PaleoBios 39:1–38, March 31, 2022

PaleoBios

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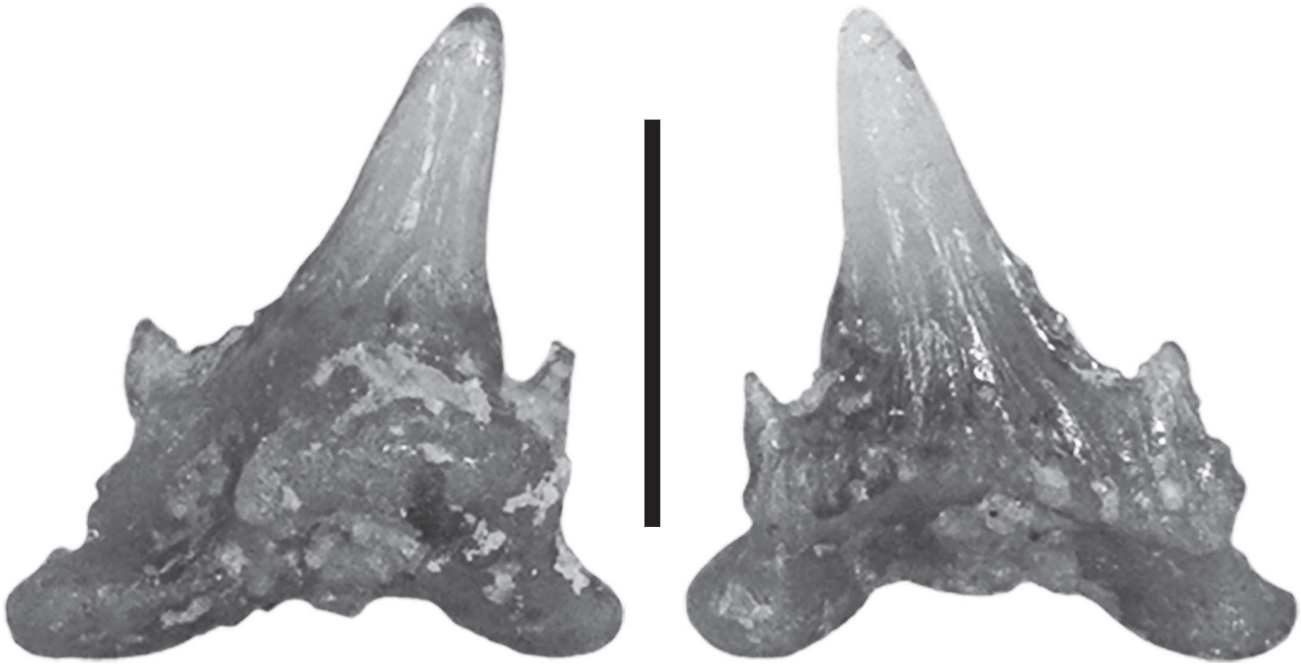

DAVID J. CICIMURRI, JAMES L. KNIGHT & JUN A EBERSOLE (2022). Early Oligocene (Rupelian) fishes (Chondrichthyes, Osteichthyes) from the Ashley Formation (Cooper Group) of South Carolina, USA

Cover: Tooth of the new Oligocene catshark species, *Scyliorhinus weemsi*, in lingual (left) and labial (right) view.
Citation: Cicimurri, D.J., J.L. Knight and J.A. Ebersole, 2022. Early Oligocene (Rupelian) fishes (Chondrichthyes, Osteichthyes) from the Ashley Formation (Cooper Group) of South Carolina, USA. *PaleoBios,* 39. ucmp_paleobios_56976. doi: https://doi.org/10.5070/P939056976.

Early Oligocene (Rupelian) fishes (Chondrichthyes, Osteichthyes) from the Ashley Formation (Cooper Group) of South Carolina, USA

DAVID J. CICIMURRI*[1], JAMES L. KNIGHT[2], and JUN A EBERSOLE[3]

[1]South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina 29201
dave.cicimurri@scmuseum.org
[2]University of South Carolina Aiken, 471 University Parkway, Aiken, South Carolina 29801
karin@gforcecable.com
[3]McWane Science Center, 200 19th Street North, Birmingham, Alabama 35203
jebersole@mcwane.org

Matrix surrounding a dermochelyid carapace and two cetacean skulls recovered from the Givhans Ferry Member of the Ashley Formation (lower Oligocene, Rupelian Stage) in South Carolina, USA yielded a surprisingly diverse assemblage of euselachian and teleost fishes. We identified 21 elasmobranch taxa, including 13 selachians and eight batoids, nearly all of which are known to occur in the overlying upper Oligocene (Chattian) Chandler Bridge Formation. Notable occurrences within the Ashley Formation paleofauna include a new shark, *Scyliorhinus weems*i n. sp., and the first South Carolina Oligocene records of *Squalus* sp., *Pristiophorus* sp., and *Pachyscyllium* sp. Numerous teleost taxa were also documented based on isolated teeth, including species of Albulidae, Paralichthyidae, Osteoglossidae, Sparidae, Sciaenidae, Sphyraenidae, Scombridae, Trichiuridae, and possibly Labridae.

Keywords: Atlantic Coastal Plain, elasmobranch, teleost, Givhans Ferry Member, North America

INTRODUCTION

Ongoing investigations of the upper Eocene (Priabonian Stage) and Oligocene (Rupelian and Chattian stages) marine deposits of the ancient Charleston Embayment that are exposed in the southeastern part of South Carolina are expanding our knowledge of the fish paleofaunas from this region. Vertebrate assemblages currently under study that were recovered from Priabonian units occurring near the study area discussed herein (Parkers Ferry and Harleyville formations) are incredibly diverse but remain to be formally reported. The Chattian Chandler Bridge Formation yielded a significant elasmobranch paleofauna (Cicimurri and Knight 2009a), but although the Rupelian Ashley Formation is broadly distributed within southeastern South Carolina, the fossil fishes occurring within this unit have not been intensively studied. Müller (1999) reported a small number of sharks and rays from the Ashley Formation in South Carolina but did not list any teleosts, and he specifically noted that otoliths were lacking. The alopiid shark, *Trigonotodus alteri* Kozlov, 2001 was described based on teeth collected from the Ashley Formation, and numerous billfish and cetacean taxa have been identified from this lithostratigraphic unit (Fierstine and Weems 2009, Godfrey et al. 2016, Albright et al. 2018, 2019).

Herein we present a report on elasmobranch and teleost teeth that were recovered from matrix associated with the carapace of a dermochelyid sea turtle and two cetacean skulls, all collected from the Givhans Ferry Member of the Ashley Formation in Dorchester County, South Carolina, USA (Fig. 1). These fossils add to our knowledge of the Ashley Formation paleofauna, and this report is part of a long-term effort to document species diversity throughout the entire formation. Our ultimate goals are to identify paleofaunas and determine what,

**author for correspondence*

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DOI: https://doi.org/10.5070/P939056976
Permalink: https://escholarship.org/uc/item/0xv324c8

LSID: urn:lisd:zoobnk.org:pub:13E6A6E9-DE0F-4C71-BE40-2957F48D9F70

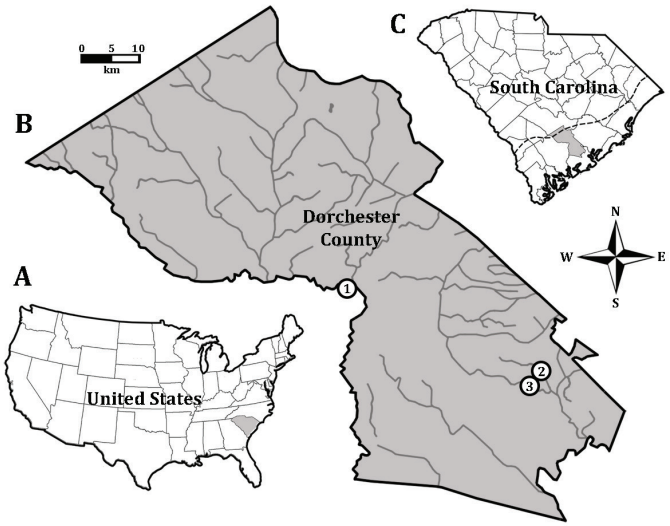

Figure 1. Geographic maps showing the generalized locations of the collection areas. **A**. Outline map of the United States showing the location of South Carolina (gray). **B**. Map of Dorchester County showing collecting localities: **1**=Edisto River; **2**=Dorchester Creek; **3**=Ashley River. **C**. County map of South Carolina showing the location of Dorchester County (gray). The dashed line indicates the location of the early Oligocene shoreline.

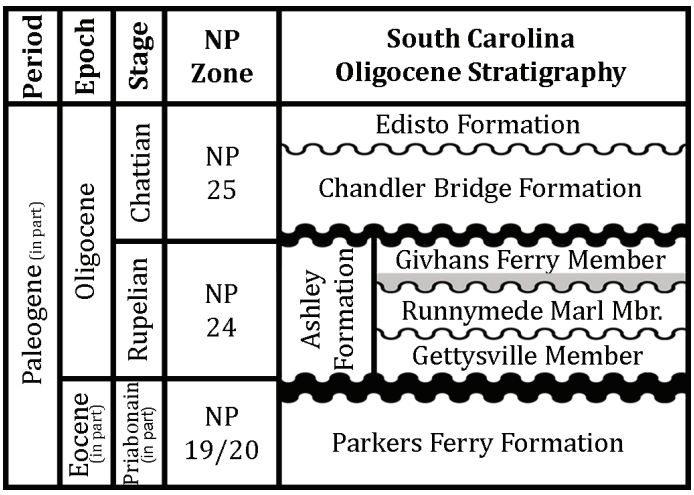

Figure 2. Generalized stratigraphic section showing lithostratigraphic units occurring in South Carolina. Note that the Gettysville Member of the Ashley Formation is restricted to a very small area, and the Runnymeade Marl Member disconformably overlies the Eocene-Oligocene Harleyville Formation (NP21–NP22) over much of its lateral extent. Irregular lines at upper/lower boundaries of units represent unconformities, with weight of the line indicating greater or lesser amounts of missing time. Weems et al. (2016) indicated up to 3.0 Ma of missing time between the Ashley and Chandler Bridge formations. **NP**=nannoplankton zone.

if any, changes occurred between the assemblages in response to the significant climatic shifts that took place from the late Eocene through the late Oligocene.

GEOGRAPHIC AND GEOLOGICAL SETTING

The Eocene-Oligocene Transition was a time of profound global temperature change and sea level fluctuation. The opening of the Drake Passage and development of the Antarctic Circum-Polar Current near the Eocene-Oligocene boundary (e.g., Miller and Wright 1991, Miller et al. 2008, Vandenberghe et al. 2012) resulted in multiple global Oligocene cooling events (Zachos et al. 2001, Pälike et al. 2006). Several embayments were located along the Atlantic Coastal Plain of the present-day United States (USA) during the Oligocene, including the Salisbury Embayment in the region of the mid-Atlantic states, the Albemarle Embayment of North Carolina, and the Charleston Embayment of South Carolina (Fig. 1). The Charleston Embayment provided the setting for marine deposition during the Rupelian (Ashley Formation) and Chattian (Chandler Bridge Formation) stages, from approximately 29 to 24 Ma.

The specimens discussed herein were obtained from the Ashley Formation in Dorchester County, South Carolina, USA. The Ashley Formation is the oldest of three formally named Oligocene lithostratigraphic units that accumulated within the Charleston Embayment, and this formation has recently been subdivided into three members, including (in ascending order) the Gettysville, Runnymeade Marl, and Givhans Ferry, all of which occur within Calcareous Nannofossil Zone NP24 (Weems et al. 2016, Albright et al. 2019) (Fig. 2). The Givhans Ferry Member has yielded nearly all the vertebrate fossil material that has been collected from the Ashley Formation (Weems et al. 2016), including the leatherback sea turtle carapace and the cetacean skulls noted above, which were collected in and around the city limits of Summerville. The Givhans Ferry Member is resistant to overburden compaction, and the fossilized bones of these larger vertebrates were preserved with little distortion of their original morphology. The Givhans Ferry Member may have been deposited during a relatively narrow 300,000-year window, as Weems et al. (2016) reported an absolute age range of 28.43 to 28.75 Ma for this unit.

The Ashley Formation has been interpreted as representing a middle to outer neritic shelf environment (Weems and Lewis 2002), with water depth of at least 100 meters (Fierstine and Weems 2009). Although the three Ashley Formation members are difficult to distinguish in outcrop or through microfossil analyses, the base of the Givhans Ferry Member is distinguished by a concentration of phosphate pebbles and phosphatic

mollusk and scleractinian coral steinkerns (Weems et al. 2016). The Givhans Ferry Member represents a period of highstand during third-order sequence 4.5 of the Tejas A4 supercycle (Coffey and Read 2004) of the late Rupelian. Subsequent to this time, a regressive event occurred that continued into the Chattian (Zachos et al. 2001, Coffey and Read 2004, Pälike et al. 2006), during which time nearshore marine deposits of the overlying Chandler Bridge Formation accumulated within the Charleston Embayment (Sanders et al. 1982, Katuna et al. 1997, Cicimurri and Knight 2009a).

MATERIALS AND METHODS

Specimen collection

The specimens described herein were recovered from matrix surrounding the skeletal remains of two fossil odontocete whales and a dermochelyid sea turtle. All the specimens occurred within the Givhans Ferry Member of the Ashley Formation. With permission from the city of Summerville (Dorchester County), in 2007 the South Carolina State Museum (**SC**) in Columbia, USA excavated the dermochelyid carapace (SC2007.36.1) from the bottom of Dorchester Creek (locality 2 in Fig. 1B). The carapace occurred dorsal surface up, and the specimen was removed in one large block that included approximately 45 kg of matrix at the ventral surface. It should be noted that although it is permissible to recover *ex situ* fossils within areas maintained by the City of Summerville, permission must be obtained to collect *in situ* remains or blocks of matrix.

One of the odontocete skulls (SC2015.29.1), currently under study, was recovered by SC personnel in 2015 from the bottom of the Ashley River, south of downtown Summerville (locality 3 of Fig. 1B). It was preserved ventral side up and extricated with approximately 7 kg of surrounding matrix. The second cetacean skull represents the type specimen of *Ediscetus osbornei* Albright et al., 2018 (SC2015.33.1) and it was collected from the banks of the Edisto River by an avocational collector in 2012 (locality 1 of Fig. 1B). SC received this fossil fully prepared, but a single associated shark tooth was provided with the skull. Fossils in South Carolina Coastal Plain tidal waterways are State property and covered by the South Carolina Underwater Antiquities Act, and special licenses and permissions are necessary to collect them. Although the precise geographic location of the collecting site for these specimens is also protected by the Act and therefore not disclosed herein, these data are on file at SC and available to researchers upon request.

Specimens SC2007.36.1 and SC2015.29.1 were prepared in the laboratory at SC, and the associated matrix was soaked in water after removal. The disaggregated material was then screen washed down to 0.25 mm (#60 US standard soil sieve) and the remaining concentrates were sorted under a binocular microscope. Because of the small mesh size used to process this matrix, miniscule fossils like placoid scales, ostracode valves, and foraminiferan tests were recovered.

Repository

The specimens discussed herein consist of isolated euselachian teeth and placoid scales, as well as teleost teeth and assorted cranial/postcranial bones. All these specimens are housed at SC and included within accessions SC2007.36, SC2015.29, and SC2015.33. Material from the Chandler Bridge Formation was examined for comparative purposes, and these are curated under accessions SC2005.2 and SC2009.18. Fossils from the Pungo River Formation (Miocene) of North Carolina, curated under accessions SC98.46 and SC2012.33, were also examined. Many of the fossil elasmobranch and teleost specimens described herein were compared to Recent comparative specimens housed at SC and McWane Science Center (**MSC**) in Birmingham, Alabama, USA.

SYSTEMATIC PALEONTOLOGY

Higher taxonomic rankings generally follow that of Nelson et al. (2016), with additional rankings for extinct species adopted from Reinecke (2015) and Reinecke and Radwański (2015). We attempted to provide a comprehensive ranking for each taxon, but it is important to note that some rankings, like subfamily, have not been assigned for many of the species we discuss herein. Authorities for extant taxa follows that of van der Laan et al. (2014) and Froese and Pauly (2021). Many of the elasmobranch taxa reported herein were previously described by Müller (1999) and Cicimurri and Knight (2009a), and the information we present for those species is therefore limited to taxonomic issues and/or paleobiogeographic and temporal distributions. The synonymy listings for the elasmobranchs are largely restricted to previously reported Oligocene occurrences from the southeastern USA. For those taxa that are new to the South Carolina Oligocene record, descriptions and taxonomic remarks are provided.

CHONDRICHTHYES Huxley, 1880
EUSELACHII Hay, 1902
ELASMOBRANCHII Bonaparte, 1838

SELACHII Cope, 1871
GALEOMORPHI (*sensu* Nelson et al., 2016)
ORECTOLOBIFORMES Applegate, 1974
ORECTOLOBOIDEI Applegate, 1974
ORECTOLOBOIDEA Naylor et al., 2012
GINGLYMOSTOMATIDAE Gill, 1862
GEN. ET SP. INDET.
Fig. 3A–C

Referred specimens (n=1)—SC2007.36.208.

Description—Our sample consists of a single partial tooth that preserves two lateral cusplets (and possibly part of a third) and a small portion of the internal dentine. Both cusplets are rather tall and broad, and the second, more distal cusplet is of slightly smaller size. The cusplets are largely united to each other, and the distal cutting edges are convex. Both lateral cusplets have a slight mesial curvature, and apices are rounded due to wear (Fig. 3A, C). In profile view, the tooth has an evenly concave labial face and slightly convex lingual face (Fig. 3B). The enameloid is smooth on both crown faces. Unfortunately, no additional notable features are preserved.

Remarks—Although SC2007.36.208 is only a partial tooth, the concave labial face, convex lingual face, multiple cusplets of diminishing size, and smooth cutting edges indicate it represents a tooth of a species of Ginglymostomatidae as opposed to some lamniform or carcharhiniform taxon discussed herein. Cappetta (2012) recognized five Paleogene genera within the Ginglymostomatidae, including *Delpitoscyllium*, *Ginglymostoma*, *Hologinglymostoma*, *Nebrius*, and *Protoginglymostoma*. Based on the morphology of SC2007.36.208, it belonged to an Oligocene representative of either *Ginglymostoma* or *Nebrius*, the latter of which was reported from the Chattian Chandler Bridge Formation by Cicimurri and Knight (2009a). Unfortunately, the incomplete preservation of SC2007.36.208 does not allow us to identify the tooth beyond the familial level.

CARCHARHINIFORMES Compagno, 1973
SCYLIORHINIDAE Gill, 1862
PREMONTREINAE Cappetta, 1992
PACHYSCYLLIUM Reinecke et al., 2005
Pachyscyllium sp.
Fig. 3D–F

Type species—*Pachyscyllium albigensis* Reinecke et al., 2005; lower Oligocene Stadecken Formation, Rhineland-Pfalz, Germany.

Referred specimen (n=1)—SC2007.36.5.

Description—The specimen lacks the mesial corner of the crown and most of the root. As preserved, the crown measures 2.0 mm in height and consists of a rather tall main cusp, with a single lateral cusplet occurring on the distal side. The main cusp is distally inclined, the cutting edges are smooth, and the apex is blunt (Fig. 3D, E). The mesial cutting edge is sinuous, whereas the distal edge is rather straight. The labial face is convex and generally smooth, but the thickened crown foot bears very short and wide vertical ridges across the entire crown width (Fig. 3D). The lingual face is very convex and smooth except for some short vertical ridges on the mesial side of the crown (Fig. 3F). The preserved cusplet is rather short but wide, located very low on the crown, and bluntly pointed. Additionally, its labial face bears vertical ridges but the lingual face is smooth.

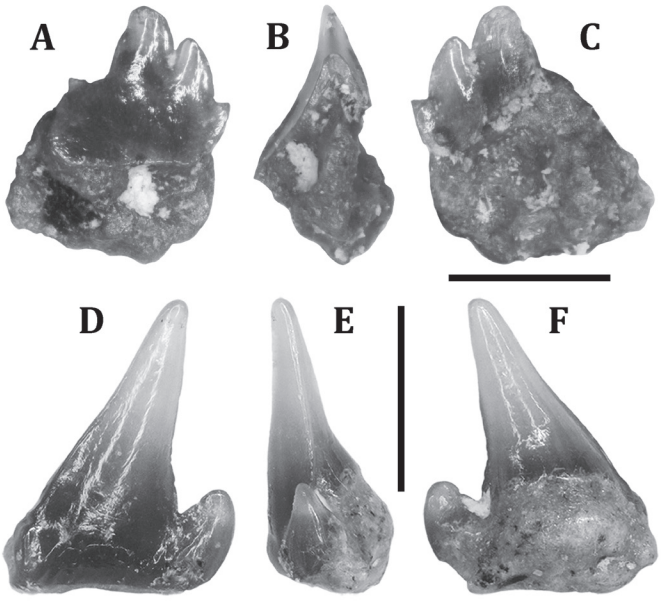

Figure 3. Selachian teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A–C**. Ginglymostomatidae indet. tooth, SC2007.36.208 in labial (**A**), profile (**B**), and lingual (**C**) views. **D–F**. *Pachyscyllium* sp. tooth, SC2007.36.5 in labial (**D**), distal (**E**), and lingual (**F**) views. Scale bars=1 mm.

Remarks—The gross morphology of SC2007.36.5 differs significantly from that of a second scyliorhinid taxon that we recovered, which is discussed in more detail below. Although it superficially resembles the Oligo-Miocene species *Pachyscyllium albigensis* Reinecke et al., 2005, *P. braaschi* Reinecke et al., 2005, *P. dachiardii* (Lawley, 1876), and *P. distans* (Probst, 1879), SC2007.36.5 clearly differs from those species by having robust vertical ridges at the labial crown foot. In contrast, the former three species appear to have completely smooth labial crown faces. Specimen SC2007.36.5 and teeth of *P. distans* have labial ornamentation, but the singular cusplet preserved on the South Carolina tooth is much shorter than

those occurring on *P. distans* teeth (Case 1980, Reinecke et al. 2001, Reinecke et al. 2005, Collareta et al. 2020).

There are only two other Oligocene records of *Pachyscyllium* in North America, including one from North Carolina (Atlantic Coastal Plain) and one from Alabama (Gulf Coastal Plain). Specimen SC2007.36.5 differs from *P. distans* reported from North Carolina (Case 1980) by the features outlined above, and it differs from *Pachyscyllium* sp. recently reported from Alabama (Ebersole et al. 2021) by having short labial longitudinal plications. The *P. distans* teeth from North Carolina were originally reported as being derived from the Trent Marl and considered of early Miocene (Aquitanian) age, but this fossiliferous deposit is now regarded as part of the River Bend Formation of Oligocene age (Rossbach and Carter 1991, Harris et al. 2000). The Alabama specimen was collected from the Rupelian Glendon Limestone Member of the Byram Formation (Ebersole et al. 2021) and is slightly older than the Ashley Formation tooth.

SCYLIORHININAE Gill, 1862

SCYLIORHINUS de Blainville, 1816

Scyliorhinus weemsi n. sp.

Fig. 4

Type species—*Squalus canicula* Linnaeus, 1758; Recent, Mediterranean Sea.

2009a *Bythaelurus* sp.; Cicimurri and Knight, p. 634–635, fig. 5M.

Diagnosis—Diminutive teeth measuring just over 1 mm in total height and 1 mm in crown width. Two morphotypes occur, including one with robust longitudinal ridges on the labial and lingual faces, and one exhibiting longitudinal ridges on the lingual face but having a smooth labial face. When present, labial ridges extend from one-third to three-quarters of the crown height. Lingual ridges always extend nearly to the apex of the main cusp. Cusplets are small or may be lacking altogether.

Holotype—SC2007.36.133 (Fig.4A–D), from locality 2 of Fig. 1B

Paratype—SC2015.29.7 (Fig. 4E–G), from locality 3 of Fig. 1B.

Referred specimens (n=9)—SC2007.36.6 (Fig. 4K-M), SC2007.36.160 (Fig. 4Q–S), SC2007.36.203 (Fig. 4T–V), SC2007.36.204 (Fig. 4W–Y), SC2007.36.205 (Fig. 4Z-BB), SC2007.36.206, SC2007.36.207, SC2015.29.6 (Fig. 4N–P), SC2015.29.8 (Fig. 4H–J).

Etymology—This species is named in honor of Robert E. Weems to recognize his contributions to our understanding of the stratigraphy and paleontology of the Atlantic Coastal Plain, and specifically for his extensive work on the Ashley Formation of South Carolina.

Description—Specimen SC2007.36.133 (Fig. 3A–D) is designated as the holotype because of its completeness. This tooth measures 1.1 mm in height and 0.9 mm in mesiodistal width. The specimen exhibits a tall, distally inclined main cusp that sharply tapers apically. In profile view the crown curves labially. A single pair of lateral cusplets occurs low on the crown, and the mesial cusplet is conspicuously wider than the distal one. The labial crown face is very weakly convex, and numerous coarse ridges occur on its lower one-third. The crown foot clearly overhangs the root and is medially concave but drawn into projections on the mesial and distal sides. The lingual crown face is very convex, and coarse longitudinal ridges nearly reach the apices of the main cusp and lateral cusplets. The cutting edge is smooth and continuous to the lateral side of the cusplets. The lingual root boss is large, and although the root lobes are both rather short, the mesial lobe is slightly wider. A large margino-lingual foramen occurs on each side of the boss.

SC2015.29.7 (Fig. 4E–G) is designated as a paratype. This specimen is morphologically similar to the holotype (Fig. 4A–D) and appears to represent a similar tooth file. SC2015.29.7 differs from the holotype by having a labio-lingually thinner crown (Fig. 4E), lower but wider lateral cusplets, and a smooth labial face (Fig. 4G). As on the holotype, robust longitudinal ridges extend nearly to the apex of the main cusp and lateral cusplets (Fig. 4E).

SC2007.36.6, SC2007.36.160, SC2015.29.6 and SC2015.29.8 are comparable to each other, and to the type specimens, by having a rather straight but distally inclined main cusp, as well as coarse longitudinal ridges that extend nearly to the apex of the main cusp and lateral cusplets. However, there are slight differences among these teeth. For example, SC2007.36.6 (Fig. 4K–M) compares well to the paratype (Fig. 4E–G) but has a labio-lingually thicker crown, larger lateral cusplets, and robust plications at the labial crown foot, whereas SC2007.36.160, SC2015.29.6 and SC2015.29.8 are similar to the holotype by having coarse labial and lingual crown ornamentation. Specimen SC2007.36.160 has a very broad main cusp compared to the other specimens (Fig. 4R), and the preserved distal cusplet is broad but poorly differentiated from the main cusp (Fig. 4S). SC2015.29.6 differs by having a mesio-distally wider crown (Fig. 5O), that lacks a mesial cusplet but bears a diminutive distal cusplet (Fig. 5P), and the labial face is more apico-basally concave (Fig. 4N). SC2015.29.8 is unusual by having an elongated mesial shoulder that is sub-perpendicular to the main cusp, and a short distal shoulder that merges

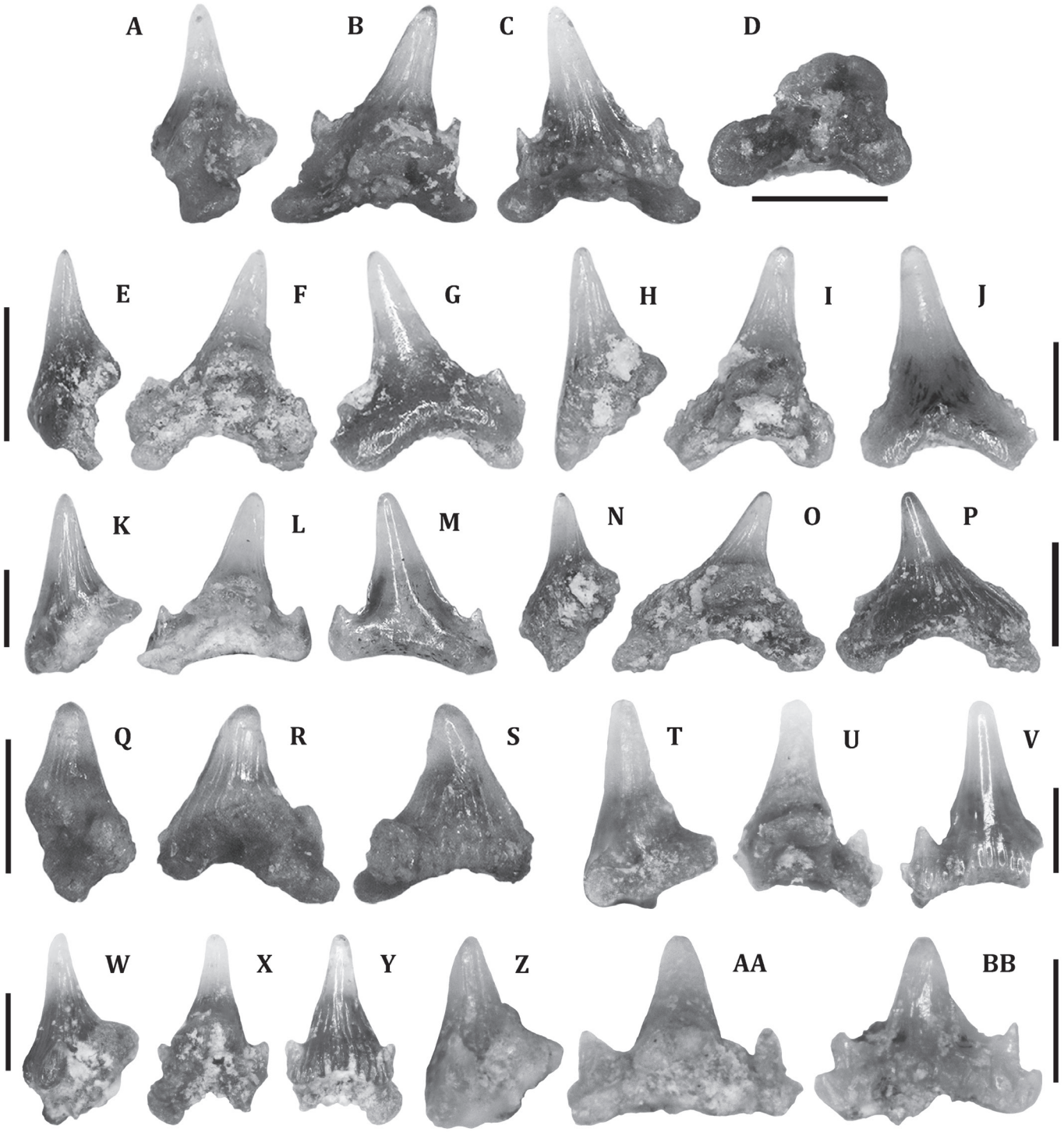

Figure 4. *Scyliorhinus weemsi* n. sp. teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A–D**. holotype, SC2007.36.133 in mesial (**A**), lingual (**B**), labial (**C**), and basal (**D**) views. **E–G**. paratype, SC2015.29.7 in mesial (**E**), lingual (**F**), and labial (**G**) views. **H–J**. SC 2015.29.8 in mesial (**H**), lingual (**I**), and labial (**J**) views. **K–M**. SC2007.36.6 in mesial (**K**), lingual (**L**), and labial (**M**) views. **N–P**. SC2015.29.6 in mesial (**N**), lingual (**O**), and labial (**P**) views. **Q–S**. SC2007.36.160 in distal (**Q**), lingual (**R**), and labial (**S**) views. **T–V**. SC2007.36.203 in mesial (**T**), lingual (**U**), and labial (**V**) views. **W–Y**. SC2007.36.204 in distal (**W**), lingual (**X**), and labial (**Y**) views. **Z–BB** SC2007.36.205 in distal (**Z**), lingual (**AA**), and labial (**BB**) views. Scale=0.5 mm in **A–D**, **H–BB**, and 1 mm in **E–G**.

with the cusp (Fig. 4I). The shoulders lack lateral cusplets, but the mesial shoulder appears weakly serrated due to the intersection of the crown ornamentation with the cutting edge (Fig. 4J).

Like the holotype, SC2007.36.204 and SC2007.36.205 have course labial and lingual crown ridges. SC2007.36.204 is unique among the sample by having a narrow crown with erect cusp that is only weakly distally curved, and there is a single pair of small, diverging lateral cusplets (Fig. 4W–Y). Although SC2007.36.205 has a rather low but very wide main cusp like that of SC2007.36.160 (compare Fig. 4R to 4AA), it differs significantly by having two pairs of large lateral cusplets, with the first pair being tall and needle like, but the second pair is diminutive and located at the very base of the crown (Fig. 4BB). Specimen SC2007.36.203 exhibits a cusplet arrangement similar to that of SC2007.36.205, but the crown of the former is comparatively higher and narrower (Fig. 4U), and the labial ornamentation is restricted to the crown foot (Fig. 4V).

Remarks—Herman et al. (1990) identified five tooth groups within scyliorhinid sharks that they differentiated largely by the root morphology. At the time of their report, the genera discussed therein were regarded as "catsharks" and subdivided into one of four subfamilies within Scyliorhinidae. However, it has since been shown that "catsharks" are a complex paraphyletic group consisting of several families and subfamilies (Iglésias et al. 2005, Weigmann et al. 2018). With respect to the tooth root, although this structure is poorly preserved on nearly all the South Carolina Oligocene specimens, the lobes are rather narrow, and the basal attachment surface is flat. These features would preclude their assignment to genera like *Atelomycterus* Garman, 1913 and *Aulohalaelurus* Fowler, 1934, both of which have rather broad root lobes, and to *Cephalurus* Bigelow and Schroeder, 1941, which has a root with a concave attachment surface. Pollerspöck and Straube (2017) noted the possible taxonomic utility of enameloid ornamentation on catshark teeth, which can occur as reticulated ridges at the base of the labial face on the genera *Apristurus* Garman, 1913, *Bythaelurus* Compagno, 1988, *Galeus* Cuvier, 1816, *Haploblepharus* Garman, 1913, and *Holohalaelurus* Fowler, 1934 (Herman et al. 1990, Weigmann et al. 2016, Weigmann et al. 2018), and on taxa like *Scyliorhinus* (Herman et al. 1990).

The specimens in our sample are strikingly similar to the teeth of various *Scyliorhinus* species illustrated by Soares and de Carvalho (2019), and we therefore assign the Oligocene specimens to this genus. The teeth of the 11 species of extant *Scyliorhinus* shown by Soares and de Carvalho (2019) exhibit a wide range of morphologies that reflect both interspecific (among species) and intraspecific (monognathic, dignathic, gynandric heterodonty within species) variation. It can be said that the *Scyliorhinus* dentition exhibits gradual monognathic heterodonty and can be sorted into anterior, lateral, and, in the lower jaw, parasymphyseal files. Anterior teeth may be erect (roughly symmetrical) to slightly distally inclined, cusplets may be poorly developed or well-developed (generally one pair), and labial ornamentation may be absent, limited to the lower part of the crown, or extend more than halfway to the apex. Lateral teeth are typically lower crowned but broader, with a vertical (generally lower jaw, but sometimes upper) to distally inclined main cusp (generally in the upper jaw but sometimes both). These teeth also bear two or more pairs of lateral cusplets, and crown ornamentation is more conspicuous than on anterior teeth. With respect to dignathic heterodonty, crown ornamentation is usually more extensive on upper teeth when compared to lowers, and lateral cusplets of upper teeth are generally taller but narrower than those of lower teeth. Development of gynandric heterodonty has not been evaluated for all *Scyliorhinus* species, but for those species where it has been documented, female teeth are often more coarsely ornamented, the main cusps are lower but broader, and the cusplets are better developed compared to male teeth of the species (Herman et al. 1990, Soares and de Carvalho 2019).

The morphological variation within the dentitions of the various extant *Scyliorhinus* species makes it difficult to accurately interpret the Ashley formation sample (n=11). However, the generalities observed in the genus lead us to conclude that our sample reflects heterodonty within a single species rather than multiple taxa and allow us to make informed hypotheses with respect to the dentition of the Oligocene species. For example, SC2007.36.204 (Fig. 4W–Y) has a narrow, rather symmetrical crown and extensive labial and lingual ornamentation, indicating it was located within an upper anterior tooth file. The holotype, SC2007.36.133 (Fig. 4A–D) is slightly inclined, has very robust labial and lingual ornamentation, and bears a single pair of rather narrow lateral cusplets. These features indicate it was from an upper anterior/antero-lateral file. In contrast, SC2015.29 (paratype, Fig. 4E–G) has a similar main cusp shape to the holotype, but labial crown ornamentation is restricted to the crown foot, and the (single pair of) lateral cusplets are rather low but broad, indicating it is

from a lower anterior/antero-lateral position. Specimen SC2007.36.203 (Fig. 4T–V) has an erect main cusp, ornamentation is limited to the crown foot, and two pairs of lateral cusplets (which are only preserved on the distal side), suggesting it is a lateral tooth, possibly from the lower dentition. Similarly, SC2007.36.2005 (Fig. 4Z–BB) appears to be a lateral tooth based on the presence of two pairs of lateral cusplets, but it may be representative of a female dentition based on the low but very broad main cusp and greater development of labial ornamentation and lateral cusplets (compare Fig. 4BB to 4V). Specimens SC2015.29.8 (Fig. 4H–J) and SC2015.29.6 (Fig. 4N–P) could represent male anterior and lateral teeth, respectively, as they have tall and narrow main cusps and lack lateral cusplets. In contrast, SC2007.36.160 (Fig. 4Q–S) has a very wide main cusp, more robust labial ornamentation, and larger lateral cusplet (which is only preserved on the distal side), indicating a female individual.

Although roughly the same size as the Chattian *Scyliorhinus biformis* Reinecke (2014), *S. weemsi* n. sp. teeth differ by having a much less medially concave labial crown base, the main cusp is broader, the cusplets are shorter, and the lingual ornamentation is more extensive. Among teeth with conspicuous labial ornamentation, those of *S. weemsi* n. sp. differ from *S. biformis* by having more robust ridges that extend higher on the crown. In addition, *S. biformis* exhibits one or two pairs of rather large cusplets, whereas *S. weemsi* n. sp. lacks or has only diminutive cusplets. Regarding teeth having much reduced ornamentation, those of *S. weemsi* n. sp. have a shorter main cusp, less convex labial crown foot, and smaller cusplets than *S. biformis*,

Teeth of Chattian *Scyliorhinus suelstorfensis* Reinecke, 2014 are two-thirds larger than those of *S. weemsi* n. sp., and they have a more gracile crown and much more medially concave labial crown foot. Also, vertical labial ridges on *S. suelstorfensis* are restricted to the lower one-third to one-half of the crown, whereas labial ridges can extend up to two-thirds or more of the crown height on *S. weemsi* n. sp. Finally, *S. weemsi* n. sp. differs from the Oligocene *Scyliorhinus kannenbergi* Leder, 2015 by being smaller in overall size and more gracile in appearance, having higher labial longitudinal ridges, and having fewer and smaller lateral cusplets.

Specimen SC2007.36.160 (Fig. 4Q–S) is nearly identical to the specimen identified as *Bythaelurus* sp. by Cicimurri and Knight (2009a: fig. 5M) from the Chattian Chandler Bridge Formation (overlying the Ashley Formation). Although both specimens are imperfectly preserved, together they show that only a single pair of lateral cusplets was developed in this jaw region. Hovestadt and Hovestadt-Euler (1995) were the first to identify *Bythaelurus* in the fossil record when they reassigned teeth formerly identified as *Scyliorhinus* aff. *coupatezi* (i.e., Steurbaut and Herman 1978, Génault 1993) to their new taxon, *B. steurbauti*. Cicimurri and Knight (2009a) considered their singular specimen as conspecific with *Bythaelurus*. However, teeth of extant *Bythaelurus*, like *B. canescens* (Günther, 1878) (see Herman et al. 1990), *B. giddingsi* McCosker et al., 2012, *B. bachi* Weigmann et al., 2016 and *B. stewarti* Weigmann et al., 2018 have one or more pairs of very large lateral cusplets. This contrasts strikingly with the teeth of the South Carolina Oligocene taxon, which have rather small cusplets or lack them altogether. The teeth of *Pachysyllium* sp. described earlier differ from those of *S. weemsi* n. sp. by being approximately twice the size, having larger lateral cusplets compared to crown size, and labial and lingual ornamentation is restricted to the crown foot.

HEMIGALEIDAE Hasse, 1878

HEMIPRISTIS Agassiz, 1835

Hemipristis cf. *H. serra* Agassiz, 1835

Fig. 5A

Type species—*Hemipristis serra* Agassiz, 1835; Miocene, Germany.

1999 *Hemipristis serra* Agassiz; Müller, p. 54, plate 8, fig. 9.

2009*a Hemipristis serra* Agassiz; Cicimurri and Knight; p. 634, fig. 5I.

Referred specimens (n=6)—SC2007.36.7 (Fig. 5A), SC2007.36.8, SC2007.36.9 (four teeth).

Remarks—Cicimurri and Knight (2009a) reported *Hemipristis serra* from the Chattian Chandler Bridge Formation, and the taxon has been reported from the Oligocene Old Church Formation of Virginia (Müller 1999). Interestingly, although *Hemipristis* has been documented from Oligocene strata of Pakistan (Adnet et al. 2007) and Oman (Thomas et al. 1989), it is not known from the European Oligocene. Müller (1999:54) commented that *H. serra* was common in warm waters during the Neogene, and von der Hocht (1978b) hypothesized that the absence of *Hemipristis* in the European Rupelian is related to the colder water conditions that existed during that time.

Adnet et al. (2007) and Ebersole et al. (2021) considered the possibility that their Oligocene *Hemipristis* teeth represented a transitional species from *H. curvatus* Dames, 1883 (Eocene) to *H. serra* (Oligocene to Early Pleistocene), and Chandler et al. (2006) reported

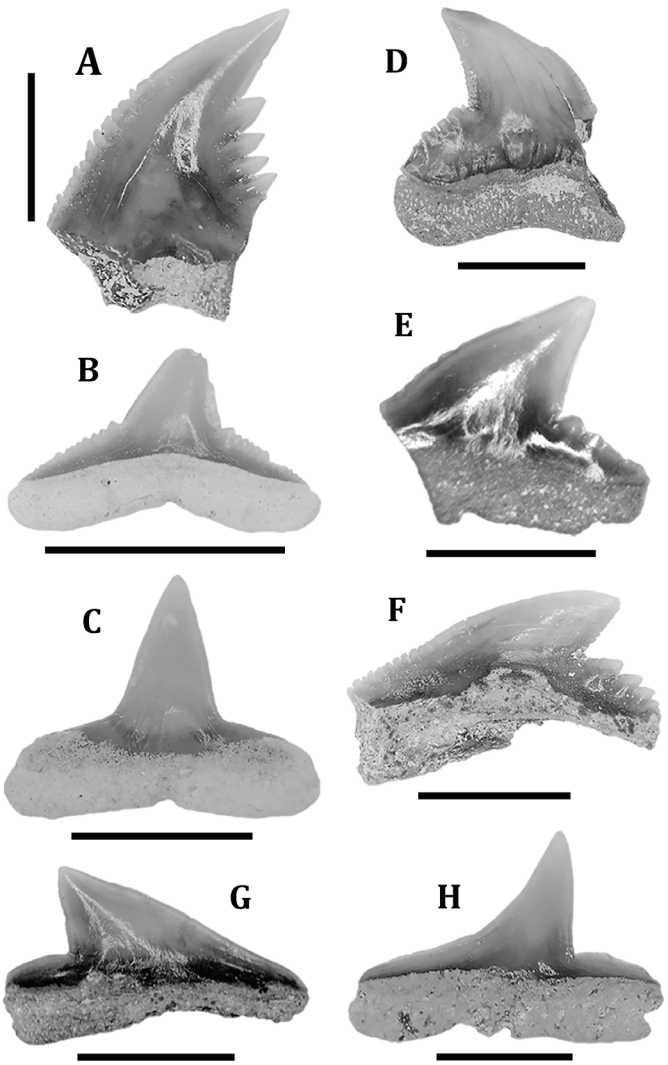

Figure 5. Selachian teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A**. *Hemipristis* cf. *H. serra* tooth, SC2007.36.7 in labial view. **B**. *Carcharhinus gibbesi* upper tooth, SC2007.36.14 in labial view. **C**. *Carcharhinus gibbesi* lower tooth, SC2007.36.15 in labial view. **D**. *Physogaleus* cf. *P. contortus* tooth, SC2007.36.19 in labial view. **E**. *Physogaleus* sp. tooth, SC2007.36.21 in labial view. **F**. *Galeocerdo aduncus* tooth, SC2007.36.17 in labial view. **G**. Sphyrnidae Morphotype 1 tooth, SC2007.36.26 in labial view. **H**. Sphyrnidae Morphotype 2 tooth, SC2007.36.24 in labial view. Scale bar=3 mm in **E**; 5 mm in **A, C, D, F, G**; 10 mm in **B**.

a trend towards increased tooth size in *H. serra* from the Oligocene to the Pliocene. Although imperfectly preserved, the Ashley Formation specimens are larger than any specimens of Eocene *H. curvatus* known to us from the Southeastern United States, and they also bear more serrations on the cutting edges, particularly on the mesial side (Cicimurri and Knight 2019, Ebersole et al. 2019, DJC unpublished data Tupelo Bay Formation). Comparison of the Ashley Formation teeth to a limited sample from the Chandler Bridge Formation (SC2005.2) revealed close similarities in both tooth size and number of mesial/distal serrations, and the material appears to be conspecific. The *H. serra* teeth from the Miocene Pungo River Formation of North Carolina (SC98.46) are much larger than the South Carolina Oligocene teeth, and for this reason we only tentatively identify the Ashley Formation specimens to *H. serra*.

CARCHARHINIDAE Jordan and Evermann, 1896
CARCHARHINUS de Blainville, 1816
Carcharhinus gibbesii (Woodward, 1889)
Fig. 5B, C

Type species—*Carcharias melanopterus* Quoy and Gaimard, 1824; Recent

2009a *Carcharhinus gibbesi*; Cicimurri and Knight, p. 632, fig. 5A–D.

Referred specimens (n=92)—SC2007.36.10, SC2007.36.11, SC2007.36.12 (ten teeth), SC2007.36.13 (32 teeth), SC2007.36.14 (Fig. 5B), SC2007.36.15 (Fig. 5C), SC2007.36.16 (25 teeth), SC2007.36.58, SC2007.36.59 (14 teeth), SC2015.29.21, SC2015.29.22, SC2015.29.23 (2 teeth), SC2015.29.24, SC2015.29.25.

Remarks—As was the case in the Chattian Chandler Bridge Formation assemblage described by Cicimurri and Knight (2009a), *Carcharhinus gibbesii* is the most common shark in our limited Ashley Formation sample. Müller (1999) identified *C. elongatus* (Leriche, 1910) in the Ashley Formation and the Old Church Formation of Virginia, and he reported *C. gibbesii* as occurring in the Belgrade Formation of North Carolina and questionably within the Ashley Formation. Specimens we examined from both the Ashley and Chandler Bridge formations revealed that serration size and density varies, and *C. gibbesii* upper teeth have lateral heels that are more regularly and more coarsely serrated than those of *C. elongatus* from the European Oligocene (i.e., Baut and Génault 1999, Reinecke et al. 2001, Reinecke et al. 2005). The material Müller (1999) illustrated as *C. elongatus* (pl. 6, particularly figs. 7–8) exhibit rather coarsely serrated lateral shoulders, and we associate them with *C. gibbesii* rather than *C. elongatus.* Unfortunately, Müller (1999) did not illustrate the Ashley Formation teeth he questionably assigned to *C. gibbesii*, so direct comparisons to our sample cannot be made. *Carcharhinus gibbesii* appears to have been distributed on both sides of the Oligocene Atlantic Ocean, as the species has been documented from Chattian strata of Germany (Reinecke et al. 2014).

PHYSOGALEUS CAPPETTA, 1980a
PHYSOGALEUS CF. *P. CONTORTUS* (GIBBES, 1849)
FIG. 5D

Type species—*Trigonodus secundus* Winkler, 1874; middle Eocene, Belgium.

1849 *Galeocerdo contortus* Gibbes; p. 193, pl. 25, figs. 71–74, Eocene(?) and Miocene, South Carolina and Virginia.

2009a *Physogaleus aduncus* (Agassiz, 1835); Cicimurri and Knight, p. 632–633, fig. 5F.

Referred specimens (n=6)—SC2007.36.19 (Fig. 5D), SC2007.36.20 (four teeth), SC2015.29.27.

Remarks—When Gibbes (1849) originally named and referred the *contortus* morphology to *Galeocerdo* (page 193), he did not designate a type specimen, type locality, or a type horizon/age. Gibbes (1849) stated that his sample included teeth from the Eocene of South Carolina and the Miocene of Virginia, but, unfortunately, he did not indicate which, if any, of the specimens shown in his plate XXV (figs. 71–74) were from South Carolina. Additionally, the Eocene age of Gibbes' (1849) South Carolina specimens is questionable because he included the site among his "Upper or Newer Eocene" localities (page 121). South Carolina invertebrate fossils that Gibbes (1849) noted as occurring in "Upper or Newer Eocene" beds, including *Cubitostrea sellaeformis* (Conrad, 1832), are found in the middle Eocene (Lutetian) Santee Limestone in the Coastal Plain. However, this unit seems unlikely as the source of the *contortus* specimens, as the morphology is currently unknown from the Santee Limestone (DJC personal observation), and it does not occur in temporally equivalent deposits in Alabama (Ebersole et al. 2019). Moreover, many of the invertebrate taxa Gibbes (1849) listed in his "Upper or Newer Eocene" division occur in what we now know to be lower Oligocene (Rupelian) strata of the Vicksburg Group in the Gulf Coastal Plain. It is therefore possible that the South Carolina *contortus* specimens available to Gibbes were derived from the Ashley Formation. The *contortus* morphology has more recently been referred to *Physogaleus* (see additional discussion below) and is followed herein.

The Ashley Formation specimens were compared to material from the Chattian Chandler Bridge Formation (SC2005.2) and middle Miocene Pungo River Formation (SC98.46), and all the specimens share the conspicuous "twisted" mesial cusp edge that Gibbes (1849) noted as being characteristic of his *contortus* species. For this reason, we tentatively assign the incompletely preserved Ashley Formation specimens to *P. contortus*. However, although quite similar, we note that the Oligocene specimens from South Carolina are significantly smaller than the Miocene specimens. Additional study is needed to determine if the Oligocene and Miocene species are indeed different, or if variation, like tooth size, is related to phyletic increase through time within a single species, as has been suggested for *Hemipristis serra* (Chandler et al. 2006) and *Striatolamia macrota* (Agassiz, 1838) (Cappetta 2012, Ebersole et al. 2019). Should the material be conspecific, a neotype specimen with associated age (Oligocene or Miocene) and stratigraphic occurrence (Ashley Formation?) must be determined. In turn, if the Oligocene and Miocene teeth represent distinct species, it must be determined which morphology truly represents *P. contortus* and which should be designated a new species.

Physogaleus contortus, as currently defined, clearly differs from *Galeocerdo aduncus* (Agassiz, 1835) (see below) by having a much more elongated and narrower main cusp that appears twisted in mesial view. Additionally, the mesial serrations are much finer and simple to only weakly compound, the distal cutting-edge serrations are finer. In addition, the distal heel is often marked by a rounded angle rather than distinct notch, and the distal heel has more denticles that are smooth to weakly serrated only on the mesial edge.

PHYSOGALEUS SP.
FIG. 5E

2009a *Physogaleus* sp.; Cicimurri and Knight, p. 633–634, fig. 5G.

Referred specimens (n=2)—SC2007.36.21 (Fig. 5E), SC2007.36.22.

Remarks—The two specimens compare favorably to *Physogaleus* sp. reported by Cicimurri and Knight (2009a) from the Chattian Chandler Bridge Formation, and we consider the material to be conspecific. *Physogaleus* sp. differs from *P. contortus* by having a short cusp, mesial cutting edge that is smooth except for irregular basal crenulation, the distal cutting edge is smooth, and the few cusplets on the distal heel are unserrated. Incomplete preservation and limited sample size inhibit meaningful comparison to the several Oligocene species that have been identified from Europe (Storms 1894, Baut and Génault 1999, Reinecke et al. 2001, Reinecke et al. 2005).

GALEOCERDIDAE HERMAN ET AL., 2010
GALEOCERDO MÜLLER AND HENLE, 1837
GALEOCERDO ADUNCUS AGASSIZ, 1835
FIG. 5F

Type species—*Squalus cuvier* Péron and Lesueur, 1822 in Lesueur 1822; Recent.

2001 *Physogaleus aduncus* (Agassiz, 1835); Ward and Bonavia, page 138.

2009a *Physogaleus aduncus* (Agassiz 1843); Cicimurri and Knight, p. 632–633, fig 5E.

Referred specimens (n=3)—SC2007.36.17 (Fig. 5F), SC2007.36.18 (two teeth).

Remarks—This tooth morphology was reported by Cicimurri and Knight (2009a) from the Chandler Bridge Formation, but they followed the work of Ward and Bonavia (2001) and referred the material to *Physogaleus contortus*. The possible conspecific association of the *aduncus* and *contortus* morphologies has long been considered (Applegate 1978, Gottfried 1993, Manning 2006) due to their regular co-occurrence in Neogene strata. Purdy et al. (2001) maintained the two morphologies as distinct species and considered the variation to reflect a difference in feeding preferences between two taxa. Ward and Bonavia (2001), however, considered the two morphologies as conspecific and went on to associate the material with *Physogaleus* (i.e., *P. aduncus*), a taxon known to exhibit strong dignathic and gynandric heterodonty (Cappetta 2012). Reinecke et al. (2001) later associated the two morphologies as *Galeocerdo aduncus*. However, in the German Oligocene the two morphologies have since been considered as separate species, *G. aduncus* and *P. contortus*, because they are apparently rarely, if ever, coeval (Reinecke et al. 2005, Reinecke and Hoedemakers 2006). More recently, Türtscher et al. (2021) provided morphometric data supporting both *G. aduncus* and *P. contortus* as separate and valid species.

Galeocerdo aduncus exhibits a uniformly convex mesial cutting edge bearing coarse compound serrations that extend nearly to the cusp apex, the distal cutting edge is more finely serrated nearly to the cusp apex, and the denticles on the distal heel are larger and serrated on their mesial and distal edges. These features are consistent with teeth of Recent *G. cuvier* (Lesueur, 1822) that we examined (i.e., SC2001.120.10), and contrasts with most species of *Physogaleus* (excluding *P. contortus*), on which much, if not all, the mesial edge is smooth, the mesial serrae that do occur are not compound, the distal cutting edge is smooth, and the distal heel cusplets are not serrated.

A brief discussion on the higher-level taxonomic assignment of *Galeocerdo* is warranted. Poey (1875) assigned *Galeocerdo* to the family Galeorhinidi and subfamily Galeocerdini (p. 86). In current usage, the name Galeocerdini implies Tribe ranking, and more recent taxonomic listings have placed *Galeocerdo* within the subfamily Galeocerdinae Whitley, 1934 (i.e., Cappetta 2012, Reinecke et al. 2014). However, if *Galeocerdo* is excluded from the family Carcharhinidae (to which it has classically been assigned), this subfamily attribution is unnecessary. Herman et al. (2010) advocated for the placement of Recent and fossil species of *Galeocerdo* within their Galeocerdidae, which has been followed by other authors with regard to fossil species (i.e. Ebersole et al. 2019). Most recently, Ebert et al. (2021) utilized Galeocerdidae, which is followed herein. Although Ebert et al. (2021) attributed authorship to Poey (1875), Poey's original spelling is inconsistent with that of Herman et al. (2010), and we follow the latter in this respect. Additional discussion on this topic can be found in Ebersole et al. (2019).

SPHYRNIDAE Bonaparte, 1840

Gen. et sp. indet.

Fig. 5G, H

2009a *Sphyrna* cf. *S. media* Springer, 1940; Cicimurri and Knight, page 635, fig. 5K.

2009a *Sphyrna zygaena* (Linnaeus, 1758); Cicimurri and Knight, page 635, fig. 5L.

Referred specimens (n=20)—SC2007.36.23, SC2007.36.24 (Fig. 5H), SC2007.36.25 (11 teeth), SC2007.36.26 (Fig. 5G), SC2007.36.27, SC2007.36.28 (five teeth).

Remarks—Two morphologies that have previously been assigned to *Sphyrna* Linnaeus, 1758, are present in our sample. The first morphology, represented by specimens SC2007.36.23–.25, was reported from the Chattian Chandler Bridge Formation by Cicimurri and Knight (2009a), who tentatively identified it as *Sphyrna media* Springer, 1940. The second morphology, represented by specimens SC2007.36.26–.28, was identified by Cicimurri and Knight (2009a) as *Sphyrna zygaena* (Linnaeus, 1758) because specimens were comparable to Mio-Pliocene teeth identified by Purdy et al. (2001). In their study, Purdy et al. (2001) synonymized fossil *S. laevissima* (Cope, 1867) with extant *S. zygaena*, citing that the tooth morphologies were indistinguishable.

Although the South Carolina Oligocene material appears to be similar to teeth of extant *Sphyrna* species, assigning the fossil morphologies to this genus is somewhat problematic. In a phylogenetic analysis, Lim et al. (2010) determined that the divergence of *Sphyrna* and its sister taxon, *Eusphyra* Gill, 1862, occurred during the Miocene, between 15 and 20 million years ago, and that

diversification within *Sphyrna* occurred only within the past 10 million years. The South Carolina Oligocene teeth are comparable and can be assigned to Sphyrnidae, as Lim et al. (2010) has indicated that the family diverged from *Carcharhinus* during the middle Eocene. However, based on the divergence times proposed by Lim et al. (2010), the Rupelian and Chattian teeth should not be assigned to *Sphyrna*, let alone any of the extant species. Although Carrillo-Briceño et al. (2020) and Adnet et al. (2020) have recently assigned Oligocene and Eocene (respectively) teeth to *Sphyrna*, the work of Lim et al. (2010) should not be discounted. We believe that the South Carolina Oligocene teeth could represent one or more undescribed stem members of the family, but such a determination is beyond the scope of this paper.

SQUALIMORPHI (*sensu* Nelson et al., 2016)
SQUALIDA (*sensu* Nelson et al., 2016)
SQUALIFORMES Goodrich, 1909
SQUALIDAE de Blainville, 1816
SQUALUS Linnaeus, 1758
Squalus sp.
Fig. 6A–E

Type species—*Squalus acanthias* Linnaeus, 1758; Recent.

Referred specimens (n=4)—SC2007.36.3 (Fig. 6A–C), SC2007.36.130, SC2015.29.9, SC2015.29.17 (Fig. 6D, E).

Description—SC2007.36.3 (Fig. 6A–C) is the only complete specimen in our sample. The crown is very low, and its total width measures 1.8 mm. The mesial cutting edge is smooth, elongated, sinuous along its length, and forms a sharply pointed cusp with the distal cutting edge. The cusp itself is highly distally directed, and the distal cutting edge is very short, straight, and smooth. A distal heel is elongated, and the cutting edge on this structure is smooth and somewhat angular, with a low apex that is located beyond the apex of the main cusp. The labial face is rather flat, devoid of ornamentation, with a somewhat thickened crown foot and medially located, basally directed protuberance (Fig. 6B). This protuberance extends beyond the basal attachment surface of the root. The lingual crown face is convex and smooth, and it has a medially located basal protuberance (Fig. 6A). This protuberance is very short, perpendicular to the lingual crown face, and directed mesially. There is a distinct constriction below the crown base on the labial and lingual sides, after which the thin root flares laterally a short distance. The basal attachment surface is narrow and weakly concave. A large centrally located nutritive

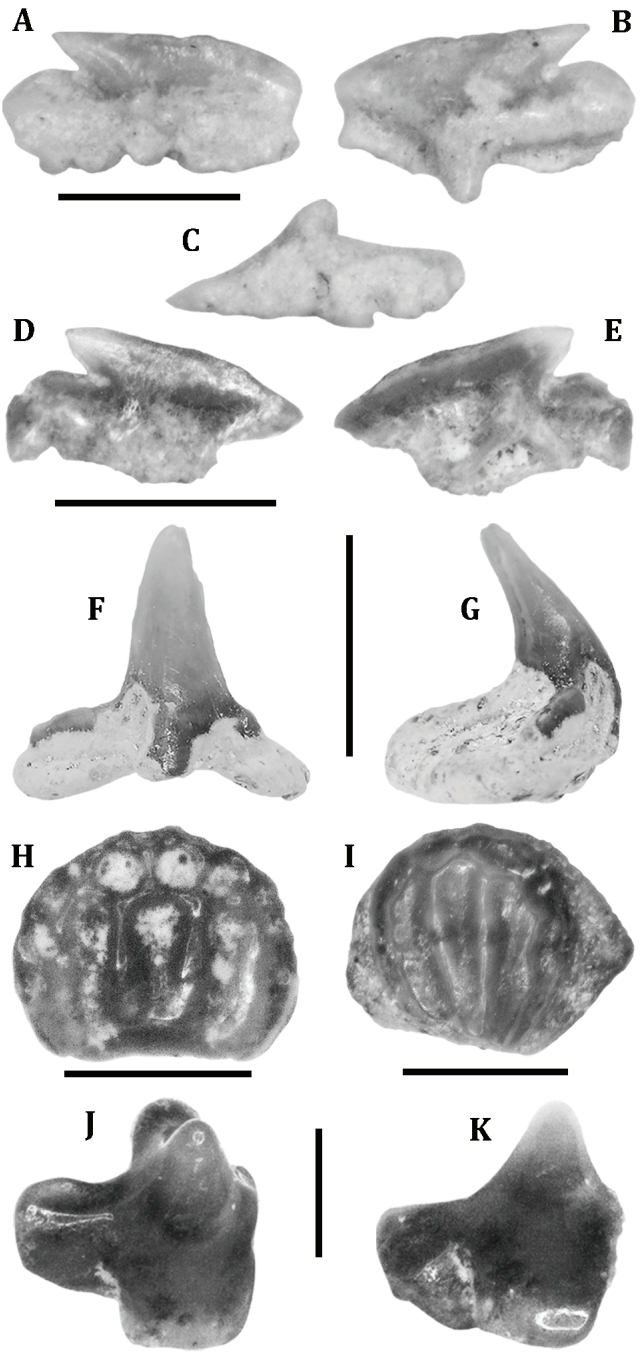

Figure 6. Selachian teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A–C**. *Squalus* sp. tooth, SC2007.36.3 in lingual (**A**), labial (**B**), and basal (**C**) views. **D–E**. *Squalus* sp. tooth, SC2015.29.17 in labial (**D**) and lingual (**E**) views. **F–G**. *Squatina* sp. tooth, SC2007.36.4 in labial (**F**) and distal (**G**) views. **H**. *Squatina* sp. placoid scale, SC2015.29.18 in apical view. **I**. *Squatina* sp. placoid scale, SC2007.36.126 in apical view. **J–K**. *Pristiophorus* sp., SC2015.29.20 in occlusal (**J**) and labial (**K**) views. Scale bar=0.5 mm in **H**; 1 mm in **I**; 5 mm in **A–G**, **J**, **K**.

foramen opens lingually (Fig. 6C).

SC2015.29.17 is a well-preserved crown (Fig. 6D, E) measuring 1.5 mm in width, the cusp angle is acute, and the apex of the distal heel lies beyond the apex of the main cusp. This crown is somewhat lower than that of SC2007.36.3.

Specimens SC2007.36.130 and SC2015.29.9 are both represented by only the posterior half of a tooth crown. Both specimens show that the highest point on the distal heel is beyond the main cusp apex. The main cusp of SC2015.29.9 is broken, but the cusp angle of SC2007.36.130 is acute.

Remarks—The Ashley Formation specimens represent the first reported fossil occurrence of *Squalus* from South Carolina. The genus has been reported from the Oligocene of Oregon (Welton 1972), and *S. alsaticus* (Andreae, 1890) was tentatively reported by Müller (1999) from the Oligocene of Virginia. The latter species is well known from the Rupelian and Chattian of Europe, having been documented in Poland (van den Bosch 1981), Belgium (Hovestadt and Hovestadt-Euler 1995, Baut and Génault 1999, Mollen et al. 2016), the Czech Republic (Brzobohaty and Kalabis 1970, Cappetta et al. 2016), France (Génault 1993), and Germany (von der Hocht 1978a, 1978b, Reinecke et al. 2001, Reinecke et al. 2005). Although the Ashley Formation sample size is small, these Oligocene teeth differ from *S. alsaticus* in two key respects – the apical angle of the main cusp (i.e., the angle formed at the cusp apex by the mesial and distal cutting edges) and the morphology of the distal heel.

Within the jaw of an extant *Squalus acanthias* Linnaeus, 1758 we examined (SC96.77.4), we observed that cusp inclination increases and, correspondingly, the crown height decreases from the symphysis to the commissure. We also observed that the apical angle was variable and decreased mesiodistally along the jaw. Reinecke et al., (2005) documented variation in the apical angle of *S. alsaticus* teeth, which ranged from 50˚ to 64˚, but they noted that the variation was not related to jaw position. Our examination of specimens shown in Reinecke et al. (2005:pl. 4-6) and Reinecke et al. (2001: pl. 6-7) showed this statement to be accurate, as anterior, lateral and posterior teeth of *S. alsaticus* can have angles in the 60˚ to 64˚ range. The apical angle of SC2007.36.3 measures only 41˚, that of SC2015.29.17 measures 47 ˚, and SC2007.36.130 is 53˚, all of which are at the low end of, or less than, the range of *S. alsaticus* teeth. The crown of SC2015.29.17 is slightly lower than that of SC2007.36.3, indicating that it was from a more distal jaw position.

With respect to the distal heel, that of *S. alsaticus* generally has a very convex to angular cutting edge with an apex that is located directly under the main cusp apex or closer to the base of the distal cutting edge. This morphology is seen on the *Squalus* aff. *alsaticus* specimens discussed by Müller (1999). In contrast, the heel apex of the South Carolina specimens lies beyond the apex of the main cusp. Although the Ashley Formation specimens may represent an undescribed species of *Squalus*, a larger sample is needed to accurately identify this Oligocene taxon and interpret its dentition.

SQUANTINIDA (*sensu* Nelson et al., 2016)
SQUATINIFORMES de Buen, 1926
SQUATINIDAE de Blainville, 1816
SQUATINA Duméril, 1805
Squatina sp.
Fig. 6F–I

Type species—*Squalus squatina* Linnaeus, 1758; Recent.

2009a *Squatina* cf. *S. angeloides* Van Beneden, 1873; Cicimurri and Knight, page 629, fig. 3A.

2009a *Cetorhinus parvus* Leriche, 1908; Cicimurri and Knight, page 631, fig. 3D

Referred specimens (n=7)—SC2007.36.4 (Fig. 6F, G), SC2007.36.126 (Fig. 6I), SC2007.36.149, SC2007.36.227, SC2015.29.18 (Fig. 6H), SC2015.29.19, SC2015.33.2.

Remarks—SC2007.36.4 and SC2015.33.2 are comparable to teeth recovered from the overlying Chandler Bridge Formation that Cicimurri and Knight (2009a) identified as *Squatina* cf. *S. angeloides* Van Beneden, 1873. Case (1980) identified *S. subserrata* (Münster, 1846) from North Carolina, which Cicimurri and Knight (2009a) considered to represent the same species as their *S.* cf. *S. angeloides*. Müller (1999) reported *S. subserrata* from the Old Church Formation of Virginia, stating that his material was more "robust" than *S. angeloides* (p. 33). We could not compare the Ashley Formation teeth to the Old Church Formation material because Müller (1999) did not illustrate these specimens. However, the jaws of a Recent *Squatina nebulosa* Regan, 1906a (SC2020.53.5) that we examined showed that the upper teeth are slightly smaller and narrower than those in the equivalent files of the lower jaw. These differences could simply be referred to as gracile (upper teeth) and robust (lower teeth) morphologies, but with the benefit of a complete dentition we know that the morphologies instead represent a single species.

Specimens SC2007.36.126, SC2007.36.149, SC2007.36.227, SC2015.29.18, and SC2015.29.19 are

isolated placoid scales that are similar to specimens from the Rupelian of Belgium (van den Bosch 1984) and the Chattian Chandler Bridge Formation of South Carolina (Cicimurri and Knight 2009a) that were referred to the cetorhinid *Keasius parvus* (Leriche, 1908). However, the Ashley Formation scales (as well as the Chandler Bridge Formation specimens) conform to scales occurring on various extant *Squatina* species (see Vaz and de Carvalho 2013) found in the Atlantic Ocean. Reinecke et al. (2011) have in fact associated such scales with *Squatina* teeth, and Case (1980) attributed a similar placoid scale from the Oligocene of North Carolina (plate 8, fig. 4) to *Squatina*.

It is important to note that, although gill rakers and teeth have been ascribed to the various Paleogene cetorhinid species (i.e., Welton 2013), no scales of the morphology that van den Bosch (1984) identified as being cetorhinid are directly associated with other remains. Hovestadt and Hovestadt-Euler (2011) described a partial skeleton of *K. parvus*, and the associated scales are dissimilar to those previously identified as *Keasius parvus* (van den Bosch 1984, Cicimurri and Knight 2009a) and to those occurring in the Ashley Formation. Although Müller (1999) reported cetorhinid gill rakers from the Oligocene Old Church Formation of Virginia, neither gill rakers nor teeth have been found in the Oligocene of South Carolina. This lack of association is understandable if the scales in question represent *Squatina* rather than Cetorhinidae.

Squatina has also been reported from the Rupelian of Oregon (Welton 1972), and the genus is known from Rupelian strata throughout Europe, including Poland (van den Bosch 1981), the Czech Republic (Brzobohaty and Kalabis 1970), Germany (von der Hocht 1978a, 1978b, Müller 1983, Reinecke et al. 2001), Belgium (Baut and Génault 1999, Mollen et al. 2016), and France (Génault 1993). A larger sample of teeth is needed to accurately identify the angel shark occurring in the Ashley and Chandler Bridge formations.

PRISTIOPHORIFORMES Berg, 1958
PRISTIOPHORIDAE Bleeker, 1859
PRISTIOPHORUS Müller and Henle, 1837
Pristiophorus sp.
Fig. 6I, K

Type species—*Pristis cirratus* Latham, 1794; Recent, Port Jackson, New Holland.

Referred specimen (n=1)—SC2015.29.20.

Description—The specimen is an incomplete crown measuring 1 mm in width as preserved. Although the mesial side is missing, the crown was mesio-distally wide. There is a large, medially located, distally inclined, pointed cusp, which is flanked by perpendicular lateral heels (not preserved on the mesial side). The labial face is weakly convex and covered with smooth enameloid, and the labial crown foot appears to have been uniformly convex (Fig. 6K). The lingual face is separated from the labial face by a continuous, smooth cutting edge that curls slightly lingually at its distal end (Fig. 6I). The lingual crown face is convex and there is a short lingually directed medial protuberance.

Remarks—The fossil record of sawsharks consists predominantly of isolated rostral spines, and three Cenozoic genera have been identified. These include the extant *Pristiophorus* Müller and Henle, 1837 (which has smooth rostral spines) and *Pliotrema* Regan, 1906b (which has serrations on the posterior edge of the rostral spines), and extinct *Ikamauius* Keyes, 1979 (which has serrations on the anterior and posterior edges of the spine). Teeth of *Ikamauius* are unknown, but those of *Pliotrema* have a distinctive labial uvula that is clearly separated from the remainder of the crown foot (Reinecke et al. 2020, Weigmann et al. 2020). In contrast, the labial crown foot of *Pristiophorus* teeth is straight to uniformly convex (Steurbaut and Herman,1978, Engelbrecht et al. 2020, Reinecke et al. 2020).

Although broken, SC2015.29.20 appears to have had a uniformly convex labial crown foot, indicating it is *Pristiophorus* as opposed to *Pliotrema*. Müller (1999) documented *Pristiophorus* sp. from the Oligocene Old Church Formation of Virginia, and SC2015.29.20 represents the first fossil record of the genus in South Carolina. *Pristiophorus* remains are known from Eocene to Pliocene-aged deposits of the Pacific (Welton 1972, Philips et al. 1976, Barnes et al. 1981, Olson and Welton 1986) and Atlantic (Case 1980, Müller 1999, Purdy et al. 2001) coastal plains. Unfortunately, the poor preservation of the single specimen available to us inhibits meaningful comparison to the several described Oligo-Miocene species (Steurbaut and Herman 1978, Reinecke et al. 2020).

BATOMORPHII Cappetta, 1980a
RAJIFORMES Berg, 1940
RAJIDAE de Blainville, 1816
RAJINAE (*sensu* McEachran and Dunn, 1998)
RAJA Linnaeus, 1758
Raja mccollumi Cicimurri and Knight 2009a
Fig. 7A–D

Type species—*Raja batis* Linnaeus, 1758; Recent.

Referred specimens (n=56)—SC2007.36.29, SC2007.36.30, SC2007.36.31 (Fig. 7C, D) SC2007.36.32,

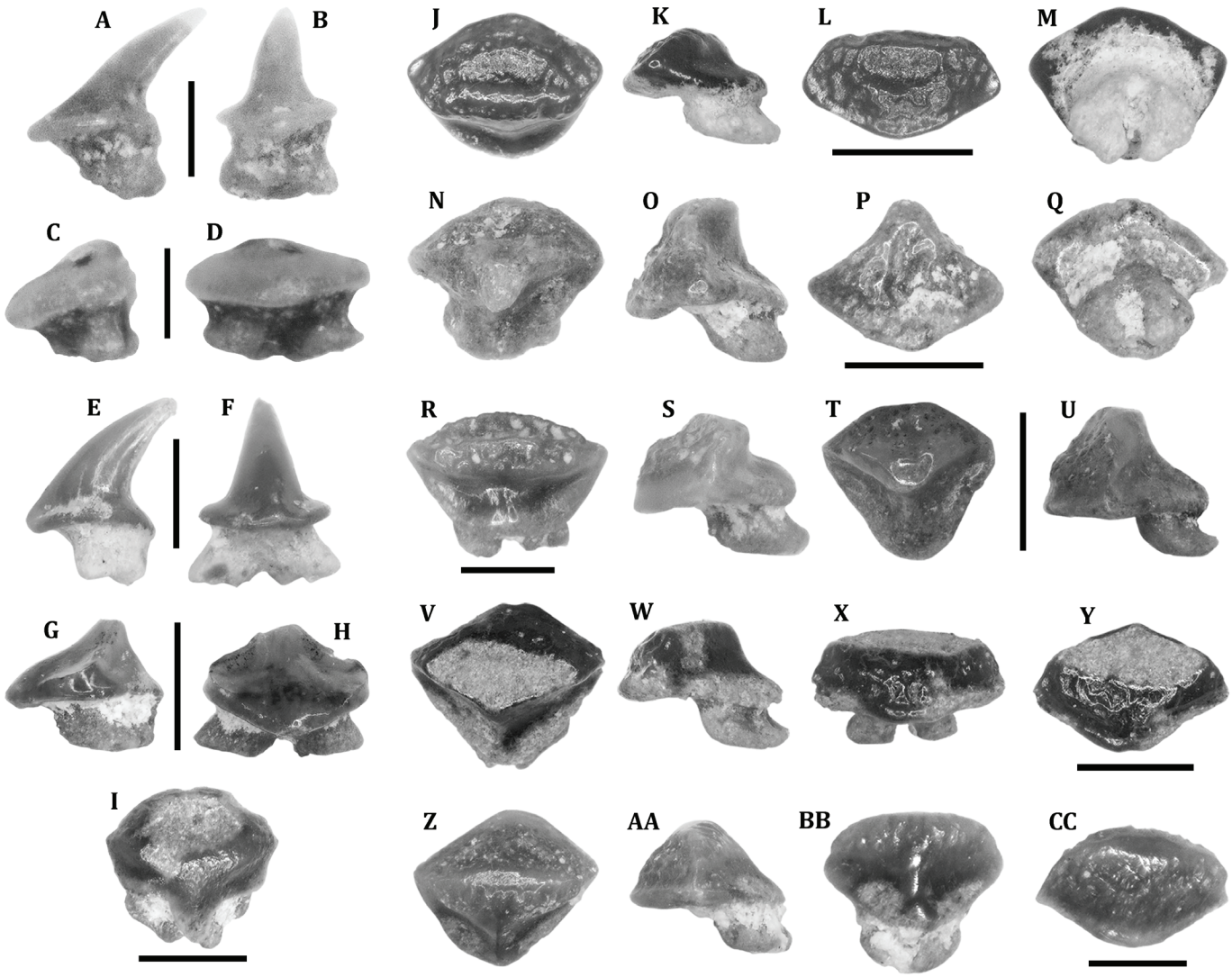

Figure 7. Batoid teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A**, **B**. *Raja mccollumi* male tooth, SC2007.36.132 in distal (**A**) and labial (**B**) views. **C**, **D**. *Raja mccollumi* female tooth, SC2007.36.31 in mesial (**C**) and labial (**D**) views. **E, F**. *Raja* sp. male tooth, SC2007.36.33 in mesial (**E**) and labial (**F**) views. **G**, **H**. *Raja mccollumi* female tooth, SC2007.36.124 in mesial (**G**) and labial (**H**) views. **I**. *Rhynchobatus* sp. tooth, SC2007.36.39 in occlusal view. **J**–**M**. "*Taeniurops*" *cavernosus* low-crowned tooth, SC2015.29.42 in occlusal (**J**), profile (**K**), labial (**L**), and basal (**M**) views. **N**–**Q**. "*Taeniurops*" *cavernosus* male tooth, SC2015.29.2 in occlusal (**N**), profile (**O**), labial (**P**), and basal (**Q**) views. **R**, **S**. "*Taeniurops*" *cavernosus* low-crowned tooth, SC2007.36.53 in occlusal (**R**) and profile (**S**) views. **T**, **U**. "*Taeniurops*" *cavernosus* male tooth, SC207.36.51 in occlusal (**T**) and profile (**U**) views. **V**–**Y**. "*Dasyatis*" sp. low-crowned tooth, SC2015.29.45 in occlusal (**V**), profile(**W**), labial (**X**), and labio-oblique (**Y**) views. **Z**–**CC**. "*Dasyatis*" sp. low-crowned tooth, SC2007.36.49 in occlusal (**Z**), profile (**AA**), lingual (**BB**), and labial (**CC**) views. Scale bar=0.5 mm in **C**, **D**, **G**, **H**; 1 mm in **E**, **F**, **I**, **T**, **U**; 2 mm in **A**, **B**; 5 mm in **J**–**S**, **V**–**CC**.

SC2007.36.131 (two teeth), SC2007.36.132 (Fig. 7A, B), SC2007.36.148 (three teeth), SC2007.36.154 (three teeth), SC2007.36.155 (ten teeth), SC2007.36.156 (two teeth), SC2007.36.157, SC2007.36.158, SC2007.36.218, SC2007.36.219 (four teeth), SC2007.36.220, SC2007.36.241, SC2015.29.3, SC2015.29.4, SC2015.29.12, SC2015.29.33 (eight teeth), SC2015.29.34, SC2015.29.35, SC2015.29.37, SC2015.29.38 (two teeth), SC2015.29.39, SC2015.29.40, SC2015.29.41 (three teeth).

Remarks—This taxon was erected by Cicimurri and Knight (2009a) based on several hundred specimens from the Chattian Chandler Bridge Formation of South Carolina. Male and female morphologies were described, and both morphotypes are represented in the Ashley Formation sample. Müller (1999) reported *Raja* sp. 1 from the Ashley Formation and the Oligocene Old Church

Formation of Virginia, but Cicimurri and Knight (2009a) could not determine if that material was conspecific with *R. mccollumi*. However, our direct comparison of Ashley Formation teeth to *R. mccollumi* from the Chandler Bridge Formation (SC2005.2) leads us to conclude that they are indeed conspecific. Thus, the paleobiogeographic range of *R. mccollumi* is herein extended to the Oligocene Salisbury Embayment of Virginia. Müller (1999) noted large numbers of *Raja* teeth in the Oligocene samples he examined, and our analyses indicate that the taxon was also common in South Carolina during the Oligocene. This diminutive species is easily missed unless a #20 (0.8 mm) or finer screen is used to process matrix.

The *R. mccollumi* male morphology (Fig. 7A, B) clearly differs from that of *Atlantoraja cecilae* (Steurbaut and Herman, 1978) from the Oligocene of Europe by having a less laterally compressed cusp that bears short apical carinae on the mesial and distal sides. Male teeth of *Raja thiedei* Reinecke, 2015 from the Chattian of Germany, although of comparable size to *R. mccollumi*, have more elongated lateral cutting edges, a depressed rather than convex area below the labial cusp base, and the lingual crown foot is more expansive. We herein retain the *mccollumi* species within *Raja* following Reinecke (2015) but note that they could represent one of the many skate genera that were once assigned to *Raja* (see McEachran and Dunn 1998). For example, *A. cecilae* was originally assigned to *Raja* by Steurbaut and Herman (1978) but placed within *Atlantoraja* by Reinecke (2015).

"*Raja*" sp.
Fig. 7E–H

2009a *Raja* sp.; Cicimurri and Knight, page 637, fig. 7A–B.

Referred specimens (n=18)—SC2007.36.33 (Fig. 7E, F), SC2007.36.34, SC2007.36.35, SC2007.36.36, SC2007.36.37, SC2007.36.38, SC2007.36.124 (Fig. 7G, H), SC2007.36.150 (two teeth), SC2007.36.151, SC2007.36.221 (two teeth), SC2007.36.222, SC2007.36.223, SC2007.36.242, SC2015.29.5, SC2015.29.15, SC2015.29.36.

Remarks—These teeth appear to be conspecific with *Raja* sp. of Cicimurri and Knight (2009a) from the Chattian Chandler Bridge Formation. The low-crowned teeth in our Ashley Formation sample, as well as low-crowned teeth of the *Raja* sp. reported by Cicimurri and Knight (2009a), have a small, medially located cusp, which is lingually directed and may be distally inclined (Fig. 7G, H). A sharp transverse ridge may extend across the entire width of the tooth (including the cusp), but on some teeth the transverse cutting edge is best developed on the mesial and distal sides of the crown, but it becomes inconspicuous at the base of the cusp and is not evident apically.

Other teeth in the sample have a very tall and conical cusp that curves lingually, and cutting edges are restricted to the postero-mesial and postero-distal sides of the upper part of the cusp (Fig. 7E, F). We interpret this variation in tooth morphology to reflect gynandric heterodonty, with the low-crowned, weakly cuspidate teeth representing females, and those teeth with distinctive conical cusps being from male individuals. Differences in cusp inclination likely reflect jaw position, with erect and symmetrical teeth occupying more anterior files, whereas those with a distally directed cusp occupying more lateral positions.

It is interesting to note that a large skate taxon (*Raja* sp.) is coeval with a smaller taxon (*R. mccollumi*) in both the Ashley Formation and overlying Chandler Bridge Formation. This scenario has also been documented in the Oligocene of Europe, where *Atlantoraja cecilae* (equivalent in size to *R. mccollumi*) and *Dipturus casieri* (Steurbaut and Herman, 1978) co-occur (Steurbaut and Herman 1978, Müller 1983, Hovestadt and Hovestadt-Euler 1995, Reinecke et al. 2005). The latter taxon was originally identified as *Raja casieri* by Steurbaut and Herman (1978), but the species was recently referred to *Dipturus* by Reinecke (2015) because of the presence of transverse cutting edges on male and female teeth (Herman et al. 1995). It is possible that the *Raja* sp. teeth from both the Ashley and Chandler Bridge Formations represent a species of *Dipturus*, but this seems unlikely because the male teeth in our sample lack complete cutting edges, and neither male nor female teeth possess a low cusplet at the mesial and/or distal crown foot (Herman et al. 1995, Reinecke 2015). These features, combined with the uniformly convex labial margin, preclude assignment of these Oligocene teeth to *Rostroraja* Hulley, 1972 (Herman et al. 1995). These Ashley Formation teeth are similar to extant *Bathyraja* Ishiyama, 1958 and *Rajella lintea* (Fries, 1838) (Herman et al. 1995), but for the purposes of this report we tentatively assign them to *Raja* due to the lack of comparative skeletal material.

RHINOPRISTIFORMES Naylor et al., 2012
RHYNCHOBATIDAE Garman, 1913
RHYNCHOBATUS Müller and Henle, 1837
Rhynchobatus sp.
Fig. 7I

Type species—*Rhinobatus laevis* Bloch and Schneider, 1801; Recent; Japan.

Referred specimens (n=3)—SC2007.36.39 (Fig. 7I),

SC2015.29.13, SC2015.29.32.

Remarks—Cicimurri and Knight (2009a) reported *Rhynchobatus pristinus* (Probst, 1877) from the Chattian Chandler Bridge Formation of South Carolina, and Cicimurri and Knight (2019) tentatively referred several late Eocene (Priabonian) specimens from the Dry Branch Formation to this species. This species has also been reported from Oligocene strata of North Carolina (Case 1980, Müller 1999) and Virginia (Müller 1999). The Ashley Formation *Rhynchobatus* specimens represent a temporally median position (ca. 28.5 Ma) between the Chattian (24.5 Ma) and Priabonian (34.5 Ma) South Carolina records. Although this suggests the Ashley Formation specimens belong to *R. pristinus*, the ablated nature of the teeth in our sample does not allow for a more refined identification.

MYLIOBATIFORMES Compagno, 1973
MYLIOBATOIDEI Compagno, 1973
FDASYATIDAE Jordan and Gilbert, 1879
TAENIUROPS Garman, 1913
"*Taeniurops*" *cavernosus* (Probst, 1877)
Fig. 7J–U

Type species—*Taeniura meyeni* Müller and Henle, 1841; Recent.

Raja cavernosa Probst, 1877; p. 75–76, plate 1, figs 1–4.

2009a *Dasyatis cavernosa* (Probst); Cicimurri and Knight, page 637–638, fig. 8A–B.

Referred specimens (n=11)—SC2007.36.52, SC2007.36.53(Fig. 7R, S), SC2007.36.54 (six teeth), SC2007.36.224, SC2015.29.2 (Fig. 7N–Q), SC2015.29.42 (Fig. 7J–M).

Remarks—The Ashley Formation specimens exhibit an ornamented labial face that is concave apically, which are features that compare to those of *Raja cavernosa* Probst, 1877. This species was later moved to *Dasyatis* Rafinesque, 1810a and more recently assigned to *Taeniurops* by Cappetta (2012). However, we prefer a more conservative approach and utilize the generic name in quotes to denote that the teeth could in fact represent some other closely related, but extinct, taxon. Although Müller (1999:60) identified *Dasyatis cavernosa* from the Ashley Formation, he did not illustrate any specimens and we cannot determine if it is conspecific with our "*Taeniurops*" *cavernosus*. Cicimurri and Knight (2009a) recorded the species from the overlying Chandler Bridge Formation of South Carolina, and it was also reported in Oligocene deposits of North Carolina (Case 1980) and Virginia (Müller 1999). *Taeniurops cavernosus* has been reported from Oligo-Miocene strata of Europe (Reinecke et al. 2001, Reinecke et al. 2005, Reinecke et al. 2008). Specimens identified as *T. cavernosus* by Reinecke and Radwański (2015) are much less ornamented than the teeth in our sample.

DASYATIS Rafinesque, 1810a
"*Dasyatis*" sp.
Fig. 7V–CC

Type species—*Dasyatis ujo* Rafinesque, 1810a; Recent.

2009a *Dasyatis rugosa* (Probst, 1877); Cicimurri and Knight, page 638, fig. 8C.

Referred specimens (n=11)—SC2007.36.49 (Fig. 7V–CC1), SC2007.36.50 (three teeth), SC2007.36.51 (Fig. 7T–U), SC2007.36.225, SC2015.29.14, SC2015.29.43, SC2015.29.44, SC2015.29.45 (Fig. 7V–Y), SC2015.29.46.

Remarks—These teeth differ from those of "*Taeniurops*" *cavernosus* discussed above by having a more convex labial face, a more angular labial crown margin (as opposed to uniformly convex), and a wider transverse crest that is crenulated. The Ashley Formation specimens are ablated but appear to be conspecific with teeth occurring in the overlying Chandler Bridge Formation identified as *Dasyatis rugosa* (Probst, 1877) by Cicimurri and Knight (2009a). Reinecke (2015) noted differences between the Chandler Bridge teeth and *D. rugosa* from Germany, and he indicated an early Chattian first appearance for this species. Reinecke et al. (2011) illustrated (plate 96, fig. 4) one of Probst's (1877) original specimens of *D. strangulata*, and the species was also reported by Reinecke et al. (2014) and Reinecke and Radwański (2015). The South Carolina specimens do appear to have a more convex labial face with less robust ornamentation, and they are more similar to *D. strangulata* than to *D. rugosa* in these respects (Reinecke et al. 2011, Reinecke et al. 2014, Reinecke and Radwański 2015).

Although teeth with this morphology have traditionally been placed within *Dasyatis* (see Cappetta 2012), recent molecular studies of extant species revealed the genus to be paraphyletic (Last et al. 2016, Nelson et al. 2016). This prompted the referral of many extant *Dasyatis* species to various other genera, like *Bathytoshia* Whitley, 1933, *Fontitrygon* Last et al., 2016, *Hemitrygon* Müller and Henle, 1838, *Hypanus* Rafinesque, 1818, *Megatrygon* Last et al., 2016, and *Telatrygon* Last et al., 2016. Because a comparative study of the dentitions of these extant taxa has yet to be undertaken, we herein conservatively retain this species within *Dasyatis* with the understanding that they may someday be referred to one of the aforementioned extant genera, or perhaps

to an unknown fossil taxon. The Ashley Formation specimens are morphologically similar to *D. strangulata*, a taxon that has tentatively been identified from the late Chattian by Reinecke et al. (2014). However, we refrain from assigning the South Carolina specimens to this species due to their much older occurrence compared to the typically Miocene range of *D. strangulata*.

MYLIOBATIDAE Bonaparte, 1835
RHINOPTERINAE Jordan and Evermann, 1896
RHINOPTERA Cuvier, 1829
"*Rhinoptera*" sp.
Fig. 8A, B

Type species—*Myliobatis marginata* Geoffroy Saint-Hilaire, 1817; Recent; Mediterranean Sea.

2009a *Rhinoptera* cf. *R. studeri*; Cicimurri and Knight, page 641, fig. 6G.

Referred specimen (n=1)—SC2015.29.30.

Remarks—The specimen consists of a broken symphyseal tooth that is very low-crowned, but the crown thickness reflects *in vivo* usage. The labial and lateral faces overhang the root, but the lingual face is even with the root. There is a thick and rounded transverse ridge located at the crown/root juncture (Fig. 8B). These features lead us to conclude that the taxon is more similar to extant *Rhinoptera* than to *Aetomylaeus* Garman, 1908 or *Myliobatis* Cuvier, 1816, which have expanded root lamellae that extend well beyond the lingual crown margin. Comparison to teeth from the Chandler Bridge Formation that Cicimurri and Knight (2009a) identified as *Rhinoptera* cf. *R. studeri* revealed that the material is conspecific.

Recent studies of the evolutionary history of the Myliobatidae by Nelson et al. (2016), Last et al. (2016), and Villalobos-Segura and Underwood (2020) utilized molecular divergence data, which suggested that the clade containing *Rhinoptera* and *Mobula* diverged from other Myliobatidae during the early Miocene, and that *Rhinoptera* diverged from its sister taxon, *Mobula*, as recently as the late Miocene. Therefore, morphologically similar Paleogene teeth cannot be referred to *Rhinoptera*. The clade Myliobatidae appears to have its origins during the middle Eocene, and from this time to the Late Oligocene, taxa with teeth morphologically similar to extant *Rhinoptera*, *Myliobatis* and *Aetomylaeus* occur (i.e., Reinecke et al. 2005, Cicimurri and Knight 2009a, Ebersole et al. 2019). These records must be reevaluated to include both molecular and morphological data to make a more

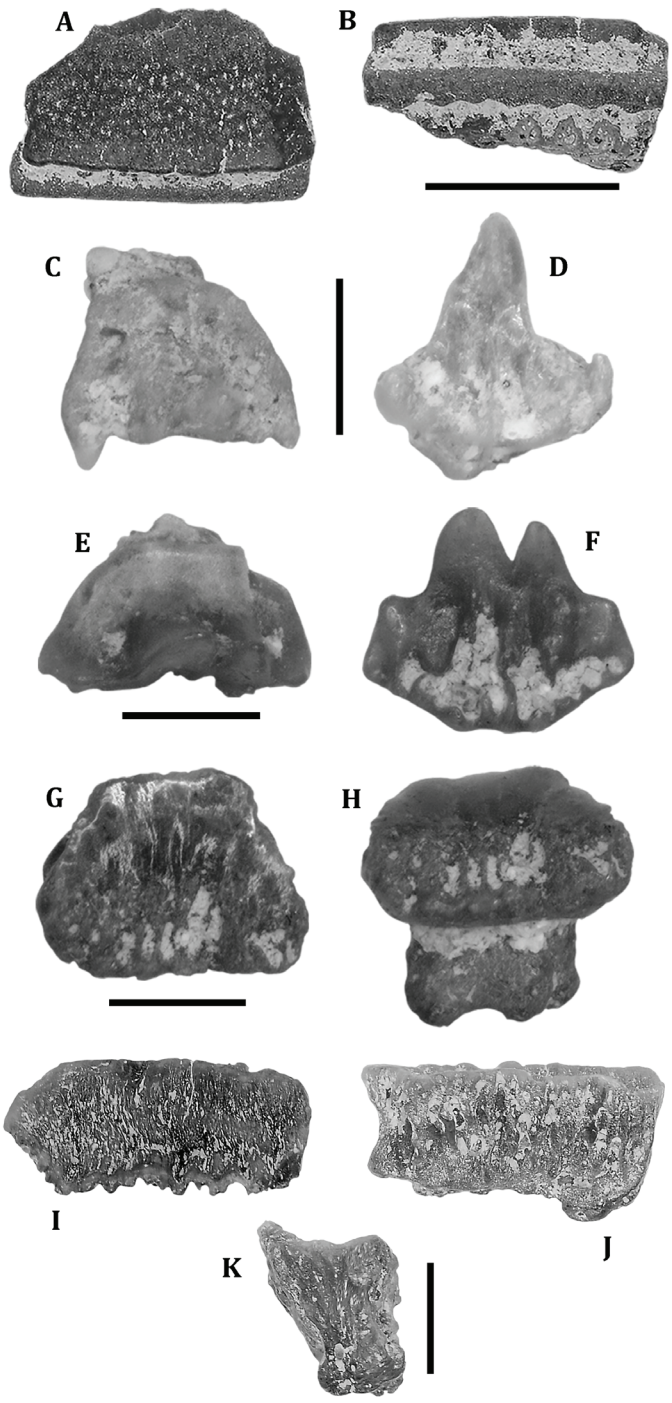

Figure 8. Batoid teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A**, **B**. "*Rhinoptera*" sp. tooth, SC2015.29.30 in occlusal (**A**) and lingual (**B**) views. **C**, **D**. "*Mobula*" sp. male tooth, SC2007.36.40 in apical (**C**) and occlusal (**D**) views. **E**, **F**. "*Mobula*" sp. male tooth, SC2007.36.42 in apical (**E**) and occlusal (**F**) views. **G**, **H**. "*Mobula*" sp. female tooth, SC2007.36.43 in occlusal (**G**) and labial (**H**) views. **I–K**. *Plinthicus* sp. tooth, SC2007.36.48 in occlusal (**I**), lingual (**J**), and profile (**K**) views. Scale bar=1 mm in **C–H**; 5 mm in **A**, **B**, **I–K**.

accurate generic determination.

MOBULINAE Gill, 1893
MOBULA Rafinesque, 1810b
"*Mobula*" sp.
Fig. 8C–H

Type species—*Mobula auriculata* Rafinesque, 1810b; Recent.

1999 *Mobula* sp.; Müller, page 66.

2009a *Mobula* cf. *M. loupianensis* Cappetta, 1970; Cicimurri and Knight, pages 639–640, fig. 9.

Referred specimens (n=11)—SC2007.36.40 (Fig. 8C, D), SC2007.36.41, SC2007.36.42 (Fig. 8E, F), SC2007.36.43 (Fig. 8G, H), SC2007.36.44, SC2007.36.45, SC2007.36.46, SC2007.36.47, SC2007.36.125, SC2015.29.16, SC2015.29.31.

Remarks—A recent molecular divergence study by Villalobos-Segura and Underwood (2020) suggested that *Mobula* diverged from its sister taxon, *Rhinoptera*, during the late Miocene. This suggests that morphologically similar Paleogene teeth cannot be referred to *Mobula*. However, the great similarity of the Oligocene taxon to both *M. loupianensis* and extant *M. rochebrunei* (Vaillant, 1879) would seem to indicate a close phylogenetic relationship. The Oligocene mobulids from South Carolina are being investigated in more detail, but for the purposes of this report we conservatively retain these specimens within the genus *Mobula* with the understanding that they likely belong to a closely related ancestral taxon.

Our small sample exhibits a remarkable amount of variation, which we attribute to gynandric heterodonty within a single taxon (see Notabartolo di Sciara 1987). The narrow, single to tri-cusped teeth represent males, whereas the wider, linguiform to multi-cuspidate teeth belong to females. This interpretation is supported by the work of Herman et al. (2000, plates 19–22), who illustrated the gynandric variation they observed in extant *Mobula rochebrunei*. The Ashley Formation morphotypes we examined match those illustrated by Cicimurri and Knight (2009a, fig. 9) from the overlying (Chattian) Chandler Bridge Formation, and we regard them as conspecific. We also concur with Cicimurri and Knight (2009a) that the *Mobula* sp. teeth reported by Müller (1999) from the Oligocene Old Church Formation of Virginia appear to fall within the range of variation observed in the South Carolina Oligocene "*Mobula*" sample. Müller (1999, page 66) reported *Mobula* sp. from the Ashley Formation, but he did not illustrate any specimens from this lithostratigraphic unit.

Although some of the South Carolina Oligocene "*Mobula*" teeth resemble the holotype of the Rupelian *Mobula irenae* Pfeil, 1981, none are similar to Pfeil's (1981:plate 1, fig. 2) paratype, and we consider the two as separate species. The Rupelian taxon *Eomanta kowaldi* Pfeil, 1981 is based on a single tooth and there is some debate as to whether it represents a distinct taxon (Adnet et al. 2012) or is conspecific with "*M.*" *irenae* (Cicimurri and Knight 2009a). The *E. kowaldi* tooth has a higher crown and the occlusal surface is unusually constricted and more embayed compared to our Oligocene specimens. The early Eocene (Ypresian) taxon *Eomobula* Herman et al., 1989 may not be a mobulid as originally thought (Adnet et al. 2012), but the superficially similar teeth can be differentiated from the South Carolina Oligocene specimens by its very low crown with no vertical wrinkling, and the root is poorly differentiated into individual root lobes. The taxon *Paramobula fragilis* (Cappetta, 1970) (which has since been assigned to *Mobula*) was reported from the Chattian Chandler Bridge Formation by Cicimurri and Knight 2009a (fig. 6D), but these teeth are more similar in morphology to those of *Plinthicus* and will not be confused with "*Mobula*" teeth described herein. Eocene and Oligocene teeth of *Argoubia* Adnet et al., 2012 apparently lack the linguiform and bi- and tri-cuspidate morphologies that occur in the dentition of the Ashley Formation taxon, and the occlusal surface is generally weakly concave (also Leder 2015). Eocene *Oromobula* Adnet et al., 2012 teeth generally are higher and much thinner (labio-lingually) than the South Carolina "*Mobula*," and the relatively small occlusal surface is very irregular.

Genus *PLINTHICUS* Cope, 1869
Plinthicus sp.
Fig. 8I–K

Type species—*Plinthicus stenodon* Cope, 1869; Miocene Kirkwood Formation(?); Cumberland County, New Jersey, USA.

2009a *Plinthicus stenodon* (Cope); Cicimurri and Knight, page 641, fig. E–F.

Referred specimens (n=1)—SC2007.36.48.

Remarks—SC2007.36.48 differs from teeth of Ashley Formation "*Mobula*" by being much larger in overall size, by having a much wider and higher crown, by bearing heavily ridged vertical crown faces (ridges extend from the crown foot nearly to the apex), and by having a concave occlusal surface that lacks elongated and lingually directed projections. This specimen differs from "*Mobula*" *fragilis* (Cappetta, 1970) reported from

the Chandler Bridge Formation (Cicimurri and Knight 2009a) by being much larger in size, labio-lingually thicker, having a concave occlusal surface, and by having better developed vertical ridges on the labial and lingual faces. Middle Oligocene teeth of *Arnomobula* Leder, 2015 differ from *Plinthicus* sp. by having a smooth lingual face and an occlusal surface consisting of irregular peaks and ridges, as opposed to a flat triturating surface. Eocene *Eoplinthicus* teeth have a distinctive low crown with an occlusal surface that is smaller in area than the crown foot (Cappetta and Stringer 2002, Adnet et al. 2012, Ebersole et al. 2019), but in contrast *Plinthicus* has occlusal and basal crown outlines of roughly the same dimensions.

The gross morphology of SC2007.36.48 is comparable to *Plinthicus*, but it differs significantly in profile view from the European Rupelian species, *P. kruibekensis* Bor, 1990. The crown of the Ashley Formation specimen is lingually inclined, with the labial and lingual faces being relatively straight (Fig. 8K). In contrast, the crown of *P. kruibekensis* is rather erect and the labial face is convex, whereas the lingual face is concave (Bor 1990). Cicimurri and Knight (2009a) reported several specimens from the Chandler Bridge Formation that they identified as *Plinthicus stenodon* Cope, 1869, citing close similarities to Mio-Pliocene teeth of this species occurring elsewhere. The crown morphology is variable in the Chandler Bridge Formation sample we examined, but SC2007.36.48 falls within the range of variation and we consider the samples from the two formations to be conspecific. Müller (1999, page 66) identified *Plinthicus stenodon* from the Ashley Formation, but he did not illustrate any specimens from this lithostratigraphic unit, and we therefore could not evaluate his material.

Our comparison of the Oligocene *Plinthicus* to Miocene specimens of *P. stenodon* (SC98.46) revealed significant differences. The Oligocene taxon exhibits a weakly inclined crown with relatively straight labial and lingual faces. The heavy vertical ridges on the labial and lingual faces are thick, highly irregular, and often interconnected via transverse ridges (Fig. 8J). In contrast, the crown of *P. stenodon* is much thinner labio-lingually, very highly lingually inclined, and near the apex the labial and lingual faces appear to curve labially. In addition, the labial and lingual ridges are very thin, sharp, straight, and not interconnected. Furthermore, the lingual ridges extend beyond the general occlusal plain, forming an irregular ridge that is separated from the occlusal surface by a shallow transverse furrow. On the Oligocene teeth, the lingual ridges terminate at the occlusal margin. The morphological differences between the Oligocene and Neogene specimens indicate that they represent different species. We refrain from naming a new species herein because the Ashley Formation specimen is broken and ablated. However, the Oligocene mobulids of South Carolina are currently under further evaluation (including specimens from the Chandler Bridge Formation). The Rupelian occurrence of *Plinthicus* in South Carolina is confirmed and thereby extends the temporal range of the genus from 24.5 Ma (Chattian) back to approximately 28.5 Ma.

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII (*sensu* Goodrich, 1930)
NEOPTERYGII Regan, 1923
TELEOSTEOMORPHA Arratia et al., 2004
TELEOSTEI Müller, 1845
TELEOCEPHALA de Pinna, 1996
ELOPOMORPHA Greenwood et al., 1966
ALBULIFORMES Greenwood et al., 1966
ALBULIDAE Bleeker, 1849
ALBULINAE Bleeker, 1849
ALBULA Scopoli, 1777
Albula sp.
Fig. 9A, B

Type species—*Esox vulpes*, Linnaeus, 1758; Recent.

Referred specimens (n=74)—SC2007.36.165, SC2007.36.228 (five teeth), SC2015.29.200 (66 teeth), SC2015.29.201, SC2015.29.204 (Fig. 9A, B).

Description—Teeth consist of an enameloid-covered crown that has a circular outline in occlusal view. The enameloid is thin and smooth and does not extend to the tooth base, exposing the interior dentine on the lower half of the tooth. The occlusal surface of unworn teeth is weakly convex, but it is often observed flat due to *in vivo* use. Lateral tooth surfaces are straight to weakly convex and taper inwards towards the base. A small, circular, centrally located and shallow basal pulp cavity is framed by a thick wall of dentine.

Remarks—This tooth morphology is reminiscent of the Eocene *Albula oweni* (Owen, 1845), as the occlusal surface of the Ashley Formation specimens is virtually flat and the crown sides are basally tapering (Weems 1999, Ebersole et al. 2019). These teeth will not be confused with those of Sciaenidae and Sparidae that also occur in the Ashley Formation (see below) because the crown has as a uniquely beveled appearance in profile view. This is the first record of bonefish from the Oligocene of South Carolina.

OSTEOGLOSSOCEPHALA Arratia, 2010
OSTEOGLOSSOMORPHA Greenwood et al., 1966
OSTEOGLOSSIFORMES Berg, 1940
OSTEOGLOSSIDAE Bonaparte, 1845

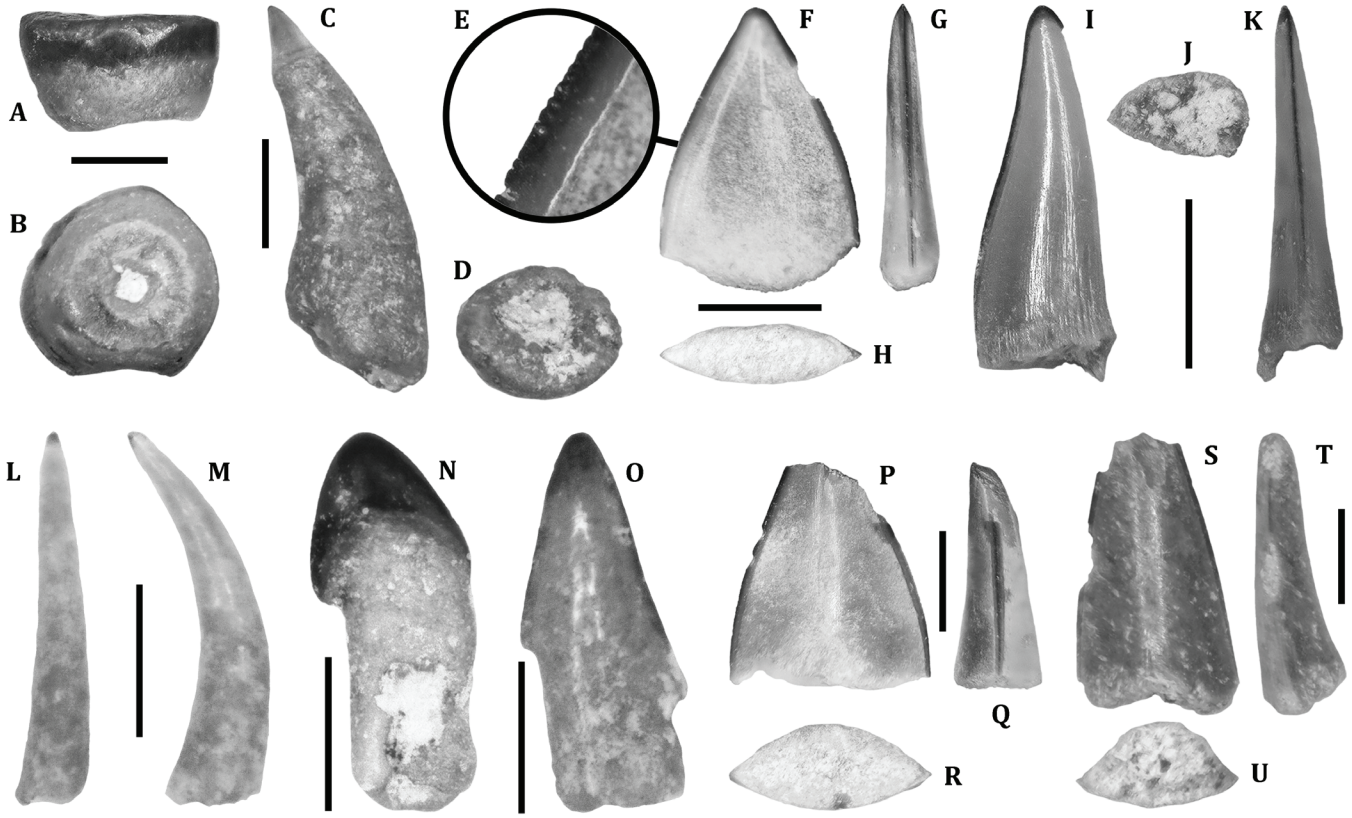

Figure 9. Teleost teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A**, **B**. *Albula* sp. tooth, SC2015.29.204 in profile (**A**) and basal (**B**) views. **C**, **D**. Osteoglossidae indet. tooth, SC2015.29.218 in profile (**C**) and basal (**D**) views. **E**–**H**. *Sphyraena* sp. cheek tooth, SC2007.36.120 in close-up showing serrations (**E**), labial (**F**), carinal (**G**), and basal (**H**) views. **I**–**K**. *Sphyraena* sp. laniary tooth, SC2007.36.190 in labial (**I**), basal (**J**), and anterior (**K**) views. **L**, **M**. Paralichthyidae indet. tooth, SC2007.36.259 in labial (**L**) and distal (**M**) views. **N**. *Trichiurides* cf. *T. sagittidens* laniary tooth, SC2015.29.185 in profile view. **O**. *Trichiurides* cf. *T. sagittidens* laniary tooth, SC2007.36.210 in profile view. **P**–**R**. *Palaeocybium* sp. tooth, SC2007.36.122 in labial (**P**), carinal (**Q**), and basal (**R**) views. **S**–**U**. *Scomberomorus* sp. tooth, SC2015.29.221 in lingual (**S**), carinal (**T**), and basal (**U**) views. Scale bar=0.4 mm in **O**; 0.5 mm in **C**, **D**, **L**–**N**, **S**–**U**; 1 mm in **A**, **B**, **I**–**K**; 3 mm in **E**–**H**, **P**–**R**.

GEN. ET SP. INDET.

FIG. 9C, D

Referred specimens (n=25)—SC2007.36.115 (10 teeth), SC2007.36.144 (six teeth), SC2007.36.211 (two teeth), SC2015.29.183 (three teeth), SC2015.29.188 (three teeth), SC2015.29.218 (Fig. 9C, D).

Description—These teeth are tall and conical, slightly postero-medially curved, and sharply pointed. The tooth apex bears a tiny enameloid cap that is translucent, and enameloid is often absent from the lateral edges of the tooth. The tooth has a circular outline in basal view and has a medially located and circular pulp cavity.

Remarks—These teeth, which consist of a very tall peduncle and comparatively small crown, are similar to Eocene osteoglossid teeth reported from Virginia and Alabama (Weems 1999, Ebersole et al. 2019). These teeth differ from the *Trichiurides sagittidens* Winkler, 1874 and *Sphyraena* spp. laniary teeth in our sample by the combination of being postero-medially curved, by having a translucent enameloid cap that lacks a posterior barb, and by having a circular cross-section in basal view. They differ from the Paralithchyidae indet. tooth in our sample by being less lingually curved and by lacking a flared apex. The Ashley Formation specimens represent the first fossil record of the family from South Carolina.

CLUPEOCEPHALA PATTERSON AND ROSEN, 1977

EUTELEOSTEI ROSEN, 1985

ACANTHOPTERYGII GREENWOOD ET AL., 1966

PERCOMORPHA (*SENSU* NELSON ET AL., 2016)

OVALENTARIA SMITH AND NEAR IN WAINWRIGHT ET AL., 2012

ISTIOPHORIFORMES BETANCUR-R ET AL., 2013

SPHYRAENIDAE RAFINESQUE, 1815

SPHYRAENA ARTEDI, 1793

SPHYRAENA SPP.

FIG. 9E–K

Type species—*Esox sphyraena*, Linnaeus, 1758; Recent; Mediterranean Sea.

Referred specimens (n=56)—SC2007.36.119 (eight teeth), SC2007.36.120 (Fig. 9E–H), SC2007.36.121 (six teeth), SC2007.36.134 (15 teeth), SC2007.36.190 (Fig. 9I–K), SC2007.36.191, SC2007.36.212, SC2007.36.213, SC2007.36.214 (two teeth), SC2007.36.215, SC2015.29.202, SC2015.29.203, SC2015.29.210 (seven teeth), SC2015.29.211 (four teeth), SC2015.29.212 (three teeth), SC2015.29.213 (three teeth).

Description—Both cheek (Fig. 9E–H) and laniary (Fig. 9I–K) teeth were identified in our sample. The cheek teeth are lanceolate, with convex anterior and posterior cutting edges that may be smooth or very finely serrated. The labial and lingual faces are only weakly convex and they appear to be unornamented, although on many specimens the enameloid is only preserved at the cutting edges. In anterior/posterior view, the crown may be straight or medially curved. The cheek teeth have an oval basal outline with sharp anterior and posterior points, and a small and shallow basal pulp cavity is preserved on some specimens. The laniary teeth are laterally compressed with rather flat labial and lingual faces. The anterior cutting edge is inclined, weakly sinuous, and may be smooth or finely serrated. The posterior edge is nearly vertical and convex basally but sharpens apically, where there is a small posterior barb on some teeth. Fine longitudinal ridges occur on the more convex portion of the posterior edge. A basal pulp cavity is small and shallow, and the teeth have a teardrop-shaped basal outline. Crown enameloid is preserved only at the anterior cutting edge on some teeth.

Remarks—Based on the jaws of Recent *Sphyraena barracuda* Catesby, 1771 (SC2018.3.1 and MSC 43215) and *S. borealis* DeKay, 1842 (MSC 43076) we examined, most of the teeth in the sample appear to have been from the dentary (both laniary and lanceolate morphotypes), but some teeth may have been located on the palatine and/or premaxilla. Additionally, the teeth of the two Recent taxa can be distinguished based on the presence (i.e., *S. barracuda*) or absence (i.e., *S. borealis*) of serrations. Within the jaws of a single individual, large and small teeth of *S. barracuda* are serrated, whereas large and small teeth of *S. borealis* are smooth. As the presence or absence of serrations appears to be a taxonomically significant character and not related to ontogeny or some other form of heterodonty, we believe that the serrated and unserrated morphologies in the Ashley Formation sample represent two species of *Sphyraena*. Cicimurri and Knight (2009a) noted the occurrence of the genus in the overlying Chandler Bridge Formation, but the specimens in our sample represent the first record of barracudas from the Ashley Formation.

PLEURONECTIFORMES Bleeker, 1859
PLEURONECTOIDEI (*sensu* Nelson et al., 2016)
PLEURONECTOIDEA Rafinesque, 1815
PARALICHTHYIDAE Regan, 1910
GEN. ET SP. INDET.
Fig. 9L, M

Referred specimen (n=1)—SC2015.36.259.

Description—This tooth is thin, needle-like, and measures approximately 1.0 mm in total height. In labial view, the margins of the tooth are relatively straight but gradually taper to a sharp point. In mesial and distal views, the tooth has a conspicuous lingual curvature, with a uniformly convex labial margin and a concave lingual margin. The main body of the tooth lacks carinae, but short labial and lingual cutting edges occur at the apex. The apex is slightly upturned and labiolingually flared. The tooth lacks ornamentation, and the enameloid at the crown apex is flared, semi-translucent, and lighter in color than that of the remainder of the tooth. The tooth has a conical cross section, and the base has a circular outline, is thin-walled and bears a shallow pulpcavity.

Remarks—The combination of features occurring on SC2015.36.259 has also been observed by us on the teeth of Recent members of the Lepisosteidae (gars) and Paralichthyidae (large-tooth flounders). However, specimen SC2015.36.259 lacks finely striated enameloid ornamentation and has a more evenly convex labial edge when compared to any of the Recent gar teeth we examined. Our specimen, however, compares very well to the dentary incisors of a Recent *Paralichthys lethostigma* Jordan and Gilbert in Jordan and Meek, 1884 specimen we studied (MSC 42999), indicating that this tooth belongs to an Oligocene member of the Paralichthyidae. Extant Paralichthyidae is an extremely diverse family consisting of at least 14 genera and approximately 111 species (Nelson et al. 2016). Unfortunately, the diversity within this family and our lack of Recent comparative material does not allow us to identify this tooth beyond the familial level. Nevertheless, Ebersole et al. (2021) recently confirmed two unspeciated, otolith-based paralichthyid genera (*Citharichthys* and *Syacium*) from the Rupelian Glendon Limestone Member of the Byram Formation in Washington County, Alabama. These occurrences show that members of the family were well-established in the nearby Gulf Coastal Plain of the USA during the Oligocene.

SCOMBRIFORMES Rafinesque, 1810b
SCOMBROIDEI Bleeker, 1859
TRICHIURIDAE Rafinesque, 1810b
TRICHIURINAE Rafinesque, 1810b
TRICHIURIDES Winkler, 1874
Trichiurides cf. *T. sagittidens* Winkler, 1874
Fig. 9N, O

Type species—*Trichiurides sagittidens*, Winkler, 1874; Belgium, Eocene.

Referred specimens (n=2)—SC2007.36.210 (Fig. 9O), SC2015.29.185 (Fig. 9N).

Description—Our sample consists of two ablated laniary teeth. As preserved, specimen SC2015.29.185 consists of a laterally compressed crown and some of the peduncle. In labial view the crown apex has a low, subtriangular outline, and in posterior view the enameloid-covered labial and lingual faces are weakly convex. The enameloid is smooth at the apex but is not preserved on the remainder of the specimen. The anterior and posterior margins are formed into a smooth, continuous and bi-convex cutting edge, and a small barb is located towards the apex on the posterior edge. The peduncle consists of dentine and is cylindrical and slightly curved medio-posteriorly. In basal view the tooth has a circular outline and a medially located pulp cavity is visible. Specimen SC2007.36.210 consists of a minute but well preserved crown apex. The crown of this specimen is triangular but taller than that of SC 2015.29.185, and the cutting edges are straight to weakly concave. The enameloid is smooth and a posterior barb is conspicuous.

Remarks—The teeth in our sample clearly differ from the Ashley Formation *Sphyraena* spp. laniary teeth by having a highly laterally compressed enameloid apex and narrow, cylindrical neck. The overall morphology of these teeth, especially the size and shape of the posterior barb, is morphologically similar to Recent *Trichiurus lepturus* Linnaeus, 1758 (MSC 42592) laniary teeth, as well as to those of the Eocene *Trichiurides sagittidens* Winkler, 1874 (see Ebersole et al. 2019). Although the Ashley Formation teeth could belong to the latter taxon,we only tentatively refer them to this species due to their incomplete preservation. Nevertheless, these teeth represent the first Oligocene records of cutlassfish in South Carolina.

SCOMBRIDAE Rafinesque, 1815
SCOMBRINAE Rafinesque, 1815
SCOMBEROMORINI Starks, 1910
PALAEOCYBIUM Monsch, 2005
Palaeocybium sp.
Fig. 9P–R

Type species—*Cybium proosti*, Storms, 1897; Eocene; Belgium and England.

Referred specimens (n=1)—SC2007.36.122.

Description—The tooth is lanceolate in labial/lingual view and higher than wide (antero-posteriorly). The anterior and posterior edges are smooth and have sharp continuous cutting edges. Both edges are convex basally, but they are straight at the upper two-thirds and converge apically (Fig. 9P). In anterior/posterior view the tooth is weakly curved lingually (Fig. 9Q). The cutting edges roughly divide the tooth into labial and lingual faces of roughly equal convexity (Fig. 9R).

Remarks—Although specimen SC2007.36.122 is comparable to non-laniary teeth of *Sphyraena* spp. in our sample, it differs by being much thicker and having more convex labial and lingual faces (compare Fig. 9R to 9H). Additionally, whereas *Sphyraena* spp. non-laniary teeth are erect and virtually straight, SC2007.36.122 exhibits a medial curvature. The features observed on SC2007.36.122 match those observed on teeth in a *Palaeocybium* dentary in the SC collection that was recovered from the Ashley Formation (SC2016.1.14), and it is therefore referred to this genus.

SCOMBEROMORUS de Lacepède, 1801
Scomberomorus sp.
Fig. 9S–U

Type species—*Scomber regalis*, Bloch, 1793; Recent.

Referred specimens (n=5)—SC2007.36.135, SC2007.36.216, SC2015.29.214, SC2015.29.221 (Fig. 9S–U).

Description—The teeth are lanceolate and higher than wide. The anterior and posterior margins are formed into smooth, continuous cutting edges that are straight basally but become convex apically, culminating in a pointed apex. These carinae asymmetrically divide the crown such that the lingual face is much larger than the labial face, a characteristic that is particularly visible in basal view. The enameloid is smooth and typically only preserved at the carinae. The labial face is flat to weakly convex, and the lingual face is very convex, and the crown may be medially curved. A basal pulp cavity is large but shallow.

Remarks—These teeth differ from those of *Palaeocybium* sp. and non-laniary teeth of *Sphyraena* spp. from the Ashley Formation (see above) by being taller and narrower antero-posteriorly, and they have labial and lingual faces of conspicuously unequal thickness. In contrast, both *Sphyraena* spp. non-laniary teeth and *Palaeocybium* sp. teeth are very wide labio-lingually,

with equally convex labial and lingual faces (Ebersole et al. 2019). Additionally, *Sphyraena* spp. non-laniary teeth typically lack medial curvature as observed on these *Scomberomorus* sp. teeth.

The Ashley Formation specimens are reminiscent of teeth of *Scomberomorus bleekeri* (Storms, 1892), a taxon known from the Claibornian (Ypresian to Bartonian) and into the Jacksonian (Priabonian) of Alabama (Ebersole et al. 2019, JAE unpublished data). The teeth differ from those of Eocene *Scomberomorus stormsi* (Leriche, 1905) by being wider antero-posteriorly and having convex carinae (as opposed to nearly parallel on the lower half). One specimen in our sample, SC2007.36.216, measures less than 1 mm in overall height. However, because it is morphologically similar to the other *Scomberomorus* teeth in our sample, we interpret this specimen as belonging to an immature individual. Although the Ashley Formation specimens compare favorably to Eocene *S. bleekeri*, they are herein not speciated because it is unclear if *S. bleekeri* persisted into the Oligocene. Nevertheless, the Ashley Formation specimens represent the first record of *Scomberomorus* from the Oligocene of South Carolina.

LABRIFORMES Kaufman and Liem, 1982
? Family LABRIDAE Cuvier, 1816
gen. et sp. indet.
Fig. 10

Referred specimens (n=6)—SC2007.36.209 (4 teeth), SC2007.36.257 (Fig. 10A–C), SC2007.36.258 (Fig. 10D, E).

Description—The teeth are minute, with most not exceeding 0.5 mm in greatest diameter. The teeth simply consist of a thick enameloid cap that has a circular to sub-circular outline in occlusal view. In profile view, the occlusal surface is uniformly convex, but the degree of convexity varies from low to high. The lateral edges are convex. The teeth are low-crowned, with their width generally being two to three times their greatest height. The crown enameloid is smooth. . In aboral view the pulp cavity is open and free of dentine.

Remarks—These teeth differ from those of sciaenids and sparids in the Ashley Formation (see below) by being very low-crowned (i.e., crown height is less than basal width) and smaller in size (>1 mm), and by always being circular or sub-circular in occlusal outline. Additionally, the teeth appear to consist of only a thick enameloid cap with an open pulp cavity, as opposed to a dentine core surrounded by enameloid and having a distinctive pulp cavity. Our sample lacks bony remains that could be used to more accurately identify the Ashley Formation labrid(s), but the teeth available to us compare well to the teeth in the pharyngeal plates of various Paleogene and Neogene genera that have been reported (Lund 1992, Oyanadel-Urbina et al. 2021).

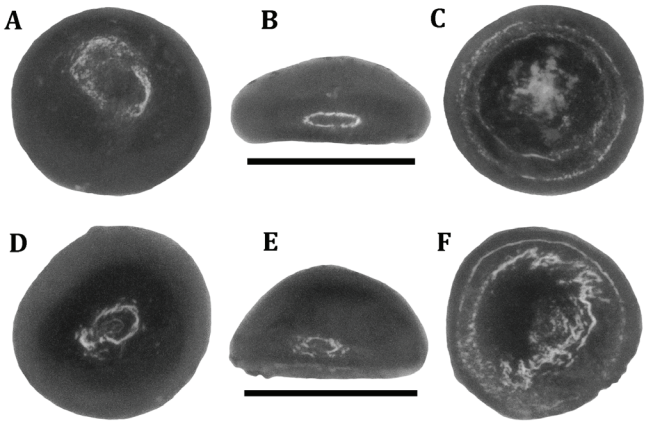

Figure 10. ?Labridae indet. teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A–C**. SC2007.36.209.1 in occlusal (**A**), profile (**B**), and basal (**C**) views. **D–F**. SC2007.36.209.2 in occlusal (**D**), profile (**E**), and basal (**F**) views. Scale bars=0.5 mm.

ACANTHURIFORMES (*sensu* Nelson et al., 2016)
SCIAENOIDEI Betancur-R et al., 2013
SCIAENIDAE Cuvier, 1829
SCIAENOPS Gill, 1863
?*Sciaenops* sp.
Fig. 11A–D

Type species—*Perca ocellata*, Linnaeus, 1766; Recent.

Referred specimens (n=281)—SC2007.36.114 (13 teeth), SC2007.36.166 (41 teeth), SC2007.36.167 (54 teeth), SC2007.36.201, SC2007.36.260 (Fig. 11AB), SC2007.36.261 (Fig. 11C–D), SC2015.29.179 (four teeth), SC2015.29.180, SC2015.29.189 (seven teeth), SC2015.29.190 (19 teeth), SC2015.29.193 (104 teeth), SC2015.29.198 (26 teeth), SC2015.29.199 (seven teeth), SC2015.29.215, SC2015.29.216.

Description—The teeth are tall and cylindrical and are slightly curved posteriorly. The upper two-thirds of the tooth are covered with a smooth enameloid whereas the lower one-third consists of exposed dentine. Unworn teeth have a bluntly pointed apex, whereas the apex on others have a flat wear facet. The apex is more recurved and often slightly smaller in diameter than the rest of the tooth. The teeth are circular in basal outline and have a small, oval, and offset pulp cavity that is surrounded by a thick wall of dentine.

Remarks—The teeth in our sample compare

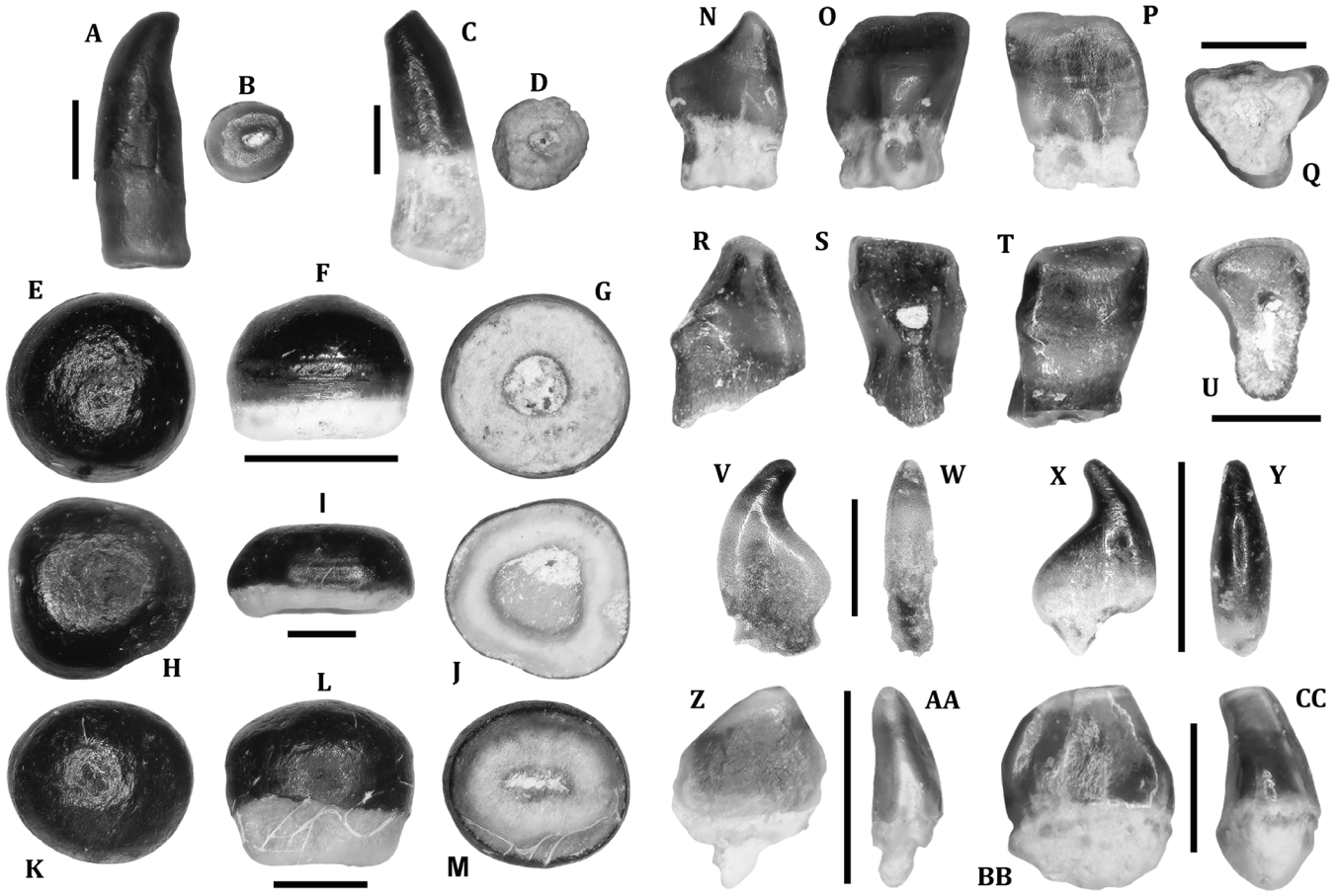

Figure 11. Teleost teeth from the Givhans Ferry Member, Ashley Formation (Rupelian), Dorchester County, South Carolina. **A**, **B**. ?*Sciaenops* sp. tooth, SC2007.36.200.1 in profile (**A**) and basal (**B**) views. **C**, **D**. ?*Sciaenops* sp. tooth, SC2007.36.200.2 in profile (**C**) and basal (**D**) views. **E–G**. ?*Pogonias* sp. tooth, SC2007.36.196 in occlusal (**E**), profile (**F**), and basal (**G**) views. **H–J**. ?*Calamus* sp. tooth, SC2007.36.198 in occlusal (**H**), profile (**I**), and basal (**J**) views. **K–M**. *Archosargus* sp. molariform tooth, SC2007.36.197 in occlusal (**K**), profile (**L**), and basal (**M**) views. **N–Q**. *Archosargus* sp. incisiform tooth, SC2007.36.200 in profile (**N**), lingual (**O**), labial (**P**), and basal (**Q**) views. **R–U**. *Archosargus* sp. incisiform tooth, SC2015.29.219 in profile (**R**), lingual (**S**), labial (**T**), and basal (**U**) views. **V**, **W**. *Archosargus* sp. pharyngeal tooth, SC2007.36.192 in profile (**V**) and anterior (**W**) views. **X**, **Y**. *Archosargus* sp. pharyngeal tooth, SC2007.36.193 in profile (**X**) and anterior (**Y**) views. **Z**, **AA**. *Diplodus* sp. tooth, SC2015.29.222 in lingual (**Z**) and posterior (**AA**) views. **BB–CC**. *Diplodus* sp. tooth, SC2015.29.224 in lingual (**BB**) and posterior (**CC**) views. Scale bar=0.5 mm in **V, W**; 1 mm in **A–U**, **X–CC**.

exceptionally well with those on the pharyngeals of a Recent *Sciaenops ocellatus* (Linnaeus, 1766) specimen we examined (MSC 42611). These specimens differ from the similar Osteoglossidae teeth in our sample by having a more recurved apex that is not translucent. Recent molecular data provided by Near et al. (2013) and Lo et al. (2015) both support the genera *Micropogonias* and *Sciaenops* as sister taxa that likely diverged from a common ancestor at some point during the late Oligocene to early Miocene. This suggests that the Ashley Formation teeth represent either a basal member of *Sciaenops* or an unknown and undescribed Rupelian sciaenid that is ancestral to both *Micropogonias* and *Sciaenops*.

POGONIAS DE LACEPÈDE, 1801

?POGONIAS SP.

FIG. 11E–G

Type species—*Pogonias fasciatus*, de Lacepède 1801; Recent.

Referred specimens (n=36)—SC2007.36.112 (33 teeth), SC2007.36.138, SC2007.36.196 (Fig. 11E–G), SC2007.36.197.

Description—These teeth are circular in occlusal outline and have a smooth enameloid crown. The enameloid does not extend to the base of the teeth, exposing a ring of dentine at the tooth base. The teeth have a strongly domed occlusal surface and slightly convex lateral edges.

In profile view, the teeth are slightly wider than tall. A shallow, rounded, and centrally located pulp cavity is visible on the tooth base that is surrounded by a thick wall of dentine.

Remarks—These specimens are comparable to teeth in the pharyngeal plates of a Recent *Pogonias cromis* (Linnaeus, 1766) we examined (MSC 42612). They differ from the *Albula* sp. teeth in our sample by having a more domed apex and the lateral edges are not straight or basally tapered as they are on the Ashley Formation *Albula*. These teeth differ from the ?*Calamus* teeth in our sample by having a circular occlusal outline, a smaller pulp cavity that is surrounded by thicker dentine walls, and by having a taller and more domed crown. They differ from the *Archosargus* sp. molariform teeth in our sample by being wider than tall, by having a circular as opposed to oval pulp cavity, and by not being as basally tapered.

Lo et al. (2015) provided molecular data that suggested *Pogonias cromis*, the only extant member of the genus, diverged from a clade consisting of the sciaenid genera *Sciaena* and *Umbrina* during the early Miocene, approximately 21.3 Ma. This suggests that the Ashley Formation teeth represent either a basal member of *Pogonias* or an unknown and undescribed Rupelian sciaenid that is ancestral to *Pogonias*, *Sciaena*, and *Umbrina.*

SPARIFORMES (*sensu* Nelson et al., 2016)
SPARIDAE Rafinesque, 1818
CALAMUS Swainson, 1839
?Calamus sp.
Fig. 11H–J

Type species—*Calamus megacephalus* Swainson 1839; Recent.

Referred specimens (n=11)—SC2007.36.117 (nine teeth), SC2007.36.198 (Fig. 11H–J), SC2007.36.199.

Description—This tooth morphotype consists of a low crown (wider than tall) that has an oval, round, squared or sub-rectangular occlusal outline. The occlusal surface is generally evenly convex, but the apex is often flat on worn teeth. Unworn teeth may have a small, but conspicuous, apical protuberance. The crown enameloid is smooth and does not extend to the base of the tooth. The tooth edges are convex in profile view, but often to varying degrees, and the tooth base is often constricted. A basal pulp cavity is extremely large and is often the same shape as the occlusal outline. The pulp cavity is relatively shallow and surrounded by a thick wall of dentine.

Remarks—The specimens in our sample are comparable to teeth occurring on the premaxillae and dentaries of an extant *Calamus leucosteus* Jordan, 1885 (MSC 43464) specimen that we examined. The pulp cavity is shallower and much larger than that on the *Albula* sp., ?*Pogonias* sp. and *Argosargus* sp. molariform teeth in our sample, and the crown width to height ratio is much lower than the teeth of these other taxa. Although these teeth may be referable to *Calamus*, our sample of sparid teeth does not include an incisiform morphology comparable to what we observed in the Recent *C. leucosteus* dentition.

ARCHOSARGUS Gill, 1865
Archosargus sp.
Fig. 11K–Y

Type species—*Sparus probatocephalus*, Walbaum 1792, Recent.

Referred specimens (n=73)—SC2007.36.111 (nine teeth) SC2007.36.146 (15 teeth), SC2007.36.163 (three teeth), SC2007.36.193 (Fig. 11X–Y), SC2007.36.200 (Fig. 11N–Q), SC2015.29.192 (20 teeth), SC2015.29.192 (Fig. 11V–W), SC2015.29.194, SC2015.29.196 (12 teeth), SC2015.29.197 (Fig. 11K–M), SC2015.29.205 (seven teeth), SC2015.29.217, SC2015.29.219 (Fig. 8R–U), SC2015.29.220.

Description—Three tooth morphologies were identified in our sample, including molariform (Fig. 11K–M), incisiform (Fig. 8N–U), and pharyngeal (Fig. V–Y). The molariform teeth have a circular to oval occlusal outline and a domed crown. The height of the teeth is nearly equal to the width. The occlusal surface is covered with enameloid, but the enameloid does not extend to the tooth base. The sides of the crown are straight to weakly convex and basally constricted where the root begins. Smaller teeth are less constricted than large ones. In basal view, the teeth have a deep, oval, and medially located pulp cavity that is framed by a thick wall of dentine.

The incisiform teeth measure less than 3.0 mm in height and up to 2.0 mm in width. In profile they are similar in appearance to the pharyngeal teeth described below, but they are much wider mesio-distally. The labial face ranges from broad and flat to weakly convex, but the lingual face bears a large, posteriorly directed boss that is narrower than the labial crown width. The upper half of the crown is developed into a broad transverse crest, which is often worn (through *in vivo* use) such that the internal dentine is exposed and framed by a thick layer of enameloid. The enameloid is smooth. The crown base is constricted at the point where the root begins. The root is comprised of dentine and is smaller in area than the crown.

The pharyngeal teeth are small, measuring less than 2.0 mm in total height and as much as 0.25 mm in width

(mesio-distal). They are highly laterally compressed but of equal apico-basal thickness. In profile the crown is antero-posteriorly wide at the lower half, but the upper part is developed into a conical, posteriorly curved cusp. The labial and lingual tooth margins are rounded. The labial margin is convex, whereas the lingual margin is sinuous due to the posteriorly expanded lower portion of the crown. The base of the crown tapers slightly at the origin of the root.

Remarks—We compared the teeth described above to those of the extant sparids *Archosargus probatocephalus* (Walbaum, 1792) (MSC 42584) and *Calamus leucosteus*, and the sciaenid *Pogonias cromis* (MSC 42612). Within the Ashley Formation sample described above, the pharyngeal teeth are comparable to those occurring along the margins of the *A. probatocephalus* pharyngeal plates. This *Archosargus*-type pharyngeal morphology appears to be lacking in the *C. leucosteus* and *P. cromis* specimens we examined.

The complex morphology of the Ashley Formation incisiform teeth compares very favorably to those of extant *Archosargus* but is very different from other sparid incisiform teeth described below. The molariform teeth also conform to large crushing-type teeth on *A. probatocephalus* pharyngeal plates. When compared to the other similar teeth identified in our Ashley Formation sample, the *Archosargus* sp. molariform teeth have a deeper and more oval pulp cavity than on *Albula* sp., ?*Calamus* sp. and ?*Pogonias* sp. In addition, the crown height to width ratio is greater than on the other taxa, and the teeth are more basally constricted than those of ?*Calamus* sp. and ?*Pogonias* sp. Finally, the crown is more dome-shaped in profile view than those of *Albula* sp. With all three of these tooth morphologies occurring within the dentition of the Recent *A. probatocephalus* examined, it is assumed that all three morphologies identified our Ashley Formation sample belong to the same taxon.

DIPLODUS Rafinesque, 1810b
Diplodus sp.
Fig. 11Z–CC

Type species—*Sparus annularis*, Linnaeus 1758; Recent.

Referred specimens (n=16)—SC2015.29.195 (13 teeth), SC2015.29.222 (Fig. 11Z, AA), SC2015.29.223, SC2015.29.224 (Fig. 11BB, CC).

Description—Tooth crowns are mesio-distally wide (less than 5 mm) but very thin labio-lingually. The labial face is weakly convex across crown width, whereas the lingual face is weakly concave. Both faces are covered by a thick layer of smooth enameloid. The occlusal surface of unworn specimens is thin and convex, but worn specimens exhibit a flat and straight occlusal surface. The crown is basally tapered, and enameloid ends where the tooth base begins. The tooth base has a deep and mesio-distally extended reniform-shaped pulp cavity.

Remarks—These labio-lingually compressed crowns are similar to the incisiform teeth identified as *Diplodus* sp. from the Miocene of Costa Rica (Laurito Mora 1999) and as *Sargus* (=*Diplodus*) *laticonus* Davis, 1888 from the New Zealand Neogene (also Chapman 1918). We have not conducted an exhaustive review of Sparidae incisiform teeth, but the specimens described herein differ from those of *Archosargus* sp. (see above) by being very antero-posteriorly compressed, with weakly convex labial face and weakly concave lingual face and lacking a well-defined lingual protuberance.

DISCUSSION

Based on the 245 galeomorph teeth and 112 batomorph teeth that we recovered from matrix samples, the Givhans Ferry Member elasmobranch paleofauna is comprised of at least 21 unequivocal taxa (including two species within Sphyrnidae). Teleost otoliths are not preserved in the Ashley Formation, but the 586 teeth that we recovered represent species within up to 14 taxa in nine families (including possible Labridae and two species of Sphyraenidae). All our specimens were recovered from matrix directly associated with skeletal remains of large marine vertebrates (a dermochelyid carapace and two odontocete cetacean skulls) that occurred in the Givhans Ferry Member of the Ashley Formation. Our sample is biased towards small specimen size, and additional larger taxa remain to be documented in detail. For example, the Ashley Formation is the type unit for *Trigonotodus alteri* Kozlov, 2001, but it is currently unclear from which of the three members the type material was derived. In addition, *Otodus* (*Carcharocles*) *angustidens* (de Blainville, 1818) occurs in the Givhans Ferry Member, as evidenced by ablated specimens observed by DJC and JLK occurring as float in the Ashley River near SC2015.29.1 (also Gibbes 1849). Teeth of the shark *Araloselachus* sp. (SC uncurated), a neurocranium and left dentary of the large scombroid fish *Palaeocybium* sp. (SC2016.4.1 and SC2016.1.14, respectively), and numerous thunniform vertebrae (SC79.38.351) may also have been derived from the Givhans Ferry Member.

The dermochelyid carapace and the two cetacean skulls do not exhibit direct evidence of predation or scavenging (i.e., bite marks or embedded tooth crowns)

by elasmobranchs. However, two genera we identified in the Ashley Formation, *Galeocerdo* and *Carcharhinus*, have fossil records of consuming cetacean remains (Cicimurri and Knight 2009b), and it is possible that the relatively small teeth of the Oligocene species simply left no physical marks on bones. It is also plausible that elasmobranchs targeted other parts of the body like limbs and tail, which were not associated with the carapace or whale skulls. Although we cannot rule out the possibility that at least some of the teeth we recovered were shed during consumption of the turtle and whale carcasses, our alternative hypothesis is that the elasmobranch and bony fish remains were detritus that was already on the sea floor or accumulated during or after soft tissue decomposition. It is unlikely that any of the rays, like "*Mobula*", *Raja*, and "*Dasyatis*", or teleosts like *Pogonias*, *Archosargus* and *Albula*, scavenged the carcasses, as these taxa are planktivorous or primarily feed on invertebrates and smaller fish. Their teeth likely accumulated on the sea floor through natural tooth replacement or death. This hypothesis is supported by the large number of placoid scales we recovered (n=566), which appear to reflect inter- (among species) and intraspecific (along the body of an individual) variation based on the differing morphologies. In addition, many of the teeth and scales are abraded and/or broken, indicating transport along the sea floor.

The teleost faunas of the Chandler Bridge Formation have not been studied in detail, so a direct comparison to the Ashley Formation bony fish assemblage is not possible. However, the elasmobranch paleofaunas of these two formations are remarkably similar, and comparisons are presented in Table 1 (selachians) and Table 2 (batoids). The similarity is surprising, considering that the Ashley Formation is roughly three million years older than the Chandler Bridge Formation, and these units represent different depositional settings. The Givhans Ferry Member of the Ashley Formation may have been deposited at a depth of approximately 100 m during a period of highstand (Miller and Wright 1991, Fierstine and Weems 2009). In addition, Miller et al. (2008) noted that water temperatures within the Rupelian Mississippi Embayment were between 17° and 19° C (63°–66° F) for 100 m water depth. In contrast, the Chandler Bridge Formation represents estuarine to middle neritic deposition (Sanders et al. 1982, Erickson 1990, Erickson and Sawyer 1996, Katuna et al. 1997), and Cicimurri and Knight (2009a) estimated that water temperature was 20° to 25° C (68°–77° F).

Weems et al. (2016) provided a revised age for the Ashley Formation, placing it entirely within calcareous nannofossil Zone NP24. The corresponding foraminiferal zone, P21a, brackets the age of the Ashley Formation at between 28.4 and 28.7 Ma within the late Rupelian (Berggren and Miller 1988, Berggren and Pearson 2005). Starting at about 26 Ma there was a mid- to late Chattian warming trend (Raffi et al. 2006, fig. 5), and it is during this warm interval that the Chandler Bridge Formation accumulated. There is evidence of a warming event at approximately the time of deposition of the Givhans Ferry Member of the Ashley Formation (i.e., Zachos et al. 2001, Westerhold et al. 2020), and it is possible that the similarity of the elasmobranch assemblages between this unit and the Chandler Bridge Formation reflects comparable water temperatures.

Müller (1999) concluded that the elasmobranch taxa he identified from the Ashley Formation were similar to those he documented from the Old Church Formation of Virginia and the Belgrade Formation of North Carolina. The Belgrade Formation is not entirely of Miocene age (i.e., Müller 1999), as the lower part of the unit is temporally equivalent to the Chandler Bridge Formation (Harris and Zullo 1991, Rossbach and Carter 1991, Kier 1997, Zachos et al. 2001). Müller (1999) thought that the high proportion of dasyatid teeth in his Ashley Formation sample indicated an inner shelf environment, and he proposed a water depth estimate of 40–100 m. It is important to note here that Müller's (1999) sample was obtained from the Givhans Ferry Member, and the upper end of his estimate is consistent with the 100 m depth (middle-to-outer neritic) postulated by Fierstine and Weems (2009) based on the occurrences of various billfish taxa. Müller (1999) stated that *Raja* teeth were common in his Ashley Formation sample, and he believed that cool and deep water provided ideal conditions for this ray. He ultimately concluded that the abundance of fish fossils in the Ashley Formation reflected high biological activity related to coastal upwelling, in combination with very low sedimentation rates.

Support for deep water accumulation and coastal upwelling may lie within the Ashley Formation itself, which was once an economically important phosphate source. The high phosphate content of the Ashley Formation (Weems et al. 2016) would seem to indicate an outer shelf-depth environment, where terrestrial input was low and coastal upwelling was active (Fillippelli 2011, Crosby and Bailey 2012). Low sedimentation rates may be indicated by the common presence of sub-millimeter glauconite grains (Hesse and Schact 2011) and could account for the long-term exposure of chelonioid and

Table 1. Oligocene selachian faunas from Dorchester County, South Carolina, USA. Chandler Bridge Formation records are based on Cicimurri and Knight (2009a). The *Trigonotodus* record is based on Kozlov (2001). **FM**=Formation

Taxon	Ashley FM	Chandler Bridge FM
Alopias cf. *A. vulpinus*		X
Araloselachus sp.	X	X (*A. cuspidatus*)
Carcharhinus gibbesi	X	X
Galeocerdo aduncus	X	X
Galeorhinus sp.		X
Hemipristis cf. *H. serra*	X	X *Hemipristis serra*
Ginglymostomatidae	X	X (*Nebrius* cf. *N. serra*)
Otodus (*Carcharocles*) sp.	X	X (*O.(C.) subauriculatus*)
Pachyscyllium sp.	X	
Physogaleus cf. *P. contortus*	X	X (*Physogaleus contortus*)
Physogaleus sp.	X	X
Pristiophorus sp.	X	
Rhincodon cf. *R. typus*		X
Rhizoprionodon sp.		X
Scyliorhinus weemsi n. sp.	X	X (*Bythaelurus* sp.)
Sphyrnidae	X	X (*Sphyrna media*)
Sphyrnidae	X	X (*S. zygaena*)
Squalus sp.	X	
Squatina sp.	X	X (*S. angeloides*)
Trigonotodus alteri	X	

Table 2. Oligocene batoid faunas from Dorchester County, South Carolina, USA. Chandler Bridge Formation records are based on Cicimurri and Knight (2009a). **FM**=Formation.

Taxon	Ashley FM	Chandler Bridge FM
"Dasyatis" sp.	X	X (*D. rugosa*)
Gymnura sp.		X
"*Mobula*" sp.	X	X (*M. loupianensis*)
Myliobatinae indet.		X
Paramobula fragilis		X
Plinthicus sp.	X	X (*P. stenodon*)
Raja mccollumi	X	X
Raja sp.	X	X
"*Rhinoptera*" sp.	X	X (*R. studeri*)
Rhynchobatus sp.	X	X (*R. pristinus*)
"Taeniurops" cavernosa	X	X (*Dasyatis cavernosa*)

cetacean remains occurring within the Givhans Ferry Member, which often bear encrusting organisms like bryozoa, serpulid worms and barnacles. Winnowing by bottom currents could also have led to the breakage of the teeth and scales, and to the disarticulation of large vertebrate skeletons. One cetacean skull noted herein (SC2015.29.1) occurred upside down with its palate up, and the dermocheylid carapace (SC2007.36.1) lacked almost all the elements from the shell margins. Sections of the shell from the posterior end had also become detached and transported towards the anterior end.

Müller (1999) believed that the Ashley Formation accumulated below storm wave base because the purported excellent preservation of the teeth indicated that they were not affected by wave action. Although we concur that deposition occurred below wave base, the Ashley Formation specimens we examined are often ablated and/or broken (even microscopic *Raja* teeth and shark scales), which contradicts Müller's (1999) assertion. We believe that ablation/breakage is due to bottom currents that were active during Givhans Ferry Member deposition. Occasional basinward transport may be indicated by very well rounded (spherical) quartz grains occurring alongside sub-angular grains. Additional breakage and disarticulation of skeletons could be attributable to bioturbation, as the Givhans Ferry Member can be heavily burrowed. We observed burrows approaching 2 cm in diameter at the collecting sites of SC2007.36.1 and SC2015.29.1.

In Europe, *Squalus alsaticus* (Andreae, 1890) sometimes constitutes a significant proportion of Rupelian elasmobranch assemblages, and the presence of this taxon is taken as an indicator of calm, cold, deep water (Steurbaut and Herman 1978, von der Hocht 1978b, Hovestadt and Hovestadt-Euler 1995). Depth ranges for extinct fish species have been inferred based on their extant relatives (i.e., Aguilera and De Aguilera 2001,

Carrillo-Briceño et al. 2020), and if such inferences hold true the genera we recovered from the Givhans Ferry Member indicate that deposition took place within a middle to outer neritic environment at a depth of at least 50 m. Putra et al. (2020) recently concluded that upwelling is an important ecological factor for extant devil rays, which appear to have a preference for areas of 200 m water depth. At least seasonal development of upwelling could explain the presence of mobulids within the Givhans Ferry Member, given the comparatively shallower water depth. Analysis of the invertebrate fossils recovered, which include foraminifera, ostracodes, solitary scleractinian corals, echinoid test plates and spines, cephalopod tentacle hooklets, various gastropods (i.e., ficids, naticids) and bivalves (anomiids, pectinids, lucinids), and articulate (terebratulinid) and inarticulate (discinid) brachiopods, could prove invaluable in elucidating water depth and temperature (surface and bottom) during Givhans Ferry Member deposition.

With regard to the bony fishes we identified in the sample, extant species within the families represented occupy a wide range of habitats within fully marine, brackish, and even freshwater environments. It is interesting to note that teeth of Sciaenidae and Sparidae represent nearly 75% of the total number of teleost teeth available to us (54% and 17%, respectively), with Albulidae constituting an additional 13% of the sample. Extant sparids live close to the sea floor and are known to occur in deeper waters of the continental shelf and slope (Iwatsuki and Heemstra 2015), and two of the three living albulid genera can be found in marine habitats where water depth is 100+ m (Musada et al. 1984, Whitehead 1990, Hidaka et al. 2016). Modern representatives of these groups are typically benthic predators that consume a variety of invertebrates as well as other teleosts. The remaining fishes comprise 16% of the teleost assemblage, with *Sphyraena* spp. being the dominant taxon (56 of 95 specimens). Extant barracudas are open-ocean, pelagic predators of other teleosts, and although these fish typically occur at depths of less than 30 m, they may be found at a depth of 100 m (Nelson et al. 2016).

CONCLUSIONS

The matrix surrounding two cetacean skulls and a dermochelyid carapace, all collected from the Givhans Ferry Member of the Ashley Formation in Dorchester County, South Carolina, USA yielded 843 isolated fish teeth and 566 placoid scales. This paleofauna includes 21 unequivocal shark and ray taxa, and up to nine teleost families are represented. Our sample was biased towards small to microscopic species, and additional, large taxa will ultimately be identified with additional investigation. For example, teeth of the lamniform sharks *Araloselachus* sp., *Otodus* (*Carcharocles*) *angustidens*, and *Trigonotodus alteri*, and vertebrae of Thunnini also occur in the Ashley Formation, although from which of the three members these were derived is unclear.

Ongoing evaluation of paleofaunas housed at SC includes samples obtained from the middle Eocene (Bartonian) Tupelo Bay Formation (NP17) and the upper Eocene (Priabonian) Parkers Ferry Formation (NP19/20). Planned future work will entail investigation of the Eocene/Oligocene Harleyville Formation (NP21–NP22), and preliminary analysis of matrix samples obtained from Dorchester County indicates the presence of an unidentified Rupelian unit in central South Carolina of NP23 age (Weems et al. 2016). Sampling of these units, along with other horizons within the Ashley Formation (including more intensive sampling of the Givhans Ferry Member), could provide a better understanding of the effect, if any, that climate fluctuation had on the Charleston Embayment from the late Eocene to the late Oligocene. In the Oligocene North Sea Basin, tropical to subtropical conditions existed during NP23 (Maxwell et al. 2016), cooler conditions prevailed during NP24 (Steurbaut and Herman 1978, von der Hocht 1978b, Hovestadt and Hovestadt-Euler 1995), and more tropical conditions were re-established during NP25 of the Chattian Stage (Reinecke 2014).

ACKNOWLEDGEMENTS

P. Bailey discovered the dermochelyid carapace and reported it to V. McCollum, who notified SC (JLK). Special thanks are extended to the Dorchester County Public Works Department, Summerville, for allowing SC to excavate the fossil. Numerous area residents supported the excavation team by providing refreshments and assistance with excavation. Bailey, McCollum, and other members of the Lowcountry Fossil Club spent considerable time helping with the excavation, and A. Shoemaker prepared the ventral surface of the carapace after it arrived at SC. Craig Garrison found SC2015.29.1 and reported its discovery, and J. Newhard (College of Charleston), K. Sawyer, and J. Armstrong are thanked for their help in excavating the specimen (even donning SCUBA gear to continue under water excavations). M. Swilp donated *Araloselachus* and *Trigonotodus* teeth and the *Palaeocybium* sp. dentary mentioned herein. We wish to thank R. Weems, P. Jambura, M. Hyzny, and an anonymous reviewer for their critical evaluation of an earlier version of this manuscript. We also sincerely appreciate

the time and effort of the editorial staff P. Holroyd, D.M. Erwin, and A. Dineen for bringing this study to print.

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