sharks, rays, and marine bony fishes, as well as occasional remains of sea birds, dugongs, and seals (mostly deposited at the USNM and the CMM). Remains of land mammals are very rare, but fossil wood and seeds of cherry, walnut, and pine, belonging to species described by Berry (1934, 1936), are moderately common in these strata. The plant remains indicate either that land was not far to the west at the time these strata were deposited or else that a strong river current then was spreading plant remains far out onto the Atlantic continental shelf.

DISCUSSION. The nearly complete Wakefield skull allows a full characterization of the external cranial elements of *T. sericodon* (Figures 4.3, 4.4). The Stratford specimen (Figure 4.5) preserves the anterior part of the skull and most of the lower jaws (Figures 4.6, 4.7). The distal end of the right quadrate is the only remnant of the posterior cranium of the Stratford specimen that was recovered (Figure 4.6). The portions of the skull preserved in both specimens are very similar, and the few teeth remaining in the jaws (as well as the numerous teeth found lying loose among the bones of both skeletons) demonstrate that this animal was markedly heterodont, with piercing teeth in the anterior part of the jaws and cutting teeth in the posterior part (Massare, 1987). The mid-jaw and anterior teeth (Figure 4.8D2,D3) are conical, recurved, and elongate; these kinds of teeth constitute the type material of *Thecachampsa sericodon*. In contrast, the posterior teeth (Figure 4.8D1) are low crowned, laterally compressed, and possess a long shearing blade; these kinds of teeth constitute the type material of *Thecachampsa sicaria*. Although such heterodonty is unusual among crocodilians, it is not unique. For example, the only tooth-bearing skull of the living tomistomine species *Tomistoma schlegelii* in the USNM collections (USNM 52972) shows a similar, although less strongly developed, heterodonty.

The most striking features of these two skulls are their elongate, narrow snouts and the elongate premaxillaries that have carried the narial opening far forward beyond the anterior end of the nasals as seen in dorsal view (Figure 4.3). These characteristics are also typical of *Gavialosuchus eggenburgensis* (Toula and Kail, 1885) and two tomistomine crocodilians previously assigned to *Tomistoma* (Capellini, 1890; Telles Antunes, 1961). In ventral view (Figure 4.4), the snout contains five premaxillary teeth and 14 maxillary teeth on each side. A distinct diastema developed between the premaxillary and maxillary teeth, and the snout is perceptibly constricted in this same region. The fifth maxillary teeth are enlarged in comparison to nearby teeth. The lower jaws are fused along a symphysis that extends 40% of the length of each jaw (Figures 4.5, 4.7) and includes the first 11 teeth; each jaw ramus contains 18 teeth. Figure 4.7

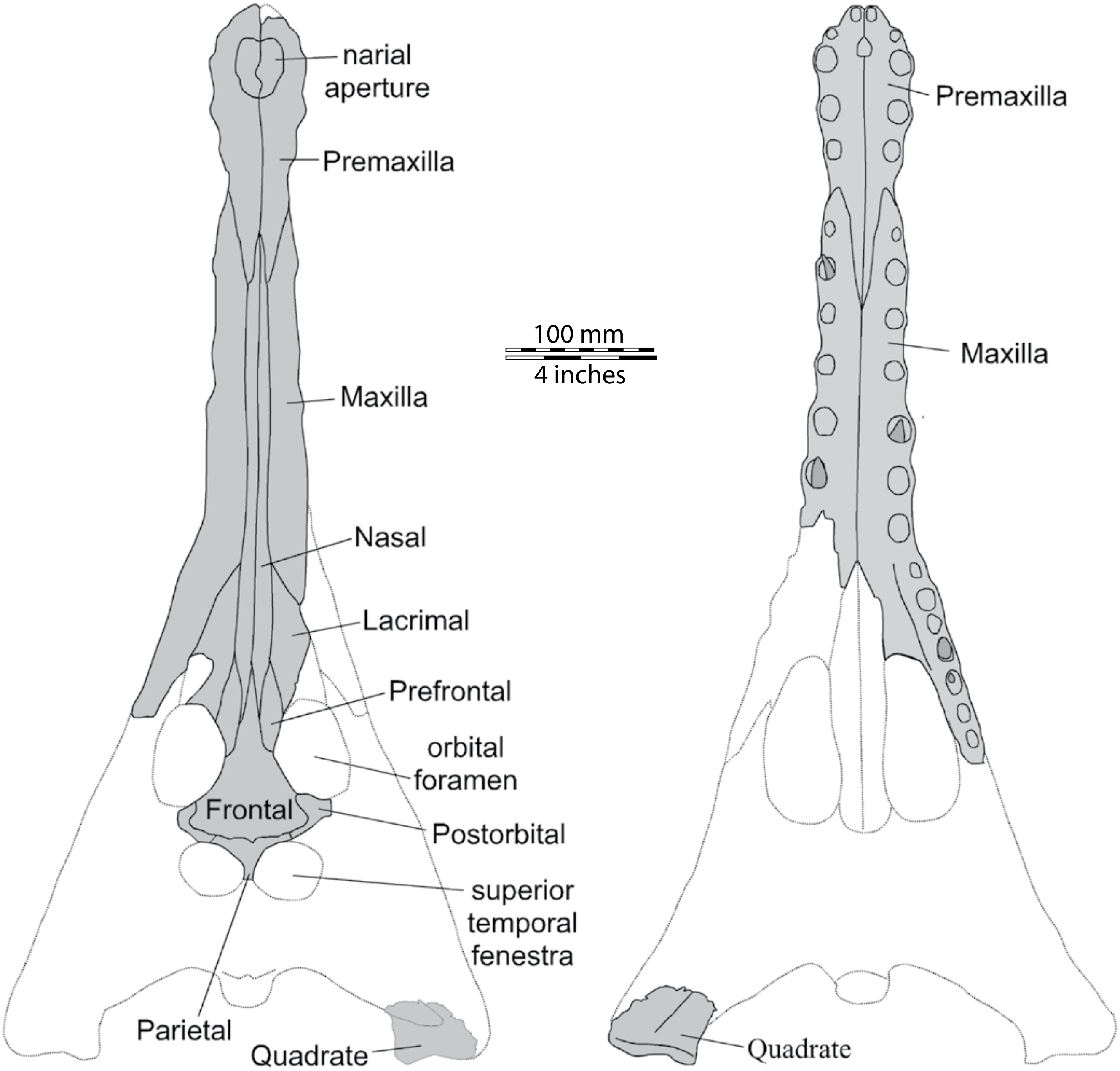

FIGURE 4.6. Restoration of the skull of the Stratford Hall Plantation specimen of *Thecachampsa sericodon* Cope (STHA1) in dorsal (left) and ventral (right) views.

shows the relative contributions of the dentary, angular, and surangular in lateral view.

No elements certainly referable to the shoulder girdle or front limbs are known, but many of the rear limb elements have been recovered. The right ilium (Figure 4.8B) was nearly complete and can be compared to the same element in *Thecachampsa carolinensis*, *Crocodylus*, and *Alligator* (Figure 4.9). It is not especially close in conformation to any of these forms. In the size of its acetabulum, it is closer to *Alligator* and *Crocodylus*; in the shape of its posterior border, it is closer to *Thecachampsa carolinensis* and *Crocodylus*; in the shape of its anterior border, it is closer to *Thecachampsa carolinensis* and *Alligator*. The femur is rather slender but normally proportioned (Figure 4.8C). The numerous osteoderms recovered with both specimens indicate that it had an

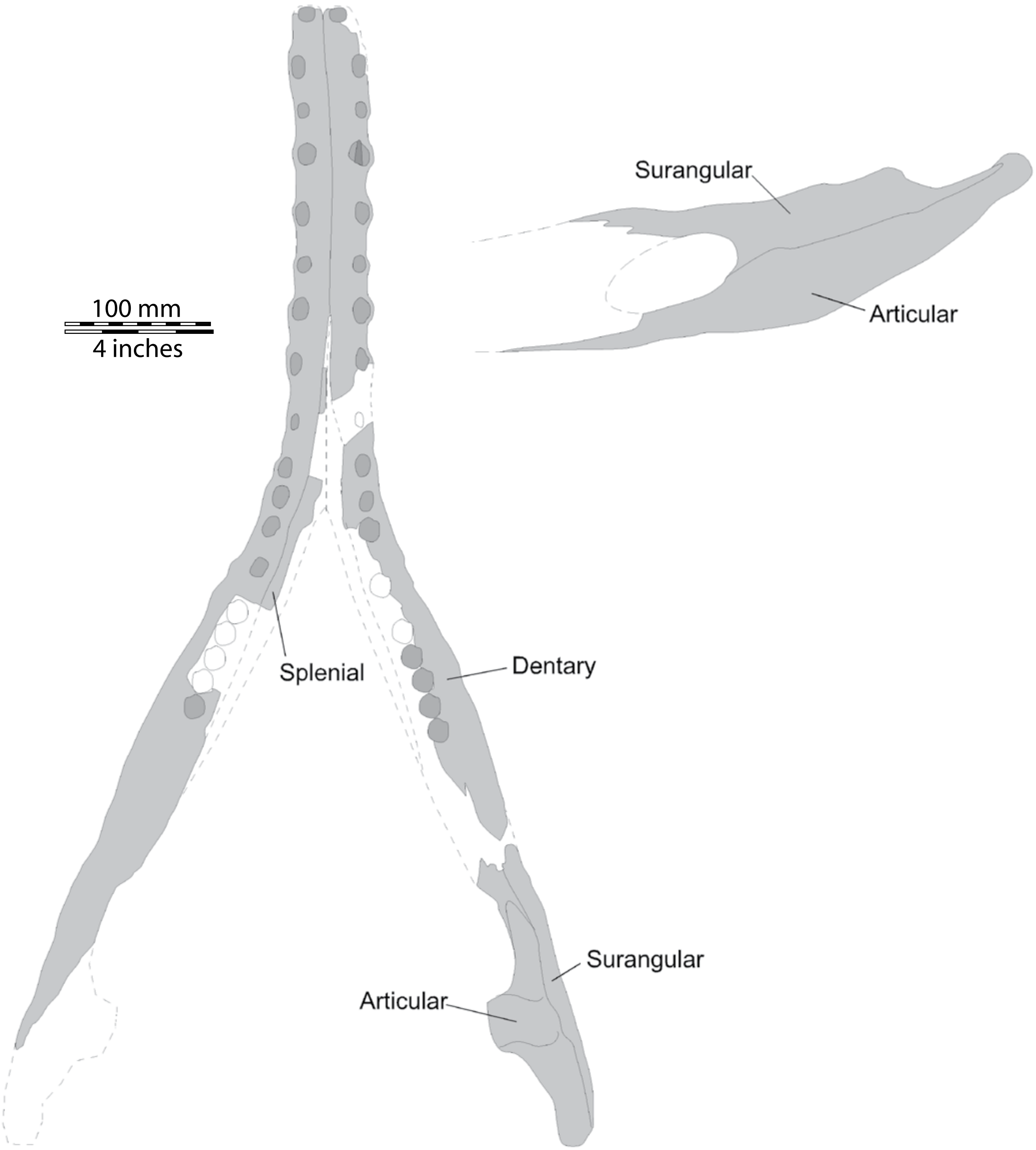

FIGURE 4.7. Restoration of the lower jaws of the Stratford Hall Plantation specimen of *Thecachampsa sericodon* Cope (STHA1) in dorsal view (left) and external posterolateral view (right).

extensive subdermal armor, with some osteoderms suturally interconnected and others smooth-bordered and floating free within the integument. Most osteoderms are unkeeled (Figure 4.8E1), but a few bear low, broad, rounded keels ranging from well developed to barely discernable (Figure 4.8E2).

Thecachampsa antiquus (Leidy, 1851)

Crocodilus antiquus, Leidy 1851a:307 (original unillustrated reference).

Crocodilus antiquus Leidy, 1852:135–138, pl. xvi (original description).

Thecachampsa contusor Cope, 1867:143.

Thecachampsa antiqua (Leidy, 1852): Cope, 1869a:64 (synonymized with *T. contusor*).

Crocodylus antiquus Leidy, 1852: Cope, 1882:983, 986.

Crocodylus antiquus Leidy, 1852: Hay, 1902:512.

Gavialosuchus americanus (Sellards, 1915): Mook, 1921a:33–41, pls. V–VII.

Gavialosuchus americanus (Sellards, 1915): Auffenberg, 1954:185–209, fig. 2.

Crocodylus antiquus Leidy, 1852: Steel, 1973:65.

Crocodylus contusor Cope, 1867: Steel, 1973:65.

Thecachampsa antiqua (Leidy, 1852) (partem): Myrick, 2001:221, fig. 2.

Etymology of Name. Although *Thecachampsa* ends in the letter *a*, "*champsa*" is not derived from a feminine first declension Latin word. Rather, *champsa* is derived from an Egyptian word for crocodile by way of Greek and is a masculine noun. Therefore, the Latin species name *antiquus* should be masculine to conform to the gender of the generic name. The name *antiquus* also has priority.

Holotype. Originally two teeth, two vertebrae, a rib fragment, and an ungual phalanx (in part illustrated in Leidy, 1852: pl. 16, figs. 1–5), collected by Robert H. Nash. According to Spamer et al. (1995:111), only the two vertebrae can be found at present (ANSP 9188, which is fig. 4 on pl. 16 in Leidy, 1852, and ANSP 9189, which is fig. 5).

Original Diagnosis. Medium-sized crocodilian, with blunt to moderately elongate conical teeth either lacking a cutting edge (carina) or with a very poorly developed carina.

Type Locality. Bluffs at Stratford Hall Plantation, Westmoreland County, Virginia, USA.

Horizon. The horizon is not indicated, but the type material is almost certainly from the Choptank Formation (upper middle Miocene) on the basis of the presence of mollusk shell material associated with the holotype. The Calvert and St. Marys Formations in the Stratford bluffs are not shelly.

Previously Referred Material. Type tooth of *Thecachampsa contusor* (Cope 1867), ANSP 9152, found near the residence of James T. Thomas near the Patuxent River, Charles County, Maryland, in the Calvert Formation (Plum Point D, middle Miocene).

Newly Referred Material. (1) CMM-V-3774, 1 tooth and numerous postcranial elements, including 9 presacral vertebrae, 2 sacral vertebrae, 10 caudal vertebrae, both ilia, 1 ischium, 1 pubis, left femur, anterior end of right femur, both tibia, 1 fibula, 6 metatarsals, and 4 tarsals, collected by Stephen Roger Horman, Robert Weems, Sankar Chatterjee, and Vincent LaPiana, 1976, from bluffs south of Popes Creek, Charles County, Maryland, Fairhaven Member (Fairhaven C) of the Calvert Formation (lower Miocene). (2) CMM-V-4668, fused frontals and fragments of surrounding bones, collected by Ron Ison from the bank of the Pamunkey River, New Kent or King William County, Virginia, Fairhaven Member (Fairhaven C) of the Calvert Formation (lower Miocene). (3) Very large mandibular tooth, in collection of Robert D. Bowes, from Pollack Farm Fossil Site, Kent County, Delaware, Fairhaven Member (Fairhaven C) of the Calvert Formation (lower Miocene; described but not illustrated in Holman, 1998). (4) USNM 25243, posterior fragment of right maxilla with 3 teeth, collector unlisted, from Lee Creek Mine, Beaufort County, North Carolina, Pungo River Formation (Myrick, 2001: fig. 2). (5) USNM 299913, cranium, collected by Vanscoy and Vanscoy, 1981, at Stratford Hall Plantation, Westmoreland County, Virginia, Choptank Formation (middle Miocene; currently on exhibit at the CMM, Solomons, Maryland). (6) CMM-V-2392, anterior tooth, south of Parkers Creek, Calvert County, Maryland, Calvert Formation, Plum Point Member (Plum Point D, Shattuck zone 14; middle Miocene). (7) USNM 25098, anterior portion of lower jaws with teeth, collected by W. L. Ashby, 1968, at Parkers Creek, Calvert County, Maryland, Choptank Formation (Choptank A, Shattuck zone 17; middle Miocene). (8) USNM 24938, posterior portion of a cranium, collected by Carla Sanchez in 1966 at Chesapeake Ranch Estates south of Little Cove Point, Calvert County, Maryland, St. Marys Formation (upper Miocene). (9) USNM 24939, anterior portion of a cranium, fragment of the right prefrontal region, and portions of mandibles, collected by Carla Sanchez in 1967 at Chesapeake Ranch Estates south of Little Cove Point, Calvert County, Maryland, St. Marys Formation (upper Miocene). (10) CMM-V-1764, mid-caudal vertebra, collected by Gary Wendt, Little Cove Point, Calvert County, Maryland, Little Cove Point Member, St. Marys Formation (upper Miocene). (11) CMM-V-3227, tooth, Windmill Point, St. Marys County, Maryland, St. Marys Formation, possibly but not certainly from the Windmill Point Member (upper Miocene). (12) AMNH 5663, largely complete skull, donated by Anton Schneider, Polk County, Florida, Bone Valley Member of Peace River Formation (middle or upper Miocene); AMNH 5662, anterior portion of skull, donated by Anton Schneider, Polk County, Florida, Bone Valley Member of Peace River Formation (middle or upper Miocene); UF 6225, largely complete skull, collector unacknowledged, Alachua County, Florida, Bone Valley Member of Peace River Formation (middle or upper Miocene).

Expanded Diagnosis. Same as for *T. sericodon* with the following exceptions: Maximum total adult body length larger, about 5 m [16 ft]. Maximum skull length approximately 80 cm [2 ft, 4 inches]. Snout of skull elongate and narrow anteriorly but less narrow than in *T. sericodon*. Dentition homodont, with stout conical crushing teeth that often lack carinas or have only weakly developed carinas; first premaxillary tooth relatively smaller than in *T. sericodon* and directed downward rather than

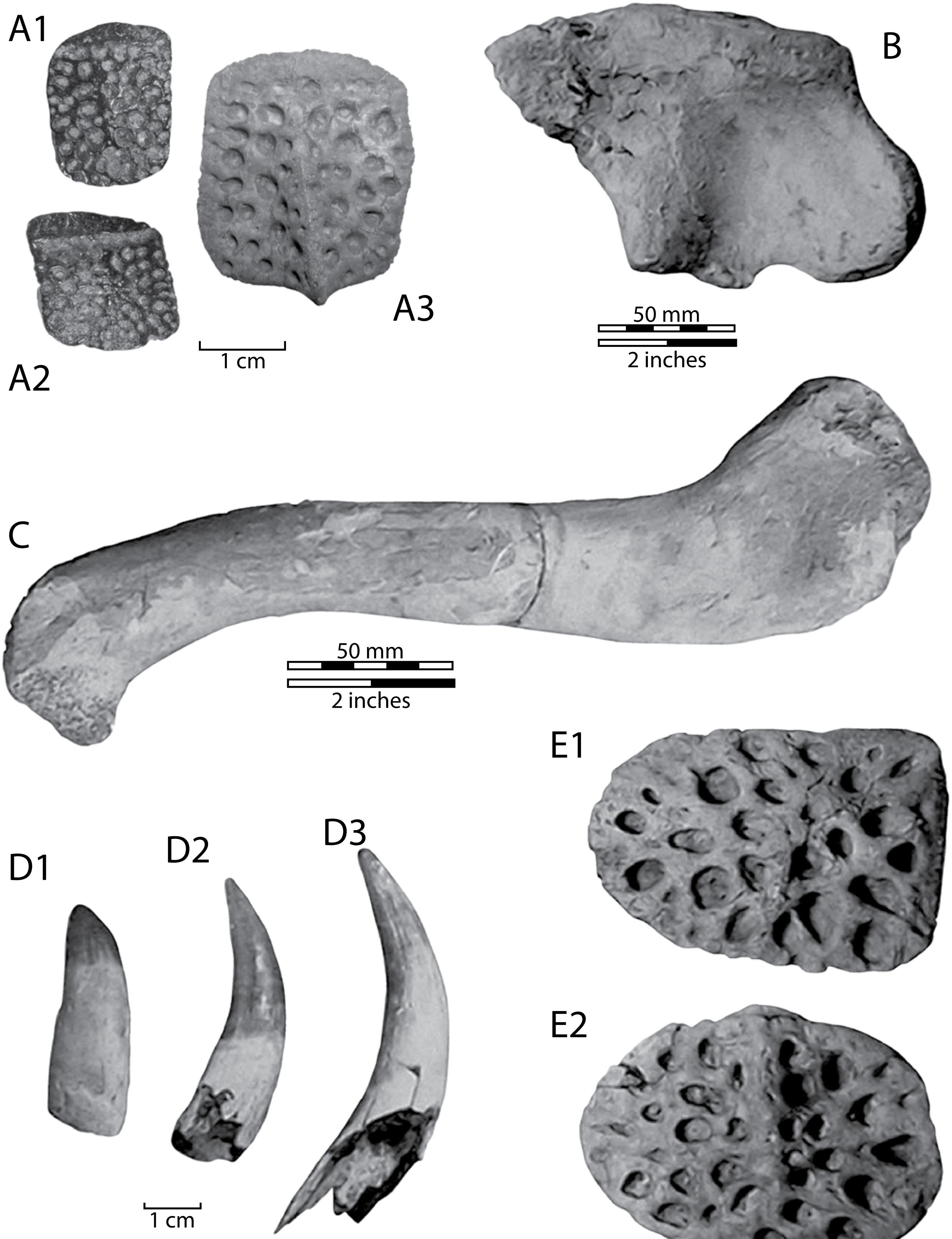
A1
A3
B
50 mm
2 inches
1 cm
A2
C
50 mm
2 inches
E1
D1
D2
D3
E2
1 cm

FIGURE 4.8. (*Facing page*) (A1, A2) Dermal armor with a low, faintly visible, vertically oriented longitudinal keel, possibly referable to *Alligator olseni* (USNM 540749 and USNM 540750, respectively). (A3) Dermal armor of *Alligator olseni* (UF 171554) with strongly developed longitudinal keel. (B–F) Postcranial elements from the Stratford Hall Plantation specimen of *Thecachampsa sericodon* Cope (STHA1). (B) Right ilium. (C) Left femur. (D1, D2, D3) Posterior, mid-range, and anterior teeth, respectively. (E1) Unkeeled armor. (E2) Keeled armor. Scale bars refer to all numbered specimens within a lettered grouping.

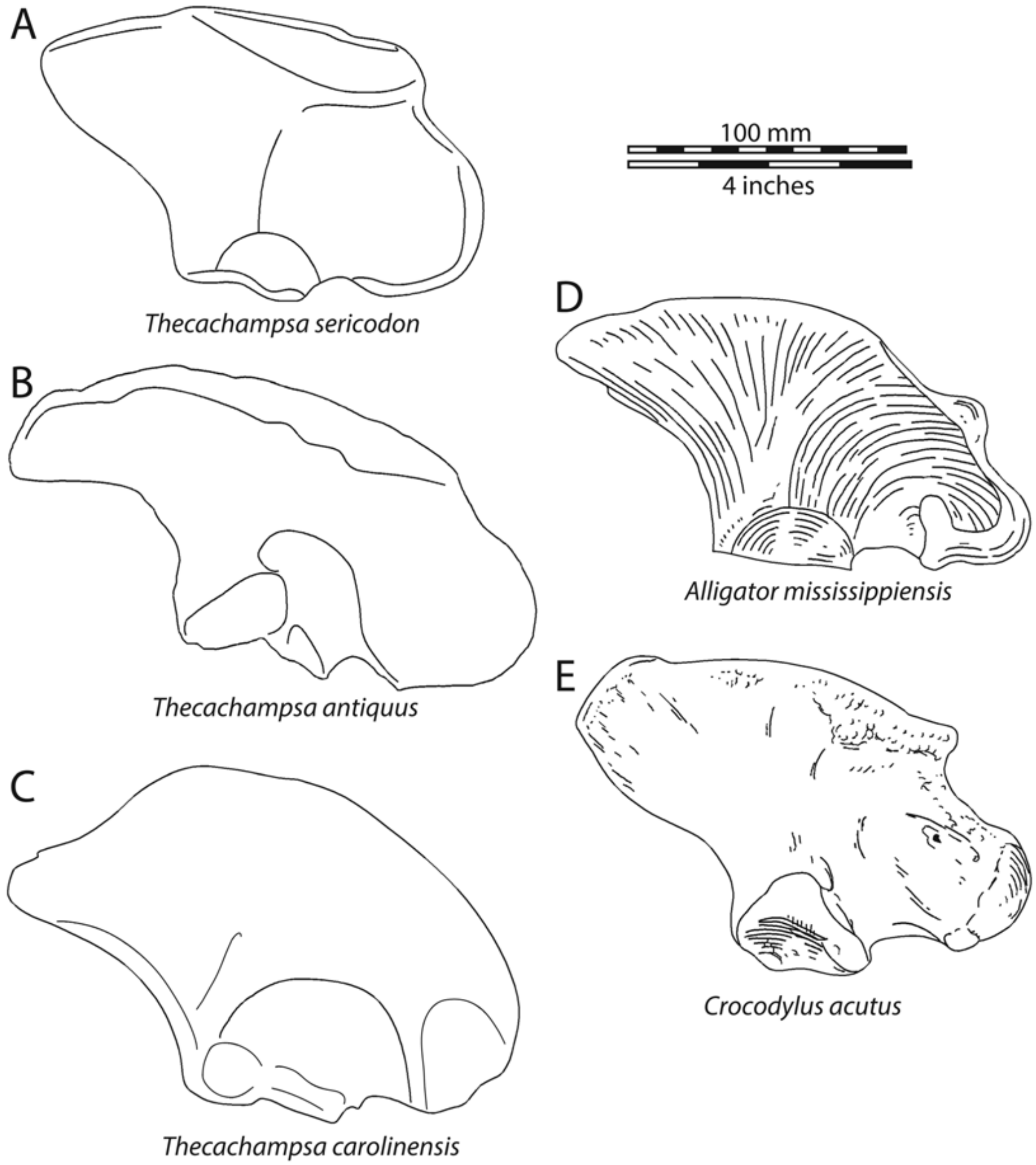

FIGURE 4.9. The left ilia of (A) *Thecachampsa sericodon* Cope, (B) *Thecachampsa antiquus* (Leidy), and (C) *Thecachampsa carolinensis* (Erickson and Sawyer) in comparison with the left ilia of (D) *Alligator mississippiensis* (Daudin) and (E) *Crocodylus acutus* Cuvier. *Alligator* from Gregory (1951), *Crocodylus* from Mook (1921a), and *T. carolinensis* from Erickson and Sawyer (1996).

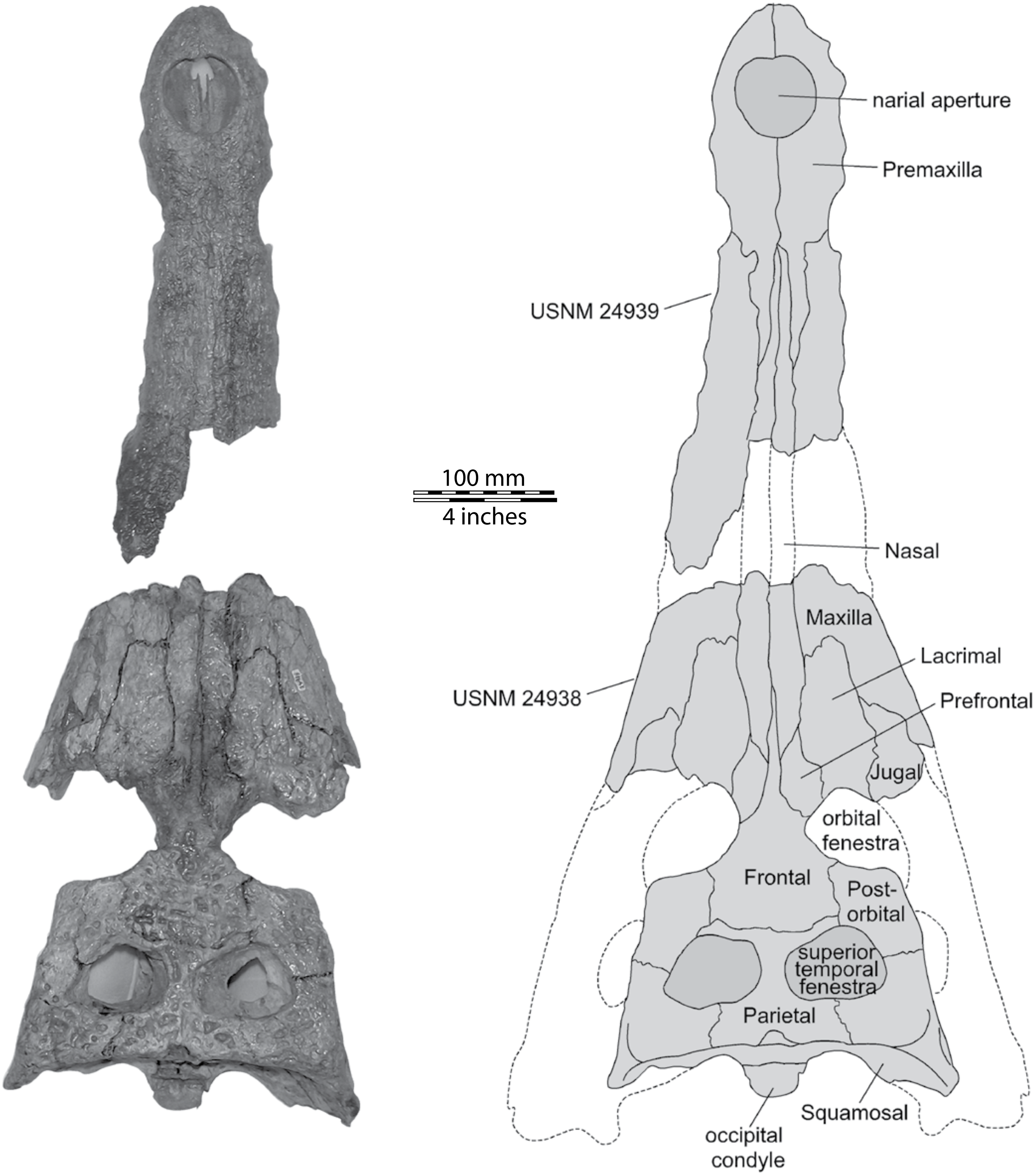

FIGURE 4.10. Photograph (left) and restoration (right) of the St. Marys Formation skull fragments of *Thecachampsa antiquus* (Leidy) (USNM 24938 and USNM 24939) in dorsal view.

forward. Posterior blade of ilium more elongated than in *T. sericodon*; fourth trochanter on femur larger and more robust than in *T. sericodon*; ventral internal border of femur straighter than in *T. sericodon*.

Horizon, Age, and Depositional Setting. Although the locality of the type material is known, the stratigraphic horizon from which it came was not indicated. The type material was associated with pectinid shells, so it came from above the Calvert Formation, which has no preserved pectinid shells at this locality. It was likely found in the overlying Choptank Formation (Choptank A). The type material of *Thecachampsa contusor* is recorded simply as being from the Calvert Formation, but the locality suggests an upper (Plum Point) Calvert horizon. The specimens described herein come from a much wider stratigraphic range than the specimens of *T. sericodon*, having been found as low as the Fairhaven Member (Fairhaven C) of the Calvert Formation and with certainty as high as the Little Cove Point Member of the St. Marys Formation. One specimen of this species, found on the beach at Windmill Point, may have come from the Windmill Point Member of the St. Marys Formation (Figure 4.1). This horizon cannot be said with certainty, however, because the specimen also could have come from the top of the Little Cove Point Member, which is exposed at beach level. The depositional setting of all of these deposits was coastal shallow marine to offshore mid-shelf.

Discussion. The two specimens from Chesapeake Ranch Estates were found at different times but at the same locality by the same collector. They are from animals of comparable size, but the snout of USNM 24939 was found in association with a large but detached fragment of its right prefrontal region that is identical in conformation to the comparable region recovered with USNM 24938. Therefore, even though these two specimens are comparable in size, they must have come from two different individuals. Between these two specimens, most features of the dorsal and ventral skull can be determined (Figures 4.10, 4.11). Although generally similar to *T. sericodon*, *T. antiquus* grew to a somewhat larger size and had a slightly more robust rostrum that held relatively larger, stout, conical teeth that were much the same in conformation from the front of the mouth to the back. These differences are consistent among the Calvert and St. Marys specimens (Figures 4.10–4.13) wherever each character state is preserved, and they all contrast with the two fairly complete skulls of *T. sericodon* described above.Similarly, the ilium and femur of *T. antiquus* are quite different in conformation from the same elements in *T. sericodon* (Figures 4.8, 4.9, 4.14), probably because *T. antiquus* had stronger rear limbs that were well suited for walking.

These consistent differences, as well as the difference in the overall stratigraphic range of the two species, demonstrate that this material represents two different but closely related species.

THE STATUS OF *GAVIALOSUCHUS AMERICANUS*

Sellards (1915) described a species of tomistomine crocodile ("*Tomistoma*" *americana*) from the anterior snout of a skull found in the Bone Valley Member of the Peace River Formation in Polk County, Florida. At that time, the Bone Valley Member was considered to be late Miocene or early Pliocene, but more recent work places the age of the tomistomine-bearing beds as middle to late Miocene (Hulbert, 2001:150). By 1915, the poorly known Maryland and Virginia Miocene crocodilian material had been assigned to *Crocodylus*. The snout described by Sellards was clearly a tomistomine, so there seemed no reason at that time to closely compare the Virginia-Maryland material to the Florida specimen. A few years later, Mook (1921a) described a much more complete tomistomine skull and other material (Mook, 1921b) from the same Florida area, referring all of this material to the species that Sellards had described. However, Mook recognized that the Florida material, although tomistomine, was closer to the genus *Gavialosuchus* than it was to *Tomistoma* and so redesignated the species as *Gavialosuchus americanus*. Much later, Auffenberg (1954) described more tomistomine material, this time from Alachua County, and again assigned it to *Gavialosuchus americanus*. Myrick (2001) synonymized all of this material with the Maryland and Virginia material and called it *Thecachampsa antiqua*.

The type of *G. americanus* is only a snout, so only this part of the Virginia and Maryland specimens can be compared with the type Florida specimen; the other two published Florida specimens can be far more fully compared. In dorsal view (Figure 4.15) the more complete specimens are separable into broader-snouted and narrower-snouted morphotypes.The type snout of *G. americanus* shows no obvious distinguishing characteristics in this view. However, in ventral view (Figure 4.16) a distinctive trait can be discerned. When the length of the portion of the snout that lies anterior to the center of the fifth maxillary tooth sockets is divided by the width of the snout at the level of the center of the fifth maxillary tooth sockets, the type specimen of *G. americanus* clearly has snout proportions identical to *T. sericodon* (Figure 4.17). In contrast, the two specimens later discussed by Mook and Auffenberg have snout proportions identical to *T. antiquus*. Thus, the type specimen of *G. americanus* is a junior synonym of *Thecachampsa sericodon*, but the other two illustrated and largely complete skulls are examples of *T. antiquus*. These conclusions are in accord with the conclusions of both Piras et al. (2007) and Brochu and Storrs (2012) that Myrick was correct in moving the Florida material from *Gavialosuchus* to *Thecachampsa*. The holotype mandible of *Megalodelphis magnidens* Kellogg, 1944, which was later referred to *Gavialosuchus americanus* by Morgan (1986), has posterior teeth that are low crowned and laterally compressed. This characteristic makes this specimen referable to *T. sericodon* rather than to *T. antiquus*. The specimen discussed by Auffenberg (1954) is unique in that the frontal does not make contact with the premaxillaries at their proximal ends; in all of the other specimens the frontal separates the prefrontals and also distinctly indents the premaxillaries (Figure 4.15). For now, this difference is assumed to be either a developmental abnormality or an interpretive drafting error, but if

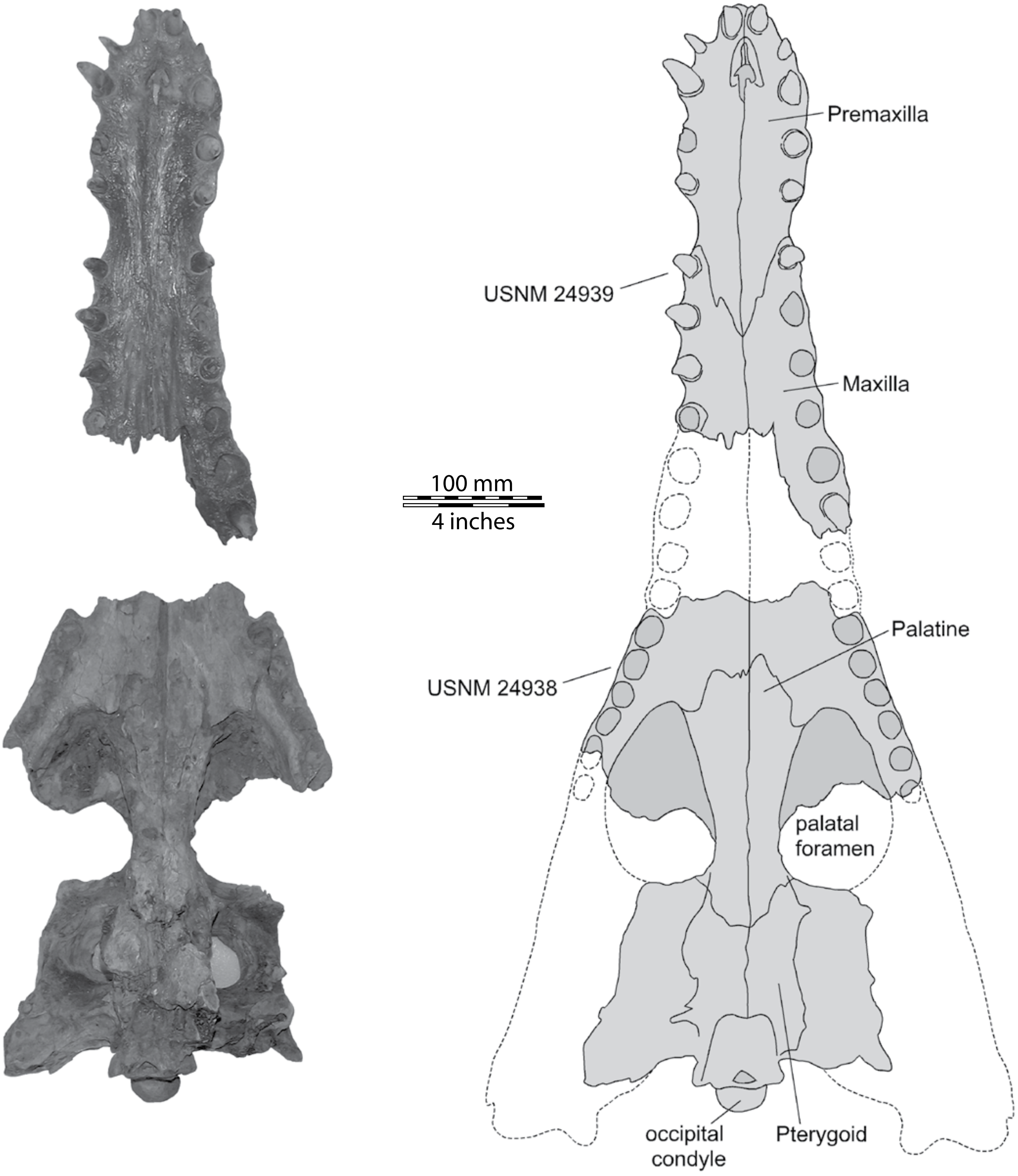

FIGURE 4.11. Photograph (left) and restoration (right) of the St. Marys Formation skull fragments of *Thecachampsa antiquus* (Leidy) (USNM 24938 and USNM 24939) in ventral view.

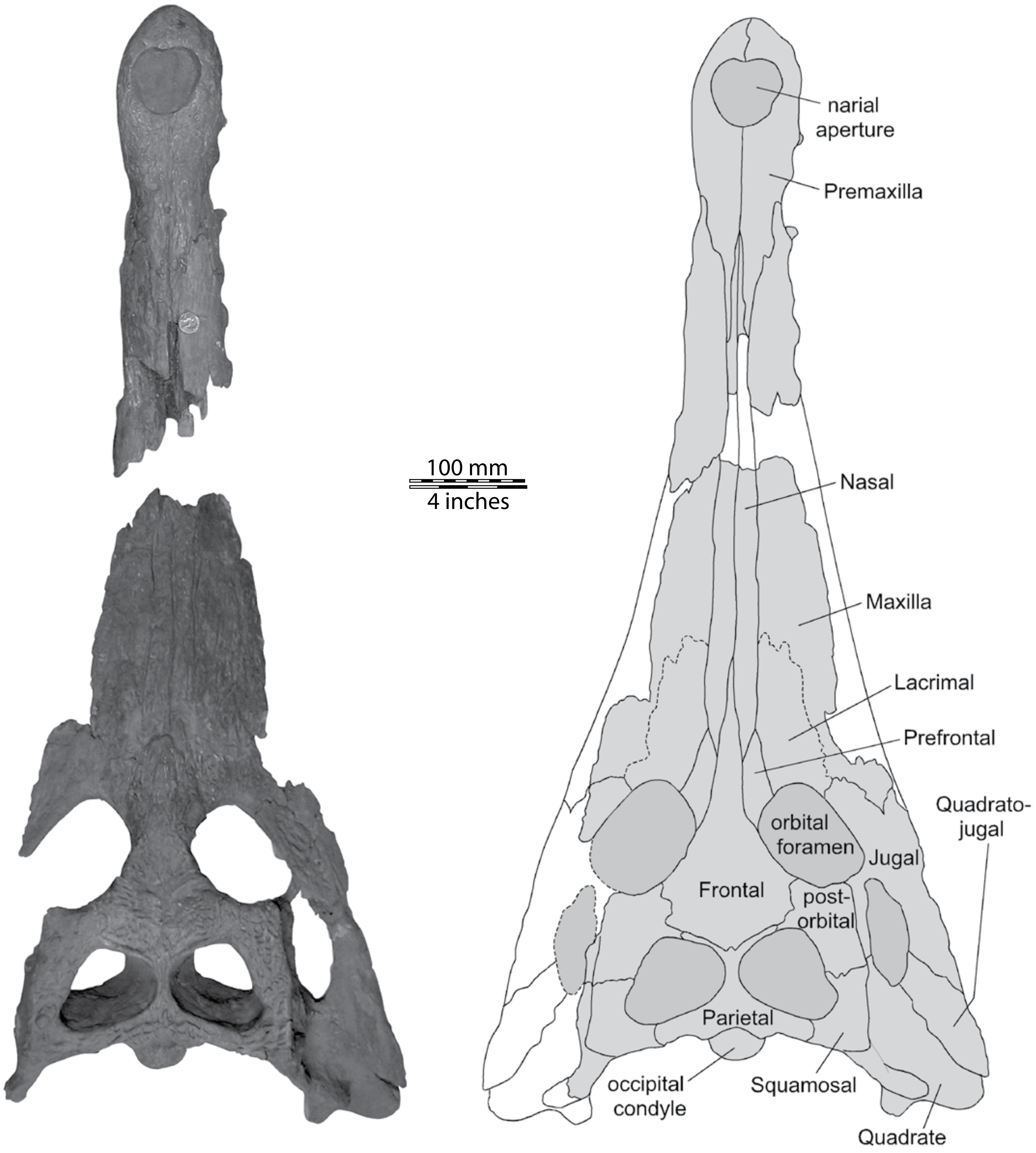

FIGURE 4.12. Photograph (left) and restoration (right) of the Calvert Formation Stratford Hall skull of *Thecachampsa antiquus* (Leidy) (USNM 299913) in dorsal view.

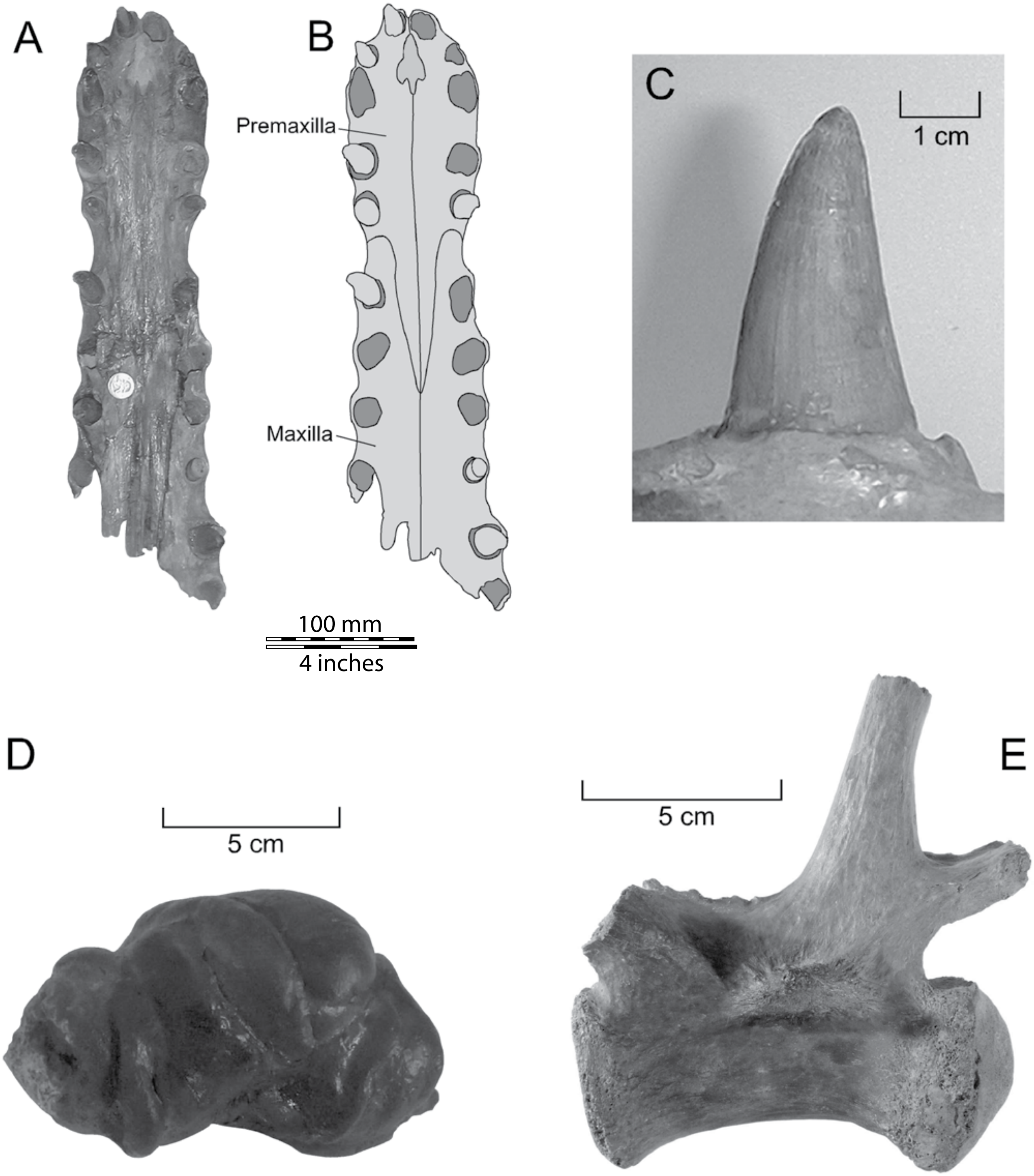

FIGURE 4.13. (A) Photograph and (B) restoration of the Stratford Hall snout of *Thecachampsa antiquus* (Leidy) (USNM 299913) in ventral view. (C) Tooth in this skull (USNM 299913). (D) Coprolite of *Thecachampsa* (CMM-V-7573) from the Plum Point Member of the Calvert Formation in lateral view. The length of animal that produced this coprolite was about 4.1 m on the basis of the ratio established by Milàn (2012). This is the size of an adult *T. sericodon* (about 4 m) or a subadult *T. antiquus* (about 5 m). (E) Caudal vertebra of *Thecachampsa antiquus* (Leidy) (CMM-V-1764) from the Little Cove Point Member of the St. Marys Formation in left lateral view.

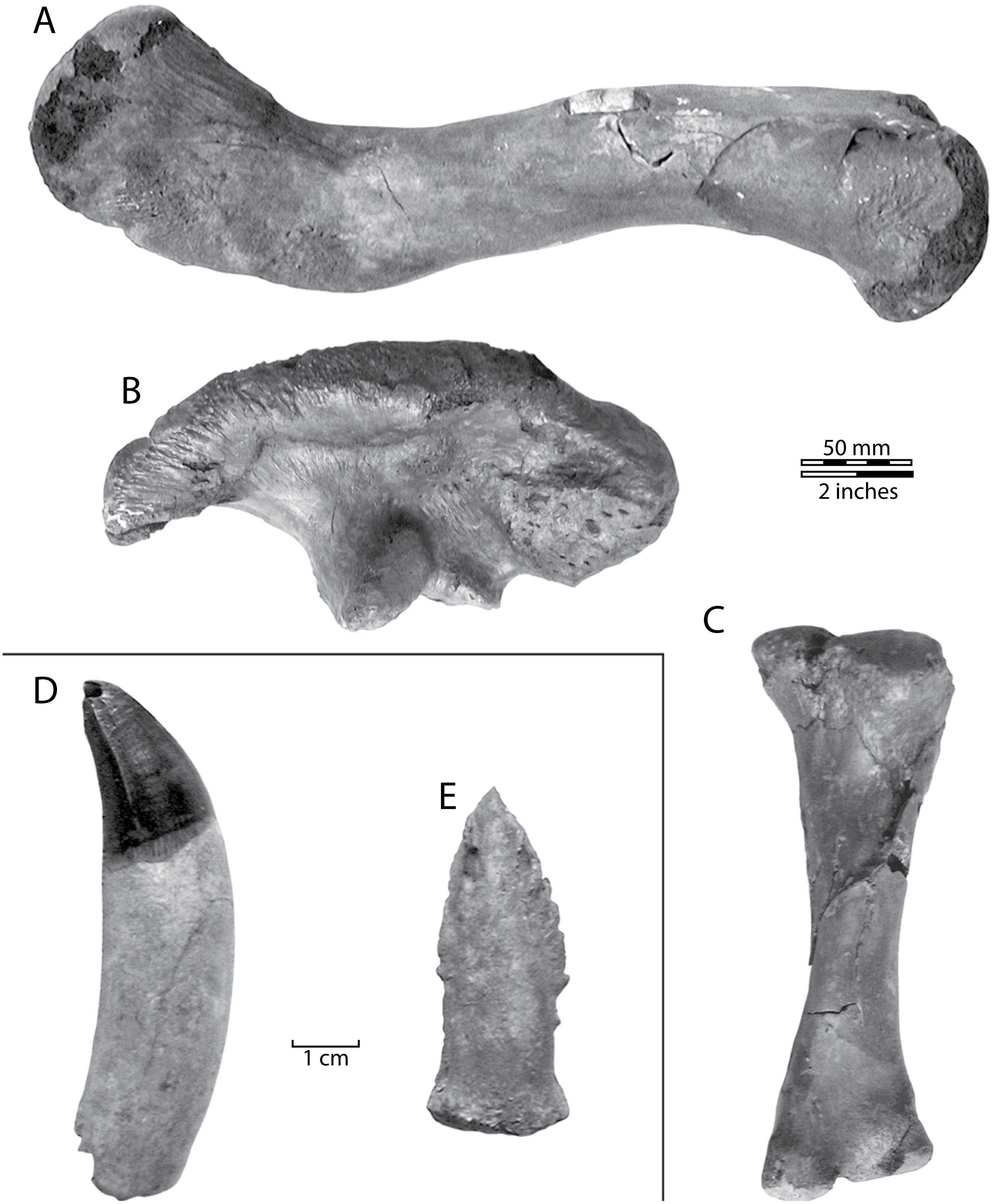

FIGURE 4.14. Postcranial elements of *Thecachampsa antiquus* (Leidy) (CMM-V-3774) from Popes Creek, Maryland. (A) Left femur in anterior view. (B) Right ilium in external lateral view. (C) Left tibia in internal view. (D) Mid-jaw or posterior tooth. (E) Ungual phalanx.

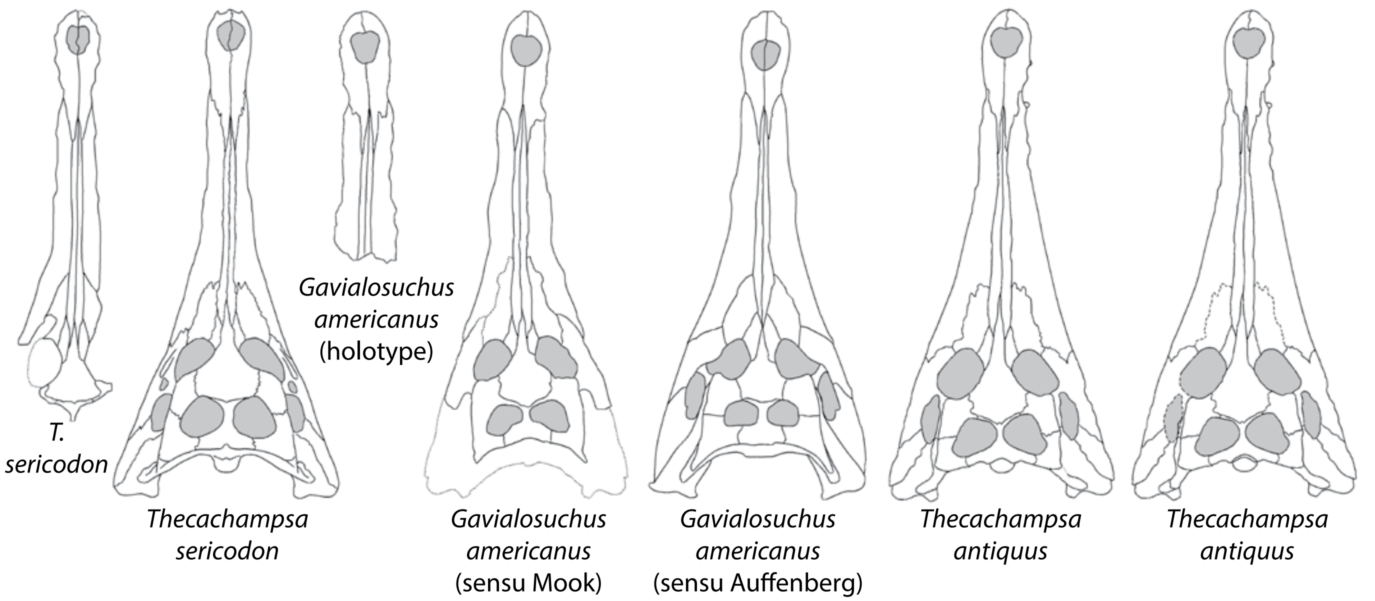

FIGURE 4.15. One nearly complete and one partial skull of *Thecachampsa sericodon* (far left), one nearly complete and one partial skull of *T. antiquus* (far right), and three partial to nearly complete skulls described as *Gavialosuchus americanus* between them. All are diagrammatically drawn in dorsal view to the same length to emphasize relative proportions.

future collecting consistently turns up more specimens like this, then this trait may be a diagnostic characteristic for an as yet unrecognized species of *Thecachampsa*.

COPROLITES OF *THECACHAMPSA*

Large coprolites (Figure 4.13D) occasionally are found in the same beds as skeletal remains of *Thecachampsa*. Many of these, and perhaps all, can be attributed to *Thecachampsa* for several reasons. First, these coprolites are large and thus pertain to a large animal. Large sharks such as *Carcharocles* could produce coprolites of this size, but they would have a strongly spiral shaped, superficially pupa-like morphology quite unlike the coprolites discussed here (see Schwimmer, 2002: fig. 8.2C,D for examples). Although possible external morphologies are rather varied, most crocodilian coprolites are elongate and cylindrical to tapering in shape and have rounded terminations (Milàn, 2012). Second, the coprolites discussed here have a faintly layered but internally massive internal texture that attests to thorough digestion of any bony material that was ingested. Study of modern crocodilian scat has shown that although hair and feathers may be present, bony remains are not (Milàn, 2012). The reason is mostly because hydrochloric acid concentrations are 50 times stronger in crocodilian digestive tracts than in the digestive tracts of mammalian carnivores (Coulson et al., 1989). Although freshly defecated feces of modern crocodilians can retain "ghosts" of bones and teeth made of organic fibrous materials, they become unrecognizable within a day or two of being produced (Fisher, 1981). Third, crocodilian feces are quite cohesive, unlike the feces of bony fishes, sea turtles, and marine mammals, and thus are much more likely to be preserved in aquatic environments. For all of these reasons, *Thecachampsa* is the only likely source of these Miocene marine coprolites.

A strong relationship exists between the diameter of crocodilian scat and the size of the animal that produced it. This relationship is expressed by the formula DS = 0.012(TL) + 1.10, where DS is the diameter of the scat and TL is the total length of the animal that produced it (Milàn, 2012). A coprolitic mass 6 cm in diameter with feather impressions, reported by Wetmore (1943) from Shattuck's zone 12 of the Calvert Formation near Parkers Creek, could belong to *Thecachampsa* because the animal that produced it was about 4 m in length and because feathers and hair are much more resistant to crocodilian digestion than bone. It should be noted, however, that hair and feather remains are found more commonly in regurgitated crocodilian stomach contents analogous to hairballs than in scat (Fisher, 1981).

It cannot be determined if coprolites of *T. antiquus* are morphologically distinguishable from coprolites of *T. sericodon* because crocodilian coprolites and skeletal remains are not yet associated in finds from the Chesapeake Group. Even if coprolites associated with skeletons are eventually found, there still is

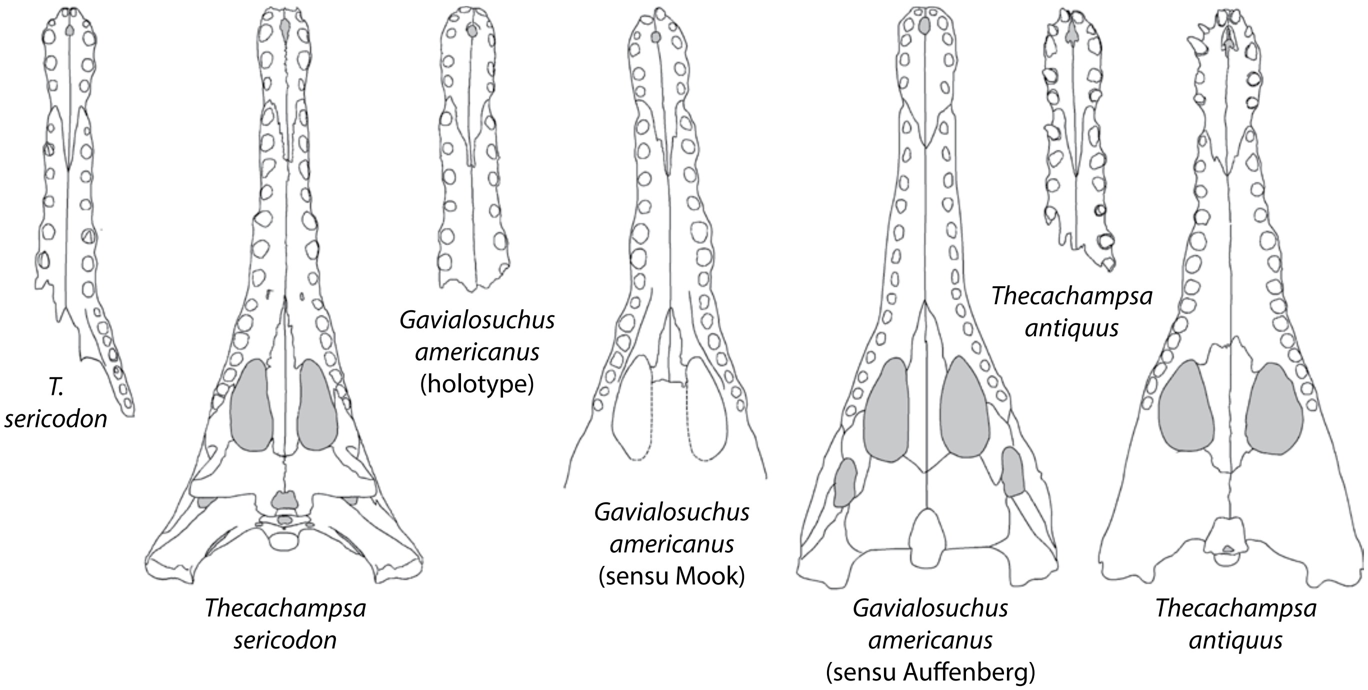

FIGURE 4.16. One nearly complete and one partial skull of *Thecachampsa sericodon* (far left), one nearly complete and one partial skull of *T. antiquus* (far right), and three partial to nearly complete skulls described as *Gavialosuchus americanus* between them. All are diagrammatically drawn in ventral view to the same length to emphasize relative proportions.

no guarantee that there will be any consistent differences that will distinguish which species produced them. On the basis of the estimated size of adults, *T. sericodon* (4 m) would have produced coprolites up to 6 cm in diameter, and *T. antiquus* (5 m) would have produced coprolites up to 7 cm in diameter. This calculation indicates that coprolites larger than 6 cm in diameter probably can be attributed to *T. antiquus*. In the St. Marys Formation, all crocodilian coprolites probably can be assigned to *T. antiquus* by default because *T. sericodon* apparently was extinct by the time of the St. Marys. Otherwise, for now large crocodilian coprolites less than 6 cm in diameter can be identified only as *Thecachampsa* sp.

DISCUSSION AND TAXONOMIC ANALYSIS

Morphological taxonomists generally have included *Tomistoma* and related extinct genera within a subfamily Tomistominae (nested within the family Crocodylidae) and placed *Gavialis* and its extinct relatives in its own family, Gavialidae (basal to all other extant crocodilians; Brochu, 1997, 2003, 2006, 2007). In contrast, molecular data set studies consistently have supported a sister group relationship between *Gavialis* and *Tomistoma* (for example, Densmore, 1983; Janke et al., 2005; Willis et al., 2007; Zhang et al., 2011). These same molecular studies strongly and consistently support a fundamental division of Crocodylia into two groups, one being Crocodylidae + (*Gavialis* + *Tomistoma*) and the other being Alligatoridae. In one variation of this phylogeny (for example, Janke et al., 2005; Zhang et al., 2011), although *Tomistoma* and *Gavialis* are both included within Crocodylidae, together they are basal to all other extant species and thus comprise either one or two separate subfamilies. A single subfamily for *Tomistoma* and *Gavialis* makes sense when only considering living forms, but because there are so many fossil relatives of both *Gavialis* and *Tomistoma* and because the separation of *Gavialis* and *Tomistoma* from the rest of Crocodylidae is so fundamental, for fossil species it makes sense to retain a threefold division of Crocodylia into the families Alligatoridae, Gavialidae, and Crocodylidae, with the clear understanding that Gavialidae and Crocodylidae are more closely related to each other than either is to Alligatoridae. This taxonomic arrangement, advocated by Poe (1996) and Willis et al. (2007), is adopted here. As *Gavialis* and *Tomistoma* are the sole surviving remnants of two quite distinct, formerly diverse and abundant clades within Gavialidae, *Gavialis* and extinct relatives are considered to comprise the subfamily Gavialinae, and *Tomistoma* and extinct relatives are considered to comprise the subfamily Tomistominae.

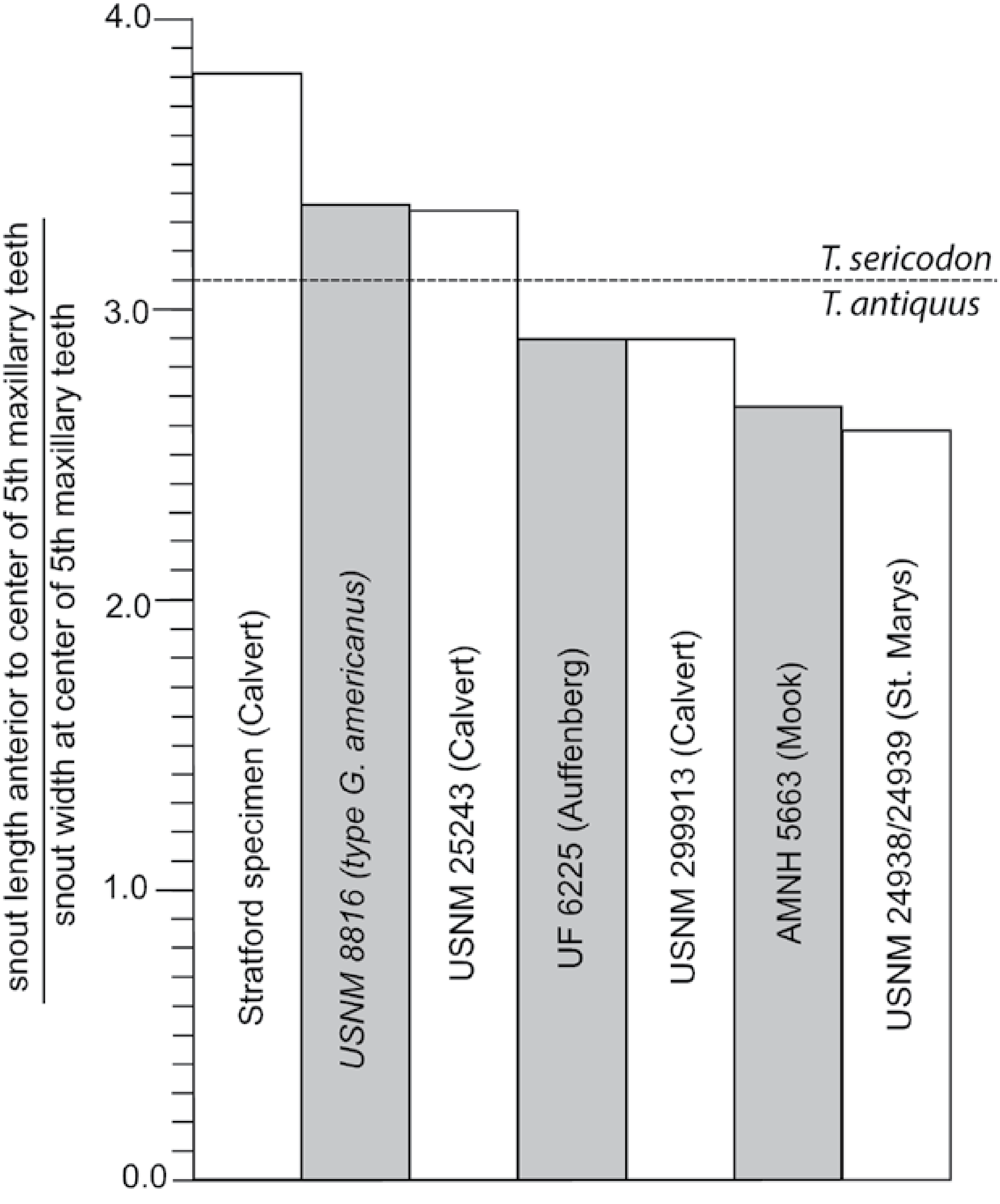

FIGURE 4.17. Bar graph showing relative snout proportions for the skulls shown in Figure 4.16. The vertical axis portrays the ratio between the length of the snout from the tip of the nose to the middle of the fifth maxillary teeth, divided by the width of the snout at the middle of the fifth maxillary teeth. Specimens from Maryland and Virginia are shown by white bars, and specimens from Florida are shown by gray bars. The Maryland and Virginia specimens contain rows of species-diagnostic teeth. One of the Florida specimens previously assigned to *Gavialosuchus americanus* (USNM 8816, the holotype) has proportions that fall in the range of *Thecachampsa sericodon*, but other published specimens have proportions typical of *T. antiquus*. Only AMNH 5663 has well-illustrated posterior teeth that independently also associate it with *T. antiquus*.

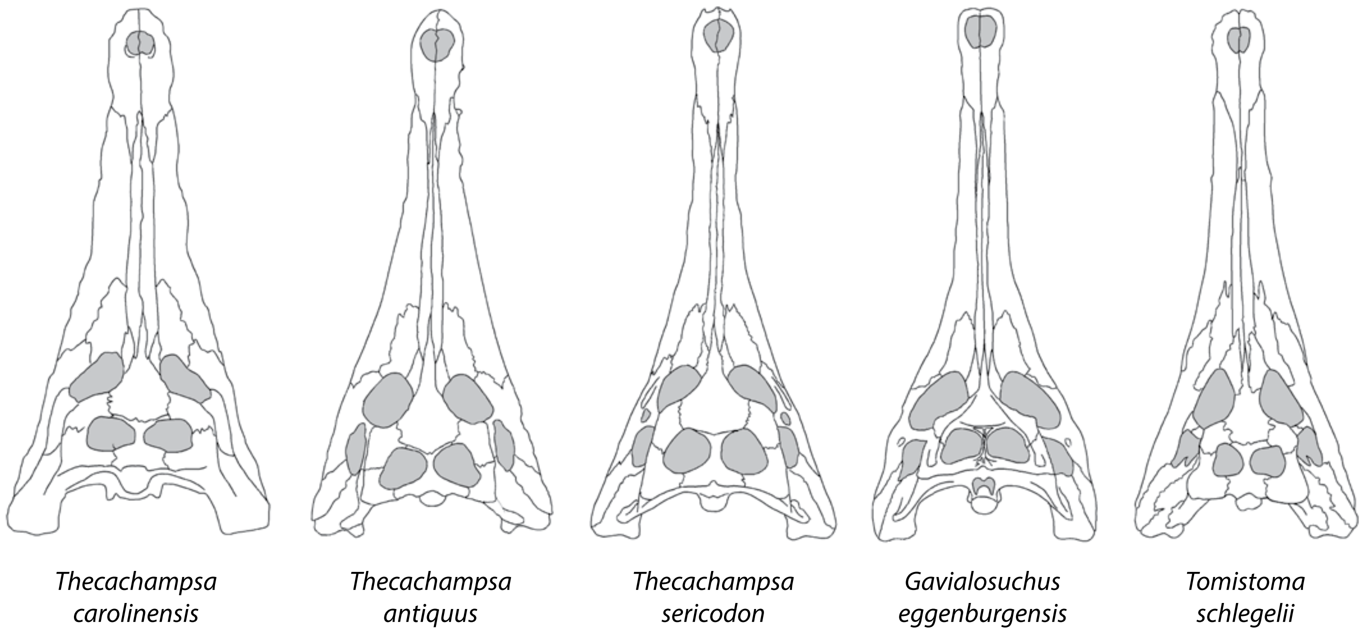

FIGURE 4.18. Comparison in dorsal view of the skulls of *Thecachampsa carolinensis*, *T. antiquus*, *T. sericodon*, *Gavialosuchus eggenburgensis*, and *Tomistoma schlegelii*. *Thecachampsa carolinensis* after Erickson and Sawyer (1996), with the left side corrected for distortion from compaction; *G. eggenburgensis* after Toula and Kail (1885); *T. schlegelii* after Mook (1921c).

The subfamily Tomistominae currently includes 13 genera: *Charactosuchus, Dollosuchoides, Ferganosuchus*, *Gavialosuchus, Kentisuchus, Maroccosuchus*, *Megadontosuchus*, *Paratomistoma*, *Penghusuchus*, *Rhamphosuchus*, *Thecachampsa*, *Tomistoma*, and *Toyotamaphimeia* (Kobayashi et al., 2005; Brochu, 2007; Piras et al., 2007; Shan et al., 2009). The oldest well-known members are the early Eocene genera *Dollosuchoides*, *Kentisuchus*, and *Maroccosuchus*. Five genera have been reported from the Miocene: *Gavialosuchus, Penghusuchus*, *Rhamphosuchus, Thecachampsa,* and, allegedly, *Tomistoma*. *Penghusuchus* and *Rhamphosuchus* are distinctive genera readily separable from *Gavialosuchus*, *Tomistoma*, and *Thecachampsa* because they both have the seventh maxillary tooth enlarged rather than the fifth.

Thecachampsa, Miocene *Tomistoma*?, and *Gavialosuchus* currently are accepted as valid groups of taxa distinctly different from each other (Brochu and Gingrich, 2000; Brochu, 2003, 2007; Piras et al., 2007).

Erickson and Sawyer (1996) named a new species of tomistomine crocodilian from the mid-Oligocene of South Carolina. They assigned their new species to the genus *Gavialosuchus* and named it *Gavialosuchus carolinensis*, but this generic assignment now seems unlikely because all other reported occurrences of *Gavialosuchus* in North America have proven to be *Thecachampsa*. *Gavialosuchus eggenburgensis* bears a striking superficial similarity to *Thecachampsa sericodon* (Figure 4.18), but the interorbital and postorbital areas of its skull table are strikingly different from the same area in the three North American species of *Thecachampsa*. In *Gavialosuchus* the frontals and postorbitals are greatly shortened anteroposteriorly, whereas in *Thecachampsa* these bones are no more shortened than in the living genus *Tomistoma*. These differences indicate that the Oligocene tomistomid from South Carolina should be classified as *Thecachampsa carolinensis*. This conclusion is in accord with the conclusions of both Piras et al. (2007) and Brochu and Storrs (2012) that *G. carolinensis* should be transferred to the genus *Thecachampsa*. It is distinguished from the two Miocene species of *Thecachampsa* by a number of characters (Table 4.1).

Laurito and Valerio (2008) described new tomistomine material from the late Miocene or early Pliocene of Costa Rica and assigned it to *Gavialosuchus americanus*. As discussed above, material formerly assigned to *G. americanus* is here considered to be in part *T. sericodon* and in part *T. antiquus*. The Costa Rican material is too fragmentary to allow species identification but clearly does pertain to *Thecachampsa* and provides a significant southward range extension for this genus.

PALEOECOLOGY

The co-occurrence of *T. sericodon* and *T. antiquus* in the same beds during the middle Miocene clearly indicates that these two species were not direct competitors in the Miocene coastal environment of the eastern United States. This conclusion is supported by the contrasting snout, dental, pelvic, and femoral features seen in these two otherwise closely related species. The very elongate and narrow snout of *T. sericodon*, with its elongate stabbing anterior teeth and laterally compressed slicing posterior teeth, is well suited for catching fish or possibly squid. The somewhat broader snout of *T. antiquus*, with its blunt, conical, alligator-like teeth, is well suited for catching turtles and crushing their shells. These two feeding styles would have minimized competition between these two species and permitted them to coexist in the same general environmental setting. Similarly, in Europe the very narrow snouts of "*Tomistoma*" *calaritanus* and *Gavialosuchus eggenburgensis* suggest piscivorous diets for those species, whereas the more robust snout of "*T.*" *lusitanica* suggests at least a tendency toward a chelonian diet in that species. The even broader snout of *Thecachampsa carolinensis*, with its enlarged sixth maxillary teeth, suggests that it was better adapted than even *T. antiquus* for crushing turtle shells.

In the Oligocene and Miocene deposits of the Atlantic Coastal Plain, remains of *Thecachampsa* have been found consistently, and sometimes abundantly, in shallow marine to mid-shelf deposits (Cope, 1867, 1869a; Marsh, 1869; Sellards, 1915; Mook, 1921c; Auffenberg, 1954; Webb and Tessman, 1968; Morgan, 1986; Erickson and Sawyer, 1996). Their occurrence in this depositional setting suggests that these animals regularly visited or normally inhabited the shallow marine waters of what is now the southeastern United States continental shelf. This observation is inherently biased by the fact that nearly all Oligocene and Miocene deposits in the Atlantic Coastal Plain are of marine origin. However, in view of the facts that (1) clearly fluvial crocodilian remains are unknown in the Oligocene and extremely rare in the Miocene and (2) remains of any other kinds of fluvial or terrestrial vertebrates of any sort are also rare in both the Oligocene and Miocene of this region, the observed abundance of remains of *Thecachampsa* far exceeds what would be expected had they been strictly freshwater animals. The general scarcity of their remains, when compared to those of whales and sea turtles, suggests that they were not extremely common in open marine environments. However, considering their large size and high position in the Miocene food chain, they should not have been extremely common. Erickson and Sawyer (1996) have suggested that *Thecachampsa carolinensis* normally nested and lived in beach to lagoonal and estuarine environments, and this seems a likely habitat preference. The Miocene species of *Thecachampsa* probably nested in this same environmental setting.

In this regard, it is interesting to note that the species *Gavialosuchus eggenburgensis,* from the Miocene of Europe, also occurs in association with remains of marine animals (Telles Antunes, 1961; Erickson and Sawyer, 1996). In Portugal, *G. eggenburgensis* not only occurs in marine environments but also is found in association with the remains of a smaller species of tomistomine crocodilian, "*Tomistoma*" *calaritanus* (Telles Antunes, 1961). The co-occurrence of a larger and smaller species of tomistomine in the Miocene coastal waters of both Portugal and the eastern United States represents a striking parallelism in niche partitioning in this group on both sides of the Atlantic.

THE DECLINE OF THE TOMISTOMINAE

During most of the Miocene, tomistomines were abundant and diverse in Europe, Asia, Africa, and the Americas (Piras et al., 2007). Although *Thecachampsa* was the only tomistomine present in the southeastern United States, it was moderately abundant there and during the middle Miocene included two species. By the early late Miocene, however, *T. sericodon* apparently had become extinct, and only *T. antiquus* persisted. The latest Miocene (Messinian) Eastover Formation has yielded no remains of tomistomines, so by then they apparently were extinct in the southeastern United States. Although there have been reports of *Thecachampsa* from the Pliocene of Florida, they probably represent nothing more than reworking of Miocene fossils into basal Pliocene deposits (Hulbert, 2001:150). By the Pliocene, all well-documented occurrences of tomistomines are from Southeast Asia. Two marine species persisted there into the Quaternary ("*Tomistoma*" *taiwanicus* in Taiwan and *Toyotamaphimeia machikanensis* in Japan). Today, only the freshwater species *Tomistoma schlegelii* survives.

It is remarkable that the Tomistominae have been reduced to a single species, considering that throughout most of the Paleogene and Neogene this was a diverse and successful group capable of dispersing across entire ocean basins. Probably, the main factor in the decline of this family was the global climatic deterioration in the late Neogene that led to Quaternary glaciation across much of the globe (Wolfe, 1994; Zachos et al., 2001; Böhme, 2003). It probably is not coincidental that the one area where a tomistomine still survives, Southeast Asia, is fully tropical and within 15° of the equator. A second possible factor in the decline of the Tomistominae may be that saltwater-tolerant species of living crocodiles (particularly *Crocodylus porosus* in the tropical Eastern Hemisphere and *Crocodylus acutus* in the tropical Western Hemisphere) now fill the coastal marine niche in tropical regions that the tomistomines once inhabited (Minton and Minton, 1973). It is not clear whether the modern crocodiles that occupy these niches do so because the tomistomines became extinct in those habitats and left them vacant or whether the modern species actively moved into those habitats while tomistomines still occupied them and drove them to extinction. In the southeastern United States, however, competitive exclusion seems unlikely because *Crocodylus acutus* today occupies only the southernmost tip of Florida. Farther north in the southeastern United States, *Alligator mississippiensis* is abundant, but it occupies only freshwater areas that lie inland of the former habitat of *Thecachampsa*. The failure of either of these two living species to occupy a major part of the former habitat of *Thecachampsa* strongly suggests that late Neogene climatic deterioration and not competition was the main factor that caused the disappearance of tomistomines in eastern North America.

AN ENIGMATIC CROCODILIAN FROM THE CALVERT FORMATION

Two small crocodilian osteoderms (USNM 540749, USNM 540750) and part of a third one, all found at the Pollack Farm fossil site in Delaware, are different from osteoderms associated with either species of *Thecachampsa* (Figure 4.8E1,E2). These osteoderms, from the Fairhaven Member (Fairhaven C) of the Calvert Formation (Figure 4.8A1,A2), are not referable to *Thecachampsa* because they have a low and narrow keel running down their longitudinal axis, they are rhomboidal to rectangular in outline, and they have smaller and more closely spaced pits on their external surfaces. This type of osteoderm does not pertain to *Thecachampsa*, although to what other kind of crocodilian it does pertain is uncertain. The only other crocodilian recognized so far from the early Miocene of the eastern United States is *Alligator olseni*. It was first recognized at the Raeford Thomas Farm site in Florida (White, 1942), which is close or identical in age to the Pollack Farm site in Delaware (Emry and Eshelman, 1998). Osteoderms of *A. olseni*, however, often have a much more pronounced keel than the ones from Pollack Farm and also are often larger (Figure 4.8A3), so reference of the Pollack Farm material to *A. olseni* is plausible but not certain. Crocodilian osteoderms of the Pollack Farm morphology occur in the midline region of modern *Crocodylus*, *Alligator*, and *Caiman*, so this type of dermal armor is not generically distinctive. What is certain, however, is that these osteoderms represent a third kind of small crocodilian that is not referable to *Thecachampsa*. This third species of crocodilian presumably was an inhabitant of freshwater environments because many freshwater and terrestrial taxa have been found at the Pollack Farm site that are extremely rare in the shallow marine environments represented by nearly all of the Calvert and Choptank Formation outcrops found elsewhere. Although this taxon has not yet been found along the Calvert Cliffs, its eventual discovery there should be expected.

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5

Fossil Sirenia (Mammalia) of the Miocene Chesapeake Group, Eastern United States

Daryl P. Domning

ABSTRACT. The extensive Miocene vertebrate fauna collected from the Chesapeake Group in New Jersey, Delaware, Maryland, Virginia, and North Carolina includes relatively rare sirenians of the family Dugongidae. They are most abundant in the early to middle Miocene Calvert and equivalent formations and in the Calvert Cliffs and nearby exposures in southern Maryland, as well as in the Lee Creek phosphate mine in North Carolina. These Calvert-correlative deposits have yielded evidence of at least three sirenian taxa: the halitheriine dugongid *Metaxytherium crataegense* (=*M. calvertense*), the dugongine dugongid *Nanosiren* sp., and another dugongine, aff. *Corystosiren* sp. A possible fourth unidentified form may also be a dugongine. The stratigraphically higher St. Marys Formation contains remains that (in view of their late Miocene age) may be referable to *Metaxytherium floridanum*, but those so far collected are too fragmentary to be distinguished morphologically from *M. crataegense*.

INTRODUCTION

Sirenians, or sea cows (manatees and dugongs), are the only completely herbivorous, completely aquatic mammals living today. They are dolphin-sized, thick-skinned, slow-swimming animals with flipper-like front limbs, a horizontal tail fin that provides their main propulsion, and no hind limbs or dorsal fin. Dense, swollen ribs and other bones (a condition known as pachyosteosclerosis) provide ballast, helping them maintain neutral buoyancy while they feed on submerged or floating aquatic plants in warm, shallow, salt or fresh waters. Their cosmopolitan fossil record spans almost 50 million years (middle Eocene to Holocene), mostly in latitudes that are now or were formerly tropical to warm temperate.

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Fossil sirenians have been collected from the Calvert Cliffs of Maryland for more than 100 years but are rare compared to Calvert cetaceans (possibly because the cliff exposures represent a deeper-water environment than the sirenians inhabited) and are still incompletely known. At least three different species of the sirenian family Dugongidae have so far been identified from the Miocene deposits of the Chesapeake Group (Calvert, Choptank, and St. Marys Formations and their equivalents) that crop out on the western side of the Chesapeake Bay, extending south into Virginia and North Carolina and north into Delaware and New Jersey (Domning, 1984a, 2006). The most important study of fossil sea cows from this region, by Remington Kellogg (1966), now requires significant updating. That three (or even more) species of dugongs might have lived together in the Chesapeake region is no longer surprising since multispecies paleofaunas of sirenians have now been discovered throughout the west Atlantic–Caribbean zoogeographic province as well as in other parts of the world (Domning, 2001; Bajpai et al., 2010; Vélez-Juarbe et al., 2012).

Besides these dugongid fossils, a radius–ulna (USNM 9346 [see Figure 5.8D and Table 5.4]) of another sirenian was reported from Fairhaven, Anne Arundel County, Maryland, by Case (1904). Although Kellogg (1966) also attributed it to the Calvert dugongid he described, it is, in fact, one of only two Maryland fossil records of the living West Indian manatee (*Trichechus manatus*), which today is an occasional summertime visitor to these waters. This bone presumably came not from any part of the Chesapeake Group (which has yielded no manatee remains) but from some overlying Pleistocene deposit (Domning, 2005:689). (The second manatee record is USNM 457373, an isolated molar from Randle Cliff, Calvert County, collected from float by William D. "Pat" Gotsis in 1990.) The remainder of this chapter will address only the Miocene dugongids.

Since sirenian remains identifiable to genus or species are uncommon in the Calvert Cliffs and in the Chesapeake Group as a whole, it is necessary to include the entire Chesapeake Group in this chapter in order to obtain anything like a clear picture of the regional sirenian fauna represented in the Calvert Cliffs. Even now, most of these sirenian taxa remain inadequately known, which was even more true when the final volume (comprising the mammals) of the Lee Creek Mine series was being prepared for publication (Ray et al., 2008). This lack of information explains why that otherwise comprehensive work has no chapter on the sirenians—an omission that I have tried to remedy with this chapter.

ABBREVIATIONS

AMNH	American Museum of Natural History, New York, New York, USA
AMNH-VP	AMNH, Department of Vertebrate Paleontology
ChM	Charleston Museum, Charleston, South Carolina, USA
CMM	Calvert Marine Museum, Solomons, Maryland, USA
coll.	collector(s)
DPUH	paleontological collection, Museo de Historia Natural Felipe Poey, Universidad de La Habana, Havana, Cuba
MYA	million years ago
SCSM	South Carolina State Museum, Columbia, South Carolina, USA
USGS	U.S. Geological Survey, Reston, Virginia, USA
USNM	Department of Paleobiology, National Museum of Natural History (formerly U.S. National Museum), Smithsonian Institution, Washington, D.C., USA
YPM	Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA

FOSSIL DUGONGIDAE IN THE MID-ATLANTIC REGION

Metaxytherium calvertense was the name given to the Calvert dugongs by Remington Kellogg (1966), distinguishing it from other fossil sirenians such as *Felsinotherium ossivallense* Simpson, 1932 (=*Metaxytherium floridanum* Hay, 1922) and *Hesperosiren crataegensis* Simpson, 1932, both of which George Gaylord Simpson had previously described from Florida—the former on the basis of teeth from the Bone Valley phosphate mines in Polk County and the latter on the basis of a skull and other remains from a fuller's earth mine in Gadsden County. Unfortunately, this latter skull (AMNH 26838) is badly crushed and distorted, leading Simpson to misinterpret some of its features, such as the degree of downturning of its snout and the presence or absence of tusks. Kellogg's Calvert skull (USNM 16757), in contrast, is undistorted but also lacks the tip of the snout, leaving the presence of tusks uncertain. As a result, Kellogg (who probably never compared the two skulls directly) did not perceive what I consider to be their basic similarity. Furthermore, they scarcely differ in their geochronological ages, which are respectively estimated as late Hemingfordian–early Barstovian for the Florida skull and late early Barstovian for the Calvert specimen; that is, both lived somewhere within the interval of roughly 15–17 MYA. For these reasons I concluded that a species distinction (let alone a generic distinction) between them could not be defended, so I synonymized them (in Aranda-Manteca et al., 1994) under the new combination *Metaxytherium crataegense* (Simpson).

In the Mid-Atlantic region, *M. crataegense* (Figures 5.1, 5.2) is best known from the Calvert Formation of Maryland and Virginia. A few specimens apparently representing *Metaxytherium* sp. have also been recovered from the overlying St. Marys and possibly the Choptank Formations in those states. Other remains referable to *M. crataegense* (as well as other dugongids) have also been found at the Lee Creek phosphate mine, North Carolina, evidently in the Calvert-correlative Pungo River Formation and possibly also in the Calvert Formation of Delaware and the Kirkwood Formation of New Jersey, as described below.

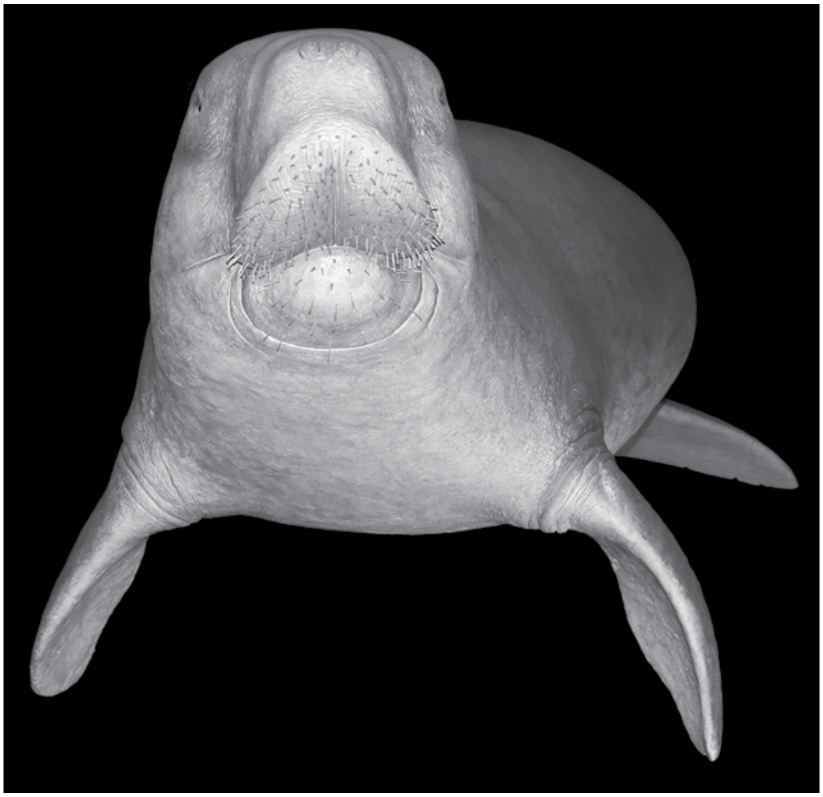

FIGURE 5.1. *Metaxytherium crataegense*, life-size body reconstruction created at the Calvert Marine Museum; anterior view.

MARYLAND

The early to middle Miocene Calvert Formation of Maryland and Virginia was divided by Shattuck (1904) into 15 lithologic beds or "zones," of which zones 1–3 corresponded to the Fairhaven Member and 4–15 correspond to the Plum Point Member. (These zones are hereinafter called beds, as they are lithologic rather than biostratigraphic units.) Gibson (1983a:43, fig. 9) restricted the Fairhaven to bed 3 and assigned beds 1 and 2 to the Popes Creek Sand Member. Kidwell et al. (2015) likewise follow Shattuck's scheme but do not recognize the Popes Creek Sand Member. Robert Weems (Calvert Marine Museum, personal communication) states that the age of the Popes Creek Sand falls between beds 3A and 3B on the basis of dinoflagellate ranges and that it is a bed within the Fairhaven Member that is missing in the Maryland section north of Popes Creek. In Kidwell et al.'s stratigraphic column (2015: fig. 2) it is represented by an unnamed sand unit between beds 3A and 3B that is correlated with dinocyst zone DN2b,c. In this chapter it is referred to as the "Popes Creek Sand bed."

Sirenian fossils have been recovered from both the Popes Creek Sand bed and the Plum Point Member. The Popes Creek Sand bed on Popes Creek, Charles County, Maryland, has yielded two partial skeletons (USNM 241562 and CMM-V-244), of which at least the former is possibly referable to the dugongid subfamily Dugonginae (see below). In contrast, most of the other Calvert Formation sirenian material represents *Metaxytherium* (in the subfamily Halitheriinae) and is from the Plum Point Member, which is extensively exposed in the Calvert Cliffs along the western shore of the Chesapeake Bay in Calvert County.

Kellogg (1966) erected the species *Metaxytherium calvertense* to include all the Calvert sirenian fossils known to him, all of which (except the manatee radius-ulna noted above) came from the Plum Point Member, specifically (insofar as their stratigraphic provenance was known) from beds 10–12. Some of these specimens, however, are now considered to represent a much smaller animal, the dugongine *Nanosiren* (Domning and Aguilera, 2008), whereas Kellogg's species is synonymized with *M. crataegense* (Simpson), as explained above.

The holotype of "*M. calvertense*" (USNM 16757) was said by Kellogg (1966:71) to have been collected by W. E. Salter, A. C. Murray, and C. W. Gilmore on 4 August 1943 and to have come from "one-half mile south of Plum Point Road end, Calvert Co., Md. In compact blue clay at base of zone 11 (below shell band) and at tide level at base of cliff." A holograph note by Gilmore himself clarifies that it was found by Salter on 4 August and collected by Salter, Murray, and Gilmore on 5 and 6 August. He also states that the locality was "1½ mi. S of Plum Point" and that the skeleton "came from layer immediately above heavy shell layer" (USNM Registrar's office, microfilm reel 624, accession number 165846). As "one-half mile south of Plum Point Road end" arguably refers to the same area as "1½ mi. S of Plum Point" itself,

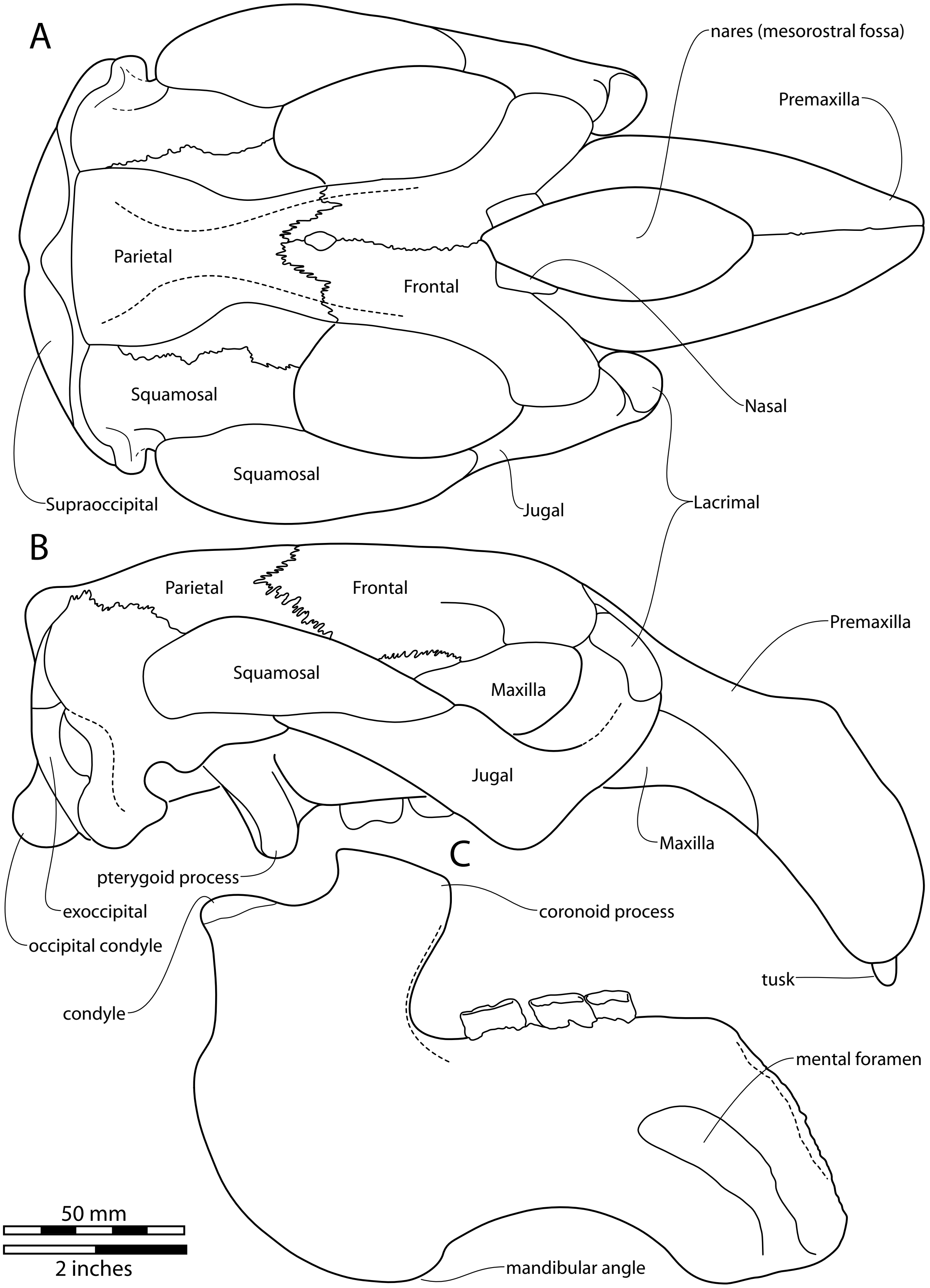

FIGURE 5.2. *Metaxytherium crataegense*, skull restoration (modified from Kellogg, 1966; based on USNM 16757, holotype of *M. calvertense*). (A) Dorsal view. (B) Right lateral view. (C) Lower jaw, right lateral view. Anterior to the right.

these two sources are not in contradiction on this. However, according to David Bohaska (USNM, personal communication), Kellogg's specification "below shell band" suggests that the skeleton was actually in bed 9 since the "shell band" was presumably bed 10; but more likely, Kellogg's "below shell band" was an error for "above shell band," as Gilmore said (hence bed 11).

Gibson (1983b:362) stated that "the probable age for bed 10 of the Calvert Formation is [planktonic foraminiferal] zone N8, and that for the overlying beds 11 and 12 is probably of lower zone N9." The lower part of zone N9, and therefore the presumed type horizon of "*M. calvertense*," is correlated with the late early Barstovian land mammal age, ca. 15 MYA (Tedford et al., 1987: fig. 6.2). This age is consistent with the correlation, based on fossil peccaries found at several horizons in this section, by Wright and Eshelman (1987), who correlated Shattuck's zone 10 with the late Hemingfordian or early Barstovian and zone 14 with the early late Barstovian. All of Kellogg's (1966) specimens of *M. crataegense* therefore appear to be of early Barstovian age.

Calvert County has also produced remains referable to *Metaxytherium* from the late Miocene St. Marys Formation (=beds 21–23) in the area of Little Cove Point and Chesapeake Ranch Estates. As discussed below, these specimens likely represent *M. floridanum*.

Virginia

Some other material also possibly referable to *M. floridanum* (listed below) has come from the south bank of the Potomac River in Westmoreland County, in the area from Stratford Hall past Westmoreland State Park and upriver to the George Washington Birthplace National Monument. The section here exposes beds 14–15 (Calvert Formation), 19 (Choptank Formation, Boston Cliffs Member), 21–24(?) (St. Marys Formation – east of Stratford only), plus the overlying, latest Miocene Eastover Formation (Ward and Andrews, 2008: fig. 7, sections PO-11, PO-12; R. Weems, pers. comm.).

The Carmel Church Quarry in Caroline County exposes beds 14–16 (here considered equivalent to the uppermost Plum Point Member of the Calvert Formation) at the edge of the Chesapeake Group depositional basin. It has produced a varied fauna, including fragments of "*Metaxytherium?*" (Dooley et al., 2004:454), but so far no diagnostic sirenian specimens.

A partial skeleton (USNM 377441-2, 377446-7, 377449) from a site on the Pamunkey River in King William County (Domning, 1984b) came from a pebble bed about 0.6 m [2 ft] above the unconformable contact of the Calvert Formation with the Eocene Piney Point Formation. On the basis of mollusks, the pebble bed and overlying deposits were correlated with Calvert beds 12–13, hence with the Plum Point Member, by Ward (in Ward and Krafft, 1984:272–273). However, using more recent data from dinoflagellates, Weems (pers. comm.) considers this horizon to represent the Popes Creek Sand bed. Domning (1984b) noted differences between this specimen and *Metaxytherium* but resemblances to a Calvert sirenian from Popes Creek (USNM 241562). Both the Pamunkey River and Popes Creek specimens now seem to be dugongines (see below).

Another rib fragment (USNM 377448, coll. Kurt M. Savoie and James W. Westgate) from the Pamunkey River was apparently reworked from the Calvert into the overlying, late Miocene Eastover Formation (Domning, 1984b). Also of unclear significance is a fragment of the shaft of a humerus from the Pamunkey River (AMNH 108643; cast: USNM 307603), collected by E. D. Cope in 1895. It may be a Miocene sirenian or possibly a primitive cetacean derived from the Eocene Piney Point Formation.

Dugongid rib and vertebra fragments (USNM 186898) were also collected near Weedonville, King George County, questionably from the late middle Miocene Choptank Formation.

North Carolina

The rich marine vertebrate fauna from the Lee Creek phosphate mine near Aurora, Beaufort County, North Carolina, includes an assortment of sirenian remains, all fragmentary and many abraded. They are all thought to be derived from the upper part of the Calvert-correlative Pungo River Formation, which is exposed in the base of the mine and is of earliest middle Miocene age (planktonic foraminiferal zone N8; early Barstovian, ca. 16 MYA; Gibson, 1983b:360; Tedford et al., 1987: fig. 6.2). Many, if not all, of them were probably reworked into the overlying early Pliocene Yorktown Formation (C. E. Ray, USNM, pers. comm.). Compared with bones from the Yorktown Formation, "Pungo River fossils generally are darker and more heavily mineralized, more polished in appearance, and more worn … though such characters are not infallible" (Eshelman and Whitmore, 2008:18). These specimens appear to fall into three groups corresponding to three species found in the Calvert Formation: *Metaxytherium crataegense*, *Nanosiren* sp., and aff. *Corystosiren* sp. This faunal resemblance is consistent with the correlation of both units with the same planktonic foraminiferal zones, N8 and N9.

Delaware

Bohaska (1998) reported dugongid rib fragments from the Cheswold sands of the Calvert Formation at the Pollack Farm Site in Kent County. These sands were considered by Bohaska to be equivalent in age to bed 3A of the Fairhaven Member and possibly of the same age as the Popes Creek Sand bed of the Calvert Formation in Maryland. The sirenian rib fragments (USNM 487268, 488608, plus another seen by Bohaska in a private collection) are not diagnostic; judging from their size (diameters of USNM 487268 = 38 × 16 mm; smaller diameter of USNM 488608 = 30 mm), they could represent either *Metaxytherium* or some dugongine.

NEW JERSEY

The early Miocene Asbury Park Member of the lower Kirkwood Formation in Monmouth County, coastal New Jersey, contains a fauna (the Farmingdale local fauna) considered by Tedford and Hunter (1984) to be of early Hemingfordian age (18–20 MYA) and correlated by Hunter and Huddlestun (1982) with Shattuck's zones 1–3 of the Calvert Formation in Maryland (see below). However, Lucas et al. (1998) consider a late Arikareean age for this fauna to be more likely on the basis of the presence of the rhinoceros *Diceratherium* and the strontium isotope age estimates of 19.2–22.6 ± 0.5 MYA obtained by Sugarman et al. (1993). Reworked Eocene material is also present.

The Farmingdale local fauna has produced a single, extremely waterworn shaft of a left humerus lacking both ends (USNM 243565). The shaft is mediolaterally compressed; a sharp anterior ridge extends from the area of the deltoid crest, parallel to the long axis of the shaft, and ends distally in a thickening for the insertion of the pectoralis major. In the form of this ridge as well as in the bone's overall size and shape, it most closely resembles a dugongid humerus (ChM PV2860) from the late Oligocene Chandler Bridge Formation of South Carolina; with due allowance for abrasion, it also resembles various Miocene specimens of *Metaxytherium*. I assign it to Dugongidae, cf. *Metaxytherium*.

Another worn left humerus (YPM uncataloged), fully resembling *M. crataegense* in size and shape, bears a label stating that it was "found in drawer marked Squankum, New Jersey" and that it was collected by O. B. Kinne in 1869. The Squankum area, near Farmingdale, contains outcrops of the Asbury Park Member, which are the probable source of this specimen (R. W. Purdy, USNM, pers. comm.).

Leidy (1856:165) based the name *Manatus antiquus* (a *nomen dubium*) partly "on fragments of ribs found in the miocene [sic] deposits of New Jersey." I do not know the present whereabouts of these specimens, but together with the humeri described above and a Pleistocene(?) radius-ulna of *Trichechus* sp. dredged from off New Jersey (Gallagher et al., 1989), they represent the northernmost fossil records of sirenians on the Atlantic coast of the Americas.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER SIRENIA ILLIGER, 1811

FAMILY DUGONGIDAE GRAY, 1821

SUBFAMILY HALITHERIINAE (CARUS, 1868) ABEL, 1913

Genus *Metaxytherium* Christol, 1840

Metaxytherium crataegense (Simpson, 1932) Aranda-Manteca, Domning, and Barnes, 1994

FIGURES 5.1–5.9; TABLES 5.1–5.4

Dugong: *Metaxytherium* – Dugongidae, Halitheriinae

Hesperosiren crataegensis Simpson, 1932:426 (original description).

Metaxytherium calvertense Kellogg, 1966:71 (junior synonym). (Holotype: USNM 16757, skull and partial skeleton of immature individual. Type locality: near Plum Point, Calvert County, Maryland; bed 11, Plum Point Member, Calvert Formation [see discussion above]; earliest middle Miocene [Langhian, early Barstovian; lower part of planktonic foraminiferal zone N9].)

Metaxytherium riveroi Varona, 1972:6 (junior synonym). (Holotype: DPUH 1255, partial skull and skeletal fragments of juvenile. Type locality: San Antonio de Cabezas, Matanzas, Cuba; Güines Formation.)

Metaxytherium crataegense (Simpson) Aranda-Manteca, Domning, and Barnes, 1994:192 (new combination).

HOLOTYPE. AMNH 26838, skull, vertebrae, and ribs of adult.

TYPE LOCALITY. Florida, Gadsden County, Floridin Company mine, north of Quincy.

FORMATION. Hawthorn Group, Torreya Formation, Dogtown Member.

AGE. Early to middle Miocene (late Hemingfordian or early Barstovian; Bryant, 1991).

REFERRED SPECIMENS.

Maryland (Calvert, Prince Georges, and Anne Arundel Counties; Calvert Formation, Plum Point Member): Partial skeletons: USNM 12596 (coll. Norman H. Boss and Remington Kellogg), USNM 16757 (holotype of *Metaxytherium calvertense*; coll. William E. Salter, A. C. Murray, and C. W. Gilmore; Figures 5.4A,B, 5.5A, 5.6E, 5.9A,B,C,F), USNM 23213 (coll. R. Lee Collins; Figure 5.8B), CMM-V-242 (coll. David Bohaska, Norman Riker, Wallace L. Ashby, August Selckmann, George C. Fonger, and Sandy Roberts; Figures 5.5E, 5.6B–D, 5.7J–N). *Partial braincase*: CMM-V-2202 (coll. Ralph Long). *Parietal–supraoccipital skullcaps*: USNM 16649 (coll. W. S. Cramer), USNM 23503 (coll. Albert C. Myrick Jr. and Richard Lund; Figure 5.3A,B), USNM 241563 (coll. Norman Riker; Figure 5.3C,D). *Squamosal*: USNM 244539 (coll. Wallace L. Ashby). *Maxilla with teeth*: USNM 244422 (cast; coll. Bruce Rydell; Figure 5.4F). *Cheek teeth*: USNM 23271 (coll. A. Shaftsbury; Figure 5.4H), USNM 23281 (coll. T. E. Ruhoff), USNM 23409 (coll. R. Lee Collins), USNM 437483 (cast; coll. R. S. Gladhill; Figure 5.4G), USNM 452988 (coll. Sandy Roberts). *Humeri*: USNM 5360 (coll. F.

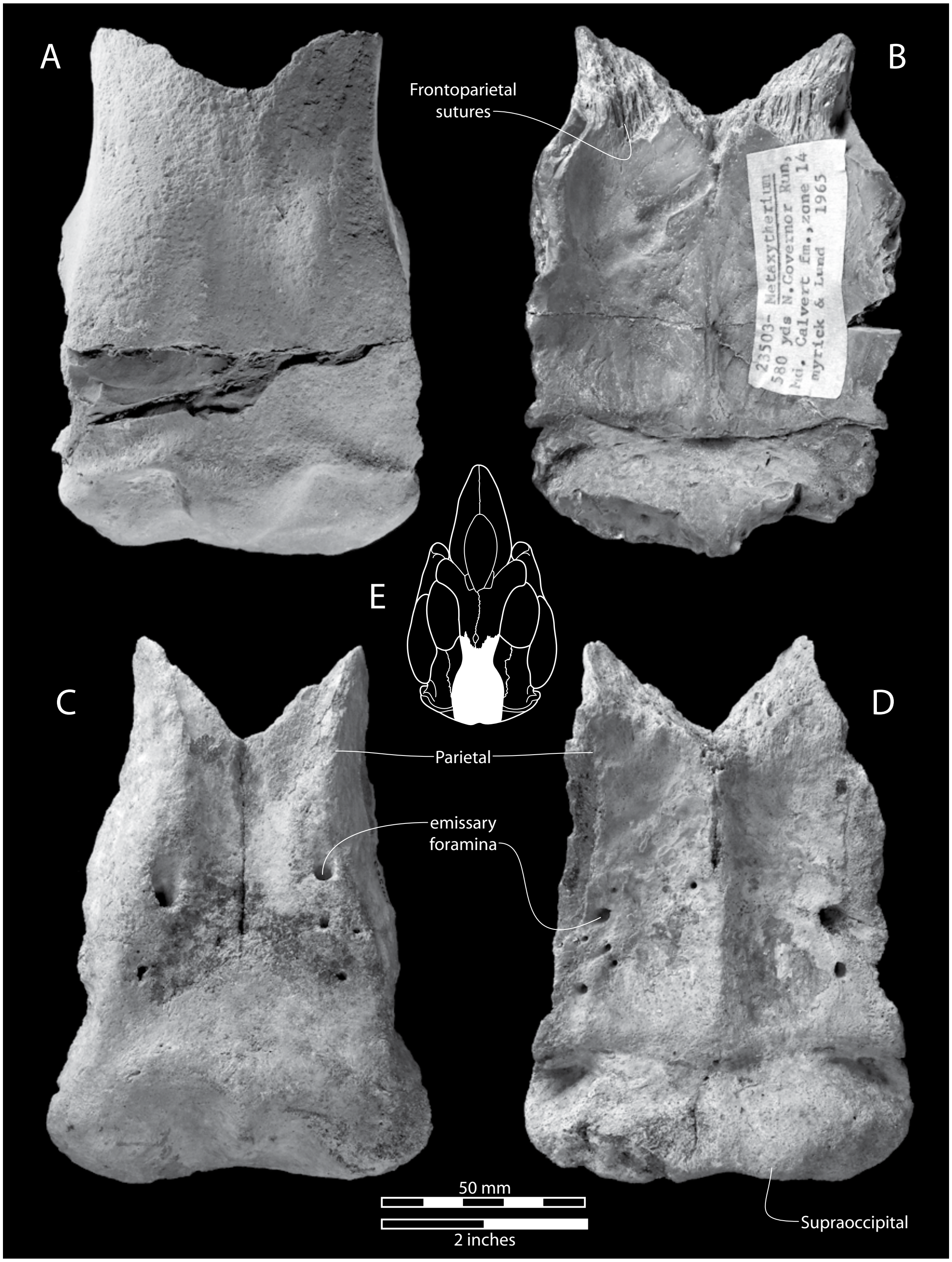

FIGURE 5.3. *Metaxytherium crataegense*, parietal-supraoccipital skullcaps. (A, B) USNM 23503 in dorsal and ventral (internal) views, respectively. (C, D) USNM 241563 in dorsal and ventral views, respectively. The numerous large and small emissary foramina in USNM 241563 are atypical and unique to this individual. (E) Line drawing of skull in dorsal view, anterior to top of page, showing in white the position of the skullcap. Specimens lightly coated with sublimed ammonium chloride.

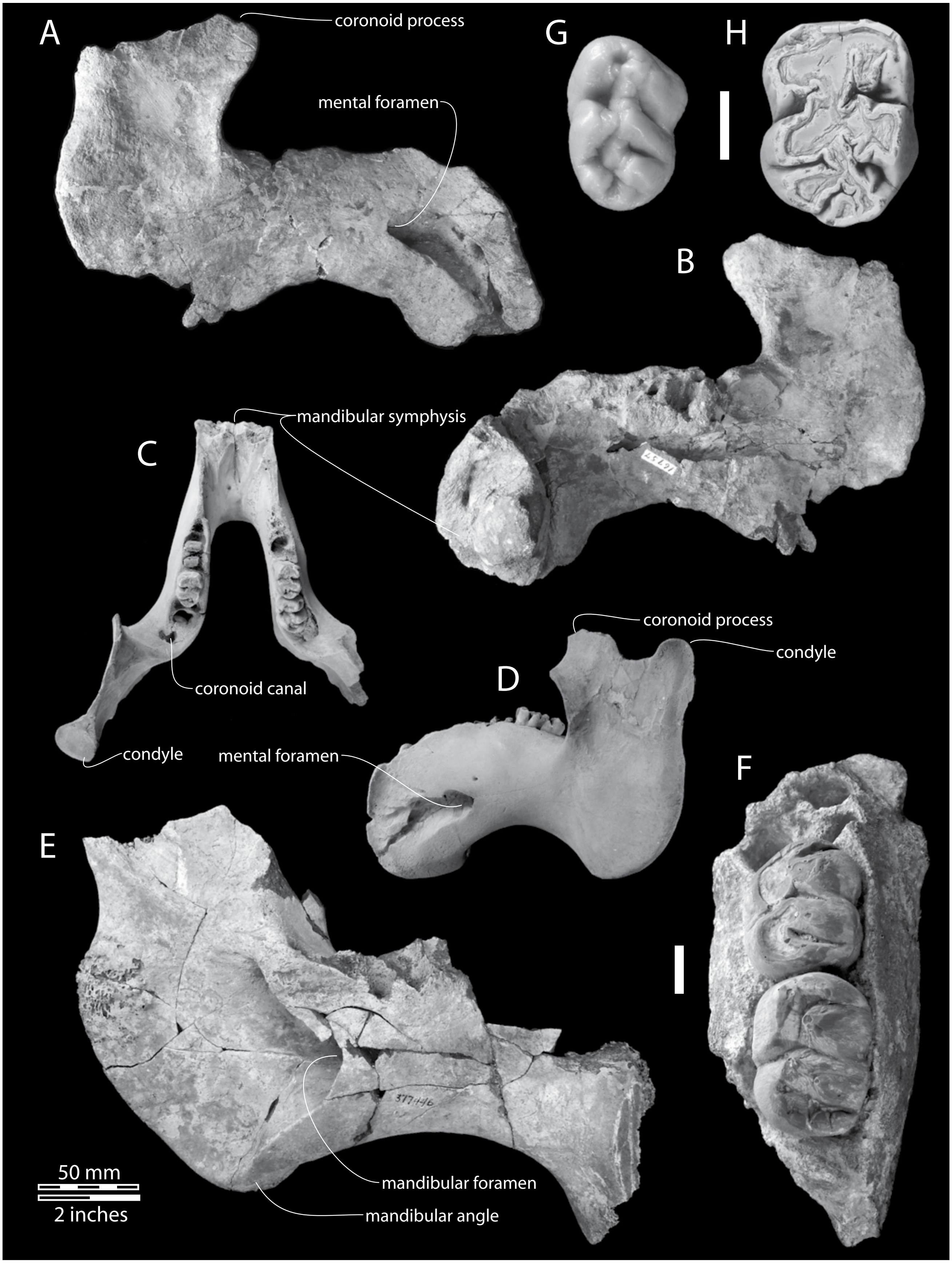
A
coronoid process
mental foramen
G
H
B
mandibular symphysis
C
coronoid process
condyle
D
coronoid canal
condyle
mental foramen
F
E
mandibular foramen
mandibular angle
50 mm
2 inches

FIGURE 5.4. (*Facing page*) Mandibles and teeth of Chesapeake Group dugongids. (A, B) *Metaxytherium crataegense*, USNM 16757 (holotype of *M. calvertense*), right half of mandible in lateral and medial views, respectively. (C, D) *Nanosiren* sp., USNM 16630, nearly complete mandible in dorsal and left lateral views, respectively. (E) Dugonginae gen. et sp. indet., Pamunkey River, Virginia, USNM 377446, left dentary in medial view. Teeth of *Metaxytherium crataegense* from Maryland, occlusal views: (F) USNM 244422, cast of left maxilla with second and third upper molars (M2–3) and alveoli of M1. (G) USNM 437483, cast, right third lower molar (m3) tooth. (H) USNM 23271, left m2. Specimens lightly coated with sublimed ammonium chloride. Scale bars for F–H equal 10 mm.

TABLE 5.1. Measurements (mm) of two specimens of skulls of *Metaxytherium crataegense* from the Chesapeake Group. Letters in parentheses denote abbreviation used by Domning (1978, 1988) for the given dimension. Other abbreviations: e = estimated; e? = identification of landmark(s) uncertain. A dash (–) indicates measurement could not be taken on specimen. Specimen USNM 16757 is the holotype of *M. calvertense*.

Dimension	USNM 16757	CMM-V-2202
Height of jugal below orbit (ab)	42	–
Rear of occipital condyles to anterior end of interfrontal suture (BI)	220	–
Zygomatic breadth (CC’)	217	–
Breadth across exoccipitals (cc’)	132e	152e
Top of supraoccipital to ventral sides of occipital condyles (de)	113	–
Length of frontals, level of tips of supraorbital processes to frontoparietal suture (F)	140e	–
Length of frontals in midline (LFr)	84	90e?
Breadth across supraorbital processes (FF’)	131	–
Breadth across occipital condyles (ff’)	88e	98e
Breadth of cranium at frontoparietal suture (GG’)	68	64
Width of foramen magnum (gg’)	44e	53
Height of foramen magnum (hi)	56	–
Width of mesorostral fossa (JJ’)	56	–
Length of zygomatic process of squamosal (OP)	131	–
Anterior tip of zygomatic process to rear edge of squamosal below mastoid foramen (OT)	163e	–
Length of parietals, frontoparietal suture to rear of external occipital protuberance (P)	97	85e?
Anteroposterior length of root of zygomatic process of squamosal (QR)	51	–
Width of supraoccipital (WSo)	94	92
Height of supraoccipital (HSo)	55	–
Minimum width of parietal roof between squamosal notches	70	78
Maximum width of braincase at level of middle part of parietal-squamosal suture	84e	77
Length of cranial portion of squamosal (ST)	93	–
Breadth across sigmoid ridges of squamosals (ss’)	186	–
Dorsoventral thickness of zygomatic-orbital bridge (T’)	10	–
Height of posterior part of cranial portion of squamosal (UV)	94	–
Dorsoventral breadth of zygomatic process (WX)	47	41
Length of jugal (YZ)	162	–
Deflection of masticating surface of rostrum from occlusal plane (RD; in degrees)	56°e	–

W. True; True, 1906: pl. 76, fig. 4), USNM 186899 (coll. William Palmer), USNM 476415 (coll. David Bohaska and William F. Douglass Jr.). *Ulna*: USNM 186896 (coll. Allan Smith). *Vertebrae*: USNM 23348 (coll. William Thomas Palmer Sr.), USNM 23367 (not 23667; axis; coll. R. Lee Collins), USNM 23666 (coll. Adolph Schultz), USNM 360706 (coll. S. F. Blake), USNM 559307 (coll. William E. Salter). *Ribs*: USNM 214431 (coll. Wallace L. Ashby); numerous uncataloged USNM specimens.

Virginia (Westmoreland County; Calvert Formation): Partial skeleton: USNM 542440 (coll. Peter McCrery, David Bohaska, Daryl Domning, Nardos Fessaha, James McDonald, and David and James Laist).

North Carolina (Beaufort County; Pungo River Formation(?), Lee Creek Mine) Exoccipitals: USNM 244182 (coll. Peter Harmatuk), USNM 476404 (coll. Becky and Frank Hyne). *Squamosal*: USNM 391875 (coll. Pam and Tom Burns). *Humeri*: USNM 476405 (coll. Peter Harmatuk), USNM 476406-8 (coll. Becky and Frank Hyne), USNM 476410 (coll. F. L. Pearce), USNM 559311 (coll. Clyde Swindell; donated by Judy Stiles). *Vertebra and rib fragments*: USNM 306481 (coll. Vincent Schneider); numerous uncataloged USNM specimens.

RANGE. Late early to early middle Miocene; from the Chesapeake Bay region, USA, to the coasts of Brazil(?) and Peru.

EMENDED DIAGNOSIS. Species of *Metaxytherium* with medium body length (2–3 m; shared with *M. serresii* and with *M. albifontanum* Vélez-Juarbe and Domning, 2014). Differs from *M. albifontanum* by the more anterior position of the ventral extremity of its jugal (character state 85[2] of Domning and Aguilera, 2008). Differs by its smaller tusk from *M. serresii* and *M. subapenninum*. Differs by its lesser rostral deflection (50°–60°) from *M. arctodites* (80°), *M. floridanum* (67°–81°), and *M. subapenninum* (57°–63°). *Metaxytherium crataegense* and the other *Metaxytherium* species also have an anteroposteriorly elongate zygomatic-orbital bridge of the maxilla (state 14[0] of Domning and Aguilera, 2008), whereas the bridge is shortened (state 14[1]) in some individuals of *M. floridanum*.

COMMENTS. *Metaxytherium* of the same general (early to middle Miocene) age and not demonstrably different from those of the Chesapeake region have also been found in Cuba (Varona, 1972), Brazil (Toledo and Domning, 1991), and Peru (Muizon and Domning, 1985). All are likely to represent the same species, which appears to differ slightly (in smaller size, slenderer mandible, and lesser rostral deflection) from the later species *M. floridanum* of Florida (Domning, 1988). However, *M. crataegense* is poorly sampled relative to *M. floridanum*, and its distinction from the latter has yet to be clearly demonstrated. For example, direct comparison of the immature dentary of USNM 16757 (Figure 5.4A,B) with immature Bone Valley dentaries of comparable growth stage (USNM 356683, 356688) shows essentially no difference in either size, depth of horizontal ramus, or rostral deflection. The depth of the ramus is greater in adult *M. floridanum*, but we still lack good, fully adult specimens of the Calvert species to compare with the Florida specimens.

An adult humerus from the Lee Creek Mine in North Carolina (USNM 559311) is, like most other remains from this mine, of uncertain stratigraphic provenance. Its proportions fall within the range of variation of *M. floridanum*: the ratio of its distal breadth (dimension EF, further defined in Table 5.3) to a measure of its overall length (QR, further defined in Table 5.3) is 0.41, compared with an average of 0.45 (observed range = 0.40–0.51; *N* = 12) in Florida specimens of *M. floridanum*. European species have similarly broad ranges of variation: for *M. krahuletzi* (early Miocene), 0.36–0.44 (*N* = 14), for *M. medium* (middle Miocene), 0.39–0.48 (*N* = 8), and for *M. serresii* (late Miocene–early Pliocene), 0.37–0.51 (*N* = 7). However, *Metaxytherium* is not recorded in the western Atlantic later than late Miocene (early Hemphillian) time (Domning, 1988), whereas the Yorktown Formation in the Lee Creek Mine is considerably later (early Pliocene, N19, Hazel, 1983; latest(?) Hemphillian, Eshelman and Whitmore, 2008). Therefore, the other, lower unit exposed in the mine—the Calvert-correlative Pungo River Formation—is more likely than the Yorktown Formation to be the source of this specimen.

Reinhart (1976:220–228) referred to *M. calvertense* several specimens from the Bone Valley Formation of Florida; these have since been placed in *M. floridanum* by Domning (1988).

One additional report of "*Metaxytherium*, cf. *M. calvertense*" is evidently also erroneous. MacPhee and Wyss (1990) described under this name a mandible (AMNH-VP 125780) and a set of vertebrae and ribs (AMNH-VP 125781) from the early Miocene Miranda Sand Member of the Cibao Formation in Puerto Rico. However, features of the mandible suggest that these specimens more likely represent a dugongine (Vélez-Juarbe, 2012).

Going back further in time, new fossils from Florida and South Carolina (*Metaxytherium albifontanum* Vélez-Juarbe and Domning, 2014) now trace the genus *Metaxytherium* as far back as the late Oligocene in the New World, significantly earlier than in Europe, where it is currently recognized only from the early Miocene onward.

Metaxytherium floridanum Hay, 1922

TYPE LOCALITY. Florida, Polk County, near Mulberry; Lower Bone Valley Formation, probably early Clarendonian (late middle Miocene).

RANGE. *Metaxytherium floridanum* has previously been recorded only from the middle and late Miocene (Clarendonian and possibly late Barstovian and early Hemphillian) of Florida (Domning, 1988).

Metaxytherium cf. *M. floridanum* Hay, 1922

FIGURES 5.5B, 5.7O–S;
TABLE 5.2

LOCALITIES, FORMATIONS, AND AGES OF INCLUDED SPECIMENS.

Maryland (Calvert County, near Little Cove Point and Chesapeake Ranch Estates): The exposures here all seem to correlate to the late Miocene St. Marys Formation (beds 21–23) and higher units (Ward and Andrews, 2008: fig. 5, sections C-16, C-17). At least the squamosal (USNM 542432) was collected in situ from the Little Cove Point Member of the St. Marys Formation.

Virginia (Westmoreland County, South Bank of the Potomac River between Stratford Hall and Westmoreland State Park): As noted above, the section here exposes parts of the Calvert, Choptank, and Eastover Formations (Ward and Andrews, 2008: fig. 7, sections PO-11, PO-12). The source of the sirenian remains is thus uncertain but is higher than the Plum Point Member of the Calvert Formation, which has produced *M. crataegense*, and thus is in either the Choptank or the Eastover Formation.

INCLUDED SPECIMENS.

Maryland: CMM-V-4074 (exoccipital; coll. John Nance), USNM 542432 (squamosal; coll. Jeff O'Neil), USNM 452480 (periotic; coll. Elizabeth M. Cridlin), USNM 241546 (immature scapula; coll. Jeff O'Neil; Figure 5.5B), USNM 451030 (scapula fragment; coll. Elizabeth M. Cridlin), USNM 542433 (cast of humerus; coll. Oliver Goldsmith), USNM 542434 (anterior rib; coll. David Bohaska), CMM-V-4748 (rib; coll. John Nance), CMM uncataloged (miscellaneous rib and vertebra fragments).

Virginia: USNM 542436 (large adult humerus; coll. David Blondin; Figure 5.7O–S), USNM 542437-38, 542440-41 (clusters of vertebrae and ribs), USNM 377443-5 (other vertebra fragments and a rib).

COMMENTS. The specimens from the St. Marys Formation are significantly later chronostratigraphically than those from the Calvert Formation and are roughly contemporaneous with *M. floridanum* from Florida; I tentatively assign them to the latter species on that chronostratigraphic basis. As noted above, these Florida animals may have been slightly larger than *M. crataegense*, with deeper mandibles and greater rostral deflections. The squamosal (USNM 542432) closely resembles some *M. floridanum*, such as USNM 323127 (Domning, 1988). The large humerus from Virginia (USNM 542436; Figure 5.7O–S, Table 5.2) is at or above the maximum recorded size of *M. floridanum* (Domning, 1988: tbl. 10). It could have come from the upper part of the Calvert Formation, which is exposed along with the Choptank and Eastover Formations in the area where it was collected; however, its size seems more consistent with the age of the higher units, so it and the other remains from the same site are likewise tentatively assigned to *M. floridanum* in order to call attention to this species' possible occurrence in the Chesapeake Group. However, until *M. crataegense* and *M. floridanum* are more adequately distinguished and Chesapeake Group specimens clearly showing diagnostic features of *M. floridanum* are found, the latter name cannot be applied in this region without qualification.

SUBFAMILY DUGONGINAE (GRAY, 1821) SIMPSON, 1932

Genus *Nanosiren* Domning in Domning and Aguilera, 2008

TYPE SPECIES. *Nanosiren garciae* Domning in Domning and Aguilera, 2008.

TYPE LOCALITY. Florida, Manatee County, Four Corners Mine; Upper Bone Valley Formation, latest Hemphillian (early Pliocene), ca. 5.3–4.9 MYA.

RANGE. The genus *Nanosiren* is believed to have lived from the early Miocene through the early Pliocene and inhabited the eastern and southeastern United States, the Caribbean region, and northern South America, as well as the Pacific coast of South America (Domning and Aguilera, 2008). Its late Miocene representative, *N. sanchezi* Domning and Aguilera, 2008, known from Venezuela is the only other named species of the genus.

Nanosiren sp.

FIGURES 5.4C,D, 5.5C, 5.7A–D, 5.8C, 5.9E;
TABLES 5.1–5.4

Metaxytherium calvertense Kellogg, 1966:71 (in part: USNM 16630, 16715).
Nanosiren sp., Domning and Aguilera, 2008:486, 496.

LOCALITIES, FORMATIONS, AND AGES OF INCLUDED SPECIMENS.

Maryland (Calvert County): Calvert Formation, Plum Point Member, beds 11–12; early middle Miocene, probably in the lower part of planktonic foraminiferal zone N9, late early Barstovian North American Land Mammal Age, ca. 15 MYA (Gibson, 1983b:362; Tedford et al., 1987: fig. 6.2).

Virginia (Westmoreland County, Wakefield): Calvert Formation, bed 10 or 11 (R. Weems, pers. comm.); middle Miocene.

North Carolina (Beaufort County, Lee Creek Mine): Pungo River Formation(?), upper part; latest early Miocene, planktonic foraminiferal zone N8, early Barstovian, ca. 16 MYA (Gibson, 1983b:360; Tedford et al., 1987: fig. 6.2).

INCLUDED SPECIMENS.

Maryland: USNM 16630 (subadult partial skeleton; coll. George E. Marsh; Figures 5.4C,D, 5.9E), USNM 16715 (scapula; coll. William E. Salter; Figure 5.5C), USNM 23246 (humerus; coll. W. H. Boss and Remington Kellogg), USNM 25902 (radius-ulna; coll. unknown; Figure 5.8C), USNM 186897 (thoracic vertebra; coll. R. Lee Collins), USNM 215078 (humerus; coll. MacKenzie L. Kelly; Figure 5.7A–D), USNM 546149 (humerus; coll. Russell Sennett, donated by George Klein), USNM 559306 (2 partial ribs; coll. William E. Salter; may be part of the same individual as USNM 16630), USNM 559310 (7 complete or partial ribs; coll. Paul Moffett), CMM-V-2690 (juvenile humerus; coll. William F. Douglass Jr.).

Virginia: USNM 542439 (right rib; coll. Frank C. Whitmore Jr. and James Kaltenbach).

North Carolina: USNM 546113 (symphyseal portion of left dentary; coll. Peter Harmatuk and sons), USNM 205472 (adult humerus; coll. William Bennett), USNM 321923 (immature humerus; coll. Peter Harmatuk), USNM 460119 (thoracic vertebra; coll. Anne Leightner Kienlen).

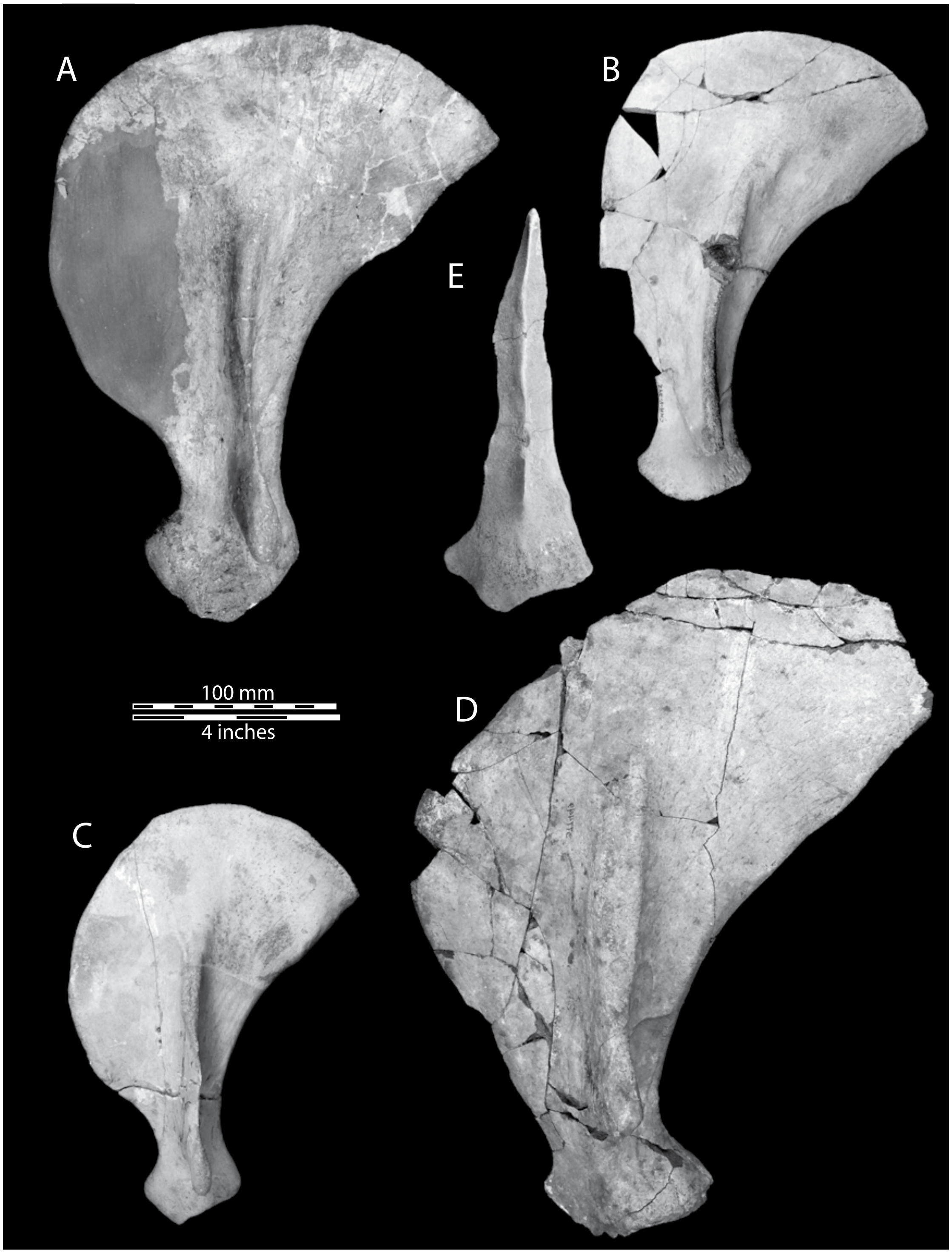

FIGURE 5.5. Scapulae of Chesapeake Group dugongids, lateral views. (A) *Metaxytherium crataegense*, USNM 16757 (holotype of *M. calvertense*), right scapula reversed. (B) *Metaxytherium* cf. *M. floridanum*, USNM 241546, left scapula (immature). (C) *Nanosiren* sp., USNM 16715, left scapula. (D) Dugonginae, gen. et sp. indet., Pamunkey River, Virginia, USNM 377449, right scapula reversed. (E) *Metaxytherium crataegense*, CMM-V-242, partial right scapula reversed (eroded by unknown cause). See also the cranial elements of this specimen in Figure 5.6B–D and the humerus of this specimen in Figure 5.7J–N.

TABLE 5.2. Measurements (mm) of scapulae of sirenians from the Chesapeake Group. Letters in parentheses denote abbreviation used by Domning (1978, 1988) for the given measurement. Other abbreviations: d = lacking distal epiphysis; e = estimated; + = broken. A dash (–) indicates measurement could not be taken on the specimen. Specimen USNM 16757 is the holotype of *M. calvertense*.

	Halitheriinae			**Dugonginae**			
	Metaxytherium crataegense		***M.* cf. *floridanum***	***Nanosiren* sp.**		**Dugonginae gen. et sp. indet.**	
Dimension	**USNM 16757 (subadult, right)**	**USNM 23213 (adult, right)**	**USNM 241546 (immature, left)**	**USNM 16630 (subadult, right)**	**USNM 16715 (subadult, left)**	**USNM 241562 (adult, right)**	**USNM 377449 (adult, right)**
Maximum length, vertebral border to border of glenoid fossa (AB)	281	–	224d	199	200	–	292
Mediolateral width of glenoid fossa (BI)	47e	41	30d	25	24	47	42e
Lateral border of glenoid fossa to to inside of concave distal end of spine (BJ)	49	–	–	26e	25	–	46
Maximum breadth of blade dorsally (CD)	208	–	137	133	132	–	219e
Minimum anteroposterior breadth of neck (EF)	44	42	32	29	29	–	49
Maximum anteroposterior breadth of distal end (GH)	74	77	52d	47	46	95	74
Summit of spine to medial side of blade, measured parallel to plane tangent to posterior edges of spine and neck (KL)	57	–	40	–	38	–	47
Anteroposterior length of glenoid fossa (MN)	50	51	–	35	33	58	52
Length of teres major origin from teres protuberance to posterior corner of blade (TMO)	73	–	51	44	44	–	60+

COMMENTS. Kellogg (1966) included in his concept of *Metaxytherium calvertense* some remains of small sirenians, which he regarded as juveniles of the larger *M. calvertense*. Principal among these was the partial skeleton USNM 16630, which included the mandible (Figure 5.4C,D). However, Kellogg misinterpreted its dentition as showing it to be much less mature than USNM 16757, the holotype of *M. calvertense*, which is itself immature. In fact, both specimens are of roughly the same life stage, with unerupted third molars (Domning and Aguilera, 2008), which shows that they represent different species of markedly different sizes. "*Metaxytherium calvertense*" is likely to have been close to 3 m in body length, whereas the early Pliocene species *Nanosiren garciae* is estimated to have been only about 2 m long (Domning and Aguilera, 2008; Sarko et al., 2010), although the Calvert *Nanosiren* was slightly larger. The specimens from the Lee Creek Mine, North Carolina, are here deemed to come from the Pungo River Formation and to represent the same unnamed species as the Calvert Formation specimens; however, given their fragmentary nature, derivation from the overlying, early Pliocene Yorktown Formation cannot be excluded on the basis of their morphology, in which case they would presumably represent *N. garciae*.

There is further confusion regarding USNM 16630. Kellogg (1966:71) reported this skeleton as including the right scapula and as having been collected by "G[eorge]. E[verett]. Marsh, Dec. 24, 1939; 646 yards south of mouth of Parker Creek, Calvert Co.,

TABLE 5.3. Measurements (mm) of humeri of sirenians from the Chesapeake Group. Letters in parentheses denote abbreviation used by Domning (1978, 1988) for the given measurement. Other abbreviations: e = estimated; p = lacks proximal epiphysis; * = measurement taken on right humerus. A dash (—) indicates measurement could not be taken on the specimen. Specimen USNM 16757 is the holotype of *M. calvertense*.

	Halitheriinae					**Dugonginae**						
	Metaxytherium crataegense			*M.* cf. *floridanum*		*Nanosiren* sp.			Dugonginae gen. et sp. indet.			
Dimension	**USNM 16757 (immature, left)**	**USNM 476415 (adult, left)**	**USNM 559311 (adult, right)**	**USNM 542436 (adult, left)**	**USNM 542433 (adult, left)**	**USNM 23246 (adult, right)**	**USNM 215078 (immature, left)**	**USNM 546149 (immature, right)**	**USNM 241562 (adult, left)**	**USNM 241562 (adult, right)**	**USNM 377442 (adult, right)**	**USNM 437570 (adult, left)**
Maximum length, greater tubercle to distal end (AB)	—	—	233	252	—	—	110p	—	191	191	—	—
Maximum breadth, greater to lesser tubercle (CD)	76	103	107	118	—	—	45	39	93	91	77	85
Maximum breadth, ectepicondyle to entepicondyle (EF)	68*	—	82	101	75	43	42	—	89	—	—	—
Maximum thickness, posterior side of head to anterior side of greater tubercle (GH)	—	98	110	112e	88	—	—	—	98	99	65	—
Maximum thickness, posterior to anterior ends of medial rim of trochlea (IJ)	—	—	33	34e	34	18	19	—	31	30	—	—
Proximolateral-mediodistal breadth of head (KL)	53	56	67	72	42e	—	—	—	62	56	51	63
Proximomedial-distolateral breadth of head (MN)	46	57	65	71	41	—	—	—	53	53	45	59
Breadth of anterior side of trochlea (OP)	—	—	57	72e	56e	24	27	—	54	—	—	—
Length, saddle between head and greater tubercle to saddle of trochlea (QR)	—	—	199	213e	166	—	—	—	171	165	—	—
Maximum mediolateral diameter perpendicular to lateral surface, midshaft (MLD)	25	36	34	51	40	14	15	13	30	30	26	—

Md., in bluish sandy clay, zone 12, Calvert Formation." A label with the specimen adds that it was found "at base of cliff, found within a space 6′ × 6′." Kellogg (1966:71) next reported USNM 16715, a left scapula (Figure 5.5C) collected by "William E. Salter, July 11, 1942; 1,400 feet south of mouth of Parker Creek (in second cliff), Calvert Co., Md., in blue clay of zone 11, about 3 feet below top of zone, Calvert formation." However, Kellogg (1966: pl. 43, fig. 2) then illustrated this left scapula but misidentified it in the caption as part of "USNM 16630"—the skeleton that did not include a left scapula. This mistaken citation of the number is understandable: direct comparison of the left and right scapulae reveals that they are of identical size (Table 5.2), morphology, osteological maturity (with fully fused distal epiphyses), and preservation, so they surely represent parts of the same individual, collected 2.5 years apart by two different people. The discrepancies in the reported localities and horizons are harder to explain. The difference between "646 yards" (=1,938 ft or ~591 m) and "1,400 feet" (~427 m) might be ascribed to inaccurate estimation of the distance or to different definitions of the "mouth of Parker Creek," or the mouth may even have shifted because of storms, as sometimes happens (D. Bohaska, USNM, and S. Godfrey, CMM, pers. comm.). The identification of bed 12 as the source of USNM 16630 may also be wrong since "bluish sandy clay" is more typical of bed 11 (Bohaska and Godfrey, pers. comm.). But any or all of these errors seem more likely than two scapulae being so similar in size and shape yet from different strata and different individuals of a species rare in these deposits.

Finally, two *Nanosiren* ribs (USNM 559306) and a *Metaxytherium* vertebra (USNM 559307) were collected by William E. Salter on 8 August 1943 "in the water at the bog iron N. of Scientists Cliff," a location arguably close or identical to those of the two finds described above. One rib is the right second rib; the other is the distal part of a left mid-thoracic rib. Both could pertain, without duplication, to the partial ribcage (12 ribs) of USNM 16630, which they match in size and preservation. It is easy to envision USNM 16630 as a tight cluster of bones comprising most of the skeleton, excavated in 1939, the scapula USNM 16715 becoming exposed close by in 1942, and the ribs USNM 559306 having been washed out of the cliff by 1943. I believe that all of these most likely represent the same individual.

Genus *Corystosiren* Domning, 1990

Type Species. *Corystosiren varguezi* Domning, 1990.

Type Locality. Mexico, state of Yucatán, between Tizimín and Colonia Yucatán; Carrillo Puerto Formation, early Pliocene.

Range. Early Pliocene; Yucatán and Florida. An undescribed primitive species occurs in the South Carolina phosphate deposits, whose fauna includes early and middle Miocene elements (Domning, 1989, 1990, 2001).

Aff. *Corystosiren* sp.

FIGURES 5.6A, 5.8E

Locality, Formation, and Age of Included Specimen 1. Maryland, Prince Georges County, Potomac Knolls, SW side of North Star Drive just W of Old Lantern Court, 38°43′46.0″N, 76°58′56.2″W: green clay with small shark teeth and phosphate pebbles; lower Calvert Formation, just above its contact with the Eocene Nanjemoy Formation. Outcrops approximately 2.5 km S of this locality are assigned by Glaser (1986:64–65) to the "basal Calvert Formation," which there consists of "3 to 4 feet of dense, clayey olive-green to olive-brown sand" overlying the Nanjemoy Formation. Early Miocene.

Included Specimen 1. USNM 542442 (tusk fragment; coll. George C. Fonger; Figure 5.8E).

Description. A triangular fragment of a large, flattened tusk, 73 × 48 × 10 mm thick, black, partly covered on the outer surface with paper-thin gray enamel. The slightly convex outer surface exhibits shallow longitudinal grooves 8–12 mm wide; the enamel has faint growth lines perpendicular to these grooves.

Comments. This fragment is too broad and flat to represent a form like *Dioplotherium*, but it compares well with the medial surfaces of tusks of large dugongines such as *Corystosiren* (cf. Domning, 1990: fig. 4B). Indeed, the overall convexity and the spacing of the grooves exactly match those of such a tusk (SCSM 2013.33.1) collected by Vance McCollum from the Wando Shipping Terminal spoils near Charleston, South Carolina. Since an unnamed species of *Corystosiren* is otherwise known to be present in the South Carolina phosphate deposits (as noted above), it would not be surprising to encounter it in the Calvert Formation or its equivalents.

Locality, Formation, and Age of Included Specimens 2 and 3. North Carolina, Beaufort County, Lee Creek Mine: specimen 2's white or light gray indurated limy silt matrix, firmly attached to the bone, contains phosphatic sand grains and abundant molds of shells. According to D. Bohaska and R. Purdy (pers. comm.), this lithology almost certainly represents the indurated unit 4 or 5 of the Pungo River Formation, the matrix of which "tends to be firmly attached to the specimens derived from" that bed (Kazár and Bohaska, 2008:271). Late early Miocene.

Included Specimen 2. USNM 498744 (skullcap; coll. Gaye Williams; Figure 5.6A).

Included Specimen 3. USNM 476409 (skullcap fragment; coll. Robert W. Purdy et al.).

Description. USNM 498744, the skullcap of a juvenile animal (Figure 5.6A), consists of the parietals fused to the broken supraoccipital; they were joined to the frontals by a broad, deep, interdigitated sutural surface, which has a 1 cm long anterior protuberance at its center. The temporal crests are widely (6.5 cm) separated anteriorly and converge posteriorly; they are low (~4 mm high), distinct, located on the overhanging edges of the flat or slightly convex parietal roof, and separated by ~2.5 cm where they are closest together (~2 cm in front of the nuchal ridge, which

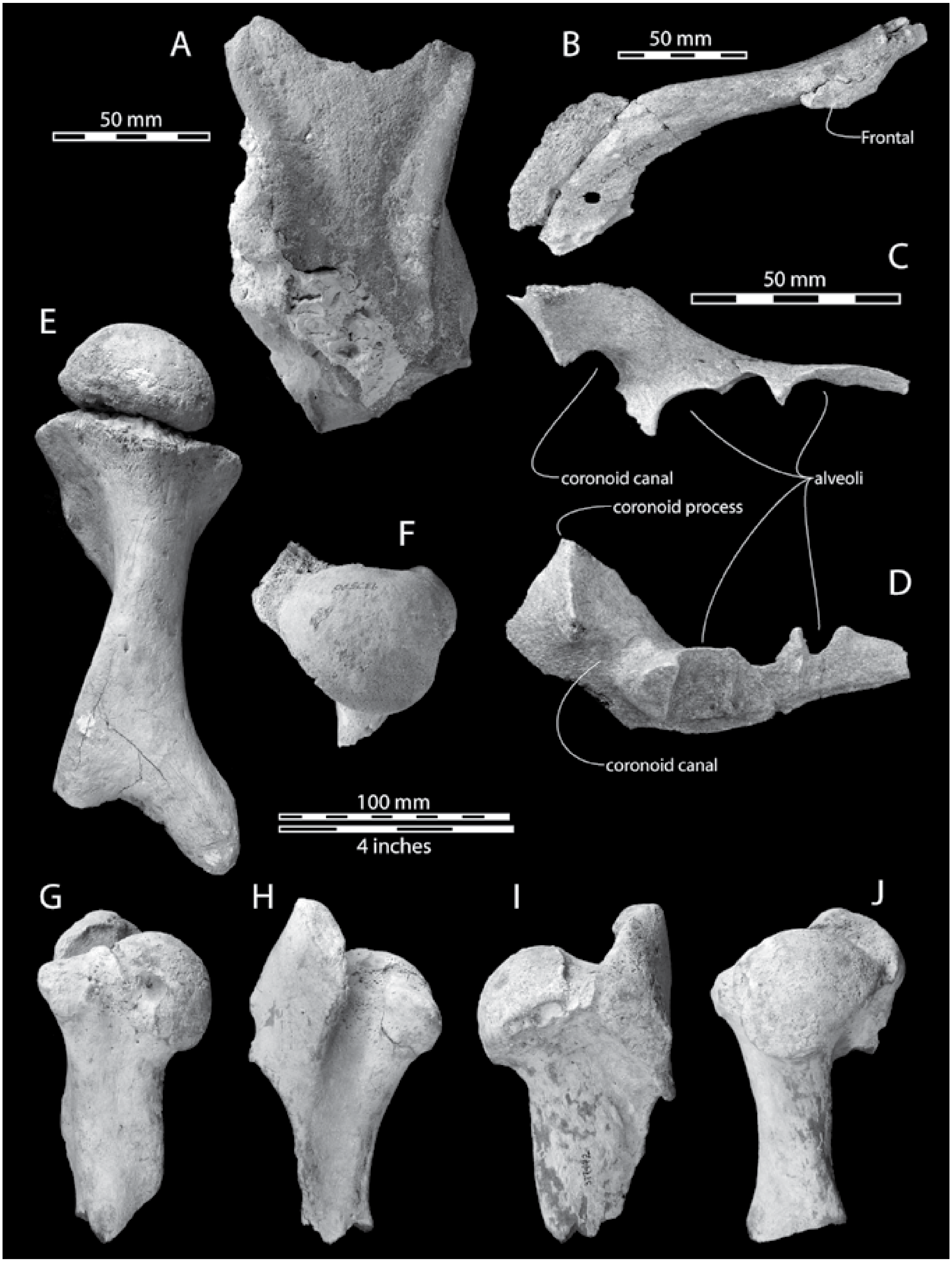
A
50 mm
B
50 mm
Frontal
C
50 mm
coronoid canal
alveoli
coronoid process
D
coronoid canal
E
F
100 mm
4 inches
G
H
I
J

FIGURE 5.6. (*Facing page*) (A) Parietal-supraoccipital skullcap of aff. *Corystosiren* sp., Lee Creek Mine, North Carolina, USNM 498744 (juvenile), with some adhering matrix, dorsal view. (B–D) *Metaxytherium crataegense*, Maryland (CMM-V-242), parts of associated adult skull eroded by unknown cause: (B) Left premaxilla with attached supraorbital process of frontal, lateral view. (C, D) Fragment of left dentary (base of ascending ramus and part of alveolar process, showing coronoid canal at left and labial sides of m2–3 alveoli at right), dorsal view and medial views, respectively. Note the knife-sharp eroded edges and thinness of bone labial to alveoli. See also the scapula of this specimen in Figure 5.5E and the humerus of this specimen in Figure 5.7J–N. (E–J) Humeri of Chesapeake Group dugongids: (E) *Metaxytherium crataegense*, USNM 16757 (holotype of *M. calvertense*), Maryland, left humerus with unfused epiphysis, posterior view. (F) Dugonginae, gen. et sp. indet., Lee Creek Mine, North Carolina, USNM 437570, head of left humerus in posteroproximal view. (G–J) Dugonginae, gen. et sp. indet., Pamunkey River, Virginia, USNM 377442, right humerus in medial, anterior, lateral, and posterior views, respectively. The 100 mm scale applies to images E–J.

intersects them). The crests are sharp posteriorly and as narrow there as they are anteriorly. The parietal roof is convex anteroposteriorly. The external occipital protuberance is large. Endocranially, the posteriorly sharp bony falx cerebri is flattened at the frontoparietal suture, which is more or less straight. The internal occipital protuberance is distinct but blunt. The skullcap is 36 mm thick in the anterior midline and 70 mm wide across its divergent, broken anterior extremities. The maximum width of the parietals below the level of the roof (measurement GG′ [defined in Table 5.1]) is about 75 mm; the midline length from the frontoparietal suture to the rear of the external occipital protuberance (measurement P [see Table 5.1]) is about 100 mm.

USNM 476409 is a similar but less complete fragment, preserving only the anterior part of the parietals with their anteriorly diverging, overhanging temporal crests, and is 31 mm thick in the anterior midline. The parietal roof is flat, with a slight median ridge.

Comments. USNM 498744 resembles adult skullcaps of *Corystosiren varguezi* (Domning, 1990) in its overall length, but its width and thickness are much smaller, and it lacks their strong sculpture on the posterior part of the roof. This difference may be due to its immaturity, and/or it may represent a different, more primitive species.

Subfamily Dugonginae, gen. et sp. indet.

FIGURES 5.6F, 5.7E–I, 5.8A, 5.9D;
TABLES 5.1–5.4

Locality, Formation, and Age of Included Specimens 1 and 2. Maryland, Charles County, Popes Creek: Popes Creek Sand bed of the Calvert Formation. Early Miocene.

Included Specimen 1. USNM 241562 (right scapula, right and left humeri [Figure 5.7E–I], left radius, ulna [Figure 5.8A], and unciform(?); 12 ribs and 14 fragments; coll. Norman Riker and Ralph Eshelman).

Included Specimen 2. CMM-V-244 (approximately 6 fragments of vertebrae and 26 of ribs; coll. Norman Riker and Calvin Taylor; not part of same specimen as USNM 241562; taxonomic referral provisional; see below).

Locality, Formation, and Age of Included Specimen 3. Virginia, King William County, Pamunkey River between Piping Tree Ferry and Grimes Landing: pebble bed about 0.6 m [2 ft] above the unconformable contact of the Calvert Formation with the Eocene Piney Point Formation (Domning, 1984b). The pebble bed and overlying deposits are here considered part of the Popes Creek Sand bed of the Calvert Formation (early Miocene).

Included Specimen 3. USNM 377441-2, 377446-7, 377449 (left dentary, atlas, axis, 3 other cervical and 4 anterior thoracic vertebrae, about a dozen ribs [Figure 5.9D], right scapula, proximal part of right humerus, and miscellaneous bone fragments; recovered over several years by David Bohaska, Lauck Ward, Robert Weems, Norman Riker, Ralph Eshelman, Bruce Alsopp, and Daryl Domning, 1973–1983, but almost certainly representing the same individual; Domning, 1984b).

Locality, Formation, and Age of Included Specimen 4. North Carolina, Beaufort County, Lee Creek Mine: Pungo River Formation(?) (latest early Miocene).

Included Specimen 4. USNM 437570 (proximal end of left humerus; coll. Peter Harmatuk; Figure 5.6F).

Locality, Formation, and Age of Included Specimen 5. Maryland, Calvert County, beach at Kaufmann Camp, S of Plum Point: Calvert Formation(?) (early middle Miocene(?)).

Included Specimen 5. USNM 363456 (distal end of left humerus; coll. George C. Fonger).

Comments. In the absence of cranial material, the best evidence for the dugongine identity of these specimens comes from the humerus. Surprisingly, humeri of only three fossil dugongines are known: a complete one belonging to the holotype of *Crenatosiren olseni* (latest Oligocene, Florida; Domning, 1997: fig. 6B), the proximal half of one associated with an unpublished skull of *Dioplotherium* cf. *D. allisoni* (USNM 521235; middle Miocene, California), and several humeri of *Nanosiren* spp. (Miocene–Pliocene, southeastern USA; Domning and Aguilera, 2008: fig. 6A). Although differing in other respects, all of these (as well as the living *Dugong dugon*; Sukhanov et al.,

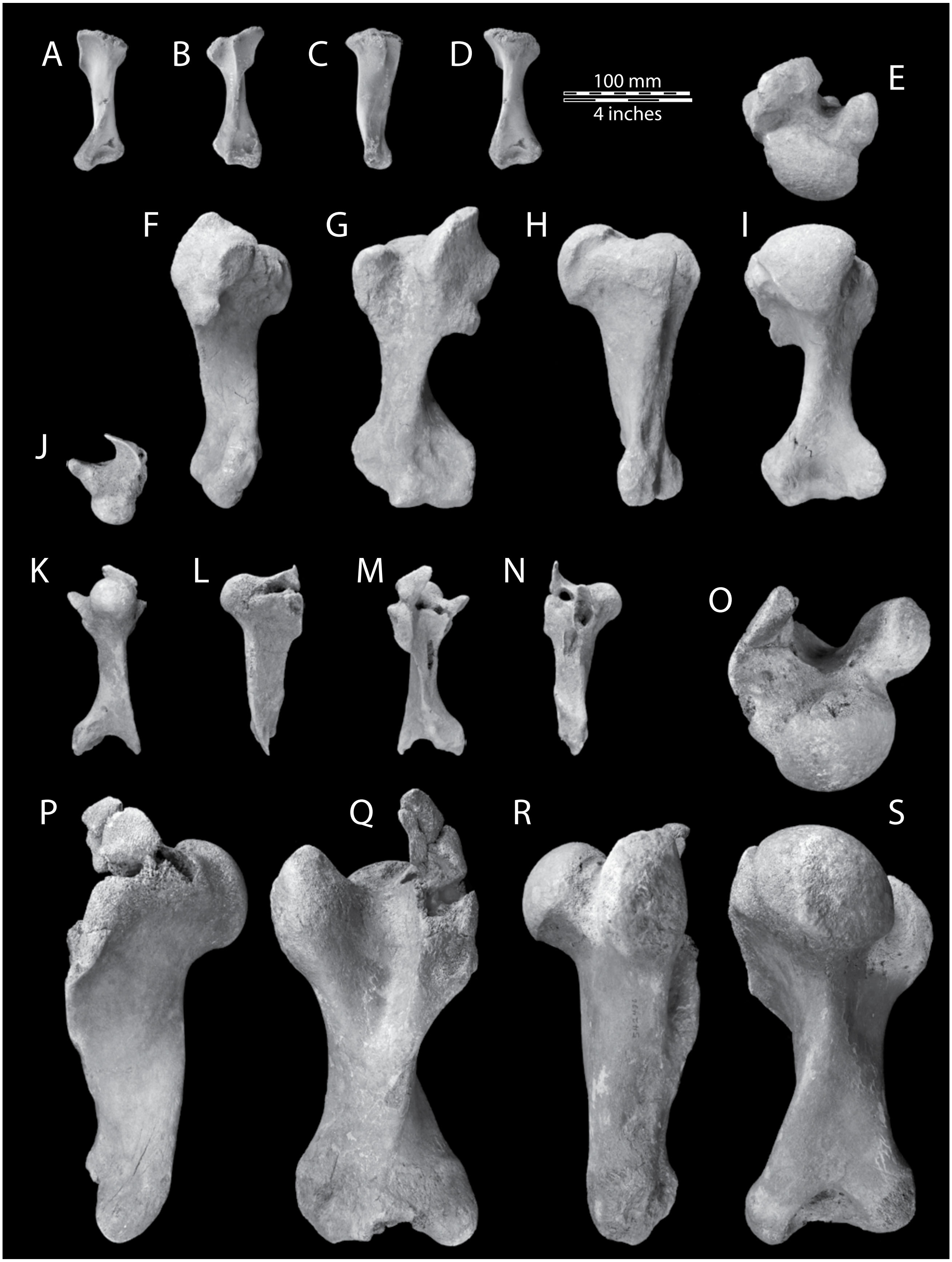
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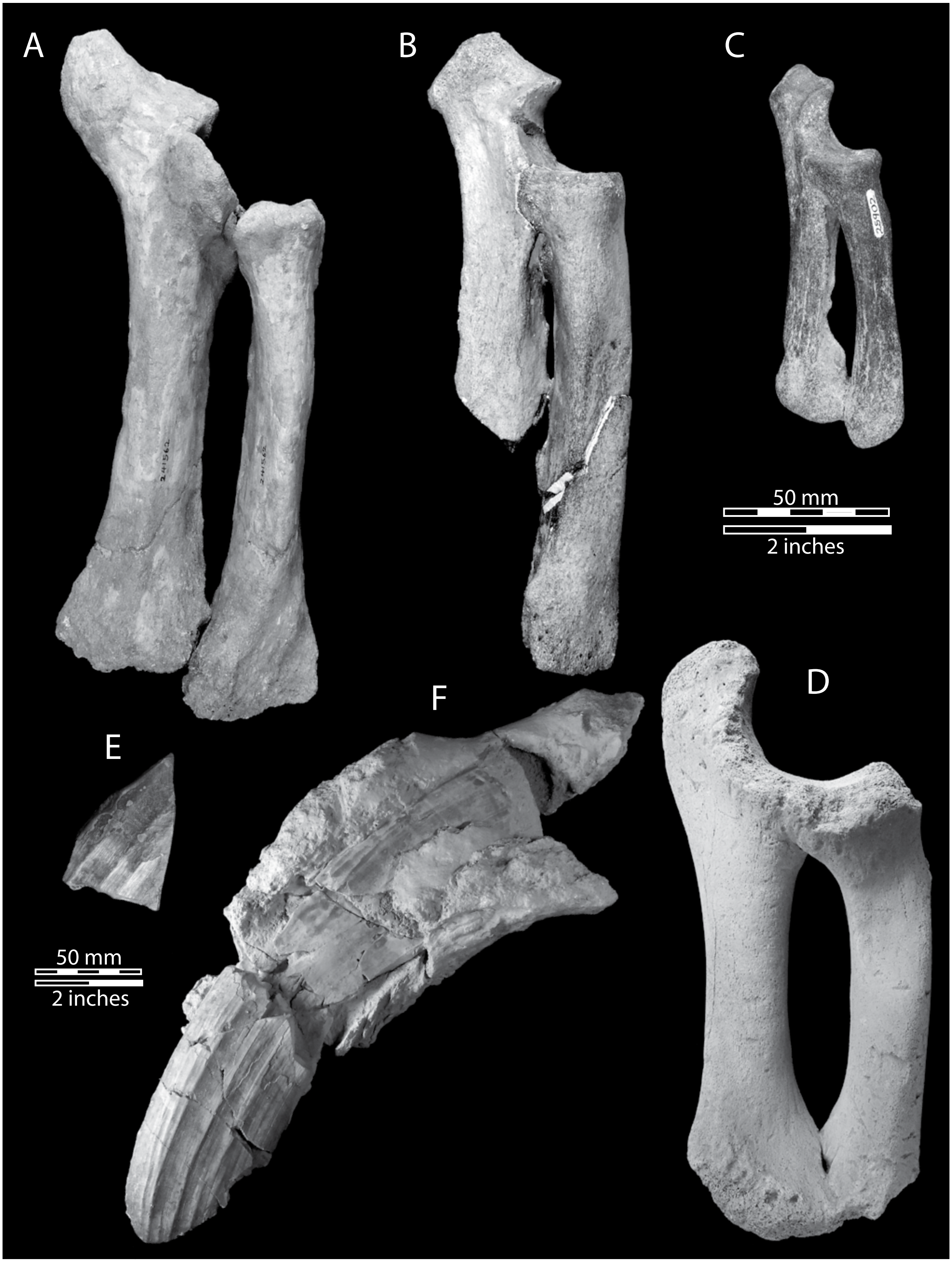
FIGURE 5.7. (*Facing page*) Humeri of Chesapeake Group dugongids. (A–D) *Nanosiren* sp., USNM 215078, left humerus in posterolateral, anterior, medial, and posterior views, respectively. (E–I) Dugonginae, gen. et sp. indet., Popes Creek, Maryland, USNM 241562, left humerus in proximal, lateral, anterior, medial, and posterior views, respectively. (J–N) *Metaxytherium crataegense*, CMM-V-242, right humerus showing extensive postmortem erosion by unknown cause, in proximal, posterior, lateral, anterior, and medial views, respectively. See also the scapula of this specimen in Figure 5.5E and the cranial elements of this specimen in Figure 5.6B–D. (O–S) *Metaxytherium* cf. *M. floridanum*, Stratford Hall, Virginia, USNM 542436, left humerus in proximal, lateral, anterior, medial, and posterior views, respectively. Specimens lightly coated with sublimed ammonium chloride.

TABLE 5.4. Measurements (mm) of radii and ulnae of sirenians from the Chesapeake Group and (for *Trichechus*) overlying Pleistocene(?) deposits. Letters in parentheses denote abbreviation used by Domning (1978, 1988) for the given measurement. Other abbreviations: d = lacking distal epiphysis; e = estimated; + = broken. A dash (–) indicates measurement could not be taken on the specimen.

	Metaxytherium crataegense		***Nanosiren* sp.**	**Dugonginae gen. et sp. indet.**	***Trichechus manatus***
Dimension	**USNM 23213 (adult, right)**	**USNM 186896 (adult, right)**	**USNM 25902 (adult, right)**	**USNM 241562 (adult, right)**	**USNM 9346 (adult, left)**
Total length of ulna (AB)	–	–	103d	193d	157+
Total length of radius, anterior lip of semilunar notch to distal end (CD)	139d	–	83d	160d	117+
Height of semilunar notch, anterior tip of olecranon to anterior radial lip of notch (EC)	30	–	20	32	39
Thickness of olecranon, anterior tip to posterior side (EF)	36	37	21	40	27
Distal thickness, anterior side of radius to posterior side of ulna (GH)	–	–	38	83	60
Maximum mediolateral breadth, radial portion of semilunar notch (IJ)	44	–	23	53	39
Maximum mediolateral breadth, ulnar portion of semilunar notch (KL)	22	45	–	58	–
Minimum mediolateral breadth, of semilunar notch at its midsection (MN)	22	21	14	26e	27
Minimum thickness of olecranon, posterior side to semilunar notch (OP)	27	27	15	26	24

1986: fig. 54) share the unusual trait of a humeral head that is transversely expanded in its proximal portion, giving it a more or less triangular shape overall (Figures 5.6F,J, 5.7I). This trait contrasts with the condition both in halitheriine dugongids (such as *Metaxytherium*; e.g., Domning, 1988: fig. 11B) and in hydrodamalines (Domning, 1978: pl. 13g,h), where the head is more or less elliptical and oriented obliquely to the shaft (Figure 5.7S). I hypothesize that a roughly triangular, transversely expanded humeral head characterizes the Dugonginae, and on this basis I refer the specimens listed above to that subfamily.

Included specimens 1, 3, and 4—the humeri from Popes Creek (USNM 241562; Figure 5.7E–I), the Pamunkey River


A
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241562
25902
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2 inches
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2 inches

FIGURE 5.8. (*Facing page*) (A–D) Radii and ulnae of Chesapeake Group sirenians, lateral views: (A) Dugonginae, gen. et sp. indet., Popes Creek, Maryland, USNM 241562, right radius-ulna. (B) *Metaxytherium crataegense*, Maryland, USNM 23213, right radius and partial ulna. (C) *Nanosiren* sp., Maryland, USNM 25902, right radius-ulna. (D) *Trichechus manatus*, Fairhaven, Maryland, USNM 9346, right radius-ulna. Note the short olecranon process and the proximally curved radius that distinguish the Pleistocene manatee (D) from the Miocene dugongids (A–C). (E, F) Tusks of dugongine dugongids: (E) Right tusk fragment of aff. *Corystosiren* sp., Potomac Knolls, Maryland, USNM 542442, anterior to left; medial surface showing enamel with growth lines and longitudinal fluting. (F) For comparison, left partial premaxilla and complete tusk (cast, reversed) of cf. *Rytiodus* from Brazil, MPEG 206-V (Toledo and Domning, 1991), in medial view. The entire medial surface of each tusk was covered with paper-thin enamel, producing a self-sharpening posteroventral edge. Specimens lightly coated with sublimed ammonium chloride.

(USNM 377442; Figure 5.6G–J; Domning, 1984b: figs. 3–4), and the Lee Creek Mine (USNM 437570; Figure 5.6F), respectively—have several traits in common. All share a subtriangular head with the lateral corner extended markedly laterad, an irregular cavity bordering the medial edge of the head, and a very distinct insertion scar for the infraspinatus muscle. They also share a prominent, strongly recurved deltoid crest that extends farther laterad from the shaft than in most dugongids; indeed, the distance is almost equal to the diameter of the shaft itself (Figure 5.7G,I). USNM 377442 (Figure 5.6G–J) is slightly smaller than the others, but all are mature, with fully fused epiphyses. The Californian specimen (USNM 521235) differs from these in that its head is less triangular, the medial cavity and muscle scar are less distinct, the deltoid crest does not extend so far laterad, and the bicipital groove is much narrower. Therefore, I surmise that the Chesapeake Group specimens do not represent *Dioplotherium*. They may possibly pertain to the aff. *Corystosiren* reported above.

The Pamunkey River scapula (USNM 377449; Figure 5.5D) lacks the proportionately narrower neck and broadly concave anterior outline consistently seen in species of *Metaxytherium* (Figure 5.5A,B) or *Nanosiren* (Figure 5.5C). Preliminary data suggest that this condition may be characteristic of some, though not all, dugongines.

Included specimen 5 (USNM 363456), an eroded humerus, resembles the humerus of USNM 241562 in that the ridge leading down to the ectepicondyle curves outward more than in *Metaxytherium*; this gives the complete bone a more strikingly dumbbell-like shape. Its dimension measurements are EF = 67 mm, IJ = 24e mm, and OP = 46e mm (see Table 5.3 for definitions).

The dentary of included specimen 3, the Pamunkey River specimen (USNM 377446; Figure 5.4E; Domning, 1984b: fig. 1), is incomplete anteriorly and less distinctive than the humeri, but it appears to have been more downturned anteriorly than *Metaxytherium* and perhaps more like USNM 521235. This might further support a referral to the Dugonginae.

Since included specimen 2 lacks a humerus or other parts diagnostic of the Dugonginae, it is listed here on the conjectural basis that a unique feature of its ribs may exclude it from the Halitheriinae. In CMM-V-244, unlike other dugongids, the rib capitula are abruptly constricted and much narrower anteroposteriorly (<1.5 cm) than the width of the rib at the level of the tuberculum and are deeper dorsoventrally (1.5–2.0 cm) than they are wide.

A TAPHONOMIC MYSTERY

A peculiarity of some sirenian fossils, observed in several parts of the world and at different geological periods, is that the individual bones or parts of them have been worn away as though they had been sandblasted (Van Orden and Godfrey, 2008). The normally robust ribs, for example, may be smoothly sharpened to a point at one end, as if they were sculpted out of ice that partly melted, preserving the bone's shape in "emaciated" form. They are found in this condition when excavated, so it is not the result of postburial erosion. Rather, we seem to be dealing here with a phenomenon in the realm of taphonomy (the study of how fossils get buried and preserved from death to fossilization). It happens that perhaps the most dramatic and revealing example of this unexplained phenomenon is a specimen from the Calvert Formation in Maryland. (Other Chesapeake Group examples are known from Virginia [USNM 542440] and from the Lee Creek Mine.)

Almost nothing has been written on this subject; the only detailed discussions I have seen are found in papers in German by Erich Thenius (1952:33–36) and Otto Sickenberg (1934:128, 215–218, pl. 6, figs. 3–4). Thenius concluded that the attrition of the bones is due to just what it looks like: wind erosion. However, it seems questionable whether sirenian bones would be exposed very often to subaerial sandblasting before burial, which would require long exposure to strong winds in a sandy environment, and under such dynamic conditions on a beach, small bones would be unlikely to remain associated (see below). Other possibilities come to mind: underwater sandblasting by strong bottom currents, for example, or slow erosion by weak currents (as favored by Sickenberg), chemical dissolution by acids, or even the action of living organisms.

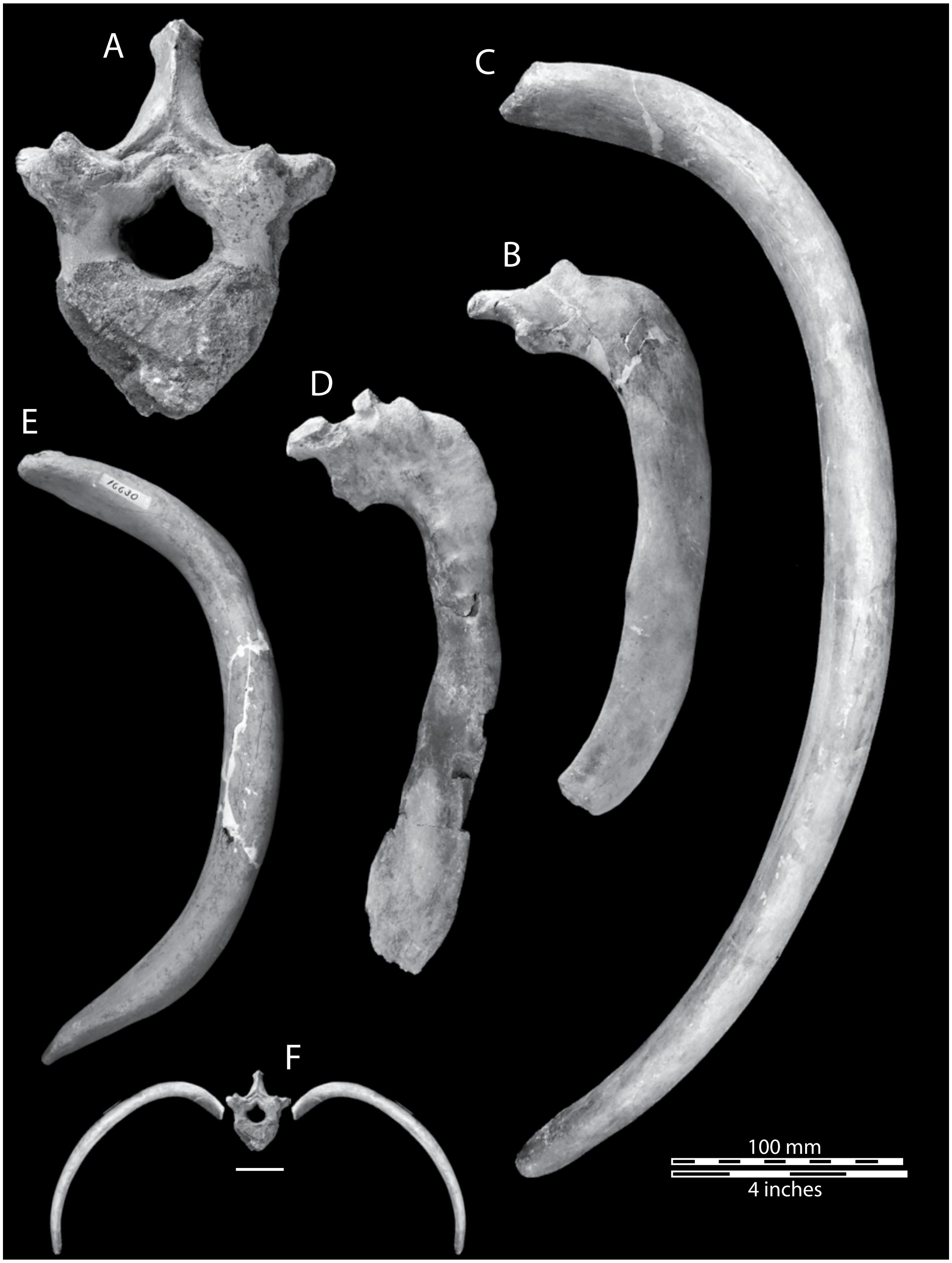

FIGURE 5.9. (A–C) *Metaxytherium crataegense*, USNM 16757 (holotype of *M. calvertense*): (A) Mid-thoracic vertebra in anterior view. (B) First left thoracic rib in anterior view. (C) Left mid-thoracic rib in anterior view. (D) Dugonginae, gen. et sp. indet., USNM 377449, first right thoracic rib in posterior view. (E) *Nanosiren* sp., USNM 16630, left mid-thoracic rib in anterior view. (F) Representation of mid-thoracic section of rib cage of *Metaxytherium crataegense*, based on (A) and (C). Scale bar for F equals 100 mm.

Some of these possibilities, however, can be ruled out by simple observations of the bones. They show no signs of tooth marks or attachment or encrustation by marine life that could account for the attrition and sharpening of their extremities. Their eroded surfaces are not pitted but are as smooth as the unaltered parts of the same or other bones. Underwater transport and tumbling by waves might account for the wear on isolated bones, as is commonly the case with other fossils, but this process would not account for the fact that many of these bones (such as ribs) are eroded on only one end, with the remainder of the bone pristine. Neither would it explain various examples of this erosion seen in still-associated skeletons that plainly did not undergo transport and scattering before burial.

Of these specimens, the most impressive example known to me is CMM-V-242 (Figures 5.5E, 5.6B–D, 5.7J–N), a subadult partial skeleton of *Metaxytherium crataegense* from the gray clay of bed 13 (3.2 m [10.5 ft] above the top of bed 12) near Parkers Creek, found by Joseph Turner and collected by David Bohaska, Norman Riker, Wallace Ashby, August Selckmann, George Fonger, and Sandy Roberts in 1983. It comprises parts of the left premaxilla attached to the supraorbital process of the frontal, a maxilla, the left dentary, a heavily worn upper molar, both scapulae, the right humerus with the proximal epiphysis attached, about 5 vertebrae, and 27 ribs, with other bone fragments. Kidwell (2006:19) stated that "Zones 11–13 reflect the deepest water and most offshore conditions — specifically, water depths >~40–50 m"—of the Calvert Cliffs stratigraphic sequence.

Besides the ribs of this specimen, several of which are sharpened at one end or on one surface, some other bones are eroded on all sides, even to the extent of becoming barely recognizable. They include several parts of the skull and mandible that have largely wasted away: the premaxilla plus frontal (Figure 5.6B), weighing only 57.5 g; the dentary (Figure 5.6C,D), weighing 30.9 g; and the maxilla, weighing 16.9 g. The small size of these fragments tells us that the agent of erosion probably did not have a lot of energy: strong waves or currents would easily have carried away such small, light, delicate objects if they lay loose on the bottom, yet they were found still associated with each other and with the heavy ribs. The clay sediment itself indicates a low-energy environment. Either the bones were stuck on or in the sediment so that they were hard to move, or else the erosion was caused by very gentle "sandblasting" or by chemical dissolution.

Van Orden and Godfrey (2008:156A) suggest that "either the bones were winnowed mechanically through the activity of organisms (akin to bone-eating worm action on whale bones in whale-fall communities) or they were dissolved chemically." If the latter occurred, they were unable to determine "if it was biologically mediated or happened in the absence of a biological agent (i.e. abiotic chemical winnowing) either before or after the skeletons were entombed in sediment."

Questions remain. Why has this kind of attrition been observed only on sirenian bones and not on those of other marine vertebrates like whales? Are only sirenians exposed to the corrosional agent (unlikely), or is the reason simply because sirenians have thick, dense bones that are relatively homogeneous throughout—and thus suitable material for "sculpture"—whereas other vertebrate bones are typically spongy on the inside and so would not stand up to such corrosion and preserve its effects?

A very promising possibility is that some sort of bacterial film covered the partly exposed bones embedded in the seafloor and secreted corrosive substances that dissolved them. Studies of deep-sea whale falls have called attention to the role of microbial mats in the destruction of bones. Such mats are "largely absent" from buried bones; "no evidence of bacterial mats was observed on bone surfaces originally lying below the sediment-water interface" (Bennett et al., 1994:212). Moreover, "there is evidence to suggest that microbial bioerosion is negatively correlated to the oil content of the bone" (Higgs et al., 2011:14). If this destructive mechanism works in shallow water as it does in the deep sea, it could explain why dense bones of sirenians, with their low lipid content, may be more prone to this kind of erosion than the spongier and oilier bones of other marine mammals.

We still do not have the complete solution to this minor mystery of science, which presents an opportunity and a challenge for clever investigators.

DISCUSSION

The sirenians of the Chesapeake Group are significant in that they are the northernmost Tertiary sirenians in the entire geological record of the western Atlantic bioprovince. As such, we might expect them to represent a depauperate sample of the Miocene sirenian diversity encountered at lower latitudes. This depauperate condition remains a possibility since only three distinct dugongid lineages (*Metaxytherium*, *Nanosiren*, and at least one other dugongine, probably *Corystosiren*) have so far been identified in the Chesapeake region, compared with at least four lineages (including the dugongines *Dioplotherium* and *Corystosiren*), and probably more, in the overall west Atlantic and Caribbean during the early and middle Miocene (Domning, 2001). It will be interesting to learn whether any (and which) of the larger dugongines were indeed absent from the Mid-Atlantic coast and what this implies about paleoenvironmental conditions there.

Large-tusked dugongines like *Dioplotherium* and *Corystosiren* seem to have specialized on uprooting and eating the tough, fibrous rhizomes of the larger species of seagrasses (Domning and Beatty, 2007). These are "climax" species that tend to dominate seagrass communities if left undisturbed. Sirenians that disturbed them by disrupting and removing their rhizome mats would have acted as "keystone species," pushing the seagrass communities to earlier, more diverse, and more productive successional stages. Earlier successional stages in turn would have provided ecological niches for additional, more delicate species of seagrasses and for species of sirenians less able to feed on the large rhizomes (Domning, 2001; Vélez-Juarbe et al., 2012). If one or more of the known west Atlantic large-tusked keystone sirenians were absent from the Mid-Atlantic region, this absence might reflect an absence of their favored seagrasses or some other undesirable characteristic of the environment. Sensitivity to cool temperatures at Mid-Atlantic latitudes, however, seems unlikely to have been a problem, given global temperatures in the early to middle Miocene that were higher than today's (Zachos et al., 2001).

Besides the three Chesapeake Group sirenian lineages indicated so far, however, it would not be surprising to find additional ones. At any rate, more complete specimens of both Calvert and Choptank/St. Marys *Metaxytherium* spp., and especially the dugongines, are eagerly awaited. The Chesapeake Group *Nanosiren* and aff. *Corystosiren* are evidently undescribed species. Properly identifying and naming these and any other new ones will require reasonably complete skulls at a minimum, so there is certainly important work for the collector to do.

Once we have a better idea of what these animals looked like, we can say with more confidence what they ate and how they divided up the available food resources. Analyses of the stable isotopes in their tooth enamel may also shed light on their diets. At present, such analyses (e.g., Clementz and Sewall, 2011) have been able to confirm only that all these sirenians fed on seagrasses, but in the future, more detailed distinctions may be possible.

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