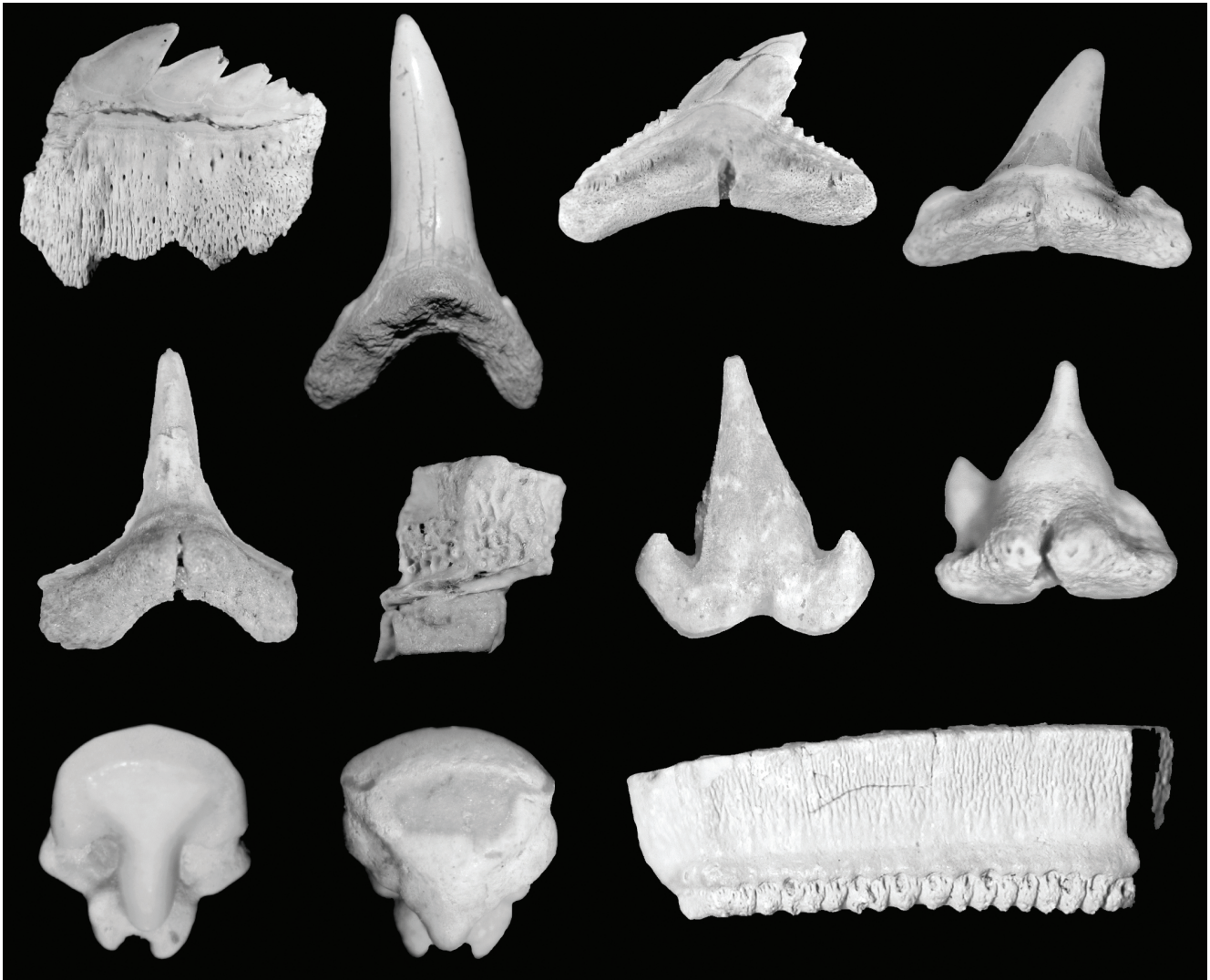


# *PaleoBios*

---

OFFICIAL PUBLICATION OF THE UNIVERSITY OF CALIFORNIA MUSEUM OF PALEONTOLOGY



**DAVID J. CICIMURRI & JAMES L. KNIGHT (2019). Late Eocene (Priabonian) elasmobranchs from the Dry Branch Formation (Barnwell Group) of Aiken County, South Carolina, USA.**

**Cover:** Various late Eocene shark and ray teeth from the Dry Branch Formation, Aiken County, South Carolina.

**Citation:** Cicimurri, D.J. and J.L. Knight. 2019. Late Eocene (Priabonian) elasmobranchs from the Dry Branch Formation (Barnwell Group) of Aiken County, South Carolina, USA. *PaleoBios*, 36. [ucmp\\_paleobios\\_43964](https://doi.org/10.2307/43964).

# Late Eocene (Priabonian) elasmobranchs from the Dry Branch Formation (Barnwell Group) of Aiken County, South Carolina, USA

DAVID J. CICIMURRI<sup>1\*</sup> and JAMES L. KNIGHT<sup>2</sup>

<sup>1</sup>South Carolina State Museum, 301 Gervais Street, Columbia, SC 29201 [dave.cicimurri@scmuseum.org](mailto:dave.cicimurri@scmuseum.org)

<sup>2</sup>Department of Biology and Geology, University of South Carolina Aiken, 476 University Parkway, Aiken, SC 29801  
[karin@gforcecable.com](mailto:karin@gforcecable.com)

A survey of the Eocene (Priabonian) Dry Branch Formation exposed in Aiken County, South Carolina, resulted in the collection of thousands of fossil teeth and bone fragments. Two sites located near the city of Aiken proved to be particularly productive, and 24 species of elasmobranchs, 11 osteichthyans, and three reptiles (one crocodylian and two turtles) have been identified. Herein we focus on the elasmobranch species (17 sharks and seven rays) that are part of the assemblage, which includes a new species of daggernose shark, *Isogomphodon aikenensis* n. sp. Cicimurri and Knight. The fossils are derived from the upper part of the Dry Branch Formation, and the fossiliferous strata accumulated within a high energy nearshore marine depositional environment that was influenced by a river system. Based on the vertebrate and invertebrate fossils we identified, the water depth was less than 40 m, and surface water temperature was at least 22° C. Elasmobranch species composition is similar to other late Eocene elasmobranch assemblages reported from the Gulf and Atlantic Coastal plains, particularly Georgia, and several of the taxa indicate affinities to the Tethyan region.

**Keywords:** fossil, elasmobranch, Eocene, Dry Branch Formation, South Carolina

## INTRODUCTION

Although Eocene strata within the South Carolina coastal plain have been extensively mapped and studied lithologically, only scattered accounts of the elasmobranch fossils these units contain have been published (Gibbes 1848, 1850, Leidy 1877, Leriche 1942, White 1956, Müller 1999, Cicimurri and Ebersole, 2015). Several reports on the elasmobranch species occurring in the Barnwell Group of Georgia, which includes the Clinchfield, Dry Branch, and Tobacco Road Formations, have been published (Case 1981, Case and Borodin 2000, Parmley and Cicimurri 2003), but such fossils occurring within equivalent strata in South Carolina have been only casually mentioned in the literature (Zullo et al. 1982, Zullo and Kite 1985, Steele et al. 1986). Cicimurri and Ebersole (2015) reported a new species of ray, *Pseudotobatus undulatus*, from the Dry Branch Formation in Aiken County, but only briefly noted other coeval species of Myliobatidae Bonaparte, 1838.

Our paper presents the first comprehensive analysis

of elasmobranch fossils from the Dry Branch Formation of South Carolina. More than 3,000 shark and ray teeth were collected from two sites in Aiken County (Fig. 1A), but only approximately 2,100 of these were complete enough to be identified to genus or species, and included discovery of a new species of daggernose shark described here as *Isogomphodon aikenensis* n. sp. Cicimurri and Knight. In addition to the taxonomic discussions about the elasmobranchs we identified, we compare the two Aiken assemblages to each other, as well as to those previously reported from the Barnwell Group of Georgia. We also present our interpretation of the depositional environment as inferred from the lithostratigraphy, taphonomic indicators, and paleoecology of the extant representatives of fossil taxa we have identified.

## GEOLOGICAL CONTEXT

### Stratigraphic framework

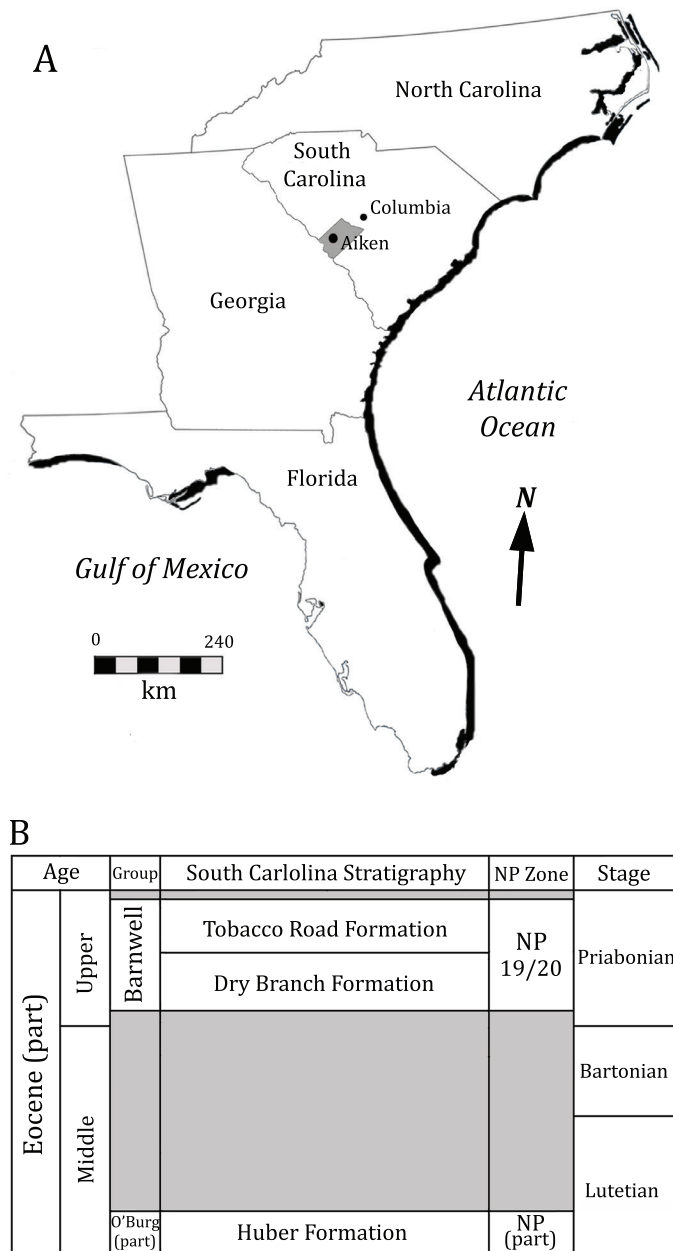
The fossils described herein were all collected from the Eocene Dry Branch Formation in Aiken, Aiken County,

\*author for correspondence

**Citation:** Cicimurri, D.J. and J.L. Knight. 2019. Late Eocene (Priabonian) elasmobranchs from the Dry Branch Formation (Barnwell Group) of Aiken County, South Carolina, USA. *PaleoBios*, 36. [ucmp\\_paleobios\\_43964](https://doi.org/10.21955/paleobios.43964).

**Permalink:** <https://escholarship.org/uc/item/0fh2f5n3>

**Copyright:** Published under Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International (CC-BY-NC-SA) license.  
LSID urn:lisd:zoobank.org:pub:3F95876E-933FF-48AF-9CF0-A840A333220B



**Figure 1.** **A.** Outline map of southeastern US coastal states showing South Carolina, Aiken County (shaded region), and the city of Aiken. **B.** Generalized stratigraphic section of Barnwell Group strata in the Aiken, South Carolina area. The fossiliferous horizon at the South Aiken Site occurs approximately 2 m below the base of the Tobacco Road Formation. A and B modified from Cicimurri and Ebersole (2015). Abbreviations: NP=calcareous nannoplankton zone, O'burg=Orangeburg.

South Carolina. The Dry Branch Formation is part of the Barnwell Group, which also includes the subjacent Clinchfield Formation and superjacent Tobacco Road Formation. Although the Clinchfield Formation occurs in the subsurface of the western part of Aiken County,

South Carolina (Fallaw and Price 1995, Falls and Prowell 2001), in central Aiken County the Dry Branch Formation disconformably overlies kaolinite deposits of the lower-to-middle Eocene Huber Formation (Fig. 1B). The contact between these two formations has been reported as a sequence boundary, with the base of the Dry Branch Formation consisting of a lag deposit (Harris et al. 2002, Schroeder et al. 2002) that formed during the initial transgression of the Jackson Sea into the region (Huddlestun and Hetrick 1986, Huddlestun 1993) at the start of the Tejas A4.2 cycle (Harris and Zullo 1991). The Dry Branch Formation is disconformably overlain by the Tobacco Road Formation (Fig. 1B), and these two units have been studied extensively for economically important occurrences of kaolinite (Buie and Schrader 1982). The base of the Tobacco Road Formation may be very pebbly, but it is also relatively easy to identify because of its indurated nature, compared to the unconsolidated sands of the Dry Branch Formation. In some areas the Dry Branch Formation is absent and the Tobacco Road Formation disconformably overlies Huber Formation kaolinite.

The Dry Branch Formation extends laterally into central Georgia, and within this region the formation has been subdivided into three members, including the Griffins Landing Sand, Twiggs Clay, and Irwinton Sand (Huddlestun and Hetrick 1979). The stratigraphic relationships between the members may not be as simple as sub- and superjacent units, as Huddlestun and Hetrick (1986) observed intertonguing lateral facies changes. Additionally, Huddlestun and Hetrick (1979) and Eversull (2005) reported clay beds within the Griffins Landing and Irwinton sands that were similar to those occurring within the Twiggs Clay. Identification of Eocene units within Georgia is facilitated by exposures of relatively thick and fossiliferous sections, but identifying and correlating strata in South Carolina has been hampered by lack of thick exposures, and those that could be examined are often highly weathered and devoid of fossils (Huddlestun 1982).

In Aiken County, the Dry Branch Formation is at least 28 m thick, and Twiggs Clay, Griffins Landing Sand, and Irwinton Sand have been identified (Mittwede 1982, Nystrom and Willoughby 1982, Zullo and Kite 1985). Invertebrate fossils may be common within calcareous sediments of the Griffins Landing Sand of Georgia and South Carolina, and species include various types of barnacles, benthonic foraminifera, a few echinoderm and crustacean remains, and the ostreid *Crassostrea gigantissima* (Finch, 1824) may be locally abundant (Huddlestun and Hetrick 1979). Zullo and Kite (1985) reported that

preservation of invertebrate fossils within the Griffins Landing Sand was excellent, and that *C. gigantissima* occurs in Allendale County but not in Aiken County. Further to the south in Allendale County, strata attributed to the Griffins Landing Sand disconformably overlie the McBean Formation (Steele et al. 1986), whereas in Aiken County, Griffins Landing deposits disconformably overlie the Huber Formation (Zullo and Kite 1985). Both Zullo and Kite (1985) and Steele et al. (1986) noted occurrences of shark and ray teeth within the Griffins Landing Sand, but no details were provided.

Strata assigned to the Twiggs Clay in the Graniteville and Hollow Creek quadrangles (west and southwest of Aiken, respectively) typically occur as well-layered sequences of clay varying in color from gray, green, brown, and purple, and clay beds are separated by fine-grained quartz sand (Nystrom and Willoughby 1982). Further to the south in the Jackson quadrangle, Mittwede (1982) reported mustard-yellow to orange-yellow loose, fine- to medium-grained quartz sand containing thin, discontinuous clay beds that were attributed to the Irwinton Sand, and he noted that the unit thickened markedly towards the Aiken area. The fossiliferous Dry Branch Formation deposits we examined are consistent with Mittwede's (1982) description of the Irwinton Sand. Non-quartz grains that we recovered along with the fossils include zircon, kyanite, and muscovite mica, and several types of igneous and metamorphic rocks occurring in the Aiken area could have been source rocks for these Dry Branch sediments (Snoke and Secor 1982, Speer 1982).

### Depositional setting

During the Eocene, deposition of marine strata in South Carolina and Georgia occurred within the Gulf Trough as the Suwanee Current flowed northeastward from the Gulf of Mexico (Huddlestun 1990, Eversull 2005). At this time, siliciclastic deposition (i.e., Dry Branch Formation) dominated on the northern side of the Gulf Trough, whereas carbonate deposition (i.e., Ocala Limestone) dominated to the south (Huddlestun, 1990, Eversull 2005).

Zullo and Kite (1985) concluded that the Griffins Landing Sand in Aiken County represented subtidal to inner shelf deposition, whereas Fallaw and Price (1995) suggested a bay or lagoon to open ocean environment based on foraminifera they studied. Kirby (2000) believed that the occurrence of *Crassostrea gigantissima* (Griffins Landing Sand) indicated fully marine environments as opposed to brackish environments. In Georgia, the Irwinton Sand Member is locally fossiliferous and has

been interpreted as representing inner neritic (sands) and bay or lagoonal environments (clays), and scour structures could represent tidal channels (Huddlestun and Hetrick 1986, Fallaw and Price 1995). Overall, the formations within the Barnwell Group of South Carolina represent a transgressive-regressive sequence, with the lower portion of the Dry Branch Formation representing a high-energy mixed siliciclastic-carbonate shelf that periodically received input from a shoreward source, the upper part of the formation being deposited in a shallow siliciclastic shelf environment, and the Tobacco Road Formation accumulating in a lower delta plain environment, with occasional shoreward transport of marine sediments (Segalla et al. 2000).

### Age of deposits

The late Eocene (Priabonian) age of the Dry Branch Formation in South Carolina has been demonstrated by the various barnacle and clypeasteroid echinoderm species that are known to occur (Zullo and Kite 1985, Steele et al. 1986, Carter 1987). Huddlestun and Hetrick (1986) placed the Twiggs Clay of the Dry Branch Formation within calcareous nannofossil Zone NP19/20, and tektites in the Dry Branch Formation that formed during the Chesapeake Bay Impact have a laser fusion age of approximately 34.5 Ma (Albin and Wampler 1996, Albin 1999, Povenmire and Povenmire 2002, Schroeder et al. 2002, Harris et al. 2002, 2004).

### METHODS

The fossils in this report were collected from two locations in the Aiken city area, Aiken County, South Carolina. The first is the North Aiken Site (NAS), a clay pit south of the Aiken Municipal Airport (33.624867, -81.681713 W at the eastern entrance). Fossils were recovered as float over the course of several years and are included within accession SC96.97. This site is currently being developed as a housing subdivision and our recent exploration of it yielded only a few additional shark teeth near the southern limit of the pit. The second is the South Aiken Site (SAS) located in a housing subdivision south of the Aiken city limit (33.504444, -84.742778). Both sites require entry through private property, and permission must be obtained before visiting them.

The SAS is the type locality for *Pseudaetobatus undulatus* (Cicimurri and Ebersole 2015). Its primary exposure consists of a 0.6 m-thick section covering a six-square-meter area. We collected more than 100 kg (dry) of *in situ* bulk matrix from a very fossiliferous horizon within the section, and recovered macrofossils that had weathered

out of place. A second, mostly covered and nearly vertical section, occurs in an E-W trending wall approximately 5 m to the north, where up to 5 m of thickness is preserved. Although no fossils were recovered from this section, we were able to determine that the fossiliferous horizon within the Dry Branch Formation occurs approximately 2.0 m below the base of the Tobacco Road Formation.

In the laboratory, Dry Branch Formation matrix was disaggregated in water and gently rinsed through U.S.A. Standard Testing Sieves down to 0.25 mm (#60 screen). Matrix that passed through this screen was also saved, and the resulting concentrates were dried and sorted under a binocular microscope. The SAS matrix sample yielded about 30 specimens per kilogram, and these fossils are included under accessions SC2001.1 and SC2013.38.

In order to more accurately identify the many broken teeth of Myliobatidae we recovered (particularly those in median positions), we repaired as many as possible using thin butvar (B-76 in acetone). Specimens were photographed with a Nikon Coolpix 995 digital camera attached to a Wild compound microscope. The teeth are white and details in unretouched photographs were difficult to discern, but brightness and contrast were adjusted slightly for clarity using Adobe Photoshop software.

In many cases, identification of the elasmobranch teeth beyond the generic level was hampered due to small sample size and diagenetic alteration of the remains. Overall, teeth have a chalky preservation, enameloid has been partly or completely leached away, and roots are eroded and/or incomplete. Comparison of the Dry Branch material to a sample of several thousand teeth from the Clinchfield Formation of central Georgia, housed at the South Carolina State Museum, and to specimens recovered from the Griffins Landing Sand of South Carolina, housed at the McKissick Museum at the University of South Carolina, allowed us to more accurately identify some of our Dry Branch Formation material. The features that we used to identify specimens and distinguish between similar morphologies are provided in the Remarks section for each taxon. Higher level taxonomy largely follows Naylor et al. (2012).

**Institutional abbreviations**—SC, South Carolina State Museum, Columbia, South Carolina; MSC, McWane Science Center, Birmingham, Alabama.

#### SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES HUXLEY, 1880  
 HEXANCHIFORMES BUEN, 1926  
 HEXANCHIDAE GRAY, 1851

#### NOTORYNCHUS AYRES, 1855

NOTORYNCHUS SP. CF. NO. KEMPI WARD, 1979A  
 (FIG. 2A–D)

**Referred specimens**—SC96.97.4, incomplete lower right tooth; SC2001.1.46, lower tooth fragment; SC2013.38.1, incomplete lower left tooth.

**Remarks**—The incompleteness of the three specimens inhibits our ability to accurately identify the Dry Branch hexanchid. However, when compared to taxa identified from Eocene deposits elsewhere, we found that the acrocone mesial cusplets of SC96.97.4 (Fig. 2C–D) are more numerous but much smaller than those of *Notidanodon Cappetta, 1975*, and the distal cusplets of SC2013.38.1 (Fig. 2A, B) also conspicuously diminish in size away from the acrocone (Gurr 1962, Casier 1967, Ward 1979a). Lower teeth of *Hexanchus agassizi Cappetta, 1976* are smaller and have 7–12 distal cusplets, as opposed to less than six on the Dry Branch taxon (Cappetta 1976, Ward 1979a). In overall morphology, our material compares favorably to lower teeth of *Notorynchus*, particularly *No. serratissimus* (Agassiz, 1843) and *No. kempi*. Early to middle Eocene teeth of *No. serratissimus* have a smaller crown (less than 17 mm width), fewer distal cusplets, and mesial serrations on the acrocone increase in size apically (Cappetta 1976, Ward 1979a, Nolf 1988, Van den Eekhaut and De Schutter 2009). In contrast, middle to late Eocene *No. kempi* teeth are larger than the aforementioned taxon (greater than 30 mm width) and the mesial serrations are large and of relatively uniform size (Ward 1979a). The Dry Branch hexanchid appears to have been as large as *No. kempi* and the evenness of the acrocone serrations on SC96.97.4 (Fig. 2C, D) is also consistent with this species.

#### SQUATINIFORMES BUEN, 1926

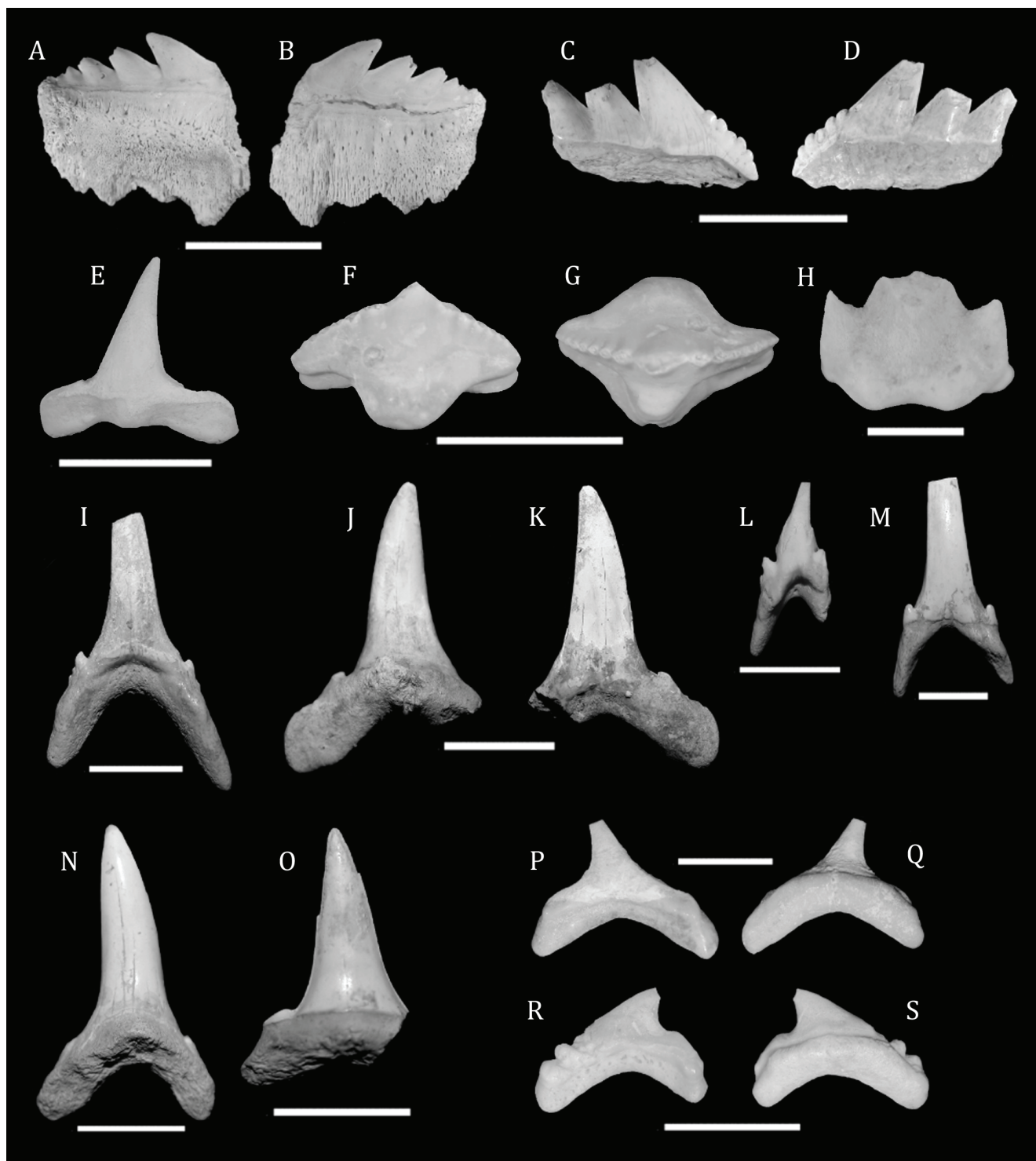
SQUATINIDAE BONAPARTE, 1838

SQUATINA DUMERIL, 1806

SQUATINA SP. CF. SQ. PRIMA (WINKLER, 1874)  
 (FIG. 2E)

**Referred specimens**—SC96.97.9, tooth (Fig. 2E), SC96.97.10, tooth; SC2001.1.40, tooth; SC2013.38.2, incomplete tooth.

**Remarks**—The four Dry Branch Formation teeth are morphologically similar to those of Eocene *Squatina prima* reported elsewhere (Case 1981, Kemp et al. 1990, Parmley and Cicimurri 2003), and our specific identification is tentative because of the small and imperfectly preserved sample. Additionally, *Squatina* tooth morphology has remained conservative and relatively stable since the Jurassic, largely consisting of a narrow cusp flanked by elongated lateral shoulders and low, roughly triangular



**Figure 2.** Shark teeth from the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A–D.** *Notorynchus* sp. cf. *No. kempii* teeth. Lower left tooth in lingual (**A**) and labial (**B**) views, SC2013.38.1. Lower right tooth in labial (**C**) and lingual (**D**) views, SC96.97.4. **E.** *Squatina* sp. cf. *Sq. prima*. Antero-lateral tooth in labial view, SC96.97.9. **F, G.** *Nebrius* sp. cf. *Neb. thielensi*. Antero-lateral tooth in labial (**F**) and occlusal (**G**) views, SC2013.38.5. Labial at top in **G**. **H.** Ginglymostomatidae. Tooth in labial view, SC2013.38.7. **I–O.** *Carcharias* sp. Third lower right anterior tooth in labial (**I**) view, SC2001.1.55. Third upper right anterior tooth in lingual (**J**) and labial (**K**) views, SC2001.1.57. First lower right anterior tooth in labial (**L**) view, SC2001.1.59. Second lower right anterior tooth in labial (**M**) view, SC96.97.44.1. Second upper right anterior tooth in lingual (**N**) view, SC96.97.42. Lower left lateral tooth in lingual (**O**) view, SC96.97.43. **P–S.** *Alopias* sp. Tooth in labial (**P**) and lingual (**Q**) views, SC2001.1.65. Tooth in labial (**R**) and lingual (**S**) views, SC2001.1.66. Scale bars=1 cm in A–D, I–K, N, O; 5 mm in E–G, L–M, P–S; 1 mm in H.

(in basal view) root (Cappetta 1987).

ORECTOLOBIFORMES APPLGATE, 1972

GINGLYMOSTOMATIDAE GILL, 1862

*NEBRIUS* RÜPPELL, 1837

*NEBRIUS* SP. CF. *NEB. THIELENSI* (WINKLER, 1874)

(FIG. 2F, G)

**Referred specimens**—SC96.97.1, three incomplete teeth; SC2001.1.41, incomplete tooth; SC2013.38.3, anterior tooth; SC2013.38.4, posterior tooth; SC2013.38.5, anterior tooth (Fig. 2F, G); SC2013.38.6, two incomplete teeth.

**Remarks**—We identify these nine orectolobid teeth as *Nebrius* because they have a wide crown bearing a central cusp that is flanked by up to seven pairs of lateral cusplets. In contrast, teeth of morphologically similar *Ginglymostoma* Müller and Henle, 1837 have up to two pairs of lateral cusplets flanking the main cusp (Herman et al. 1992, Purdy et al. 2001). Unfortunately, identifying fossil *Nebrius* teeth is often hampered by the fact that original descriptions of fossil species are based on relatively few specimens, and the degree of morphological variation within true biological species is unknown. There is a lack of agreement as to species occurrences within Eocene strata of North America, with *Neb. thielensi* (Case and Borodin 2000, Parmley and Cicimurri 2003), *Neb. blackenhorni* (Stromer, 1903) (Thurmond and Jones 1981), *Neb. serra* (Manning and Standhardt 1986), and *Neb. obliquus* (Leidy 1877) (*Ginglymostoma obliquum* of Case 1981) being recognized in the literature. Kent (1994) reported *Neb. thielensi* (p. 34, fig. 8.3b) and *Neb. blackenhorni* (p. 34, fig. 8.3a) from the lower Eocene Nanjemoy Formation of Maryland and Virginia (Kent 1999), and he considered the possibility that the morphologies represented heterodonty within a single species. Woodward (1889: pl. 16, fig. 9) identified teeth from the Eocene of Alabama as *Gi. serra* (Leidy 1877), but Leriche (1942:27, 28) and White (1956:146) synonymized the record with *Neb. obliquus*. However, Thurmond and Jones (1981:44) reported that the middle Eocene Gosport Sand of Alabama contained a continuous morphological series between the *obliquus* and *serra* morphologies, and they synonymized *obliquus* with *serra*. Unfortunately, Thurmond and Jones (1981) only provided an illustration of Leidy's (1877) original material, not specimens from the Gosport Sand. Noubhani and Cappetta (1997) considered the identification of Eocene teeth as *Neb. serra* to be incorrect and preferred instead to identify teeth as *Neb. obliquus* (also Darteville and Casier 1943). The precise geologic age of *Neb. serra*, collected from South

Carolina coastal plain deposits is unknown, and the fossils could be as old as Eocene or as young as Pleistocene (see Leidy 1877: pl. 34). Although *Neb. obliquus* was based on a single tooth from the Eocene of New Jersey, it has been reported as being common in lower Eocene (Ypresian) strata elsewhere (Noubhani and Cappetta 1997, Cappetta 2012).

Morphologically, *Neb. thielensi* was differentiated from *Neb. blackenhorni* in having a crown that is wide but rather low, a larger and less distally inclined main cusp, fewer lateral cusplets, and a shorter but conspicuously flat or slightly bifid labial protuberance (Winkler 1874, Arambourg 1952). In contrast, *Neb. blackenhorni* has a rather high crown in proportion to width, there are ten or more cusplets on the mesial side of the main cusp, and the labial protuberance is more elongated and rounded basally. These generalities are seen in the suite of teeth illustrated in Arambourg (1952, pl. 22), as well as Stromer 1905, and teeth originally identified as *Ginglymostoma fourtaui* (Priem, 1905) (Priem 1907, 1909).

Noubhani and Cappetta (1997) used features like tooth size, labial crown profile, shape of the labial protuberance, and concavity of the basal attachment surface to separate *Neb. thielensi* from *Neb. obliquus*. Some late Eocene records of *Nebrius*, including teeth identified as *Neb. thielensi* (Case and Borodin 2000, Parmley and Cicimurri 2003) and *Neb. obliquus* (Case 1981), appear to be conspecific, as all have a large and rather erect main cusp flanked by 7–9 cusplets, and a basal protuberance that is moderately elongated and often weakly bifid. The Dry Branch *Nebrius* teeth lack enameloid, making direct comparisons to other specimens difficult, but they are comparable to *Neb. thielensi* (note that the name has also variously been published as *Neb. thielensis* and *Neb. thielense*; see Cappetta [2012] for further discussion on spelling) in that they are larger than *Neb. obliquus* sensu Leidy (1877: pl. 34, fig. 14), have a larger main cusp, fewer lateral cusplets, and shorter and weakly bifid labial protuberance.

GINGLYMOSTOMATIDAE GEN. ET SP. INDET.

(FIG. 2H)

**Referred specimen**—SC2013.38.7, incomplete anterior tooth.

**Remarks**—This specimen differs from *Nebrius* sp. cf. *Neb. thielensi* (see above) in having only a single pair of large lateral cusplets, and the labial crown foot is distinctively bifid but not drawn out into an elongate basal protuberance. SC2013.38.7 is similar to the anterior teeth

of Cretaceous *Plicatoscyllium* Case and Cappetta, 1997, but there is no indication of labial crown ornamentation. The single pair of lateral cusplets also distinguishes SC2013.38.7 from the various early Paleogene species of *Ginglymostoma* (Noubhani and Cappetta 1997). In terms of gross morphology, SC2013.38.7 is similar to *Protoginglymostoma ypresiensis* (Casier, 1946) from the early to middle Eocene of Belgium and Morocco (Casier 1946, Herman 1977, Tabuce et al. 2005), but the poor condition of the only available tooth makes a more precise identification difficult.

LAMNIFORMES BERG, 1958  
ODONTASPIDIDAE MÜLLER AND HENLE, 1838  
CARCHARIAS RAFINESQUE, 1810  
CF. CARCHARIAS SP.  
(FIG. 2I–O)

**Referred specimens**—SC96.97.42, second upper right anterior tooth (Fig. 2N); SC96.97.43, lower left lateral tooth (Fig. 2O); SC96.97.44.1, second lower right anterior tooth (Fig. 2M); SC96.97.44.2, four teeth; SC96.97.45, 236 incomplete teeth; SC2001.1.55, third lower right anterior tooth (Fig. 2I); SC2001.1.56, anterior tooth; SC2001.1.57, third upper right anterior tooth (Fig. 2J, K); SC2001.1.58, six incomplete anterior teeth; SC2001.1.59, first lower right anterior tooth (Fig. 2L); SC2001.1.60, three posterior teeth; SC2001.1.61, 40 incomplete teeth; SC2013.38.8, anterolateral tooth; SC2013.38.9, four partial teeth; SC2013.38.10, three partial teeth; SC2013.38.11, lateral tooth; SC2013.38.12, 14 tooth fragments; SC2013.38.13, tooth; SC2013.38.14, two incomplete anterior teeth.

**Remarks**—The 332 teeth in the sample are similar to extant *Carcharias taurus* Rafinesque, 1810, and examination of two Recent dentitions of this species (SC2001.120.6 and SC86.62.2) allowed us to identify various anterior and lateral positions in the fossil species. Unfortunately, diagenetic alteration of the teeth makes confidently assigning the fossil material to any of various species that have been reported from Eocene strata difficult, as characteristics that have been used for species identification, like the number and shape of lateral cusplets and crown ornamentation, are generally not evident or imperfectly preserved.

ALOPIIDAE BONAPARTE, 1838  
ALOPIAS RAFINESQUE, 1810  
ALOPIAS SP.  
(FIG. 2P–S)

**Referred specimens**—SC2001.1.65, tooth; SC2001.1.66,

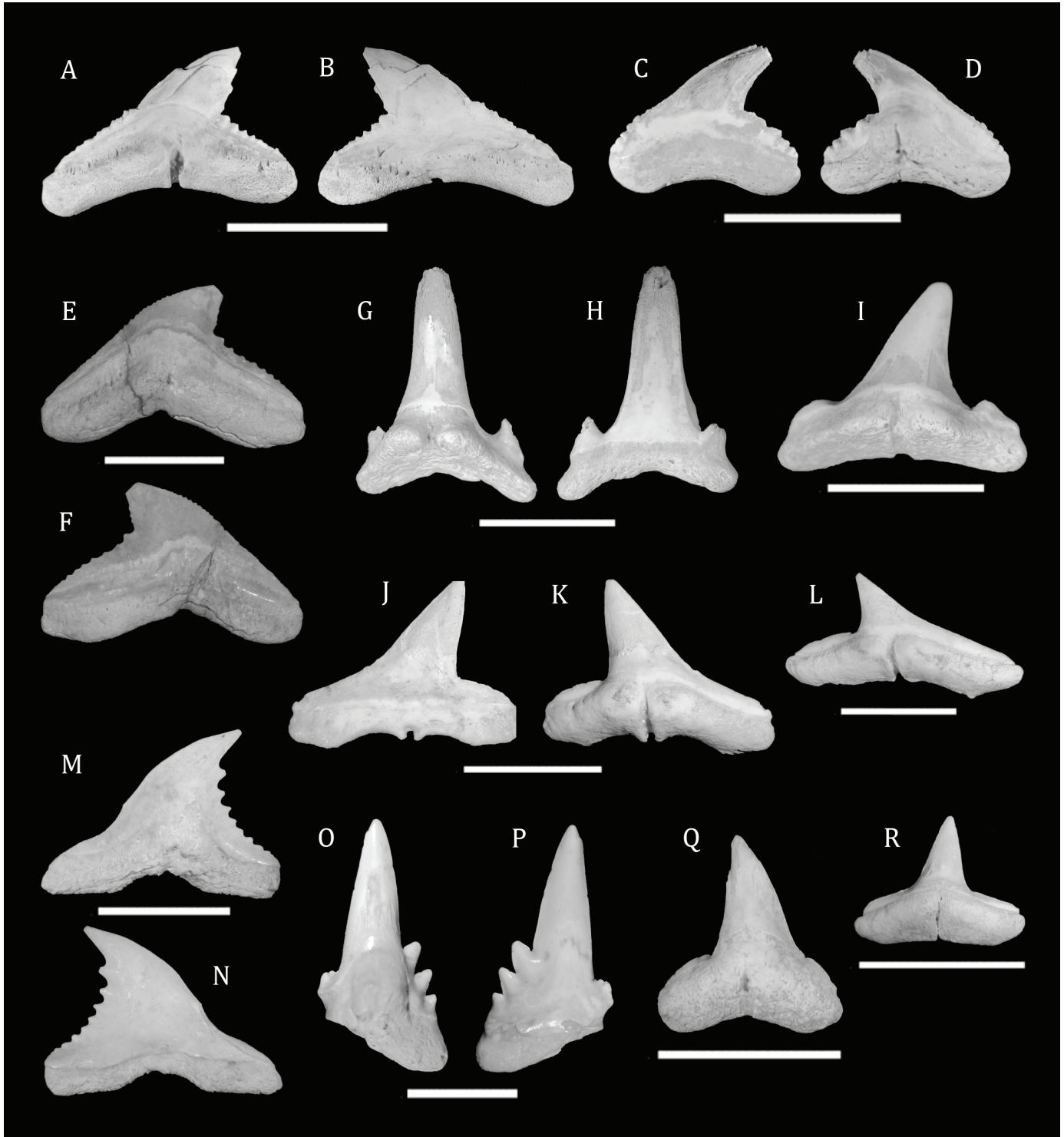
tooth.

**Remarks**—Specimens bear a broadly triangular, distally curving crown. Unfortunately, the enameloid is lacking due to taphonomic processes, and the dentine cores are exposed. There is no indication that lateral cusplets are present on SC2001.1.65 (Fig. 2P, Q), but dentine cores of what appear to be two mesial basal cusplets and an incipient distal cusplet are visible on SC2001.1.66 (Fig. 2R, S). Unfortunately, the enameloid on the two specimens is imperfectly preserved, and the shape of the crown may not be accurately reflected. Coupled with the very limited sample size (n=2), we could therefore not effectively compare the Dry Branch *Alopias* teeth to those of any of the several Eocene species that have been described, which include *Al. crochardi* Ward, 1978, *Al. leensis* Ward, 1978, *Al. denticulatus* Cappetta, 1981, and *Al. alabamensis* White, 1956. The crown foot of both Dry Branch Formation teeth is very convex and obviously overhangs the root (Fig. 2Q, S), and the lingual side of the root is bisected by a shallow nutritive groove (Fig. 2P, R). These features are consistent with teeth of *Al. crochardi* and *Al. denticulatus*, but our specimens appear to have lacked cusplets like those seen on *Al. denticulatus*. Teeth of *Al. leensis* and *A. alabamensis* lack nutritive grooves and crowns appear much wider than seen on the Dry Branch Formation specimens. Our two specimens are similar to teeth we observed within the jaws of *Al. superciliosus* (Lowe, 1841) housed at SC, and perhaps the Dry Branch Formation taxon is related to this “group” (sensu Cappetta, 2012). A larger and better preserved sample is needed for a more specific determination.

CARCHARHINIFORMES COMPAGNO, 1973  
GALEOCERDIDAE HERMAN AND VAN DEN EECKHAUT, 2010  
GENUS GALEOCERDO MÜLLER AND HENLE, 1837  
GALEOCERDO SP.  
(FIG. 3E, F)

**Referred specimens**—SC96.97.11, three incomplete teeth; SC2001.1.8, incomplete anterior tooth; SC2001.1.9, lateral tooth; SC2001.1.10, three partial teeth; SC2013.38.16, anterolateral tooth (Fig. 3E, F); SC2013.38.17, incomplete lateral tooth; SC2013.38.18, incomplete tooth; SC2013.38.19, four incomplete teeth.

**Remarks**—All 15 specimens lack enameloid but they are morphologically consistent with *Galeocerdo*, having an elongated and broadly convex mesial edge, short distal edge that forms a triangular cusp with the mesial edge, and elongate, serrated distal heel. In terms of gross morphology, the Dry Branch Formation specimens differ from Eocene *Galeocerdo eaglesomei* White, 1926 in having a



**Figure 3.** Carcharhiniform shark teeth the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A–D.** *Physogaleus* sp. cf. *Ph. latus*. Upper left lateral tooth in lingual (**A**) and labial (**B**) views, SC2013.38.65. Lower left anterior tooth in labial (**C**) and lingual (**D**) views, SC96.97.26. **E, F.** *Galeocerdo* sp. Anterolateral tooth in lingual (**E**) and labial (**F**) views, SC2013.38.16. **G–I.** *Abdounia* sp. cf. *Ab. enniskilleni*. Anterior tooth in lingual (**G**) and labial (**H**) views, SC96.97.30. Lateral tooth in lingual (**I**) view, SC96.97.31. **J–L.** *Rhizoprionodon ?ganntourensis*. Anterolateral tooth in labial (**J**) and lingual (**K**) views, SC2013.38.98. Lateral tooth in lingual view (**L**), SC2013.38.99. **M–P.** *Hemipristis* sp. cf. *He. curvatus*. Upper left lateral tooth in lingual (**M**) and labial (**N**) views, SC2001.1.21. Lower right anterior tooth in lingual (**O**) and labial (**P**) views, SC2013.28.35. **Q, R.** *Negaprion gilmorei*. Upper right anterior tooth in lingual (**Q**) view, SC2013.38.61. Lower right anterolateral tooth in lingual (**R**) view, SC2013.38.64. Scale bars=1 cm in A–F, M–N, Q–R; 5 mm in G–L, O–P.

lower and more uniformly convex mesial cutting edge, as opposed to a rather high and conspicuously convex apical portion to the mesial edge. We believe that the Dry Branch Formation *Galeocerdo* teeth are comparable to specimens from the Clinchfield Formation of Georgia identified as *Ga. alabamensis* Leriche, 1942 by Parmley and Cicimurri (2003). However, the specific identification made by those authors appears to be in error, as examination of Leriche's (1942) *alabamensis* holotype leads us to conclude that it is actually *Physogaleus* Cappetta, 1980. The assignment of the Clinchfield material to *Ga. alabamensis* by Parmley and Cicimurri (2003) was based on White's (1956) identification of specimens from South Carolina as *Ga. alabamensis*, which are not conspecific with Leriche's (1942) taxon.

In addition to Alabama (White 1956, Thurmond and Jones 1981), *Ga. alabamensis* was also documented from Arkansas (Westgate 1984) and Louisiana (Manning and Standhardt 1986). Another species, *Ga. clarkensis*, was founded by White (1956) based on a small number of teeth from the late middle Eocene of Alabama, but Manning and Standhardt (1986) synonymized this taxon with *Ga. alabamensis*, considering the former to represent upper teeth and the latter lower teeth in the same dentition. However, as noted above, the "*Galeocerdo*" *alabamensis* morphology is more appropriately identified as *Physogaleus*. In Georgia, Case (1981) identified *Ga. clarkensis* from the Clinchfield and Dry Branch (Twiggs Clay Member) Formations, but Case and Borodin (2000) later reported *Ga. latidens* Agassiz, 1843 from the Dry Branch Formation (Irwinton Sand Member). It is apparent that Eocene records of *Galeocerdo* from North America are in further need of evaluation.

Our examination of *Ga. clarkensis* teeth from the middle Eocene (Bartonian) Gosport Sand (Claiborne Group) of Alabama, housed at MSC, showed that the mesial cutting edge bears coarse, compound serrations (largest serrations bear smaller serrations). Additionally, examination of *Ga. eaglesomei* teeth from the middle Eocene (Lutetian) Lisbon Formation (Claiborne Group) of Alabama, also at MSC, revealed that serration on the mesial edge is simple (large serrations do not bear smaller serrations). As our specimens are incompletely preserved, we cannot determine the precise shape of the original crown or if the serrations were simple or compound (serrations on serrations), and we refrain from making a specific identification.

CARCHARHINIDAE JORDAN AND EVERMANN, 1896  
*PHYSOGALEUS* CAPPETTA, 1980

*PHYSOGALEUS* SP. AFF. *PH. LATUS* (STORMS, 1894)  
 (FIG. 3A–D)

**Referred specimens**—SC96.97.26, anterior tooth; SC96.97.27, lateral tooth; SC96.97.28, lateral tooth; SC96.97.29, 18 incomplete teeth; SC2001.1.51, anterior tooth; SC2001.1.52, lateral tooth; SC2001.1.53, posterior tooth; SC2001.1.54, five incomplete teeth; SC2013.38.56, lateral tooth; SC2013.38.57, anterior tooth; SC2013.38.58, lateral tooth; SC2013.38.59, tooth; SC2013.38.60, six incomplete teeth.

**Remarks**—Dignathic heterodonty is evident among the 39 Dry Branch specimens, with upper teeth having a broader central cusp and better developed serrations on the lateral shoulders (Fig. 3A, B) compared to lower teeth. Lower teeth have a very narrow, sigmoidal cusp and significantly thickened root (Fig. 3C, D). The *Physogaleus* teeth are similar in gross morphology to those of *Galeocerdo*, but they are smaller in overall size and development of serrations (especially on the mesial edge) is much reduced. For example, only the basal half of the mesial cutting edge of *Physogaleus* teeth is serrated, whereas the apical half is smooth. This phenomenon can be discerned even on teeth lacking enameloid, as the dentine core preserves small denticulation basally, but the edge is smooth apically.

Several of the species that White (1926) described from the Eocene of Nigeria, including *Eugaleus falconeri*, *Sphyrna itoriensis*, *Sph. tortilis*, and *Carcharhinus nigeriensis*, have been placed within *Physogaleus* (Cappetta, 2006), but it is as yet unclear if the morphologies represent multiple species or heterodonty within a single species (monognathic, dignathic, and gynandric heterodonty). The teeth we tentatively identify as *Ph. latus* compare favorably to teeth described by Storms (1894) from the lower Oligocene of Belgium, and several of the Dry Branch teeth (i.e., Fig. 3A, B) are practically identical to the specimen he illustrates in plate 6, figure 17c. These particular teeth differ from other Eocene and Oligocene species of *Physogaleus* in that the cusp is broad with bi-convex cutting edges, and the cusp is well differentiated from the coarsely serrated distal heel and basal half of the mesial cutting edge (Winkler 1876, Reinecke and others 2005, Haye et al. 2008, Reinecke et al. 2008). Teeth that we identify as being from anterior files (i.e., Fig. 3C, D) are comparable to the specimen illustrated by Storms (1894; pl. 6, fig. 18).

Case (1981) named *Galeorhinus huberensis* (= *Ph. huberensis*) from the Dry Branch Formation of Georgia, and we consider that taxon to be conspecific with *Ph. secundus*

(Winkler, 1876) as reported by Parmley and Cicimurri (2003) from the Clinchfield Formation of central Georgia. The South Carolina Dry Branch taxon appears to differ from the Georgia material in that the teeth can attain larger size, the cusp is wider, distal serrations are smaller and more numerous, and the mesial serrations may be larger or more numerous.

*ABDOUNIA* CAPPETTA, 1980  
*ABDOUNIA ENNISKILLENI* (WHITE, 1956)  
 (FIG. 3G–I)

**Referred specimens**—SC96.97.30, anterior tooth; SC96.97.31, lateral tooth; SC96.97.32, 43 teeth; SC2001.1.43, anterior tooth; SC2001.1.44, three teeth; SC2013.38.15, incomplete tooth.

**Remarks**—Gradient monognathic heterodonty is evident among the 50 specimens we examined, with anterior teeth having tall vertical main cusps (Fig. 3G, H), but cusps becoming lower, broader, and distally curved (Fig. 3I) in lateral and posterior positions. Fine vertical enameloid ridges are preserved on specimens from the NAS, and this feature, combined with the gross morphology of teeth, leads us to assign them to *Abdounia enniskilleni*. This species has been reported from several upper Eocene localities in the Gulf and Atlantic coastal plains (often identified as *Scyliorhinus enniskilleni* prior to 1987), including Louisiana (Manning and Standhardt 1986), Arkansas (Westgate 1984), Alabama (White 1956), North Carolina (Timmerman and Chandler 1995), and Georgia (Case 1981, Case and Borodin 2000, Parmley and Cicimurri 2003). Within the Dry Branch sample, *Ab. enniskilleni* can be differentiated from small odontaspid teeth in that the lateral cusplets are large in relation to the main cusp, the lingual root face is flat, and root lobes are shorter and more triangular in outline.

*RHIZOPRIONODON* WHITLEY, 1929  
*RHIZOPRIONODON* ?*GANNTOURENSIS* (ARAMBOURG, 1952)  
 (FIG. 3J–L)

**Referred specimens**—SC96.97.2, four teeth; SC2001.1.18, tooth; SC2001.1.19, 40 teeth; SC2013.38.98, anterior tooth (Fig. 3J, K); SC2013.38.99, lateral tooth (Fig. 3L); SC2013.38.100, 18 teeth; SC2013.38.101, 32 teeth; SC2013.38.102, eight posterior teeth; SC2013.38.103, eight distal lateral teeth.

**Remarks**—One hundred thirteen Dry Branch Formation teeth are similar to those of extant *Rhizoprionodon*, and to Eocene *Rhiz. ganntourensis*, in particular. The distal heel of *Rhizoprionodon*, including *Rhiz. ganntourensis*,

is generally cuspidate (Arambourg 1952, Herman et al. 1991, Case et al. 1996, Noubhani and Cappetta 1997, Mustafa et al. 2005), but our specimens lack enameloid and this feature is not preserved. However, we examined a tooth of *Rhiz. sp. cf. Rhiz. ganntourensis* that was recovered by Zullo and Kite (1985) from the Griffins Landing Sand (see Appendix 1), and found that it is very similar to the material listed above. The well preserved Griffins Landing Sand tooth exhibits a cuspidate distal heel, but the translucent enameloid allows us to view the uniformly convex dentine core of the heel, as can be seen on the specimens in our sample.

*NEGAPRION* WHITLEY, 1940  
*NEGAPRION GILMOREI* (LERICHE 1942)  
 (FIG. 3Q, R)

**Referred specimens**—SC96.97.37, upper right anterior tooth; SC96.97.38, upper right antero-lateral tooth; SC96.97.39, upper right lateral tooth; SC96.97.40, 101 upper teeth; SC96.97.41, 24 lower teeth; SC2001.1.47, upper tooth; SC2001.1.48, tooth; SC2001.1.49, lower tooth; SC2001.1.50, 75 teeth; SC2013.38.61, upper anterior tooth; SC2013.38.62, upper right lateral tooth; SC2013.38.63, upper right tooth; SC2013.38.64, lower tooth; SC2013.38.65, seven lower teeth; SC2013.38.66, seven upper anterior teeth; SC2013.38.67, 29 teeth; SC2013.38.68, 14 lower teeth.

**Remarks**—This species is represented by 267 specimens that exhibit dignathic heterodonty, with upper teeth having a broader cusp flanked by elongate, oblique lateral shoulders (Fig. 3Q), whereas lower teeth have a shorter and narrower cusp, and smooth shoulders that are nearly perpendicular to the cusp (Fig. 3R). Although the enameloid is often missing, the remaining dentine core of the lateral shoulders on some upper teeth shows indications that they were at least weakly serrated.

Leriche (1942) erected *Sphyrna gilmorei* based on teeth occurring in upper Eocene deposits of Alabama. White (1956) assigned the morphology to the subspecies *Negaprion gibbesi gilmorei*, and Müller (1999) and Adnet et al. (2007) used the name *Carcharhinus gilmorei*. Underwood et al. (2011) and Underwood and Gunter (2012) identified unserrated to weakly serrated teeth, such as those reported here, as *Negaprion* rather than *Carcharhinus*. If our association is correct, the dignathic heterodonty of *Neg. gilmorei* is more pronounced than in a dentition of Recent *Neg. brevirostris* (Poey, 1868) we examined (SC uncurated).

We believe that Eocene material from North Carolina

and Georgia that was referred to *Neg. eurybathrodon* (Blake, 1862) is more appropriately identified as *Neg. gilmorei* (Case 1981, Case and Borodin 2000, Parmley and Cicimurri 2003). Teeth of Miocene *Neg. eurybathrodon* are up to 2 cm in height and width, much larger than Eocene specimens attributed to this species. The main cusp of *Neg. eurybathrodon* upper teeth is also much taller but narrower than the Eocene specimens, and the lateral shoulders are more evenly serrated (White 1955). *Negapriion gilmorei* is common in the Dry Branch Formation, and it is the dominant elasmobranch taxon within the Clinchfield Formation of Georgia, based on several thousand teeth within two SC accessions (SC2004.34 and SC2013.44; also Parmley and Cicimurri 2003).

GENUS *ISOGOMPHODON* GILL 1862

*ISOGOMPHODON AIKENENSIS* CICIMURRI AND KNIGHT N. SP.  
(FIG. 4E–P)

**Holotype**—SC2013.38.110 (Fig. 4E), upper anterior tooth.

**Paratypes**—SC2013.38.111 (Fig. 4P), upper anterolateral tooth; SC2013.38.119 (Fig. 4H, I), lower anterior tooth; SC2013.38.112 (Fig. 4J, K), upper lateral tooth; SC2013.38.115 (Fig. 4N, O), posterior tooth.

**Referred specimens**—SC2001.1.62, upper tooth; SC2001.1.63, lower tooth; SC2001.1.64, 97 teeth; SC2013.38.113, symphyseal tooth; SC2013.38.114, posterolateral tooth (Fig. 4L, M); SC2013.38.116, upper tooth; SC2013.38.117, 15 symphyseal teeth; SC2013.38.118, anterior tooth; SC2013.38.120, four anterior teeth; SC2013.38.121, six anterior teeth; SC2013.38.122, 52 teeth; SC2013.38.123.1 lower lateral tooth (Fig. 4F, G), SC2013.38.123.2, 84 teeth; SC2013.38.124, 112 teeth; SC2013.38.125, 16 posterior teeth.

**Occurrence**—Type locality: South Aiken Site (SAS) 33.504444, -84.742778, Aiken County, South Carolina; yellow, orange and red variegated sand, Upper Eocene (Priabonian) Dry Branch Formation, approximately two meters below the contact with the overlying Tobacco Road Formation.

**Etymology**—The species name recognizes the city of Aiken and Aiken County, South Carolina, the only known area from which Eocene *Isogomphodon* have thus far been documented from North America.

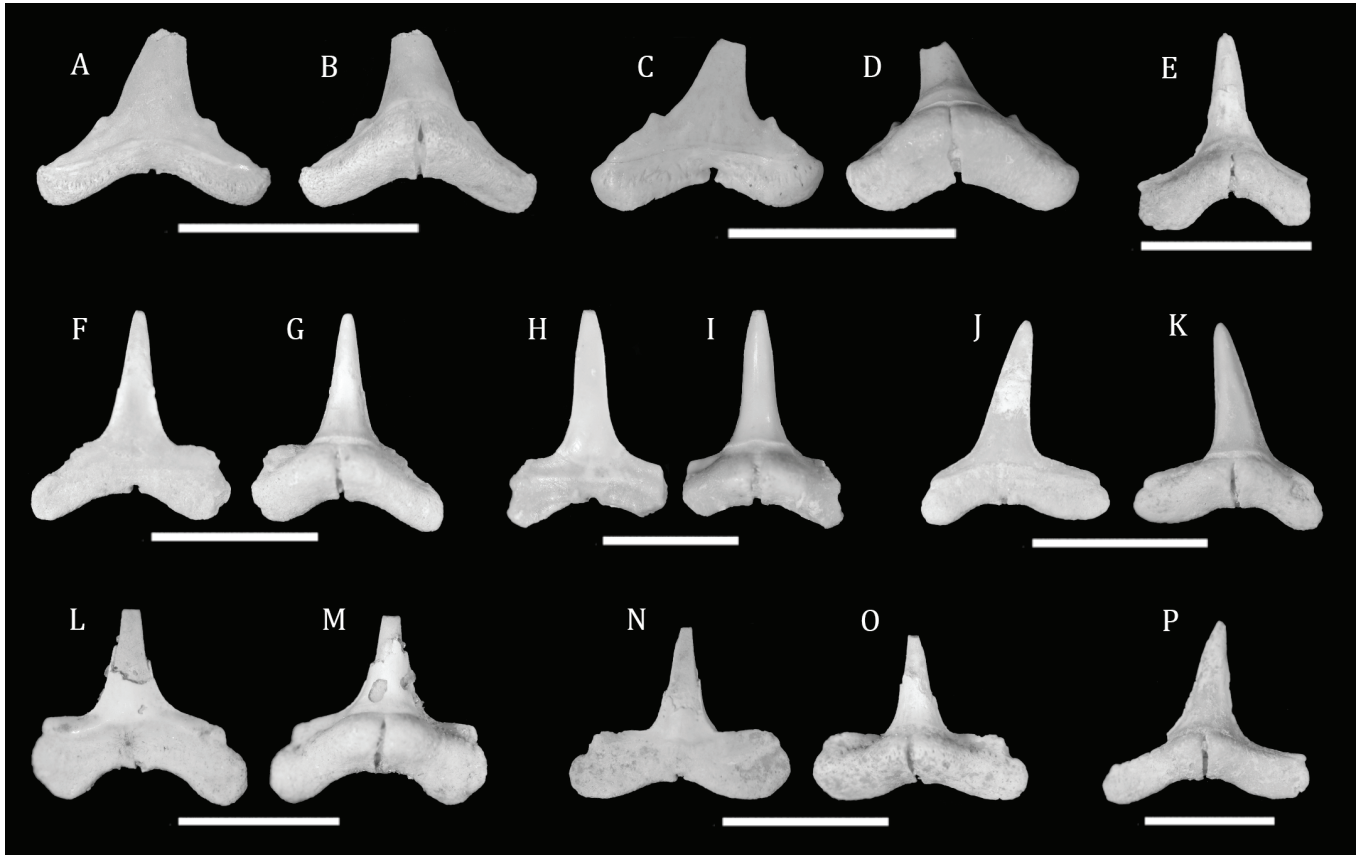
**Diagnosis**—Nearly 400 specimens are referred to the new species, which differs from Recent *Isogomphodon oxyrhynchus* (Müller and Henle 1841) in that all teeth have smooth cutting edges extending from the apex to the very base of the crown. In contrast, the upper teeth

of the extant species are weakly serrated and edges of lower anterior teeth are often limited to the upper half of the crown. In addition, the Eocene teeth have shorter cusps, many exhibit very convex lateral shoulders (especially more lateral positions), and the root lobes are more elongated and divergent (Herman et al. 1991, Compagno et al. 2005).

The new species differs from the fossil species *I. acuaris* (Probst 1879), *I. lerichei* (Darteville and Casier 1943), *I. caunellensis* (Cappetta 1970), and *I. gracilis* (Jonet 1966) in being smaller in overall size. Additionally, the Dry Branch species has narrower upper anterior teeth and complete cutting edges on all teeth when compared to *I. caunellensis*, and the convexity of the lateral shoulders of anterior teeth appears to be more pronounced than on *I. acuaris* (Cappetta 1970, Case 1980, Müller 1999). The transition from main cusp to lateral shoulders appears to be slightly more angular on teeth of *I. lerichei* (Darteville and Casier 1943).

**Description**—These 393 distinctive teeth generally measure less than 5 mm in total height, although some anterior teeth are up to 7 mm. All teeth have a tall and narrow cusp, and enameloid shoulders that extend nearly to the tips of the root lobes. The cutting edges of all teeth are smooth and extend to the tips of lateral shoulders. The holotype, SC2013.38.110, is an upper anterior tooth that is slightly asymmetrical (Fig. 4E). The crown consists of a tall, narrow and erect cusp, with cutting edges that diverge slightly towards the crown base. Elongate lateral shoulders extend obliquely onto the root lobes. The root is bilobate, with rather short and sub-rectangular lobes that are separated by a narrow but deep U-shaped interlobe area. The mesial lobe is slightly smaller than the distal lobe, and a deep but narrow nutritive groove bisects the flat lingual root face. Upper anterolateral teeth (Fig. 4P) are wider than those near the jaw symphysis. The cusp is narrow and flat as seen in more anterior positions, but slightly distally inclined. The lateral shoulders are more elongated and nearly horizontal. The sub-rectangular root lobes are lower, more elongated and divergent than on anterior teeth, and the interlobe area is wider but shallower.

Lower anterior teeth (Fig. 4H, I) have a very tall and narrow cusp, with sub-parallel cutting edges. Lateral shoulders are short and nearly horizontal. The bilobate root is bisected by a deep, narrow nutritive groove, and the short lobes are widely separated by a U-shaped interlobe area. Lower lateral teeth (Fig. 4F, G) are similar to those in the upper jaw, but the cusp is narrower, lateral shoulders are shorter, the transition from cusp



**Figure 4.** Carcharhiniform shark teeth from the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A–D.** Carcharhinidae indeterminate. Anterolateral tooth in labial (**A**) and lingual (**B**) views, SC2013.38.105. Anterolateral tooth in labial (**C**) and lingual (**D**) views, SC2001.1.43. Labial at right in **C**. **E–P.** *Isogomphodon aikenensis* n. sp. Upper anterior tooth in lingual view (**E**), SC2013.38.110 (Holotype). Lower lateral tooth in labial (**F**) and lingual (**G**) views, SC2013.38.123.1. Lower anterior tooth in labial (**H**) and lingual (**I**) views, SC2013.38.119 (Paratype). Upper lateral tooth in labial (**J**) and lingual (**K**) views, SC2013.38.112 (Paratype). Posterolateral tooth in labial (**L**) and lingual (**M**) views, SC2013.38.114. Posterior tooth in labial (**N**) and lingual (**O**) views, SC2013.38.115 (Paratype). Upper anterolateral tooth in lingual (**P**) view, SC2013.38.111 (Paratype). Scale bars=1 cm in A–D; 5 mm in E–P.

to shoulder is more angular, and the mesial root lobe is shorter than the distal one. The root is low and bilobate, with rounded and diverging lobes that are separated by a wide and shallow U-shaped interlobe area. A narrow but deep nutritive groove is located on the lingual face.

Posterolateral and posterior teeth (Fig. 4L–O) are small with a T-shaped outline. The cusp is triangular but sharply tapering apically, rather low compared to teeth in more anterior positions. The cusp is vertical to slightly distally inclined, flat in profile. Lateral shoulders are short to elongate, perpendicular to the cusp, and the transition from cusp to shoulder is more angular than seen on more anterior jaw positions. The lateral shoulders in these positions are very convex at their distal extremities, resulting in a cusp-like appearance in lingual view. The root is bilobate with short, rounded, highly diverging lobes, which are separated by a broad, shallow to deep U-shaped interlobe area. The lingual face bears

a centrally located narrow but deep nutritive groove.

**Remarks**—A number of fossil species have been assigned to *Aprionodon* Poey, 1868, a junior synonym of *Isogomphodon*, including *Ap. acuarias* (Probst, 1879), *Ap. amekiensis* White, 1926, *Ap. caunellensis* Cappetta, 1970, *Ap. collata* (Eastman, 1904), *Ap. elongatus* (Leriche, 1910), *Ap. gibbesi* (Woodward, 1889), *Ap. gracilis* (Jonet, 1966), *Ap. frequens* (Dames, 1883), *Ap. lerichei* Darteville and Casier, 1943, *Ap. macrorhiza* Jonet, 1966, *Ap. marçaisi* Arambourg, 1952, and a subspecies, *Ap. lerichei* var. *minuta* Jonet, 1966. Although some of these species are at least in part based on specimens correctly assigned to the genus, most are appropriately referred to other genera or are perhaps *nomina dubia*.

For example, *Carcharhinus collata* Eastman, 1904 was referred to *Aprionodon* by Powlowska (1960), but illustrations of three teeth in Eastman (1904: pl. 22, figs. 3–5) show them to represent *Carcharhinus* and, possibly,

*Negaprion*. Antunes and Jonet (1970) concluded that Jonet's (1966) *Ap. macrorhiza* represents symphyseal teeth of indeterminate Carcharhinidae. The teeth that White (1926) illustrated as *Ap. amekiensis* (pl. 8, figs. 11-26) largely appear to be *Carcharhinus* (with some possibly representing *Negaprion*), and Arambourg's (1952) *Ap. marçaisi* morphology was identified as *Carcharhinus marçaisi* by Noubhani and Cappetta (1997: 151). Teeth of the *Ap. gibbesi* (Woodward 1889) and *Ap. elongatus* (Leriche 1910) species have weakly to coarsely serrated heels, particularly the uppers, and both species have been placed within *Carcharhinus* (Reinecke et al. 2001, 2005, Haye et al. 2008, Cicimurri and Knight 2009).

With regard to Jonet's (1966) *Ap. lerichei* var. *minuta* subspecies, Cappetta (1970) considered the material to represent the lateral teeth of *Isogomphodon acuaris*, but he later (2006) treated the morphology as a valid species distinct from *I. acuaris* without providing supporting evidence. However, our examination of the teeth illustrated in Jonet's (1966) plate II leads us to conclude that many of them, including the type specimen shown in figure 1, are not *Isogomphodon*. Specimens shown in figures 7, 11 and 13 in Jonet's (1966) plate II appear to be *Isogomphodon*, but the specific attribution is in need of further evaluation.

Dames' (1883) *Carcharhinus (Aprionodon) frequens* from the late Eocene of Egypt contains more than one species of shark. His description of the teeth (pp. 143, 144) and accompanying illustrations (pl. 3, figs. 7a-p) indicate that some specimens he examined (figs. 7b, f) are *Isogomphodon*. However, the *frequens* morphology is considered valid but has been attributed to *Carcharhinus* (i.e., Cappetta 1970) and, more recently, *Negaprion* (Underwood et al. 2011). As is the case with Jonet's (1966) *gracilis* morphology, the *Isogomphodon* teeth reported by Dames (1883) are in need of further study.

Cappetta (1970) believed that Jonet's (1966) *Ap. gracilis* species was actually the anterior teeth of *I. acuaris*. However, Cappetta (2006) later treated the species as valid, but in doing so provided no comment supporting the conclusion. We concur with Cappetta (1970) that teeth illustrated by Jonet (1966: pl. 2, figs. 14-21) represent anterior teeth, and they are not dissimilar from those of *I. acuaris*. Regardless of whether Jonet's (1966) species is valid or conspecific with *I. acuaris*, the teeth are both larger and have more elongated cusps than *I. aikenensis* n. sp. Case and Cappetta (1990) placed Cappetta's (1970) *Ap. caunellensis* species within *Carcharhinus*, but later Cappetta (2006, 2012) supported identification as *Isogomphodon caunellensis*. If valid, *I. caunellensis* teeth

are larger than *I. aikenensis*, have wider upper anterior teeth, and lower anterior teeth with incomplete cutting edges. Probst (1879) illustrated a specimen (pl. 1, figs. 76-77) of *I. acuaris* from his sample of approximately 50 teeth that is not dissimilar to anterior teeth of *I. aikenensis*. However, his description of the material (p. 140) is generic for the genus, but the maximum tooth size he reported (10 mm) is larger than that of *I. aikenensis* (7 mm).

*Isogomphodon lerichei* was based on a suite of Miocene teeth described by Darteville and Casier (1943). However, this taxon also appears to be a mixture of multiple species, with teeth of *Isogomphodon* and non-*Isogomphodon* species included in the illustrated suite of teeth provided by Darteville and Casier (1943: i.e., pl. 13, figs. 41, 42, 49, 50). This calls into question the validity of *I. lerichei*, but examination of the daggernose shark teeth shown by Darteville and Casier (1943: i.e., pl. 13, figs. 37, 39, 43-46) show that they are much larger and the angle between the cusp and lateral shoulders may be sharper than *I. aikenensis*. Antunes et al. (1981) tentatively reported *I. lerichei* from the Miocene of Portugal, but the two referred teeth (pl. 2, figs. 13 and 17) are, in our opinion, more appropriately referred to *Carcharhinus*.

*Isogomphodon oxyrhynchus* is the only extant species of daggernose shark, and it is largely restricted to coastal waters of northeastern South America (Lessa and others 1999, Lessa et al. 2016). Teeth of fossil *Isogomphodon*, particularly *I. acuaris*, are predominantly known from Mio-Pliocene deposits of the Tethyan regions of Europe and Africa, but an increasing number of reports document the taxon from temporally equivalent strata in South America (i.e., Carrillo-Briceño et al. 2016). Some of these latter records, however, are based on inaccurate identifications of teeth belonging to other Carcharhinidae (i.e., Mora 1999). Two reports of *I. acuaris* from North Carolina in the eastern United States have been published (Case 1980; Müller 1999). The strata yielding the fossils were considered to be of Miocene age, but the deposits are actually of Oligocene age (Harris and Zullo 1991; Zullo et al. 1992; Denison et al. 1993). Considering the limited geographic distribution and habitat preference of extant *I. oxyrhynchus*, it may be prudent to re-evaluate Oligo-Miocene records of the genus. Discovery of *I. aikenensis* in the Dry Branch Formation unequivocally extends the temporal range of the genus back to the late Eocene, and it is the only Eocene record in North America.

**Referred specimens**—SC2013.38.104, tooth; SC2013.38.105, tooth; SC2013.38.106, tooth; SC2013.38.107, tooth; SC2013.38.108, tooth; SC2013.38.109, three teeth.

**Remarks**—Unfortunately, the eight teeth lack enameloid. However, they are distinguished by the presence of a single pair of cusplets that mark the base of the main cusp and beginning of short enameloid shoulders (Fig. 4A, C). These teeth are superficially similar to *Abdounia enniskilleni*, but whereas the cusplets of *Ab. enniskilleni* form the mesial and distal ends of the crown, cusplets of Carcharhinidae indet. are comparatively smaller and located near the middle of the crown (compare Fig. 3H, I to Fig. 4A, C). Some of the specimens are very similar to White's (1926) *Hypoprion overricus* (reassigned to *Abdounia overrica* by Cappetta 2006), but the teeth in the Dry Branch sample differ in that cusplets appear to have been smaller. The Dry Branch teeth also bear similarities to Case's (1980) *Negaprion furimskyi* (Cappetta [2006] considers this species to belong within *Abdounia*), but a significant difference between the two morphologies is that the diminutive cusplets occur at the ends of the lateral shoulders on *Ab. furimskyi*, whereas they are between the end of the shoulder and the base of the cusp of the Dry Branch teeth.

Comparison of the Dry Branch material to some of the late Eocene teeth identified by Case and Cappetta (1990) as *Carcharhinus frequens* (pl. 5, figs. 100–103, 106–107; pl. 7, figs. 143–144, 146–148, 151–159) revealed striking similarities. Case and Cappetta's (1990) assignment of the Egyptian material to *Carcharhinus frequens* is in error because the teeth differ from most of the specimens illustrated by Dames (1883: pl. 3, fig. 7), which clearly possess a broader, lower cusp and exhibit serrated lateral shoulders. The *frequens* morphology was considered to be a species of *Negaprion* by Underwood et al. (2011), and they concluded that the sample examined by Case and Cappetta (1990) contained teeth of *Negaprion* and an undescribed species of *Abdounia*.

HEMIGALEIDAE HASSE, 1879

HEMIPRISTIS AGASSIZ, 1835

HEMIPRISTIS SP. CF. *H. CURVATUS* DAMES, 1883

(FIG. 3M–P)

**Referred specimens**—SC96.97.33, upper lateral tooth; SC96.97.34, upper lateral tooth; SC96.97.35, lower lateral tooth; SC96.97.36, 13 incomplete teeth; SC2001.1.20, incomplete upper tooth; SC2001.1.21, upper tooth; SC2001.1.22, five upper teeth; SC2001.1.23, four incomplete teeth; SC2013.38.20, lower anterior tooth; SC2013.38.21, lower lateral tooth; SC2013.38.22,

two juvenile upper tooth; SC2013.38.23, lower anterior tooth; SC2013.38.24, lower anterolateral tooth; SC2013.38.25, lower lateral tooth; SC2013.38.26, five incomplete upper teeth.

**Remarks**—Monognathic and dignathic heterodonty can be discerned within the sample of 39 teeth. Upper anterior teeth are narrow and rather erect, whereas lateral teeth are broadly triangular with a crown apex that is distinctively distally curved. The mesial edge of upper lateral teeth is completely smooth or weakly serrated on its basal half, but the distal edge is coarsely serrated nearly to the apex (Fig. 3M). Lower anterior teeth are comparatively narrower, erect, and serrations on cutting edges are restricted to the crown base (Fig. 3P).

*Hemipristis* teeth are distinctive in having very large cusplets along the distal crown edge, a characteristic evident even on teeth lacking enameloid (Fig. 3N). *Hemipristis curvatus* (identified as *He. wyattdurhami* White, 1956 in older literature) appears to have been widespread in the Eocene Atlantic and Gulf coastal regions, having been reported from North Carolina (Timmerman and Chandler 1995), Georgia (Case 1981, Case and Borodin 2000, Parmley and Cicimurri 2003), Alabama (White 1956, Thurmond and Jones 1981), Louisiana (Manning and Standhardt 1986), and Arkansas (Westgate 1984). This taxon is easily separated from the temporally younger *He. serra* Agassiz, 1835 in that teeth are much smaller in size and the mesial cutting edges of lateral teeth are nearly or completely devoid of serrations.

SCYLORHINIDAE GILL, 1862

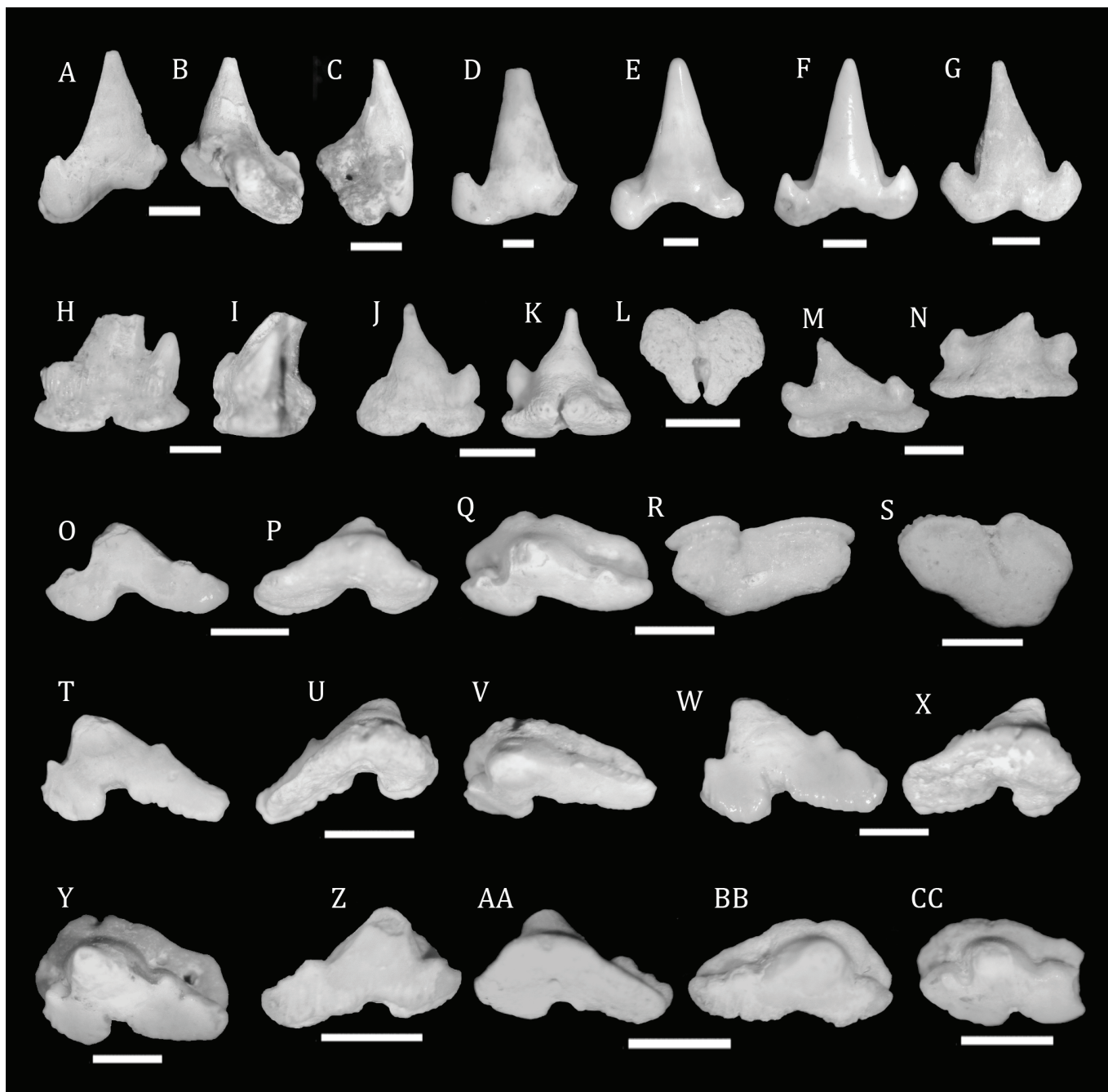
FOUMTIZIA NOUBHANI AND CAPPETTA, 1997

FOUMTIZIA SP.

(FIG. 5A–G)

**Referred specimens**—SC96.97.5, incomplete tooth (Fig. 5D); SC96.97.6, incomplete tooth (Fig. 5E); SC96.97.7, incomplete tooth (Fig. 5F); SC96.97.8, incomplete tooth (Fig. 5G); SCSC2001.1.42, incomplete tooth; SC2013.38.27, incomplete tooth (Fig. A–C); SC2013.38.28, two incomplete teeth; SC2013.38.159, lateral tooth.

**Remarks**—These scylorhinid teeth are large enough (up to 4 mm in height) to be found in the field with the naked eye. Tooth crowns consist of a tall, erect, basally broad but sharply tapering cusp that is flanked by a pair of large lateral cusplets. The labial crown foot is thick, overhangs the root, and bears a conspicuous medial concavity. A blunt cutting edge extends across the main cusp and generally only onto the inner side of the lateral cusplets. In terms of overall morphology these



**Figure 5.** Scyliorhinid shark teeth from the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A–G.** *Fountizia* sp. Anterior tooth in labial (**A**), lingual (**B**) and profile (**C**) views, SC2013.38.27. Anterior tooth in labial (**D**) view, SC96.97.5. Anterior tooth in labial (**E**) view, SC96.97.6. Anterior tooth in labial view (**F**), SC96.97.7. Anterior tooth in labial view (**G**), SC96.97.8. **H–N.** *Premonotreia (Oxyscyllium)* sp. cf. *Pr. (O.) gilberti*. Anterior tooth in labial (**H**) and distal (**I**) views, SC2013.38.29. Labial at left in **I**. Anterior? tooth in labial (**J**), lingual (**K**) and basal (**L**) views, SC2013.38.30. Lateral tooth in labial (**M**) and lingual (**N**) views, SC2013.38.31. **O–CC.** *Scyliorhinus* sp. Lateral tooth in labial (**O**), lingual (**P**), occlusal (**Q**), and basal (**R**) views, SC2013.38.36. Anterolateral tooth in basal (**S**) view, SC2013.38.35. Lateral tooth in labial (**T**), lingual (**U**), and occlusal (**V**) views, SC2013.38.39. Lateral tooth in labial (**W**), lingual (**X**), and occlusal (**Y**) views, SC2013.38.37. Lateral tooth in labial (**Z**), lingual (**AA**), and occlusal (**BB**) views, SC2013.38.38. Anterior? tooth in occlusal (**CC**) view, SC2013.38.40. Labial at top in **L, R, S**; at bottom in **Q, V, Y, BB, CC**. Scale bars=1mm.

teeth compare well to *Fountizia*, but the Dry Branch teeth are larger than any species previously attributed to that genus (Cappetta 1976, Noubhani and Cappetta

1997, Malyshkina 2006). The preservation of our material and small sample size ( $n=9$ ) leads us to refrain from making a more specific identification. The morphological

features noted above, along with larger size and lack of enameloid ornamentation, distinguish the teeth from two other scyliorhinids occurring in the Dry Branch sample (see below).

*PREMONTREIA* CAPPETTA, 1992  
*PREMONTREIA (OXYSCYLLIUM)* SP.  
 CF. *PR. (O.) GILBERTI* (CASIER, 1946)  
 FIG. 5H–N

**Material examined**—SC2013.38.29, tooth (Fig. 5H, I); SC2013.38.30, tooth (Fig. 5J–L); SC2013.38.31, tooth (Fig. 5M, N); SC2013.38.32, tooth; SC2013.38.33, tooth; SC2013.38.34, incomplete tooth.

**Remarks**—The root morphology of our six specimens leads us to assign the teeth to Premontreinae Cappetta, 1992, which currently contains the genera *Premontreia* and *Pachyscyllium* Reinecke and others, 2005. Noubhani and Cappetta (1997) have since divided *Premontreia* into two subgenera: *Premontreia* and *Oxyscyllium*. Although only the dentine core of the Dry Branch Formation specimens is preserved, we can discern that the tooth crowns bore coarse basal longitudinal ridges and they were distally inclined, which is in contrast to what is seen on teeth of the various Oligocene to Pliocene species of *Pachyscyllium* that have been described (Cappetta, 1970, Reinecke and others 2005, Haye et al. 2008, Reinecke et al. 2008). With respect to crown shape, the Dry Branch Formation teeth are identifiable to the subgenus *Premontreia (Oxyscyllium)* Noubhani and Cappetta, 1997 because of the large and well differentiated lateral cusplets. Additionally, we believe that the teeth compare favorably to *Pr. (O.) gilberti*, a species formerly placed within *Scyliorhinus* (Casier 1946, Bor 1985, Nolf 1988, Kemp et al. 1990, Case et al. 1996, also Reinecke et al. 2008). We also consider specimens that Parmley and Cicimurri (2003) identified as *Scyliorhinus gilberti* and material identified as *Scy. distans* (Probst, 1879) by Manning and Standhardt (1986:fig. 1, no. 2) to be conspecific with the Dry Branch taxon.

*SCYLIORHINUS* BLAINVILLE, 1816  
*SCYLLIORHINUS* SP.  
 (FIG. 5O–CC)

**Referred specimens**—SC2001.1.42, incomplete tooth; SC2013.38.35, tooth; SC2013.38.36, tooth; SC2013.38.37, tooth; SC2013.38.38, tooth; SC2013.38.39, tooth; SC2013.38.40, tooth; SC2013.38.160, anterior tooth.

**Remarks**—Unfortunately, our eight teeth lack enameloid and/or have broken cusps, and the true

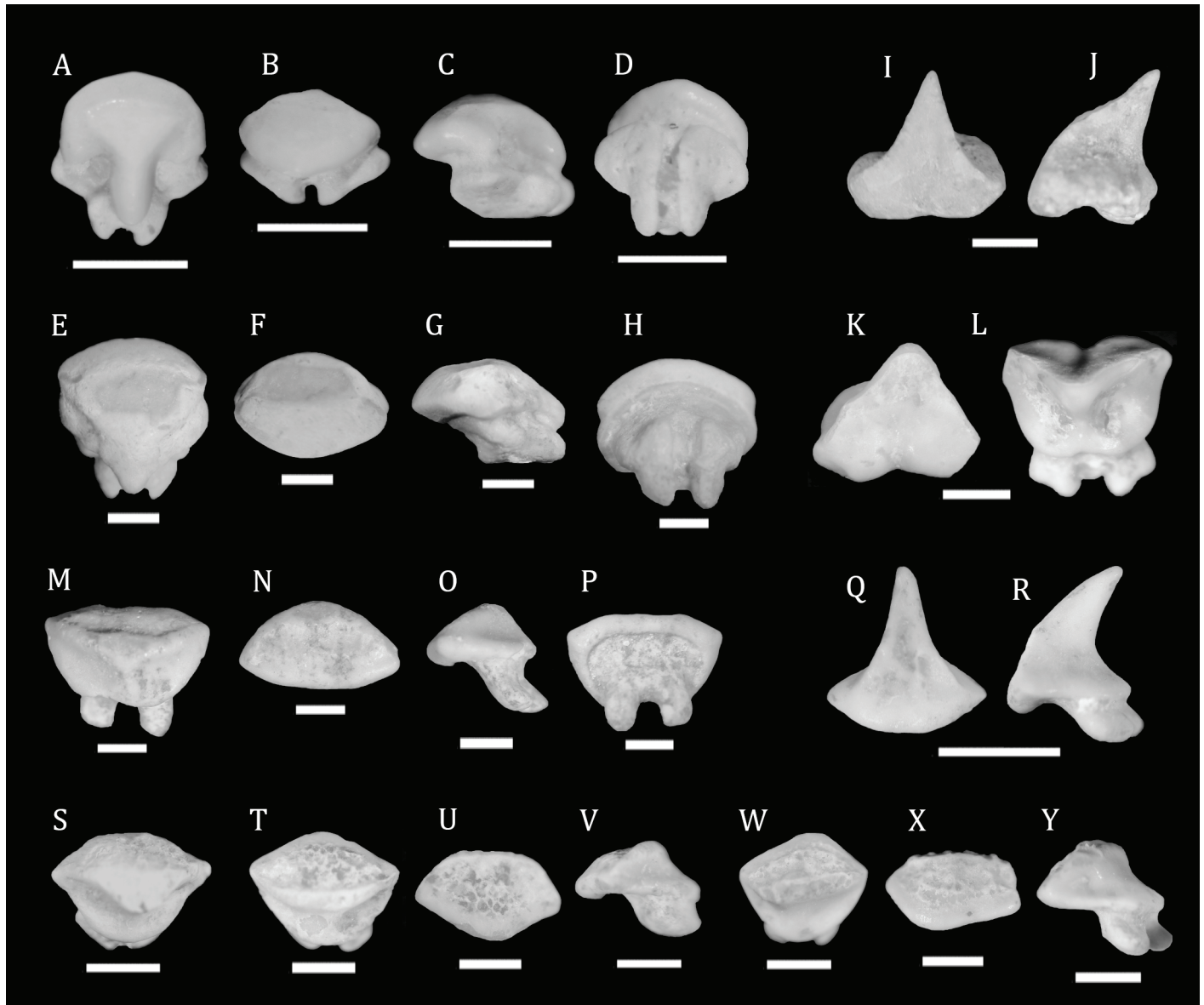
height of the main cusp and lateral cusplets cannot be determined. Teeth are distinctive in that the labial crown foot is highly concave so that two lobes, a short mesial and a more elongated distal lobe, are developed. One or two cusplets are found on the mesial lobe, but only one large cusplet occurs on the distal lobe. The specimens exhibit crown ornamentation and lateral cusplets, and they are of similar size to other scyliorhinid teeth in our sample that we identify as *Premontreia* (see above). However, the root morphology and strongly asymmetrical nature of the crown are not typical of species within the genus *Premontreia* (Noubhani and Cappetta 1997, Malyshkina 2006, Mollen 2008).

The discontinuous nature of the nutritive groove on our teeth is consistent with the morphology of *Scyliorhinus* species identified elsewhere (Noubhani and Cappetta 1997). The preservation of the Dry Branch teeth inhibits our ability to compare them to known species, but in terms of overall morphology they are similar to Paleocene *Sc. entomodon* Noubhani and Cappetta, 1997 of Morocco and *Sc. joleaudi* Cappetta, 1970 from the lower Miocene of France. However, the Dry Branch teeth differ from the Moroccan species in that the crown lobes are much more widely separated, and all specimens exhibit enameloid ornamentation (Noubhani and Cappetta 1997). The main cusp of *Sc. joleaudi* appears to have been larger than the Dry Branch taxon, the crown lobes are closer together, and cusplets are also larger (Cappetta 1970). A larger sample size and more complete material will help with making a more specific determination.

RHINOPRISTIFORMES NAYLOR ET AL., 2012  
 RHINOBATIDAE BONAPARTE, 1835  
 RHINOBATOS LINCK, 1790  
 RHINOBATOS SP.  
 (FIG. 6A–D)

**Referred specimen**—SC2013.38.45, tooth.

**Remarks**—The single tooth can be distinguished from teeth of *Rhynchobatus* Müller and Henle, 1837 (see below) in lacking crown ornamentation, the medial lingual protuberance is very narrow, and flanking lateral protuberances are present (Fig. 6A). The crown apex is worn, and it is unclear if this tooth was low-crowned (female) or cuspidate (male). The tooth is identical to *Rhinobatos* teeth from the temporally older Clinchfield Formation of central Georgia (DJC, unpublished data). Although represented by a single specimen, the Dry Branch *Rhinobatos* exhibits features in common with middle to late Eocene *Rhinob. steurbauti* Cappetta and Nolf, 1981, including an elongated central lingual protuberance flanked by much



**Figure 6.** Batoid teeth from the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A–D.** *Rhinobatos* sp. Tooth in occlusal (**A**), labial (**B**), profile (**C**), and basal (**D**) views, SC2013.38.45. **E–H.** *Rhynchobatus* sp. cf. *Rhy. pristinus*. Tooth in occlusal (**E**), labial (**F**), profile (**G**), and basal (**H**) views, SC2013.38.46. **I–P.** *Dasyatis* sp. cf. *D. tricuspoidatus*. Male anterior tooth in labial (**I**) and distal (**J**) views, SC2013.38.42. Tooth in labial (**K**) and occlusal (**L**) views, SC2013.38.43. Tooth in occlusal (**M**), labial (**N**), profile (**O**), and basal (**P**) views, SC2013.38.41. **Q–Y.** *Dasyatis* sp. SC2013.38.49. Male anterior tooth in labial (**Q**) and distal (**R**) views. Tooth in occlusal (**S**) view, SC2013.38.55. Tooth in occlusal (**T**), labial (**U**), and profile (**V**) views, SC2013.38.52. Tooth in occlusal (**W**), labial (**X**), and profile (**Y**) views, SC2013.38.53. Labial at top in **A, D, E, H, L, M, P, S–T, W**; at left in **C, G, J, O, R, V, Y**. Scale bars=1 mm.

smaller and slightly diverging lateral protuberances (Cappetta and Nolf 1981, Case et al. 1996). *Rhinobatos* teeth occurring in upper Eocene strata of Georgia and Louisiana appear to be conspecific with the Dry Branch Formation species, and we believe that those records were erroneously identified as the Cretaceous taxon *Rhinob. casieri* Cappetta and Case, 1975 (Case 1981, Manning and Standhardt 1986). Manning and Standhardt (1986)

used the presence of *Rhinobatos* in a paleofauna as an indicator of a middle shelf-depth environment.

Cappetta and Case (2016) recently identified similar teeth from middle Eocene strata of Alabama as *Pristis* Linck, 1790. However, those teeth clearly have an elongated medial uvula flanked by lateral uvulae, whereas *Pristis* teeth lack lateral uvulae (Carrillo-Briceño et al. 2015, Carrillo-Briceño et al. 2016). Negative evidence within

the Dry Branch Formation sample, which lacks Pristidae [Bonaparte, 1838](#) rostral spines, indicates sawfish were not present at the time of deposition. For the purposes of this report we identify SC2013.38.45 as *Rhinobatos*, but our generic assignment could change with a larger sample size that will allow for better comparisons to the tooth morphologies of other extant rhinopristiform genera. The Dry Branch Formation tooth bears some similarity to *Glaucostegus typus* [Bennett, 1830](#) ([Underwood et al. 2015](#)), but its labial face appears to be more convex than seen on male and female teeth of *Zapteryx brevirostris* ([Müller and Henle, 1841](#)) ([Rangel et al. 2014](#)).

RHINIDAE MÜLLER AND HENLE, 1841

RHYNCHOBATUS MÜLLER AND HENLE, 1837

RHYNCHOBATUS SP. CF. RHY. PRISTINUS (PROBST, 1877)

(FIG. 6E–H)

**Referred specimens**—SC2013.38.46, tooth; SC2013.38.47, tooth; SC2013.38.48, tooth.

**Remarks**—The three teeth are easily distinguished as *Rhynchobatus* in having granular crown ornamentation and a central lingual protuberance that is long and wide, and flanking protuberances are absent (Fig. 6E). Two fossil *Rhynchobatus* species have been reported, *Rhy. vincenti* [Jaekel, 1894](#) from Eocene deposits ([Leriche 1905](#)) and *Rhy. pristinus* from Oligo-Miocene strata ([Cappetta 1970](#), [Cicimurri and Knight 2009](#)). Overall, teeth of these two species are comparable in size and morphology, but *Rhy. vincenti* has a wider, shorter lingual protuberance than *Rhy. pristinus* ([Jaekel 1894](#), [Müller 1999](#)). [Jaekel \(1894:76–77\)](#) makes no mention of ornamentation on *Rhy. vincenti*, and the Dry Branch specimens have a long and narrow protuberance similar to *Rhy. pristinus*. We tentatively refer the Dry Branch teeth to this latter species due to limited sample available to us. [Müller \(1999\)](#) reported a damaged lower Eocene *Rhynchobatus* tooth that is similar to *Rhy. vincenti*, but he did not believe the taxa were conspecific. Although similar, teeth of *Pristis* differ from those of *Rhynchobatus* in lacking crown ornamentation, but having a sharp and conspicuous transverse crest. Additionally, *Pristis* teeth have a shorter lingual face but much more elongated medial uvula ([Cappetta 2012](#), [Carrillo-Briceño et al. 2015](#), [Carrillo-Briceño et al. 2016](#)).

MYLIOBATIFORMES COMPAGNO 1973

DASYATIDAE JORDAN 1888

DASYATIS RAFINESQUE 1810

DASYATIS SP. CF. D. TRICUSPIDATUS CASIER 1946

(FIG. 6I–P)

**Referred specimens**—SC2013.38.41, tooth; SC2013.38.42, male tooth; SC2013.38.43, male tooth; SC2013.38.44, six teeth.

**Remarks**—Nine large *Dasyatis* teeth are characteristic in their lack of enameloid ornamentation, a feature that readily distinguishes them from most other species that have been reported from Eocene strata ([Ward 1979b](#), [Noubhani and Cappetta 1997](#)). The intersection of the transverse crest with a sagittal lingual crest results in a tripartite division of the crown (i.e., Fig. 6M). This species was originally reported from lower Eocene strata of Belgium ([Casier 1946](#)), and the taxon has subsequently been documented in middle Eocene strata of Europe ([Kemp et al. 1990](#), [Van den Eeckhaut and de Schutter 2009](#)).

*Dasyatis* exhibits gynandric heterodonty (male teeth differ from those of females), but the identification of male and female teeth of a fossil species may not be as clear cut as previously thought. [Kajiura and Tricas \(1996\)](#) found that male and female teeth of *Dasyatis sabina* (= *Hypanus sabinus*) ([Lesueur, 1824](#)) may be nearly indistinguishable from each other, with both sexes having low-crowned teeth. However, as mating season approaches, male teeth exhibit a transition (Fig. 6K) to taller, highly cuspidate crowns that are effective at grasping pectoral fins of females during copulation ([Kajiura et al. 2000](#)). Assuming this phenomenon was developed in Eocene fossil species, isolated low-crowned teeth (Fig. 6M–P) in the Dry Branch sample could belong to males or females, whereas high-crowned cuspidate teeth belonged to males (Fig. 6I–J).

DASYATIS SP.

(FIG. 6Q–Y)

**Referred specimens**—SC2013.38.49, male tooth; SC2013.38.51, 12 male teeth; SC2013.38.52, tooth; SC2013.38.53, tooth; SC2013.38.54, 39 teeth; SC2013.38.55, tooth; SC2013.38.161, four teeth.

**Remarks**—These 59 teeth differ from those of *Dasyatis* sp. cf. *D. tricuspoidatus* (see above) in that they are smaller in overall size and are easily distinguished by their highly ornamented labial face (Fig. 6S, U, W). It is difficult to make accurate comparisons to other species with highly ornamented teeth ([Ward 1979b](#), [Noubhani and Cappetta 1997](#)) due to the lack of enameloid on the Dry Branch specimens. However, the teeth of *D. jaekeli* ([Leriche, 1905](#)) have ornamentation that is generally restricted to the apical region of the labial face ([Leriche 1905](#)), and ornamentation on *D. wochadunensis* [Ward, 1979b](#) extends well onto the lingual side of the crown. Highly cuspidate teeth bearing weak labial ornamentation (i.e.,

Fig. 6Q–R) are herein identified as male teeth, and we associate them with *Dasyatis* sp. due to their small size and ornamented labial face, in comparison to *Dasyatis* sp. cf. *D. tricuspidatus* discussed above.

MYLIOBATIDAE BONAPARTE, 1838

*AETOMYLAEUS* GARMAN, 1908

*AETOMYLAEUS* SP.

(FIG. 7A–E)

**Material examined**—SC96.97.49, 17 incomplete median teeth; SC96.97.50, lateral tooth; SC96.97.51, lateral tooth; SC2001.1.1, eight partial median teeth; SC2001.1.2, incomplete median tooth; SC2001.1.29, lateral tooth; SC2001.1.30, three lateral teeth; SC2001.1.31, two incomplete median teeth; SC2001.1.32, five partial median teeth; SC2013.38.80, partial median tooth; SC2013.38.81, two incomplete median teeth; SC2013.38.82, four incomplete median teeth; SC2013.38.83, two lateral teeth.

**Remarks**—These 48 teeth are distinguished by their thick crowns with slightly lingually inclined labial and lingual faces. The labial face appears highly pitted (Fig. 7A), whereas the lingual face has a granular texture and a very thin and sharp transverse ridge is located at the crown-root junction (Fig. 7B). Upper median teeth can be distinguished from those in the lower dentition in being more convex overall, with a straight to curved crown base that parallels the occlusal surface. In contrast, lower median teeth have a straight crown with flat occlusal surface, and the crown foot is parallel to the basal root face. Lateral teeth are longer than wide and bear labial pitting and lingual tuberculation on crown faces (Fig. 7D, E).

The Dry Branch material appears to be conspecific with a myliobatoid occurring in the Clinchfield Formation of central Georgia (DJC *unpublished data*). In terms of overall morphology, this taxon compares quite favorably to Miocene teeth Cappetta (1970) identified as *Pteromylaeus* Garman, 1913, and to *Myliobatis meridionalis* (Gervais, 1852). Cappetta (2006) synonymized *M. meridionalis* with *Pteromylaeus*, and earlier Cappetta (1987:171) considered the possibility that the material he described in 1970 could represent old individuals of *Aetomylaeus*. Hovestadt and Hovestadt-Euler (1999) noted the difficulty of identifying isolated fossil myliobatidae teeth and stated that *Pteromylaeus* is only known from extant species. However, Hovestadt and Hovestadt-Euler (2013) later assigned several fossil species previously identified as *Myliobatis* to *Pteromylaeus* and *Aetomylaeus*, thereby extending the record of the latter genera back into the Eocene. White (2014) more recently synonymized *Pteromylaeus* with *Aetomylaeus*,

and the latter generic name is applied to the Dry Branch sample listed above.

*PSEUDAETOBATUS* CAPPETTA, 1986

*PSEUDAETOBATUS UNDULATUS* CICIMURRI AND EBERSOLE, 2015

(FIG. 7F–I)

**Referred specimens**—SC96.97.52, 22 medial tooth fragments; SC96.97.53, lateral tooth; SC2001.1.3, 118 partial medial teeth; SC2001.1.4, three lateral teeth; SC2001.1.5, 10 lateral teeth; SC2001.1.6, lateral tooth; SC2001.1.7, lateral tooth; SC2013.38.84, lower medial tooth; SC2013.38.85, upper medial tooth; SC2013.38.86, upper medial tooth; SC2013.38.87, upper medial tooth; SC2013.38.88, incomplete upper medial tooth; SC2013.38.89, incomplete upper medial tooth; SC2013.38.90, lower medial tooth; SC2013.38.91, lower distal-most lateral tooth; SC2013.38.92, upper distal-most lateral tooth; SC2013.38.93, five lower distal-most laterals; SC2013.38.94, 12 upper distal-most lateral teeth; SC2013.38.95, lateral tooth; SC2013.38.96, five lateral teeth; SC2013.38.97, 87 incomplete medial teeth.

**Remarks**—We assign 275 teeth in our sample to *Pseudaetobatus*. Upper median teeth of *Pseudaetobatus* are wide and straight (Fig. 7F), whereas median teeth from the lower dental battery are more arcuate (Fig. 7G). Median teeth are easily distinguished from those of *Aetomylaeus* (see above) in that the labial and lingual crown faces are only weakly ornamented (as opposed to heavily pitted labially and with granular texture lingually) and the lingual ridge at the crown/root junction is thick and rounded instead of thin and sharp. These features can also be used to distinguish the lateral teeth of both species, and the distal-most lateral teeth of *Pseudaetobatus* are also sinuous (Fig. 7I).

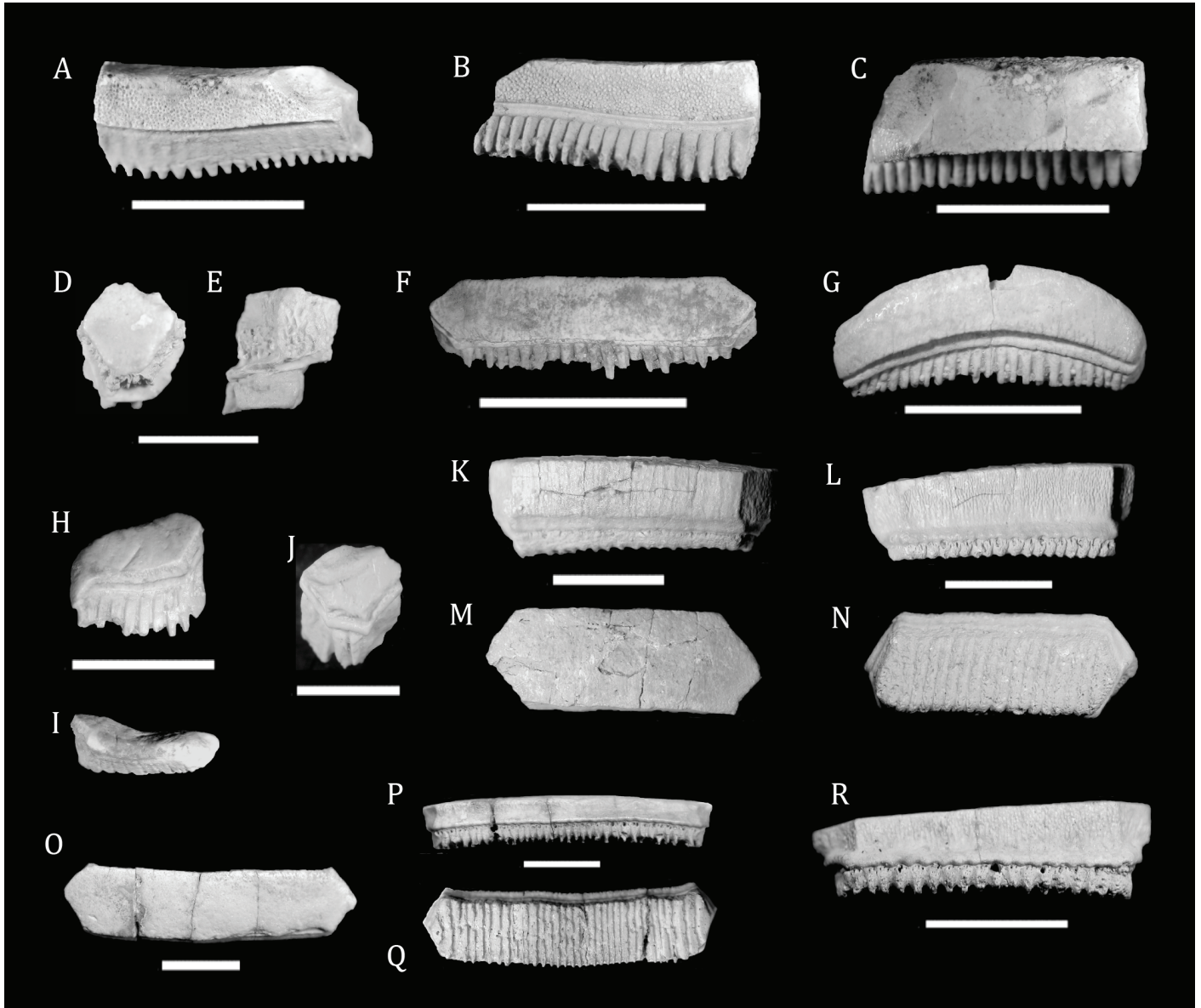
*Pseudaetobatus* has only recently been formally reported from the United States, with two new species described by Cicimurri and Ebersole (2015). *Pseudaetobatus belli* Cicimurri and Ebersole, 2015 is an early Eocene species that occurs in Mississippi and Alabama, whereas *Ps. undulatus* is thus far only known from the upper Eocene Dry Branch Formation of South Carolina.

RHINOPTERA CUVIER, 1829

RHINOPTERA SP.

(FIG. 7K–R)

**Referred specimens**—SC96.97.54, medial tooth; SC96.97.55, 8 lateral teeth; SC96.97.56, 38 tooth fragments; SC2001.1.11, 233 partial medial teeth; SC2001.1.12, lateral tooth; SC2001.1.13, lateral tooth;



**Figure 7.** Myliobatidae teeth from the Dry Branch Formation (Priabonian) of Aiken County, South Carolina. **A-E.** *Aetomylaeus* sp. Incomplete lower median tooth in labial (**A**), lingual (**B**), and occlusal (**C**) and views, SC2001.1.2. Lateral tooth in occlusal (**D**) and profile (**E**) views, SC2001.1.29. **F-I.** *Pseudaetobatus undulatus*. Upper median tooth in occlusal (**F**) view, SC2013.38.86. Lower median tooth in occlusal (**G**) view, SC2013.38.84. Upper right distal-most lateral tooth in occlusal (**H**) and labial (**I**) views, SC2013.38.91. Lateral tooth in occlusal (**J**) view, SC2013.38.96.2. **K-R.** *Rhinoptera* sp. Lateral tooth in labial (**K**), lingual (**L**), occlusal (**M**), and basal (**N**) views, SC2001.1.12. Median tooth in occlusal (**O**), lingual (**P**), and basal (**Q**) views, SC2001.1.16. Lateral tooth in lingual (**R**) view, SC2013.38.70. Labial at top in C, D, F-H, J, M-O, Q; at right in E. Scale bars=1 cm in A-C, F-I, K-R; 5 mm in D, E, J.

SC2001.1.14, lateral tooth; SC2001.1.15, lateral tooth; SC2001.1.16, medial tooth; SC2001.1.17, 19 medial teeth; SC2013.38.69, medial tooth; SC2013.38.70, lateral tooth; SC2013.38.71, lateral tooth; SC013.38.72, lateral tooth; SC2013.38.73, lateral tooth; SC2013.38.74, four medial teeth; SC2013.38.75, three medial or proximal lateral teeth; SC2013.38.76, ten lateral teeth; SC2013.38.77, eight distal lateral teeth; SC2013.38.78, distal-most

lateral tooth; SC2013.38.79, 100 incomplete teeth.

**Description**—*Rhinoptera* is represented in our material by 435 teeth. Unworn teeth have a crown measuring up to 1 cm in thickness, but in cases of extreme wear crowns are only 2 mm thick. The labial and lingual faces of all teeth are vertical and flat, and ornamented with fine vertical wrinkles which grade apically into a granular texture on the lingual face. A large rounded transverse

ridge is located at the lingual crown/root junction (Fig. 7L, P, R). The labial crown face overhangs the root, and there is a shallow groove on the ventral surface of the crown just anterior to the root (Fig. 7K). Median teeth (i.e., Fig. 7O–Q) measure up to 35 mm wide and 8 mm long (4.4:1 ratio). We observed, as did White (1926), that median teeth are evenly worn and may be arched (Fig. 7P). The largest teeth that we consider to have been from the first lateral row measure between 23 mm and 25 mm in width and 5 mm to 9 mm in length. These teeth are easy to identify because the crown is obviously thicker on the mesial side than on the distal side (Fig. 7K, L, R), and root lobes are often oblique to the long axis of the tooth (Fig. 7N). Other specimens that we believe to be from the outermost row of lateral teeth are symmetrical or only slightly wider than long (1:0.7 ratio). These teeth are distinguished by having an angular mesial margin that articulates with the remainder of the dentition, but the distal margin is rounded. At this time we cannot ascertain if intermediate lateral positions were part of the dentition.

**Remarks**—Unworn median teeth we refer to *Rhinoptera* have a square cross section, whereas those of *Pseudaetobatus* are rectangular. The labial and lingual crown faces of *Rhinoptera* sp. are vertical and bear fine vertical wrinkling, whereas the labial face of *Aetomylaeus* is concave with extensive pitting, and the lingual face is convex with granular ornamentation. In addition, the root lobes of *Rhinoptera* do not extend lingually past the crown base as they do on *Pseudaetobatus* and *Aetomylaeus*. The lingual crown/root ridge on *Rhinoptera* is thick and rounded as opposed to thin and sharp on *Aetomylaeus*.

The Dry Branch *Rhinoptera* is easily distinguished from Paleocene *Rhinop. prisca* Woodward, 1907 and *Rhinop. raeburni* White, 1934 in that the crown is not nearly as thick, labial and lingual faces are nearly vertical and straight, and ornamentation is reduced to fine wrinkles or scattered nodes. Occlusal ornamentation appears to be absent, and nutritive grooves are more numerous and more closely spaced. Although of similar morphology, Dry Branch *Rhinoptera* teeth are larger than *Rhinop. sherborni* White, 1926 from the African Eocene, with the crown of the largest complete tooth in our sample measuring 3.6 cm in width as opposed to only 1.7 cm (see White 1926: pl. 10, figs. 16–26; also Arambourg 1952). Even considering specimens originally identified as *Myliobatis* by White (1926: pl. 10, fig. 5–7) but later considered by Arambourg (1952) to be *Rhinop. sherborni* medial teeth, the largest specimen measures only 2.5 cm.

Bearing these differences in mind, assigning a species name to the Dry Branch *Rhinoptera* is somewhat problematical. The available material compares very well to Leidy's (1855) *Zygobates dubius* from the "Ashley Phosphate beds" region of South Carolina (Leidy did not illustrate teeth until 1877; see pl. 31, figs. 21–33). Leidy (1877:248) mentioned the possibility that his *Z. dubius* was conspecific with *Trygon carolinensis* named by Emmons (1858) from the Eocene of North Carolina. However, Emmons' illustrated teeth (p. 243, figs. 91, 92) appear to be undulating rather than straight or weakly arched. Cappetta (2006) synonymized *Z. dubius* with Mio-Pliocene *Rhinoptera studeri* Agassiz, 1843, but unfortunately the stratigraphic position and age of Leidy's fossils are unknown. Due to a lack of stratigraphic control and more limited knowledge of Cenozoic stratigraphy in Leidy's time, material purportedly from the "Ashley Phosphate beds" of South Carolina could range in age from the Oligocene through Pleistocene epochs (Sanders 2002).

Leriche (1927) illustrated a partial *Rhinoptera* dentition (p. 44, fig. 6) that may shed some light on the issue. That specimen, from the Swiss Miocene, was identified as *Rhinop. studeri* and it clearly shows that a median tooth row and at least three lateral tooth rows were present. The first lateral tooth of the Swiss specimen is only 86% of the width of the median tooth, but the second median tooth is only 29% of the width of the median tooth. We can only confirm two lateral tooth rows in the dentition of the Dry Branch taxon (first and distal-most lateral positions). Additionally, the first lateral tooth is 63% of the width of the median tooth. The Swiss *Rhinop. studeri* dentition appears to have been disjunct with respect to tooth size reduction towards the commissure, but size reduction within the Dry Branch appears to have been more gradual and similar to Recent *Rhinop. brasiliensis* (Bigelow and Schroeder 1953). Leidy's *Z. dubius* appears to be identical to the Dry Branch taxon, and his fossils could be older than Miocene. Unfortunately, we cannot corroborate these hypotheses, and at this time we identify the Dry Branch taxon only to the generic level. Interestingly, Darteville and Casier (1959) illustrated two teeth from the Eocene of western Africa (pl. 34, fig. 2a–c, figs. 7, 8), identified as *Myliobatis* sp., that are very similar to the Dry Branch *Rhinoptera*.

## DISCUSSION

### Stratigraphic position of the Dry Branch elasmobranch assemblage

In the Aiken area, the Huber, Dry Branch, and Tobacco

Road Formations are generally visible at the surface as thin outcroppings along roadways and in housing subdivisions. Limited exposure, combined with a great deal of lithologic variability and inconsistent local thickening and thinning due in part to highly irregular contacts between these formations, makes identification of units and correlation of sections difficult. All of the exposures at the NAS are assignable to the Dry Branch Formation, and a thick grayish-white clay bed occurs at the base of the unit. Unfortunately, this site has been reclaimed as a housing development, and only thin patches of strata are currently exposed. Of the strata preserved in the E-W trending wall at the SAS, only the sediment within the lower 2.0–2.5 m belong to the Dry Branch Formation (we also dug a trench up to 1.3 m below ground level but only encountered more unconsolidated sand). The upper part of the section consists of indurated medium- to very coarse-grained quartz sands (grains are sub-rounded to rounded) that are poorly sorted and contain abundant interstitial clay, which we assign to the Tobacco Road Formation. A basal pebble lag is not obvious, but the contact with the Dry Branch Formation is irregular, and there is a sharp change from fine- to coarse-grained, pinkish to pale yellow quartz sand containing little interstitial clay (soft and friable=Dry Branch Formation), to medium- to coarse-grained, poorly sorted quartz sand containing abundant orange interstitial clay (more indurated=Tobacco Road Formation).

Consistent with previous observations of elasmobranch teeth occurring in the Dry Branch Formation (Zullo et al. 1982), the sample from the SAS is derived from the upper part of the formation, and the lithology is consistent with the Irwinton Sand as it is composed predominantly of golden-yellow, brownish-yellow, and pinkish to purple medium- to very coarse-grained quartz sand that is moderately well-sorted and generally contains very little interstitial clay.

The fossiliferous horizon at SAS is approximately 15 cm thick and has variegated red and white color, with lesser amounts of yellow and orange. Within this horizon, vertebrate fossils are common and haphazardly distributed and oriented, small white clay clasts are common, and larger quartz clasts (>1 cm) are uncommon. Numerous small phosphatic steinkerns representing at least ten species of bivalves, ten species of gastropods, a scaphopod, a barnacle, possible branching bryozoa, and chelipeds of at least three species of decapod crustaceans are associated. The fossil horizon is located approximately two meters below the contact with the overlying Tobacco Road Formation. The unit directly underlies at

least 15 cm of thin alternating beds of red sand and white sandy clay, and overlies a loose sand of more uniform yellow-orange color.

### Composition of the Dry Branch elasmobranch assemblage

As noted earlier, identification of the Dry Branch shark teeth to the species level was sometimes hampered by the preservation of the material. The enameloid was often partly or completely leached, and the presence of crown ornamentation, height of lateral cusplets, and the nature of cutting edge serrations was difficult to discern on many specimens. For example, Figure 3A, B and 4L–M show teeth on which the enameloid is partially lost, whereas Figure 3 provides a contrast between teeth with (3O–P) and without (3M–N) enameloid. However, it can be said that carcharhiniform sharks dominate the Dry Branch elasmobranch assemblage, with 11 taxa having been identified. The remaining component consists of one hexanchid, one squatid, two orectolobiforms, and two lamniforms. The batiod portion of the fauna is composed of two rhinopristiform rays and five myliobatiform rays. Twenty-one taxa have presumed benthic/epibenthic habits (including *Squatina*, most of the carcharhiniforms, batoids). These far outnumber the three with presumed pelagic habits that include *Galeocerdo*, *Alopias*, and *Carcharias*. The varied tooth morphologies in our sample are indicative of clutching, cutting, tearing, and crushing dentitions (Cappetta 1987), and a larger array of prey species was probably available, both vertebrate and invertebrate, than is presently indicated by the fossil record.

### Depositional environment

Vertebrate species occurrences at the NAS and SAS are very similar, and we believe that the depositional settings at the two sites were comparable. For both sites, evidence suggests shallow, subtropical, high-energy environments. The lithology and presence of terrestrial/brackish water vertebrates like gars, trionychid turtles, and crocodylians indicates very close proximity to the shoreline and influx of sediment via a river system. Minerals like kyanite and amphibole suggest local igneous and metamorphic rocks were sediment sources for the fossiliferous bed at the SAS.

If extant elasmobranchs can be utilized as proxy environmental indicators for fossil species, the taxa we identified from the Dry Branch Formation support the above hypotheses. Tawny nurse sharks (*Nebrius*) and sevengill sharks (*Notorynchus*) are predominantly inshore

inhabitants where water depth is between five to 30 m and one to 50 m, respectively, whereas daggernose sharks (*Isogomphodon*) prefer turbid waters near river mouths to depths of 40 m; the latter two species are apparently intolerant of hyposaline conditions (Compagno et al. 2005). The discovery of a hexanchid in the Dry Branch Formation, occurring at both NAS and SAS, is particularly notable because these sharks have not previously been reported from the late Eocene of the Gulf and Atlantic coastal plains. Stingrays currently inhabiting coastal waters of South Carolina, including *Hypanus sabinus*, *Hy. say* (Lesueur, 1817), and *Hy. americanus* (Hildebrand and Schroeder, 1928), occur at depths of nine to 25 m (Snellson et al. 1988, McEachran and Carvalho 2002, Farmer 2004, Aguiar et al. 2009). Wedgefish (*Rhynchobatus*) commonly occur in coastal waters to depths of 25 m (Compagno and Last 1999a), and cow-nosed rays (*Rhinoptera*) inhabit a variety of nearshore habitats in water depths up to 26 m (Compagno and Last 1999b). Although extant angel sharks (*Squatina*) inhabit a wide range of habitats, primarily remaining buried in the substrate waiting to ambush prey (Compagno 1984, Compagno et al. 2005), Case (1981) considered *Squatina* to be indicative of an estuarine depositional environment, whereas Manning and Standhardt (1986) believed the absence of the genus was evidence for fully marine conditions.

Barnacle faunas reported from the Griffins Landing Sand have been used as an indication of a subtidal to inner shelf environment, and the SAS Dry Branch sample contains at least one taxon (cf. *Hesperibalanus* Pilsbury, 1916). We recovered several specimens of the coral *Endopachys* Milne Edwards and Haime, 1848, and extant species of this genus can be found in subtropical inner to middle shelf environments (20–100 m) where water temperatures are between 21° and 22° C (Brook 1999, Keller and Os'Kina 2008). An additional, unidentified coral, represented by several small and poorly preserved conical calyces, occurs at the SAS.

Many specimens recovered from both sites exhibit unusual circular depressions, including teeth of *Hemipristis*, *Carcharias*, *Negaprion*, Myliobatidae, *Sphyræna*, and crocodile, as well as mollusk steinkerns, phosphate pebbles, and coprolites. These features are usually isolated and penetrate various depths into an object, and sometimes completely through. The surfaces of the markings are white. The marks are found primarily on the roots of the selachian teeth (one was observed at the crown base of a *Carcharias* tooth, where the enameloid covering is thinnest), directly on the crown of *Sphyræna*, and on the crown and root of Myliobatidae teeth. These markings are

similar to features of bioerosion reported on Cretaceous fish teeth by Underwood et al. (1999:fig. 2e). However, we also observed the markings on steinkerns, phosphate pebbles and coprolites, and it is unclear if these are the result of pre-fossilization bioerosion or post-fossilization chemical alteration.

### Connection to the Tethys Sea

The Dry Branch Formation elasmobranch assemblages from NAS and SAS share generic similarities to the Eocene Tethyan region, with *Squatina*, *Alopias*, *Galeocerdo*, *Abdounia*, *Physogaleus*, *Negaprion*, *Rhinoptera*, and *Rhinoptera* having been reported from Europe, Africa, and Asia (Arambourg 1952, Adnet et al. 2010, Underwood et al. 2011, Zalmout et al. 2012, Malyshkina et al. 2013). *Hemipristis curvatus* has been identified in Jordan (Mustafa and Zalmout 2002) and northern Africa (Dames 1883, Priem 1905, Stromer 1905, Case and Cappetta 1990), and *Pseudaetobatus* was originally described from the Eocene of Morocco (Cappetta 1986). *Dasyatis tricuspidatus* is known from Eocene strata of Belgium and England (Casier 1946, Kemp et al. 1990), and *Rhinobatos steurbauti* has been reported from the Paris Basin (Cappetta and Nolf 1981) and Uzbekistan (Case et al. 1996). *Notorynchus kemp* occurs in the Eocene of England (Ward 1979a, Kemp et al. 1990).

### Comparison to Barnwell Group elasmobranch assemblages from Georgia

At the generic level, the elasmobranch assemblages reported from Barnwell Group strata of Georgia (Clinchfield and Dry Branch Formations) are similar in faunal composition, and the South Carolina Dry Branch assemblage contains most of these genera, including *Galeocerdo*, *Squatina*, *Nebrius*, *Carcharias*, *Premontreia*, *Hemipristis*, *Abdounia*, *Negaprion*, *Physogaleus*, *Rhinoptera*, *Aetomylaeus*, and *Dasyatis* (Case 1981, Case and Borodin 2000, Parmley and Cicimurri 2003, DJC and JLK unpublished data). The Georgia assemblages also contain taxa not yet known in the South Carolina Dry Branch Formation, including *Otodus* (*Carcharocles*) Jordan and Hannibal, 1923, *Macrorhizodus* Glikman, 1964, *Heterodontus* Blainville, 1816, *Pristis*, and *Propristis* Dames, 1883 (see references cited above). Conversely, the South Carolina Dry Branch paleofaunas contain taxa not known from Georgia, including *Notorynchus*, *Isogomphodon*, *Rhynchobatus*, and *Pseudaetobatus*. These differences could be related to collecting biases, but the samples from the Dry Branch Formation of South Carolina and the Clinchfield Formation of Georgia that we examined were obtained during

multiple site visits over the course of several years, through prospecting surfaces for exposed macrofossils and processing bulk matrix samples for microfossils. These units are not time-equivalent, and the differences could be related to variations in depositional environment, with, for example, absence of *Otodus* (*Carcharocles*) and *Macrorhizodus* from the South Carolina assemblage reflecting the very shallow, probably turbid conditions and/or coarse sandy substrate. However, Zalmout et al. (2012) reported both *Otodus* (*Carcharocles*) and *Macrorhizodus* from river-influenced bay/estuarine deposits in Egypt, and perhaps these larger sharks were attracted to the area, where marine mammals were apparently plentiful. Marine mammals are thus far unknown from the Dry Branch Formation.

### CONCLUSIONS

Not surprisingly, comparison of the vertebrate assemblages from the NAS and SAS revealed a similar taxonomic composition within the fish component. Both assemblages are derived from the upper part of the Dry Branch Formation and are separated by only 13 km (SAS is nearly 7 km further inland). Both sites are thought to have been very close to the late Eocene shoreline, as crocodylian and trionychid turtle fragments were found at both sites. The SAS is thus far the furthest inland within the South Carolina Coastal Plain from which Eocene marine vertebrates have been reported. The SAS is also significant because it has now yielded two new elasmobranch species, including *Pseudaetobatus undulatus* (Cicimurri and Ebersole 2015) and *Isogomphodon aikenensis* described herein. The Dry Branch Formation sediments occurring at both sites, especially SAS, may have been derived from metamorphic rocks and/or pegmatites located in Aiken County. The two elasmobranch assemblages we recovered are similar to, but less diverse than, those reported from the Clinchfield (Parmley and Cicimurri 2003) and Dry Branch (Case 1981, Case and Borodin 2000) Formations of central Georgia. Close proximity to the shoreline could account for lower taxonomic diversity in the South Carolina Dry Branch assemblages, and large pelagic sharks like *Macrorhizodus* and *Otodus* (*Carcharocles*) may have preferred deeper water. However, diagenetic alteration/obliteration of remains (i.e., current action, bioerosion, chemical leaching) may also be a phenomenon affecting species diversity. The variety of elasmobranch and teleost tooth morphologies occurring in the Dry Branch Formation indicates greater prey species richness (i.e., invertebrates and small vertebrates) than is currently known.

There are tantalizing clues that additional vertebrate faunas are preserved within other Eocene deposits in the region. We examined two small collections of vertebrate fossil that were made by Zullo and Kite (1985) during a study of barnacles from the Dry Branch Formation. Both samples were recovered from deposits attributed to the Griffins Landing Sand, and the various elasmobranch and bony fish species we identified are listed in Appendix 1. The shark teeth are well preserved and helped confirm the identity of some species that we collected from the Irwinton Sand. Kite (1982a) collected an assortment of elasmobranch remains from the middle Eocene Huber Formation, which underlies the Dry Branch Formation to the east of Aiken, and the species we identified from her illustrated material are listed in Appendix 2. She also noted that her material was poorly preserved, fragile, and had been altered to clay.

Finding additional vertebrate faunas within the Dry Branch Formation and other Barnwell Group strata in South Carolina may be a difficult task. It is interesting to note that, of eight stratigraphic sections of the Dry Branch Formation prepared by Kite (1982b), none were reported to contain vertebrate fossils. Attempts to revisit these sites have been thwarted because of landscape alteration or they no longer exist. For example, a borrow pit in northeastern Hollow Creek Quadrangle (stop 7 of Kite 1982b) is now used as an inert landfill. Other sites, like Kite's (1982a) Huber Formation site and stop 4 of Zullo et al. (1982; locality SCGS-004, 33° 29' 27" N lat., 81° 49' 5" W long.), are overgrown and part of housing subdivisions (as are the NAS and SAS). Additionally, the Griffins Landing Sand largely occurs in the subsurface of the region.

Even with abundant exposures, discovering elasmobranch teeth at other sites may not occur unless lithostratigraphic beds contain large fossils and/or concentrations of remains. Teeth are easily eroded from the fossiliferous horizon at the SAS, and larger specimens occurring as float are common around the base of the exposure. As control samples, we collected matrix randomly from 110 cm, 100 cm, 60 cm, and 30 cm below the fossil horizon, as well as 10 cm and 165 cm above. We obtained two additional samples from the Tobacco Road Formation, one from within the lowermost 5 cm, and one 30 cm above the base. Of the 4.5 kg of matrix processed from each of these horizons, only two teeth were recovered in the sample from 60 cm below the fossiliferous horizon, and a few from the sample 10 cm above (thin-bedded red sand and white sandy clay). In contrast, the fossiliferous horizon at the SAS yielded approximately 30 specimens

per kg of matrix sampled.

#### ACKNOWLEDGEMENTS

We would like to express our appreciation to Andrew Scheffield, Katie White, and David Briedis for the long hours they spent sorting through matrix with a binocular microscope and counting specimens. Karin, Ryan, and Stacy Knight helped JLK recover fossils during many visits to the Nouth Aiken site (NAS), and Christian and Morgan Cicimurri accompanied DJC and JLK to the North and South Aiken sites (SAS). Mike Bruggeman assisted JLK at the NAS, and Ralph Willoughby confirmed that the strata at the NAS belonged to the Dry Branch Formation. Bobby and Susan Congdon donated a large collection of fossils from the SAS to SC. Scott Harris determined that greenish-black grains occurring in matrix from the SAS were an amphibole mineral. Mark Smith and Christian Cicimurri arranged for the loan of McKissick Museum (University of South Carolina, Columbia) specimens to DJC. Editorial comments provided by Peter Kloess and Diane M. Erwin, as well as input from Will Doar (South Carolina Geological Survey, Columbia, SC) and Charlie Underwood (Birkbeck, University of London), improved upon our original manuscript.

#### LITERATURE CITED

- Adnet, S., P.-O. Antoine, S.R. Hassan Baqri, J.-Y. Crochet, L. Marivaux, J.-L. Welcomme, and G. Metais. 2007. New tropical carcharhinids (Chondrichthyes, Carcharhiniformes) from the late Eocene-early Oligocene of Balochistan, Pakistan: paleoenvironmental and paleogeographic implications. *Journal of Asian Earth Sciences* 30:303–323. <http://dx.doi.org/10.1016/j.jseas.2006.10.002>
- Agassiz, L. 1835. Revue critique des poissons fossils figurés dans l'ittologia veronesé. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde* 1835:290–316.
- Agassiz, L. 1843. Recherches sur les Poissons Fossiles. Tome IV (livr. 4). Neuchatel: Imprimerie de Petitpierre. Pp. 33–52.
- Aguiar, A.A., J.L. Valentin, and R.S. Rosa. 2009. Habitat use by *Dasyatis americana* in a south-western Atlantic oceanic island. *Journal of the Marine Biological Association of the United Kingdom* 89(6):1147–1152.
- Albin, E.F. 1999. Regional stratigraphic correlation of North American Tektites. Abstracts of the 30<sup>th</sup> Lunar and Planetary Science Conference, abstract 1357.
- Albin, E.F., and J.M. Wampler. 1996. New potassium-argon ages for georgiites and the Upper Eocene Dry Branch Formation (Twiggs Clay Member): Inferences about tektite stratigraphic occurrence. *Lunar and Planetary Science* 27:5–6.
- Antunes, M.T., and S. Jonet. 1970. Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. *Revista da Faculdade de Ciências da Universidade de Lisboa* 16(1):119–280.
- Antunes, M.T., S. Jonet, and A. Nascimento. 1981. Vertébrés (crocodiliens, poissons) du miocène marin de l'alagarve occidentale. *Ciências da Terra* 6:9–38.
- Applegate, S.P. 1972. A revision of the higher taxa of Orectoloboids. *Journal of the Marine Biological Association of India* 14(2):743–751.
- Arambourg, C. 1952. Les vertébrés fossils des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc* 92:1–372.
- Ayres, W.O. 1855. Description of new species of California fishes. *Proceedings of the California Academy of Natural Sciences* 1(1):23–77.
- Bennett, E.T. 1830. Class Pices. Pp. 686–694 in *Memoir of the Life and Public Services of Sir Thomas Stamford Raffles, particularly in the government of Java, 1811–1816, and of Bencoolen and its dependencies, 1817–1824: with details of the commerce and resources of the Eastern Archipelago and selections from his correspondence*. Lady Stamford Raffles, London, 851pp.
- Berg, L.S. 1958. System der Rezenten und Fossilen Fischartigen und Fische. Hochschulbücher für Biologie, Berlin. 310 pp.
- Bigelow, H.B., and W.C. Schroeder. 1953. Sawfishes, guitarfishes, skates and rays; chimaeroids. Fishes of the western North Atlantic, part two. *Memoirs of the Sears Foundation for Marine Research, Yale University*. 514 pp.
- Blainville, H.M.D. de. 1816. Prodrome d'une nouvelle distribution systematique du règne animal. *Bulletin du Société Philomathique du Paris* 8:105–112.
- Blake, C.C. 1862. Shark's teeth at Panama. *Geologist* 5:316.
- Bonaparte, C.L. 1835. *Incografia della fauna italic per le Quattro classi degli animali vertebrati*. Tomo III. Pesci.
- Bonaparte, C.L. 1838. *Selachorum tabula analytica*. *Nuovi Annali delle Scienze Naturali* 1(2):195–214.
- Bor, T.J. 1985. Elasmobranch teeth (Vertebrata, Pisces) from the Dongen Formation (Eocene) in the Netherlands. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 22(2):73–122.
- Brook, F.J. 1999. The coastal scleractinian coral fauna of the Kermadec Islands, southwestern Pacific Ocean. *Journal of the Royal Society of New Zealand* 29(4):435–460.
- Buie, B.F., and E.L. Schrader. 1982. South Carolina kaolin. Pp. 1–12 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). *Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina*. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Cappetta, H. 1970. Les sélaciens du Miocène de la région de Montpellier. *Palaeovertebrata, Memoires Extraordinaire* 1970:1–139.
- Cappetta, H. 1975. Sélaciens et Holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géologie Méditerranéenne* 2:115–134.
- Cappetta, H. 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Géobios* 9(5):551–575. [https://doi.org/10.1016/S0016-6995\(76\)80024-1](https://doi.org/10.1016/S0016-6995(76)80024-1)
- Cappetta, H. 1980. Modification du statut générique de quelques espèces de sélaciens Crétacés et Tertiaires. *Palaeovertebrata* 10(1):29–42.
- Cappetta, H. 1981. Additions à la faune de sélaciens fossils du Maroc. 1: Sur la présence des genres *Heptranchias*, *Alopias* et *Odontorhynchus* dans l'Yprésien des Ouled Abdoun. *Géobios* 14(5):563–575
- Cappetta, H. 1986. Myliobatidae nouveaux (Neoselachii, Batomorphii) de l'Yprésien des Ouled Abdoun, Maroc. *Geologica et*

- Palaeontologica* 20:185–207.
- Cappetta, H. 1987. Handbook of Paleichthyology, Vol. 3B: Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii. Gustav Fischer Verlag, Stuttgart. 193 pp.
- Cappetta, H. 1992. Carcharhiniformes nouveaux (Chondrichthyes, Neoselachii) de l'Ypresien du Bassin de Paris. *Géobios* 25(5):639–646. [https://doi.org/10.1016/0016-6995\(92\)80103-K](https://doi.org/10.1016/0016-6995(92)80103-K)
- Cappetta, H. 2006. Elasmobranchii Post-Triadici (Index speciorum et generum). Backhuys Publishers, Leiden, Germany. 142 pp.
- Cappetta, H. 2012. Handbook of Paleichthyology, Vol. 3E: Chondrichthyes, Mesozoic and Cenozoic Elasmobranchii. Verlag Friedrich Pfeil. 512 pp.
- Cappetta, H., and G.R. Case. 1975. Contribution à l'étude des Sélaciens du groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica Abteilung A* 151(1–3):1–46.
- Cappetta, H., and G.R. Case. 2016. A selachian fauna from the Middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama. *Palaeontographica Abteilung A* 307(1–6):43–103.
- Cappetta, H., and D. Nolf. 1981. Les sélaciens de l'Auvervien de Ronquerolles (Eocène supérieur du Bassin de Paris). *Mededelingen van den Werkgroep voor Tertiaire en Kwartaire Geologie* 18(3):87–107.
- Carrillo-Briceño, J.D., E. Maxwell, O.A. Aguilera, R. Sánchez, and M.R. Sánchez-Villagra. 2015. Sawfishes and Other Elasmobranch Assemblages from the Mio-Pliocene of the South Caribbean (Urumaco Sequence, Northwestern Venezuela). *PLoS ONE* 10(10): e0139230. <https://doi.org/10.1371/journal.pone.0139230>
- Carrillo-Briceño, J.D., O.A. Aguilera, C. De Gracia, G. Aguirre-Fernández, R. Kindlmann, and M.R. Sánchez-Villagra. 2016. An early Neogene elasmobranch fauna from the southern Caribbean (western Venezuela). *Palaeontologica Electronica*. 19.2.27A:1–32. <https://doi.org/10.26879/664>
- Carter, B.D. 1987. Paleogene echinoid distributions in the Atlantic and Gulf Coastal plains. *Palaios* 2:390–404.
- Case, G.R. 1980. A selachian fauna from the Trent Formation, Lower Miocene (Aquitanian) of Eastern North Carolina. *Palaeontographica Abteilung A* 171(1–3):75–103.
- Case, G.R. 1981. Late Eocene selachians from south-central Georgia. *Palaeontographica Abteilung A* 176:52–79.
- Case, G.R., and P.D. Borodin. 2000. Late Eocene selachians from the Irwinton Sand Member of the Barnwell Formation (Jacksonian), WKA mines, Gordon, Wilkinson County, Georgia. *Münchner Geowissenschaften Abhandlungen* 39:5–16.
- Case, G.R., and H. Cappetta. 1990. The Eocene selachian fauna from the Fayum Depression in Egypt. *Palaeontographica Abteilung A* 212:1–30.
- Case, G.R., and H. Cappetta. 1997. A new selachian fauna from the Late Maestrichtian of Texas (Upper Cretaceous/Navarro Group; Kemp Formation). *Münchner Geowissenschaftliche Abhandlungen* 34:131–189.
- Case, G.R., N.I. Udovichenko, L.A. Nessov, A.O. Averianov, and P.D. Borodin. 1996. A Middle Eocene selachian fauna from the White Mountain Formation of the Kizylkum Desert, Uzbekistan, C.I.S. *Palaeontographica Abteilung A* 242(4–6):99–126.
- Casier, E. 1946. La faune ichthyologique de l'Ypresien de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 104:1–247.
- Casier, E. 1967. Le Landénien de Dormaal (Brabant) et sa faune ichthyologique. *Mémoires de Musée Royal d'Histoire Naturelle de Belgique* 156:1–42.
- Cicimurri, D.J., and J.A. Ebersole. 2015. Two new species of *Pseudodaetobatus* Cappetta, 1986 (Batoidei: Myliobatidae) from the southeastern United States. *Palaeontologia Electronica*, 18(1)15A:1–17. <http://dx.doi.org/10.26879/524>
- Cicimurri, D.J., and J.L. Knight. 2009. Late Oligocene sharks and rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA. *Acta Palaontologica Polonica* 54(4):627–647.
- Compagno, L.J.V. 1973. Interrelationships of living elasmobranchs. *Zoological Journal of the Linnean Society* 53:15–61.
- Compagno, L.J.V. 1984. FAO Species Catalogue. Vol. 4: Sharks of the world, Part 1 – Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis* 4(1):1–250.
- Compagno, L.J.V., and P.R. Last. 1999a. Rhinobatiformes: Rhinidae (=Rhynchobatidae). Pp. 1418–1422 in K.E. Carpenter and V.H. Niem (eds.). FAO Species Identification Guide for Fishery Purposes. The Living marine Resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeroids, and bony fishes part 1 (Elopidae to Linophrynidae).
- Compagno, L.J.V., and P.R. Last. 1999b. Myliobatiformes: Rhinopteridae. Pp. 1520–1523 in K.E. Carpenter and V.H. Niem (eds.). FAO Species Identification Guide for Fishery Purposes. The Living marine Resources of the Western Central Pacific. Volume 3. Batoid fishes, chimaeroids, and bony fishes part 1 (Elopidae to Linophrynidae).
- Compagno, L.J.V., M. Dando, and S. Fowler. 2005. Sharks of the World. Princeton University Press, Princeton, New Jersey. 368 pp.
- Cuvier, G. 1829. Le règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Louis Hauman et Comp, Brussels, Belgium. 626 pp. <https://doi.org/10.5962/bhl.title.49223>
- Dames, W. 1883. Über eine tertiäre Wirbelthierfauna von der westlichen Insel des Birket-el-Qurūn im Fajum (Aegypten). *Sitzungsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 6:129–153.
- Darteville, E., and Casier, E. 1943. Les poisons fossils du bas-Congo et des régions Voisines (Part I). *Annales du Musée Congo belge, Minéralogique Géologique, Paléontologique* 3(2):1–200.
- Darteville, E., and Casier, E. 1959. Les poissons fossils du bas-Congo et des régions Voisines (Part III). *Annales du Musée Congo belge, Minéralogique Géologique, Paléontologique* 3(2):257–568.
- de Buen, F. 1926. Catalogo ictológico del Mediterraneo Español y de Marruecos, recopilando lo publicado sobre peces de las costas mediterráneas y próximas del Atlántico (Mar de España). Resultados de las campañas Realizadas por Acuerdos Internacionales. *Instituto Español de Oceanografía* 2:1–221.
- Denison, R.E., E.A. Hetherington, Jr., B.A. Bishop, D.A. Dahl, and R.B. Koepnick. 1993. The use of strontium isotopes in stratigraphic studies; an example from North Carolina. *Southeastern Geology* 33(2):53–69.
- Dumeril, A.H.A. 1806. Zoologie analytique, ou method naturelle de classification des animaux. Paris. 344 p.
- Eastman, C.R. 1904. Pisces (Miocene). *Maryland Geological Survey* 2(1):71–93.
- Emmons, E. 1858. Descriptions of the fossils of the marl beds.

- North Carolina Geological Survey. 314 pp.
- Eversull, L.G. 2005. The Twiggs Clay: mineralogy, origin, and industrial properties of an upper Eocene opaline claystone in the coastal plain province of Georgia, U.S.A. Ph.D. dissertation. Louisiana State University, Baton Rouge, Louisiana. 167 pp.
- Fallow, W.C., and Price, V. 1995. Stratigraphy of the Savannah River Site and surrounding vicinity. *Southeastern Geology* 35(1):21–58.
- Falls, W.F., and D.C. Prowell. 2001. Stratigraphy and depositional environments of sediments from five cores from Screven and Burke counties, Georgia. *USGS Professional Paper* 1603-A:1–20.
- Farmer, C.H., III. 2004. Sharks of South Carolina. South Carolina Department of Natural Resources, Charleston, South Carolina. 144 pp.
- Finch, J. 1824. Geological essay on the Tertiary formations in America. *American Journal of Science* 7:31–43.
- Garman, S. 1908. New Plagiostoma and Chismopnea. *Bulletin of the Museum of Comparative Zoology at Harvard College* 51:249–256.
- Garman, S. 1913. The Plagiostoma (sharks, skates and rays). *Memoirs of the Museum of Comparative Zoology at Harvard College* 36:1–528.
- Gervais, P. 1852. Zoologie et paléontologie françaises (1 ère édit). Paris. 271 pp.
- Gibbes, R.W. 1848. Monograph of the fossil Squalidae of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2(1):139–147.
- Gibbes, R.W. 1850. New species of *Myliobates* from the Eocene of South Carolina, with other genera not heretofore observed in the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 2(1):299–300.
- Gill, T.N. 1862. Analytical synopsis of the order Squali, and a revision of the nomenclature of the genera. *Annals of the Lyceum of Natural History of New York* 7:371–408. <http://dx.doi.org/10.1111/j.1749-6632.1862.tb00166.x>
- Glikman, L.S. 1964. Sharks of Paleogene and their stratigraphic significance (in Russian). Nauka Press, Moscow. 229 pp.
- Gray, J.E. 1851. List of the specimens of fish in the collection of the British Museum. Part 1. Chondropterygii. British Museum (Natural History), London. 160 pp.
- Gurr, P.R. 1962. A new fish fauna from the Woolwich Bottom Bed (Sparnacian) of Herne Bay, Kent. *Proceedings of the Geologists' Association* 73:419–447. [https://doi.org/10.1016/S0016-7878\(62\)80032-7](https://doi.org/10.1016/S0016-7878(62)80032-7)
- Harris, R.S., M.S. Duncan, S.M. Holland, M.F. Roden, and P.A. Schroeder. 2002. Probable shocked quartz as evidence for an upper Eocene impact horizon in coastal plain strata, Warren County, Georgia, U.S.A. Geological Society of America, Abstracts with Programs, 2002, paper 178-9.
- Harris, R.S., M.F. Roden, P.A. Schroeder, S.M. Holland, M. S. Duncan, and E.F. Albin. 2004. Upper Eocene impact horizon in east-central Georgia. *Geology* 32(8):717–720.
- Harris, W.B., and V.A. Zullo. 1991. Eocene and Oligocene stratigraphy of the outer Coastal Plain. In J.W. Horton, Jr. and V.A. Zullo (eds.). *The Geology of the Carolinas. Carolina Geological Society Fiftieth Anniversary Volume*:251–262.
- Hasse, C. 1879. Das Natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung Ihrer Wirbelsäule. Eine Morphologische und Paläontologische Studie. Von Gustav Fischer. 76 pp.
- Haye, T., T. Reinecke, K. Gürs, and A. Piehl. 2008. Die Elasmobranchier des Neochattiums (Oberoligozän) von Johannistal, Ostholstein, und Ergänzungen zu deren Volkomen in der Tarzeburg-Formation (Neochattium) des südöstlichen Nordseebeckens. *Palaeontos* 14:55–97.
- Herman, J. 1977. Additions to the Eocene fish fauna of Belgium. 3. Revision of the Orectolobiforms. *Tertiary Research* 1(4):127–138.
- Herman, J., M. Hovestadt-Euler, and D.C. Hovestadt. 1991. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part A: Selachii. No. 2c: Order: Carcharhiniformes. Families: Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae, and Carcharhinidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 61:73–120.
- Herman, J., M. Hovestadt-Euler, and D.C. Hovestadt. 1992. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part A: Selachii. No. 4: Order: Orectolobiformes. Families: Brachaeluridae, Ginglymostomatidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomatidae. Order: Pristiophoriformes – Family: Pristiophoridae. Order: Squatiniformes – Family: Squatinidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 62:193–255.
- Herman, J., and G. van den Eeckhaut. 2010. Inventaire systématique des Invertébrata, Vertébrata, Plantae et Fungi des Sables de Bruxelles. *Geominpal Belgica Découvertes géologiques, minéralogiques et paléontologiques en Belgique* 1(2):35–65.
- Hildebrand, S.F., and W.C. Schroeder. 1928. Fishes of Chesapeake Bay. Bulletin of the United States Bureau of Fisheries 43(1):1–366.
- Hovestadt, D.C., and M. Hovestadt-Euler. 1999. *Weissobatis micklichi* n. gen., n. sp., an eagle ray (Myliobatiformes, Myliobatidae) from the Oligocene of Frauenweiler (Baden-Württemberg, Germany). *Paläontologische Zeitschrift* 73(3/4):337–349.
- Hovestadt, D.C., and M. Hovestadt-Euler. 2013. Generic assessment and reallocation of Cenozoic Myliobatidae based on new information of tooth, tooth plate and caudal spine morphology of extant taxa. *Palaeontos* 24:1–66.
- Huddlestun, P.F. 1982. The development of the stratigraphic terminology of the Claibornian and Jacksonian marine deposits of western South Carolina and eastern Georgia. Pp. 21–33 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Huddlestun, P.F. 1990. The Paleogene of the northeastern Gulf of Mexico Coastal Plain. Pp. 23–24 in V.A. Zullo, W.B. Harris, and V. Price (eds.). *Savanna River Region: Transition Between the Gulf and Atlantic Coastal Plains*. University of North Carolina, Wilmington.
- Huddlestun, P.F. 1993. A revision of the lithostratigraphic units of the Coastal Plain of Georgia – The Oligocene. *Georgia Geologic Survey Bulletin* 105:1–152.
- Huddlestun, P.F., and J.H. Hetrick. 1979. The stratigraphy of the Barnwell Group of Georgia. *Georgia Geologic Survey, 14<sup>th</sup> Annual Field Trip of the Georgia Geological Society*:1–89.
- Huddlestun, P.F., and J.H. Hetrick. 1986. Upper Eocene stratigraphy of central and eastern

- Georgia. *Georgia Geologic Survey Bulletin* 95:1–78.
- Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880:649–662.
- Jaekel, O. 1894. Die eocänen Selachier vom Monte Bolca. Verlag von Julius Springer, Berlin 176 pp.
- Jonet, S. 1966. Notes d'Ichthyologie Miocène II. – Les Carchariniidae. *Boletim do Museu e Laboratório Mineralógico e Geológico da Faculdade de Ciências* 10:65–88.
- Jordan, D.S. 1888. A manual of the vertebrate animals of the northern United States, including the district north and east of the Ozark Mountains, south of the Laurentian hills, north of the southern boundary of Virginia, and east of the Missouri River, inclusive of marine species. A.C. McClurg Company, Chicago, Illinois. 375 pp.
- Jordan, D.S., and B.W. Evermann. 1896. The fishes of the North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum* 47:1–1240.
- Jordan, D.S., and H. Hannibal. 1923. Fossil sharks and rays of the Pacific slope of North America. *Bulletin of the Southern California Academy of Sciences* 22:27–63.
- Kajiura, S.M., and T.C. Tricas. 1996. Seasonal dynamics of dental sexual dimorphism in Atlantic stingrays, *Dasyatis sabina*. *Journal of Experimental Biology* 199(10):2297–2306.
- Kajiura, S.M., A.P. Sebastian, and T.C. Tricas. 2000. Dermal bite wounds as indicators of reproductive seasonality and behavior in the Atlantic stingray, *Dasyatis sabina*. *Environmental Biology of Fishes* 58(1):23–31.
- Keller, N.B., and N.S. Os'kina. 2008. Habitat temperature ranges of azooxantellate scleractinian corals in the world ocean. *Oceanography* 48(1):77–84.
- Kemp, D.J., L. Kemp, and D.J. Ward. 1990. An illustrated guide to the British middle Eocene vertebrates. Privately published, London. 59 pp.
- Kent, B. 1994. Sharks of the Chesapeake Bay region. Egan Rees and Boyer, Inc., Columbia, Maryland. 146 pp.
- Kent, B. 1999. Sharks from the Fisher/Sullivan site. Pp. 11–38 in R.E. Weems and G.J. Grimsley (eds.). Early Eocene vertebrates and plants from the Fisher/Sullivan site, (Nanjemoy Formation) Stafford County, Virginia. *Virginia Division of Mineral Resources* 152.
- Kirby, M.X. 2000. Paleoecological differences between Tertiary and Quaternary *Crassostrea* oysters, as revealed by stable isotope sclerochronology. *Palaios* 15(2):132–141.
- Kite, L.E. 1982a. Tertiary stratigraphy of the Oakwood quadrangle, Aiken County, South Carolina. Pp. 65–78 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Kite, L.E. 1982b. Appendix to the field guide. Pp. 132–183 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Leidy, J. 1855. Indications of twelve species of fossil fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 7:395–397.
- Leidy, J. 1877. Description of vertebrate remains, chiefly from the Phosphate Beds of South Carolina. *Journal of the Academy of Natural Sciences* 8(2):209–261.
- Leriche, M. 1905. Les poissons éocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 3:49–228.
- Leriche, M. 1910. Les Poissons oligocènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 5:229–363.
- Leriche, M. 1927. Les Poissons de la Molasse Suisse. *Mémoires de la Société Paléontologique Suisse* 46:1–55.
- Leriche, M. 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains Tertiaires de la plaine cotière Atlantique et du centre des États-Unis. *Mémoires Société Géologique de France* 45:1–110.
- Lesueur, C.A. 1817. Description of three new species of the genus *Raja*. *Journal of the Academy of Natural Sciences of Philadelphia* 1:41–45.
- Lessa, R., V.S. Batista, and Z. Almeida. 1999. Occurrence and biology of the daggernose shark *Isogomphodon oxyrinchus* (Chondrichthyes: Carcharhinidae) off the Maranhão Coast (Brazil). *Bulletin of Marine Science* 64(1):115–128.
- Lessa, R., V.S. Batista, and F.M. Santana. 2016. Close to extinction? The collapse of the endemic daggernose shark (*Isogomphodon oxyrinchus*) off Brazil. *Global Ecology and Conservation* 7:70–81.
- Lesueur, C.A. 1817. Description of three new species of the genus *Raja*. *Journal of the Academy of Natural Sciences of Philadelphia* 1:41–45.
- Lesueur, C.A. 1824. Description of several species of the Linnaean genus *Raia* of North America. *Journal of the Academy of Natural Sciences, Philadelphia* 4(1):100–121.
- Linck, H.F. 1790. Versuch einer Eintheilung der Fische nach den Zähnen. *Magazin für das Neueste aus der Physik und Naturgeschichte* 6(3):28–38.
- Lowe, R.T. 1841. A paper from the Rev. R.T. Lowe, M.A., describing certain new species of Medean fishes, and containing additional information relating to those already described. *Proceedings of the Zoological Society of London* 8:36–39.
- Malyshkina, T. 2006. Late Eocene scyliorhinid sharks from the Trans-Urals, Russia. *Acta Palaeontologica Polonica* 51(3):465–475.
- Malyshkina, T., G. González-Barba, and A.F. Bannikov. 2013. Records of elasmobranchian teeth in the Bartonian of the Northern Caucasus (Russia) and Crimea (Ukraine). *Paleontological Journal* 47(1):98–103. <https://doi.org/10.1134/S0031030113010085>
- Manning, E.M., and B.R. Standhardt. 1986. Late Eocene sharks and rays from Montgomery Landing, Louisiana. Pp. 133–161 in Montgomery Landing Site, Marine Eocene (Jackson) of Central LA. *Proceedings of the GCAGS Symposium*, Baton Rouge, LA.
- McEachran, J.D., and M.R. de Carvalho. 2002. Batoid Fishes. Pp. 508–530 in K.E. Carpenter (ed.). *The living marine resources of the western Central Atlantic*. Volume 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras. FAO Species Identification Guide for Fisheries Purposes and American Society of Ichthyologists and Herpetologists Special Publication 5.
- Milne Edwards, H., and J. Haime. 1848. Recherches sur les Polypiers, deuxième mémoire, Monographie des Turbinolides. *Annales des Sciences Naturelles (Zoologie et Biologie)* 3(9):211–344.
- Mittweide, S.K. 1982. Stratigraphy of the Jackson area, Aiken

- County, South Carolina. Pp. 65–78 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Mollen, F. 2008. A new Middle Eocene species of *Premontreia* (Elasmobranchii, Scyliorhinidae) from Vlaams-Brabant, Belgium. *Geologica Belgica* 11:123–131.
- Mora, A.C.L. 1999. Los seláceos fósiles de la localidad de Alto Guáyacan (y otros ictiolitos asociados). Mioceno Superior-Plioceno Inferior de la Formación Uscari, Provincia de Limón, Costa Rica. Privately published, San Jose, Costa Rica. 124 pp.
- Müller, A. 1999. Ichthyofaunen aus dem atlantischen Tertiär der USA. *Leipziger Geowissenschaften* 9-10:1–360.
- Müller, J., and J. Henle. 1837. Gattungen der Haifische un Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. *Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin* 1837:111–118.
- Müller, J., and J. Henle. 1838. On the generic characters of cartilaginous fishes, with descriptions of new genera. *Magazine of Natural History and Journal of Zoology, Botany, Mineralogy, Geology and Meteorology* 2:33–37, 88–91.
- Müller, J., and J. Henle. 1841. Systematische Beschreibung der Plagiostomen. Verlag von Veit und Companie, Berlin, Germany. 200 pp.
- Mustafa, H., and I.S. Zalmout. 2002. Elasmobranchs from the late Eocene Wadi Esh-Shallala Formation of Qa'Faydat ad Dahikiya, east Jordan. *Tertiary Research* 21:1–18.
- Mustafa, H., I.S. Zalmout, A.A. Smadi, and I. Nizzal. 2005. Review of the Middle Eocene (Lutetian) selachian fauna of Jebal eth Thuleithuwat, east Jordan. *Neues Jahrbuch für Geologie un Paläontologie, Abhandlungen* 237(3):399–422.
- Naylor, G.P., J.N. Caira, K. Jensen, K.A.M. Rosana, N. Straube, and C. Lakner. 2012. Elasmobranch Phylogeny: A mitochondrial estimate based on 595 species. Pp. 31–56 in J.C. Carrier, J.A. Musick, and M.R. Heithaus (eds.). *Biology of Sharks and their relatives*. CRC Press, Boca Raton, Florida.
- Nolf, D. 1988. Dents de requins et de raies du Tertiaire de la Belgique. Institut Royal des Sciences Naturelles de Belgique. 184 pp.
- Noubhani, A., and H. Cappetta, 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien-Lutétien basal): Systématique, biostratigraphie, évolution et dynamique des faunes. *Palaeo Ichthyologica* 8:1–326.
- Nystrom, P.G., Jr., and R.H. Willoughby. 1982. Cretaceous, Tertiary, and Pleistocene (?) stratigraphy of Hollow Creek and Graniteville quadrangles, Aiken County, South Carolina. Pp. 80–113 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.
- Parmley, D., and D.J. Cicimurri. 2003. Late Eocene sharks of the Hardie Mine local fauna of Wilkinson County, Georgia. *Georgia Journal of Science* 61(3):153–179.
- Povenmire, K.I., and H. Povenmire. 2002. Three well documented Georgia tektites from Montgomery, Wheeler, and Twiggs counties, Georgia. *Lunar and Planetary Science XXXIII*:1.
- Pawłowska, K. 1960. Szczałki ryb z wapieni Miocennskich Pińczowa. *Acta Palaeontologica Polonica* 5(4):421–432.
- Pilsbury, H.A. 1916. The sessile barnacles (Cirripedia) contained in the collection of the US National Museum; including a monograph of the American Species. *Bulletin of the United States National Museum* 93:1–357.
- Poey, F. 1868. Synopsis piscium cubensium. Catalogo razonado de los peces de la isla de Cuba. Repertorio Físico-Natural de la Isla de Cuba 2:279–484.
- Priem, F. 1905. Sur les poissons fossils de l'éocène moyen d'Égypte. *Bulletin de la Société Géologique de France* (new series) 5:633–641.
- Priem, F. 1907. Sur des Vertébrés de l'Eocène d'Égypte et de Tunisie. *Bulletin de la Société géologique de France* (series 4) 7:412–419.
- Priem, F. 1909. Note sur des poissons fossils des phosphates de Tunisie et d'Algérie. *Bulletin de la Société Géologique de France* (new series) 9:315–324.
- Probst, J. 1877. Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen, II: Batoidei A. Gunther. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 33:69–103.
- Probst, J. 1879. Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. Hayfische. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 35:127–191.
- Purdy, R.W., and M.P. Francis. 2007. Ontogenetic development of teeth in *Lamna nasus* (Bonnaterre, 1758) (Chondrichthyes: Lamnidae) and its implications for the study of fossil shark teeth. *Journal of Vertebrate Paleontology* 27(4):798–810. [https://doi.org/10.1671/0272-4634\(2007\)27\(798:ODOTIL\)2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27(798:ODOTIL)2.0.CO;2)
- Purdy, R.W., V.P. Schneider, S.P. Applegate, J.H. McLellan, R.L. Meyer, and B.H. Slaughter. 2001. The Neogene sharks, rays and bony fishes from Lee Creek Mine, Aurora, North Carolina. *Smithsonian Contributions to Paleontology* 90:71–202. <http://dx.doi.org/10.5479/si.00810266.90.1>
- Rafinesque, C.S. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medesimi. Part 1. 3–69. Palermo, Italy. <https://doi.org/10.5962/bhl.title.104418>
- Rangel, B.S., S. Rodrigues, E. Malavasi-Bruno, S.E.A. Will, P.O. Favaron, A.F. Amorim, and R.E.G. Ricci. 2014. 3-D aspects of the dentition in rays of the genus: *Atlantoraja*, *Rhinobatos* and *Zapteryx* from Southeastern and South of Brazil. Pp. 3–9 in A. Méndez-Vilas (ed.). *Microscopy: advances in scientific research and education*. Microscopy book series, 2014 edition, FORMATEX, Badajoz.
- Reinecke, T., H. Stapf, and M. Raisch. 2001. Die Selachier und Chimären des Unteren Meeressandes und Schleichsandes im Mainzer Becken (Rupelium, Unteres Oligozän). *Palaeontos* 1:1–73.
- Reinecke, T., H. Mohs, A. Grant, and H. Breitzkreuz. 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oligozän). *Palaeontos* 8:1–135.
- Reinecke, T., F. von der Hocht, and K. Gürs. 2008. Die Elasmobranchier des Vierlandiums, Unteres Miozän, im Nordwestdeutschen Becken aus Bohrungen und glazifluvialiten Geröllen ("Holsteiner Gestein") der Vierlande-Feinsande (Holstein) und der Kakert-Schichten (Niederrhein). *Palaeontos* 14:1–54.
- Rüppell, E. 1837. Neue Wirbelthiere zu der Fauna von Abyssinien gehörig, entdeckt und beschrieben. Fische des rothen Meeres.

- Siegmund Schemerber, Frankfurt am Main, Germany. 148 pp. <https://doi.org/10.5962/bhl.title.53778>
- Sanders, A.E. 2002. Additions to the Pleistocene mammal faunas of South Carolina, North Carolina, and Georgia. *Transactions of the American Philosophical Society* 92(5):1–152.
- Schroeder, P.A., R.S. Harris, M.F. Roden, M.S. Duncan, and S.M. Holland. 2002. X-ray diffraction evidence for shocked quartz in an upper Eocene sand deposit, Warren County, Georgia, U.S.A. Geological Society of America, abstracts with programs, 2002 annual meeting, paper 239:12.
- Segalla, M.P., D.L. Siron, and D.J. Colquhoun. 2000. Depositional and diagenetic signatures of Late Eocene–Oligocene sediments, South Carolina. *Sedimentary Geology* 134:24–47.
- Snelson, F.F., Jr., S.E. Williams-Hooper, and T.H. Schmid. 1988. Reproduction and ecology of the Atlantic stingray, *Dasyatis sabina*, in Florida coastal lagoons. *Copeia* 1988(3):729–739.
- Snoke, A.W., and D.T. Secor, Jr. 1982. The eastern piedmont fault system and its relationship to Alleghanian tectonics in the southern Appalachians: a discussion. *The Journal of Geology* 90(2):209–211.
- Speer, J.A. 1982. Descriptions of the granitoid rocks associated with two gravity minima in Aiken and Barnwell counties, South Carolina. *South Carolina Geology* 26(1):15–24.
- Steele, K.B., V.A. Zullo, and R.H. Willoughby. 1986. Recognition of the Eocene (Jacksonian) Dry Branch Formation at Usserys Bluff, Allendale County, South Carolina. *South Carolina Geology* 30(2):71–78.
- Storms, R. 1894. Troisième note sur les poissons du terrain rupélien. *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie* 8:67–82.
- Stromer, E. 1903. Haifischzähne aus dem unteren Mokattam bei Wasta in Egypten. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 1:29–41.
- Stromer, E. 1905. Die fischreste des mittleren und oberen Eocäns von Ägypten. I. Tiel: Selachii, B. Squaloidei und II. Tiel: Teleostomi, A. Ganoidei. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns* 18:163–192.
- Tabuce, R., S. Adnet, H. Cappelletta, A. Noubhani, and F. Quillevère. 2005. Aznag (bassin d'Ouazazate, Maroc), nouvelle localité à sélaciens et mammifères de l'Eocène moyen (Lutétien) d'Afrique. *Bulletin de la Société géologique de France* 176(4):381–400. <https://doi.org/10.2113/176.4.381>
- Thurmond, J.T., and D.E. Jones. 1981. Fossil vertebrates of Alabama. University of Alabama Press, Tuscaloosa. 244 pp.
- Timmerman, J., and R. Chandler. 1995. Cretaceous and Paleogene fossils of North Carolina, a field guide. North Carolina Fossil Club, Durham, North Carolina. 70 pp.
- Underwood, C.J., Z. Johanson, M. Welten, B. Metscher, L.J. Rasch, G.J. Fraser, and M.M. Smith. 2015. Development and evolution of dentition pattern and tooth order in the skates and rays (Batoidea: Chondrichthyes). *PLoS ONE* 10(4):e0122553. <http://dx.doi.org/10.1371/journal.pone.0122553>
- Underwood, C.J., and G.C. Gunter. 2012. The shark *Carcharhinus* sp. from the Middle Eocene of Jamaica and the Eocene record of *Carcharhinus*. *Caribbean Journal of Earth Science* 44:25–30.
- Underwood, C.J., S.F. Mitchell, and C.J. Veltkamp. 1999. Microborings in mid-Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society* 52(3):269–274. <http://dx.doi.org/10.1144/pygs.52.3.269>
- Underwood, C.J., D.J. Ward, C. King, S.M. Antar, I.S. Zalmout, and P.D. Gingerich. 2011. Shark and ray faunas in the Middle and Late Eocene of the Fayum area, Egypt. *Proceedings of the Geologists' Association* 122(1):47–66. <http://dx.doi.org/10.1016/j.pgeola.2010.09.004>
- Van den Eekhaut, G., and P. de Schutter. 2009. The elasmobranch fauna of the Lede Sand Formation at Oosterzele (Lutetian, Middle Eocene of Belgium). *Palaeofocus* 1:1–57.
- Ward, D.J. 1978. Additions to the fish fauna of the English Paleogene. 1. Two new species of *Alopias* (Thresher Shark) from the English Eocene. *Tertiary Research* 2(1):23–28.
- Ward, D.J. 1979a. Additions to the fish fauna of the English Paleogene. 3. A review of the Hexanchid sharks with a description of four new species. *Tertiary Research* 2(3):111–129.
- Ward, D.J. 1979b. Additions to the fish fauna of the English Paleogene. 2. A new species of *Dasyatis* (stingray) from the London Clay (Eocene) of Essex, England. *Tertiary Research* 2(2):75–81.
- Westgate, J.W. 1984. Lower vertebrates from the late Eocene Crow Creek local fauna, St. Francis County, Arkansas. *Journal of Vertebrate Paleontology* 4(4):536–546. <https://doi.org/10.1080/02724634.1984.10012029>
- White, E.I., 1926. Eocene fishes of Nigeria. *Bulletin of the Geological Survey of Nigeria* 10:1–82. <https://doi.org/10.1093/oxfordjournals.afraf.a100500>
- White, E.I., 1934. Fossil fishes of Sokoto province. *Bulletin of the Geological Survey of Nigeria* 14:1–78.
- White, E.I. 1955. On *Lamna eurybathrodon* Blake. *The Annals and Magazine of Natural History* 12(8):191–193.
- White, E.I. 1956. The Eocene fishes of Alabama. *Bulletins of American Paleontology* 36(156):122–152.
- White, W.T. 2014. A revised generic arrangement for the eagle ray family Myliobatidae, with definitions for the valid genera. *Zootaxa* 3860(2):149–166. <http://dx.doi.org/10.11646/zootaxa.3860.2.3>
- Whitley, G.P. 1929. Additions to the check-list of the fishes of New South Wales. No. 2. *Australian Zoologist* 5(4):353–357.
- Whitley, G.P. 1940. The fishes of Australia. Part 1. The sharks, rays, devil fishes and other primitive fishes of Australia and New Zealand. Royal Zoological Society of New South Wales. 230 pp.
- Winkler, T.C. 1874. Mémoire sur des dents de poissons du terrain bruxellien. *Archives du Musée Teyler* 3(4):295–304.
- Winkler, T.C. 1876. Deuxième mémoire sur des dents de poissons fossils du terrain bruxellien. *Archives du Musée Teyler* 4(1):16–48.
- Woodward, A.S. 1889. Catalogue of the fossil fishes in the British Museum. Part 1. British Museum (Natural History). 474 pp. <https://doi.org/10.5962/bhl.title.61854>
- Woodward, A.S. 1907. Notes on some Upper Cretaceous fish-remains from the Provinces of Sergipe and Pernambuco, Brazil. *Geological Magazine*, decade 5, 4:193–197.
- Zalmout, I.S.A., M.S.M. Antar, E. Abd-El Shafy, M.H. Metwally, El-Bialy E. Hatab, and P.D. Gingerich. 2012. Priabonian sharks and rays (Late Eocene: Neoselachii) from Minqar Tabaghbagh in the western Qattara Depression, Egypt. *Contributions to the Museum of Paleontology, University of Michigan* 32(6):71–90.
- Zullo, V.A., and L.E. Kite. 1985. Barnacles of the Jacksonian (upper Eocene) Griffins Landing Member, Dry Branch Formation in South Carolina and Georgia. *South Carolina Geology* 28(1):1–22.
- Zullo, V.A., M.P. Katuna, and K.C. Herridge. 1992. Scalpellomorph and balanomorph barnacles (Cirripedia) from the upper Oligocene Ashley Formation, Charleston County, South Carolina.

*South Carolina Geology* 34(1-2):57–67.

Zullo, V.A., R.H. Willoughby, and P.G. Nystrom, Jr., 1982. A late Oligocene or early Miocene age for the Dry Branch Formation and Tobacco Road Sand in Aiken County, South Carolina? Pp. 34–45 in P.G. Nystrom, Jr. and R.H. Willoughby (eds.). Geological investigations related to the stratigraphy in the kaolin mining district, Aiken County, South Carolina. *Carolina Geological Society, Field Trip Guidebook* 1982.

---

**Appendix 1.** Fossil elasmobranch and bony fish species identified from McKissick Museum samples of the Griffins Landing Sand, Dry Branch Formation, recovered by Zullo and Kite (1985).

---

**McKissick Museum locality 03, Griffins Landing (Z-622).**

Chondrichthyes

*Carcharias* sp.

*Hemipristis curvatus*

*Abdounia enniskilleni*

*Rhizoprionodon* sp. cf. *Rhiz. ganntourensis*

*Rhinoptera* sp.

*Dasyatis* sp. cf. *D. tricuspidata*

Osteichthyes

cf. *Sphyraenodus* sp.

*Seriola* sp.

**McKissick Museum locality 06 (=South Carolina Geological Survey locality 2-49), Aiken County auger hole (Z- 723).**

Chondrichthyes

*Carcharias* sp.

*Negaprion gilmorei*

*Physogaleus* sp.

*Abdounia enniskilleni*

Osteichthyes

cf. *Sphyraenodus* sp.

---

**Appendix 2.** Elasmobranch taxa from the Huber Formation exposed to the east of Aiken, Aiken County, South Carolina, based on material figured by Kite (1982a):

---

Chondrichthyes

*Carcharias* sp. (Kite 1982a:fig. 2A-B)

Carcharhiniformes indet. (Kite 1982a:fig. 2C, left)

*Rhizoprionodon* sp. (Kite 1982a:fig. 2C, right)

Myliobatinae indet. (Kite 1982a:fig. 2D)

*Rhinoptera* sp. (Kite 1982a:fig. 2E)

indeterminate batoid caudal spines (Kite 1982a:fig. 2F)