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Late Oligocene sharks and rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA

DAVID J. CICIMURRI and JAMES L. KNIGHT

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A diverse vertebrate fauna, dominated by elasmobranch taxa, was collected from the upper Oligocene (Chattian) Chandler Bridge Formation in Summerville, Dorchester County, South Carolina. Nearly 3,500 teeth and dermal denticles are assigned to 29 species of sharks and rays, and our sample includes the oldest known occurrence of the whale shark, *Rhincodon*, as well as a new skate, *Raja mccollumi* sp. nov. The Chandler Bridge elasmobranch assemblage is comparable in species diversity to Chattian assemblages of Virginia and North Carolina, USA, and Germany. Notable absences from Germany include *Rhincodon*, *Hemipristis*, and *Sphyrna zygaena*, likely reflecting the influence of colder water on the North Sea Basin during the Chattian. Squaloids, pristiophoroids, and hexanchoids are known from Chattian deposits of the Albemarle Embayment (North Carolina), Salisbury Embayment (Virginia), and North Sea Basin, but these taxa are absent from the Chandler Bridge assemblage, perhaps because of shallow, warm water (20 to 25°C) conditions within the more southerly Charleston Embayment.

Key words: Chondrichthyes, Neoselachii, Oligocene, Chandler Bridge Formation, South Carolina.

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Introduction

Vertebrate faunas within Oligocene marine deposits of the Atlantic Coastal Plain are inadequately known (Weems and Sanders 1986). Two fossiliferous Oligocene formations, the Ashley Formation and overlying Chandler Bridge Formation, occur in the coastal plain of South Carolina. Cetaceans, crocodilians, and chelonioids have been reported from the Chandler Bridge Formation, and elasmobranchs, osteichthyans, birds, and sirenians are also known to occurr (Sanders 1980; Weems and Sanders 1986; Erickson 1990; Katuna et al. 1997).

Herein we provide a detailed account of a diverse elasmobranch assemblage recovered from tan, clay-rich, fine-grained quartz sand occurring within an exposure of the Chandler Bridge Formation that was located in Summerville (33°1' 35.314"N latitude, 80°16'8.360"W longitude), Dorchester County, South Carolina (Fig. 1). We also discuss the paleoecological and paleobiological significance of the assemblage.

Institutional abbreviations.—BCGM, Campbell Geology Museum, Clemson University, Clemson, South Carolina, USA; SC, South Carolina State Museum, Columbia, USA.

Other abbreviations.—NP, nannoplankton; TB, transgressive boundary.

Geological setting

The Ashley and Chandler Bridge formations were deposited within the Charleston Embayment, a physiographic structure flanked by the Yamacraw Arch to the south and the Cape Fear Arch to the north (Katuna et al. 1997; Ward 1992). The Chandler Bridge Formation ranges from 0.3 to 5 m in thickness (Sanders et al. 1982) and its lateral distribution is patchy because of post-Oligocene erosion (Katuna et al. 1997). Weems and Sanders (1986; also Erickson 1990) suggested that the formation is generally preserved in low spots within the Ashley Formation, but Katuna et al. (1997) noted that the formation occurs on high land between river channels. Calcareous nannofossils date the formation to the upper part of zone NP 25 (23.6 to 25.7 Ma) of the Chattian Stage (Edwards et al. 2000).

Weems and Sanders (1986) proposed that the Chandler Bridge Formation represents a shallow marine transgressive sequence that was deposited on an irregular Ashley Formation erosion surface. Sanders et al. (1982) and Sanders and Weems (1986) divided the Chandler Bridge Formation into three lithostratigraphic units (see Fig. 2), with bed 1 being sparsely fossiliferous and interpreted as representing an estuarine or lagoonal environment. Bed 2 was thought to have formed in either an open shelf environment below wave

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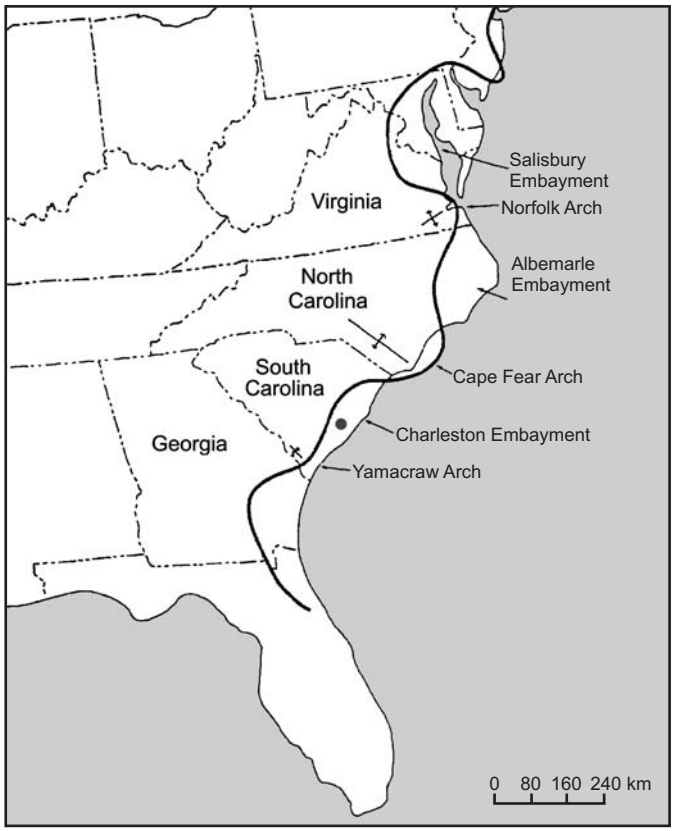


Fig. 1. Geographic map of the eastern United States showing physiographic features discussed in the text. Solid circle indicates location of the collection site. Modified from Ward (1992).

base or open bay environment (Sanders et al. 1982; Weems and Sanders 1986), and cetacean and chelonioid bones indicate more normal marine conditions. A gavialosuchid crocodilian is associated with odontocete cetacean remains in Bed 3, leading to the interpretation that the stratum represents a beach-face shallow marine environment where the carcasses of beached whales were scavenged by crocodilians (Weems and Sanders 1986; Erickson 1990).

In contrast, Katuna et al. (1997) divided the formation into four sedimentary facies, including, from bottom to top, marine, marginal marine, bay/estuarine, and fluvial/estuarine (Fig. 2). According to Katuna et al. (1997: 188), the marine facies is extremely rich in fish remains (including shark teeth and denticles). The overlying marginal marine facies was correlated to bed 1 of Sanders et al. (1982; also Weems and Sanders 1986), and sediments were interpreted as being deposited in a more restricted environment of slightly higher energy than the marine facies (Katuna et al. 1997: 189). The bay/estuarine facies was correlated to bed 2 as discussed by Sanders et al. (1982), and the rarity of dinoflagellates indicate that the facies represented a restricted brackish bay or lagoonal environment (Katuna et al. 1997). Occurrences of cetacean, chelonioid, and fish remains within the bay/estuarine facies point to at least some access to the open ocean (Katuna et al. 1997: 189). The uppermost facies, considered to be correlative to bed 3 of Sanders et al. (1982), lacks dinoflagellates but contains freshwater pollen, leading to a fluvial/ estuarine interpretation by Katuna et al. (1997: 190), who also suggested that the cetaceans discussed by Weems and Sanders (1986) and Erickson (1990) became stranded along a tidal bar or estuarine margin, rather than being stranded on a beach.

Based on the paleoenvironmental reconstructions provided by Katuna et al. (1997), the overall trend within the Chandler Bridge Formation is a shallowing-upward (and coarsening-upward) regressive sequence. Basal marine sediments accumulated during a third-order eustatic sea-level rise (sequence cycle TB 1.3), but the rather rapid shallowing within the basin has been used as supporting evidence that uplift to the north-northeast significantly affected and overprinted climate-driven coastal processes (Katuna et al. 1997; Clandenin et al. 1999). A fluvial system that drained into the Charleston Embayment from the west was a sediment source for the Chandler Bridge Formation (Katuna et al. 1997; Segall et al. 2000).

Overview of Oligocene elasmobranch assemblages

Kruckow and Thies (1990) presented a synopsis of the Paleogene and Neogene elasmobranch record from the Atlantic and Gulf coastal plains of the United States. Within the Atlantic Coastal Plain, Case (1980) described an assemblage from the Trent Formation of North Carolina that he considered to be of early Miocene (Aquitanian) age. This formation is now considered to be of Rupelian age (NP 21–NP 22) and temporally equivalent to the lower part of the River Bend Formation (Rossbach and Carter 1991; Kier 1997; Harris et al. 2000). In his work on Paleocene to Pliocene ichthyofaunas, Müller (1999) documented elasmobranch assemblages from the

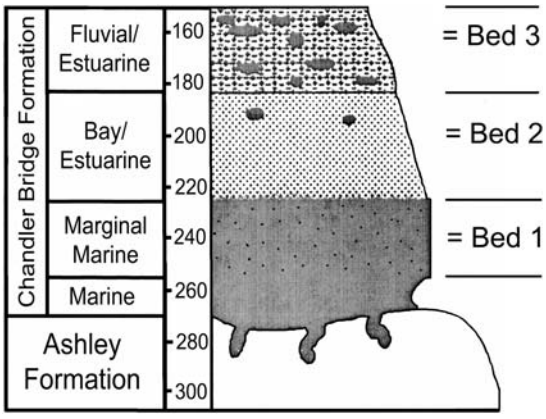


Fig. 2. Stratigraphy of the Chandler Bridge Formation showing facies designations of Katuna et al. (1997) and their correlative units (Beds 1–3) as discussed by Sanders and Weems (1986). Marine/marginal marine facies constitute a coarsening upward sequence from poorly sorted, sandy to silty clay to moderately sorted silty, very fine sand, whereas the bay/estuarine facies is poorly sorted silty to clayey fine quartz sand with occasional phosphate pebbles, and fluvial/estuarine facies consists of poorly sorted, clayey, fine sand with abundant phosphate pebbles.

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Ashley Formation, Old Church Formation of Virginia, and Belgrade and River Bend formations of North Carolina. Dinocysts were used to correlate the Old Church Formation with the Ashley Formation (NP 24 and NP 25) (Edwards et al. 1997, 2000). The upper part of the River Bend Formation is of Chattian age (NP 25) and possibly temporally equivalent to the Ashley Formation (see Rossbach and Carter 1991; Harris et al. 2000). Although Müller (1999) indicated a Miocene age, the lower Belgrade Formation (Haywood Landing Member) is correlative to the Chandler Bridge Formation (see Kier 1997; Harris and Zullo 1991; Rossbach and Carter 1991). In Georgia, *Carcharocles auriculatus* Blainville, 1818 was identified in the Rupelian Bridgeboro Formation (Freile et al. 2001).

In the Gulf Coastal Plain, *C. auriculatus* was reported from the Rupelian Byram Formation of Mississippi (Dockery and Manning 1986). Miller (2000) reported a small elasmobranch assemblage from the Mint Spring Formation of Mississippi, but most of her identifications were limited to the generic level and none of the material was illustrated. The Mint Spring Formation was deposited within zones NP 21 and NP 22 (34.6 to 35.5 Ma; see Dockery and Lozouet 2003). Stringer et al. (2001) listed two shark species from the Rosefield Marl of Louisiana, a deposit that formed within zone NP 22 (34.1 to 34.6 Ma). Oligocene records from the Pacific Coast of the USA are primarily limited to Oregon and Washington, with elasmobranchs being reported from the Keasey and Pittsburg Bluff formations (Welton 1972, 1973, 1979). The Keasey Formation spans the Eocene–Oligocene boundary (33–35 Ma), whereas the Pittsburg Bluff Formation is Rupelian and dated to 29.5–33 Ma (Hankins and Prothero 2001).

In Asia, Oligocene elasmobranch assemblages have been documented in Japan (Applegate and Uyeno 1968; Uyeno et al. 1984; Yabumoto 1987; Yabumoto and Uyeno 1994) and the Middle East (Thomas et al. 1989; Adnet et al. 2007). A limited number of species have been reported from the South Pacific, including Australia (Pledge 1967; Kemp 1982; Keyes 1982) and New Zealand (Keyes 1979; Pfeil 1984; Gottfried and Fordyce 2001).

European Oligocene elasmobranch occurrences have been well documented, with numerous Rupelian reports from Belgium (Leriche 1910; Steurbaut and Herman 1978; Baut and Génault 1999) and Rupelian/Chattian records in Germany (von der Hocht 1978a, b; Müller 1983; Reinecke et al. 2001, 2005; Haye et al. 2008). Additional records include The Netherlands (van den Bosch 1980), Poland (van den Bosch 1981), Switzerland (Leriche 1927), Czech Republic (Brzobohatý and Kalabis 1970) and France (Génault 1993). Bor (1980) described a small Belgian Lattorfian elasmobranch assemblage and calcareous nannofossils place the Lattorfian Stage within the upper Eocene (NP 19/20; see Snyder et al. 1983).

Material and methods

The SC obtained approximately 2 kg of concentrated microfossils, and the BCGM acquired approximately 55 kg of bulk matrix. In the laboratory, matrix was disaggregated in water and screened down to 0.25 mm (# 60 USA Standard Testing Sieve), with the remaining concentrate dried and then sorted under a binocular microscope. The material that passed through the # 60 screen was also saved, dried, and sorted. The specimens we recovered during this study are housed at the BCGM and SC.

Systematic paleontology

Class Chondrichthyes Huxley, 1880

Subcohort Neoselachii Compagno, 1977

Order Squatiniformes Buen, 1926

Family Squatinidae Bonaparte, 1838

Genus *Squatina* Duméril, 1906

Type species: *Squalus squatina* Linneaus, 1758, Recent, "European Seas".

Squatina cf. *S. angeloides* van Beneden, 1873

Fig. 3A.

Referred specimens.—BCGM 9042 and 9043.

Comments.—Kent (1994) reported *Squatina subserrata* (von Münster, 1846) from the Oligocene of Virginia, and Müller (1999) adopted this classification even though he noted a very close similarity to Rupelian *S. angeloides*. Case (1980) referred North Carolina Oligocene teeth to *S. subserrata*, possibly because he thought the fossils were of early Miocene age. We believe Case's (1980) material is morphologically similar to *S. angeloides*, and we tentatively assign our complete tooth to this species primarily because the lateral shoulders are virtually perpendicular to the cusp, which is characteristic of teeth that have been reported elsewhere (i.e., van den Bosch 1981; Müller 1983; Génault 1993; Baut and Génault 1999; Reinecke et al. 2001).

Stratigraphic and geographic range.—Oligocene (Rupelian and Chattian), Germany, France, Belgium, USA (North and South Carolina).

Order Orectolobiformes Applegate, 1972

Family Ginglymostomatidae Gill, 1862

Genus *Nebrius* Rüppel, 1837

Type species: *Nebrius concolor* Rüppel, 1837, Recent, New Guinea.

Nebrius cf. *N. serra* (Leidy, 1877)

Fig. 3B.

Referred specimen.—SC 2009.18.1.

Comments.—Teeth of extant *Nebrius* Rüppel, 1837 have more than three pairs of rather small lateral cusplets (our specimen has five pairs), whereas teeth of extant *Ginglymostoma* Müller and Henle, 1837 have only two or three pairs of robust lateral cusplets (Compagno 1984; Compagno et al. 2005). We concur with Cappetta (1987) and Purdy et al.

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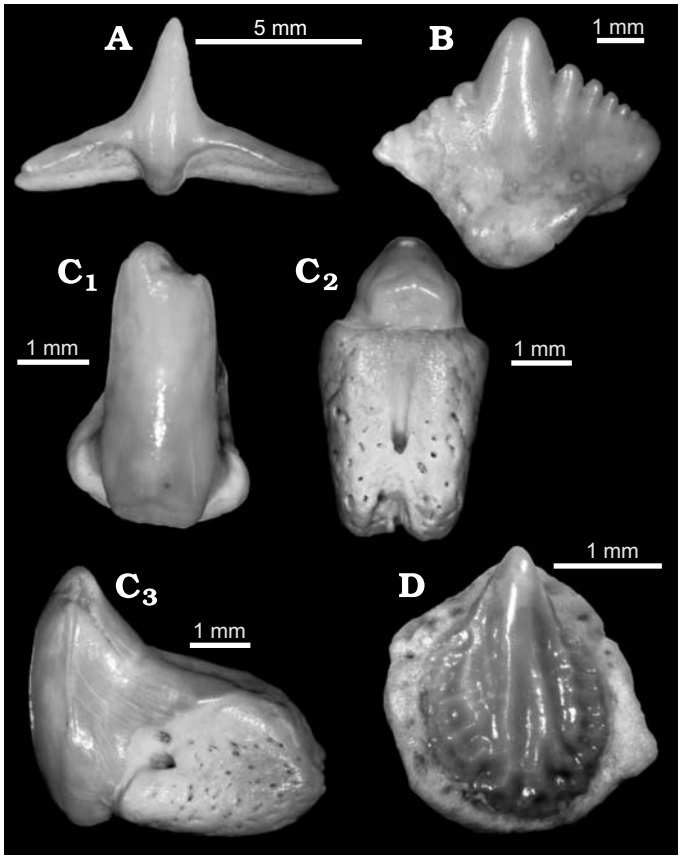


Fig. 3. Shark remains from Summerville, upper Chattian. **A**. *Squatina* cf. *S. angeloides* van Beneden, 1873, BCGM 9043, antero-lateral tooth, labial view. **B**. *Nebrius* cf. *N. serra* (Leidy, 1877), SC2009.18.1, antero-lateral tooth, labial view. **C**. *Rhincodon* cf. *R. typus* (Smith, 1828), BCGM 9045, anterior tooth, labial (C_1), lateral (C_2), and basal (C_3) view. **D**. ?*Cetorhinus parvus* (Leriche, 1908), BCGM 9050, dermal scale, dorsal view, anterior at bottom.

(2001) that fossil teeth of *Nebrius* are sometimes misidentified as *Ginglymostoma*. Our specimen is morphologically similar to *Acrodobatus serra* Leidy, 1877 (figs. 10–12) from the "Ashley phosphate beds" of South Carolina. The stratigraphic and temporal occurrence of these fossils is difficult to determine because economically important phosphate deposits occur within Oligo-Miocene units (Weems and Sanders 1986), and other fossils reportedly from "Ashley phosphate beds" are definitively of Pleistocene age (Sanders 2002). The species is, in our opinion, referable to *Nebrius*.

A very similar species, *Ginglymostoma delfortriei* Daimeries, 1889, has been reported from the Miocene of France (Cappetta 1970) and the Oligocene Belgrade Formation of North Carolina (Müller 1999). Yabumoto and Uyeno (1994) assigned the *G. delfortriei* morphology to *Nebrius*. According to Cappetta (1970), *N. serra* differs from the *G. delfortirei* morphology in having a longer labial basal protuberance that is more uniformly united with the remainder of the crown foot. If these characteristics are sufficient to separate two species, then our specimen, as well as the Oligocene material reported by Müller (1999), is closer to *N. serra*. To our knowledge, the only European Oligocene record of *Nebrius* is from the French Rupelian, and our specimen does not differ appreciably from the material discussed by Génault (1993).

Stratigraphic and geographic range.—Oligocene (Chattian), USA (North and South Carolina).

Family Rhincodontidae Garman, 1913

Genus *Rhincodon* Smith, 1829

Type species: *Rhiniodon typus* Smith, 1828, Recent, South Africa.

Rhincodon cf. *R. typus* (Smith, 1828)

Fig. 3C.

Referred specimens.—BCGM 9044 and 9045, SC 2009.18.2.

Comments.—The teeth in our sample represent the oldest fossil record of *Rhincodon* Smith, 1829. Prior to this discovery, fossil *Rhincodon* teeth were known only from the Miocene of France (Cappetta 1970, 1987) and Mio-Pliocene of Lee Creek, North Carolina (Purdy et al. 2001). An alleged lower Miocene occurrence in Delaware was reported by Purdy (1998: pl. 1: 8), but Purdy et al. (2001) later stated that the Lee Creek material represented the first record of the genus in the Atlantic Coastal Plain. Our fossils appear to be identical to the French material (Cappetta 1970: 40, text-fig. 8, pl. 7: 7), and Purdy et al. (2001) stated that their specimens are identical to teeth of extant *R. typus*. We see no appreciable morphological difference between the Chandler Bridge teeth and those of *R. typus* (see Herman et al. 1992).

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Miocene, France, USA (North Carolina), extant.

Order Lamniformes Berg, 1958

Family Alopiidae Bonaparte, 1838

Genus *Alopias* Rafinesque, 1810

Type species: *Alopias macrourus* Rafinesque, 1810, Recent, Sicily.

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

Fig. 4A, B.

Referred specimens.—BCGM 9046–9048, SC 2009.18.3.

Comments.—Several species of *Alopias* Rafinesque, 1810 have been reported from Oligocene marine strata, including *A. exigua* (Probst, 1879) and *A. latidens* (Leriche, 1909) (i.e., Leriche 1910; Steurbaut and Herman 1978; Baut and Génault 1999). The validity of these species, which have been differentiated on the basis of crown stockiness and development of cutting edges (i.e., Leriche 1908; Cappetta 1970), has been questioned by Purdy et al. (2001), citing ambiguities in the morphological criteria used to identify teeth and noting a high degree of interspecific variation between individuals within extant species. Case (1980) and Pfeil (1981) reported teeth of *A. superciliosus* (Lowe, 1841), and those specimens are similar to the *A. exigua* morphology in having rather gracile crowns. This is in contrast to our Chandler Bridge specimens, which have a wide crown as in the *A. latidens* morphology. We conclude that

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the Chandler Bridge teeth do not differ morphologically from specimens of *A*. cf. *A. vulpinus* illustrated by Purdy et al. (2001: 108, fig. 22a), and we follow their taxonomic assignment. Of three Oligocene species illustrated by Reinecke et al. (2005), *A. latidens* (pl. 24), *A. exigua* (pl. 25), and *A*. aff. *A. vulpinus* (pls. 21, 22), our sample more closely compares with the latter-most taxon.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Mio-Pliocene, USA (North Carolina), extant.

Family Cetorhinidae Gill, 1862

Genus *Cetorhinus* Blainville, 1816

Type species: *Squalus maximus* Gunner, 1765, Recent, Portugal.

?*Cetorhinus parvus* Leriche, 1908

Fig. 3D.

Referred specimens.—BCGM 9049 and 9050, SC 2009.18.4.

Comments.—Each scale consists of a circular to teardrop-shaped, cuspidate, highly ornamented crown sitting atop a dorso-ventrally flattened base that has a circular outline and convex ventral surface. Our material is identical to fossils identified as type E denticles by Cappetta (1970) and *Squatina subserrata* scales by Case (1980). Van den Bosch (1984: figs. 50–66) tentatively assigned the scales to Cetorhinidae because the morphology is apparently unique to the family. Reinecke et al. (2005) identified their scales as ?*Cetorhinus parvus*. *Cetorhinus maximus* (Gunnerus, 1765), the only living species, is widely distributed (Compagno et al. 2005), and our fossils may be conspecific with the fossils reported by van den Bosch (1984) and Reinecke et al. (2005).

Stratigraphic and geographic range.—Oligocene (Rupelian and Chattian), Belgium, Germany, USA (South Carolina).

Family Odontaspididae Müller and Henle, 1839

Genus *Carcharias* Rafinesque, 1810

Type species: *Carcharias taurus* Rafinesque, 1810, New York, USA.

Carcharias cuspidatus (Agassiz, 1843)

Fig. 4D.

Referred specimens.—BCGM 9051 and 9052.

Comments.—BCGM 9051 is a symphyseal tooth nearly identical in morphology to symphyseal teeth of Recent *Carcharias taurus* Rafinesque, 1810 that we examined (SC.86.62.2). Although teeth of *Megachasma pelagios* Taylor, Compagno, and Stuhsaker, 1983 are superficially similar to our symphyseal tooth (see Herman et al. 1993), the root of our specimen is more laterally compressed and the lingual boss not as well developed. BCGM 9052 is a lower lateral tooth, the enameloid of which is completely smooth on both crown faces, and the lateral cusplets are rather small. These characteristics lead us to assign the specimen to *C. cuspidatus* (also Génault 1993; Baut and Génault 1999; Reinecke et al. 2001, 2005; Haye et al. 2008).

Stratigraphic and geographic range.—Oligo-Miocene, Europe, Russia, USA.

Carcharias sp.

Fig. 4C.

Referred specimens.—BCGM 9053 and 9054.

Comments.—BCGM 9053 is a posterior tooth that is undiagnostic and differs little in morphology from teeth in SC.86.62.2 (jaws of *C. taurus*). BCGM 9054 is a lateral tooth from a very young individual (Fig. 4C) and has a very gracile morphology and large lateral cusplets like *C. acutissimus* (Agassiz, 1843) and *C. gustrowensis* (Winkler, 1875) (see Reinecke et al. 2001, 2005). The specimen appears to be closer to *C. gustrowensis* in its lack of lingual ornamentation (see also Haye et al. 2008), but a larger sample is needed to determine if these teeth represent a species other than *C. cuspidatus* (see above).

Family Otodontidae Glückman, 1964

Genus *Carcharocles* Jordan and Hannibal, 1923

Type species: *Carcharodon auriculatus* Blainville, 1818, Eocene, Belgium.

Carcharocles sp.

Fig. 4E.

Referred specimens.—BCGM 9055, SC 2009.18.5.

Comments.—Ward and Bonavia (2001) commented on species concepts (i.e., biological, morphological, chronological) with regard to *Carcharocles* Jordan and Hannibal, 1923. Based solely on morphology, our tooth compares favorably to Miocene *C. subauriculatus* (Agassiz, 1839). Reinecke et al. (2005) considered Oligocene *C. angustidens* (Agassiz,

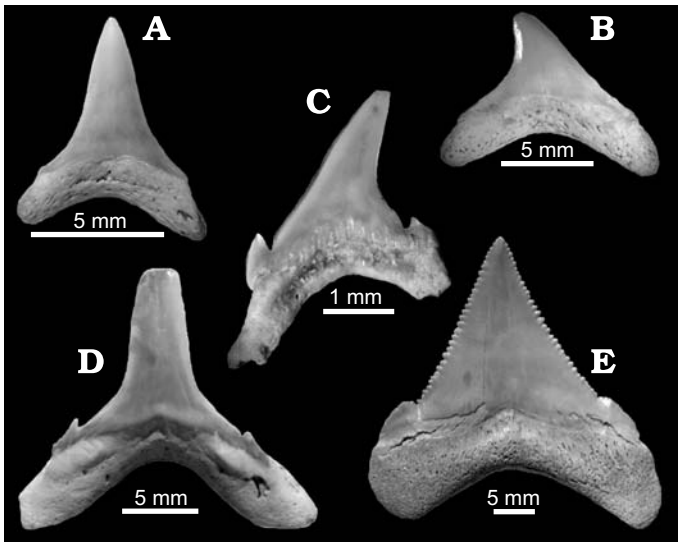


Fig. 4. Lamniform sharks from Summerville, upper Chattian. **A**, **B**. *Alopias* cf. *A. vulpinus* (Bonnaterre, 1788). **A**. BCGM 9047, anterior tooth, labial view. **B**. BCGM 9048, lateral tooth, labial view. **C**. *Carcharias* sp., BCGM 9054, labial view. **D**. *Carcharias cuspidatus* (Agassiz, 1843), BCGM 9052, lower lateral tooth, labial view. **E**. *Carcharocles* sp., BCGM 9055, labial view.

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1843) and Miocene *C. subauriculatus* as chronospecies. Purdy et al. (2001) noted that lateral cusplets of *C. subauriculatus* are not differentiated from the main cusp by a deep notch as in teeth referred to *C. angustidens* (also Marsili et al. 2007). *Carcharocles angustidens* has been identified from numerous Oligocene deposits worldwide (i.e., Uyeno et al. 1984; Génault 1993; Baut and Génault 1999; Gottfried and Fordyce 2001; Reinecke et al. 2001, 2005). Interestingly, Purdy et al. (2001) identified teeth from the Chandler Bridge Formation as *C. subauriculatus*, and some of the teeth identified as *C. angustidens* by Uyeno et al. (1984: pl. 3: 2, 3) are similar to *C. subauriculatus*. Perhaps Oligocene *C. subauriculatus*-like teeth represent the first occurrence of a distinct species, or represent variation within *C. angustidens*.

Order Carcharhiniformes Compagno, 1973

Family Carcharhinidae Jordan and Evermann, 1896

Genus *Carcharhinus* Blainville, 1816

Type species: *Carcharhinus melanopterus* Quoy and Gaimard, 1824, Recent, Waigeo Islands.

Carcharhinus gibbesi (Woodward, 1889)

Fig. 5A–D.

Referred specimens.—BCGM 9056–9062, SC 2009.18.6.

Comments.—This taxon is the most abundant non-batomorph elasmobranch in the Chandler Bridge sample. We assign two morphologies to *C. gibbesi*; one has a broadly triangular, smooth-edged cusp flanked by serrated mesial and distal shoulders (Fig. 5A–C), the other has a narrower cusp flanked by low, smooth-edged heels (Fig. 5D). We concur with White (1956: 143, text-figs. 77–94) and regard the former morphology as representing upper teeth, whereas the latter represents lower teeth (dignathic heterodonty). Upper teeth of *C. gibbesi* are similar to those of *C. elongatus* (Leriche, 1910), but the latter species may be distinguished by the more weakly serrated or smooth lateral shoulders (Génault 1993; Baut and Génault 1999; Reinecke et al. 2001, 2005; Haye et al. 2008). Cutting edges on the lower teeth of our *C. gibbesi* are completely smooth, whereas those of *C. elongatus* may be weakly serrated (see Reinecke et al. 2001: pls. 50, 52; Reinecke et al. 2005: pl. 39).

There is little indication of ontogenetic heterodonty in our sample, as small teeth from each jaw position are simply miniature versions of their adult counterparts (compare Fig. 5A to 5B). Monognathic heterodonty is more obvious in upper teeth, with specimens from anterior positions being more symmetrical (Fig. 5B), but cusps become more distally directed and lateral shoulders more elongated towards the commissure (Fig. 5C). Only in more distal positions are the cusps of lower teeth distally directed.

We believe that the *gibbesi* material described and illustrated by White (1956: 143, text-figs. 77–94) that came from the "phosphate beds" of South Carolina were derived from Oligocene as opposed to Eocene strata. We have thus far only recovered this morphology from the Ashley and Chandler Bridge formations, but the upper Eocene (Priabonian) Harleyville Formation contains the similar, but more weakly serrated (usually unserrated), *Carcharhinus gilmorei* (Leriche, 1942). Eocene *C. gilmorei* have variously been referred to in the literature as *Sphyrna gilmorei* Leriche, 1942, *Negaprion gibbesi gilmorei* (Leriche, 1942) (see White 1956), *N. eurybathrodon* (Blake, 1862) (i.e., Case 1981; Parmley and Cicimurri 2003), and *C. gibbesi gilmorei* (Leriche, 1942) (i.e., Kruckow and Thies 1990; Manning 2006). Manning (2006) noted that *C. gilmorei* and *C. gibbesi* morphologies occur together in Oligocene but not Eocene strata (no *C. gibbesi*) of the Gulf Coastal Plain, and that the morphologies were intergradational. Müller (1999) reported both *C. gibbesi* and *C. elongatus* from Oligocene deposits of the Atlantic Coastal Plain. We recovered several upper teeth that are quite similar to *Carcharhinus gilmorei* and *C. elongatus*, but we consider these specimens to represent morphological variation within *C. gibbesi*, not an additional species/subspecies.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (Gulf and Atlantic coastal Plains).

Genus *Physogaleus* Cappetta, 1980

Type species: *Trigonodus secundus* Winkler, 1874, Eocene, Belgium.

Physogaleus aduncus (Agassiz, 1843)

Fig. 5E, F.

Referred specimens.—BCGM 9063–9066, SC 2009.18.7.

Comments.—The teeth within in this sample include morphotypes traditionally identified as *Galeocerdo contortus* Gibbes, 1849 and *G. aduncus* Agassiz, 1843. Our studies of Oligocene and Miocene elasmobranch assemblages from the Atlantic Coastal plain confirm the observations of Purdy et al. (2001) and Ward and Bonavia (2001) that the two morphotypes occur together and in nearly equal numbers (see also Case 1980; Kent 1994). The morphologies could represent two coeval species, the teeth might be conspecific and represent dignathic heterodonty in a single species, (upper and lower teeth), or the teeth may be conspecific and represent gynandric heterodonty (male and female teeth).

Leriche (1927) illustrated what appear to be the "*G. contortus*" and "*G. aduncus*" morphologies under the name *Galeocerdo aduncus* (pl. 14: 1–8). Applegate (1978, 1992) discussed the possibility that the two morphologies represent dignathic heterodonty within a single species, "*G.*" *aduncus*, with palatoquadrates (upper jaws) bearing the "*G. aduncus*" morphotype and the Meckel's cartilages (lower jaws) the "*G. contortus*" morphotype. Gottfried (1993) followed Applegate (1978) when describing a dentigerous partial right Meckel's cartilage from the Miocene of Maryland, and Manning (2006) also advocated this relationship. Treating the morphologies as separate species, Purdy et al. (2001) suggested that "*G. aduncus*" fed on larger animals, whereas "*G. contortus*" was piscivorous.

Ward and Bonavia (2001) consider the "*G. contortus*" and "*G. aduncus*" morphologies to represent the same spe-

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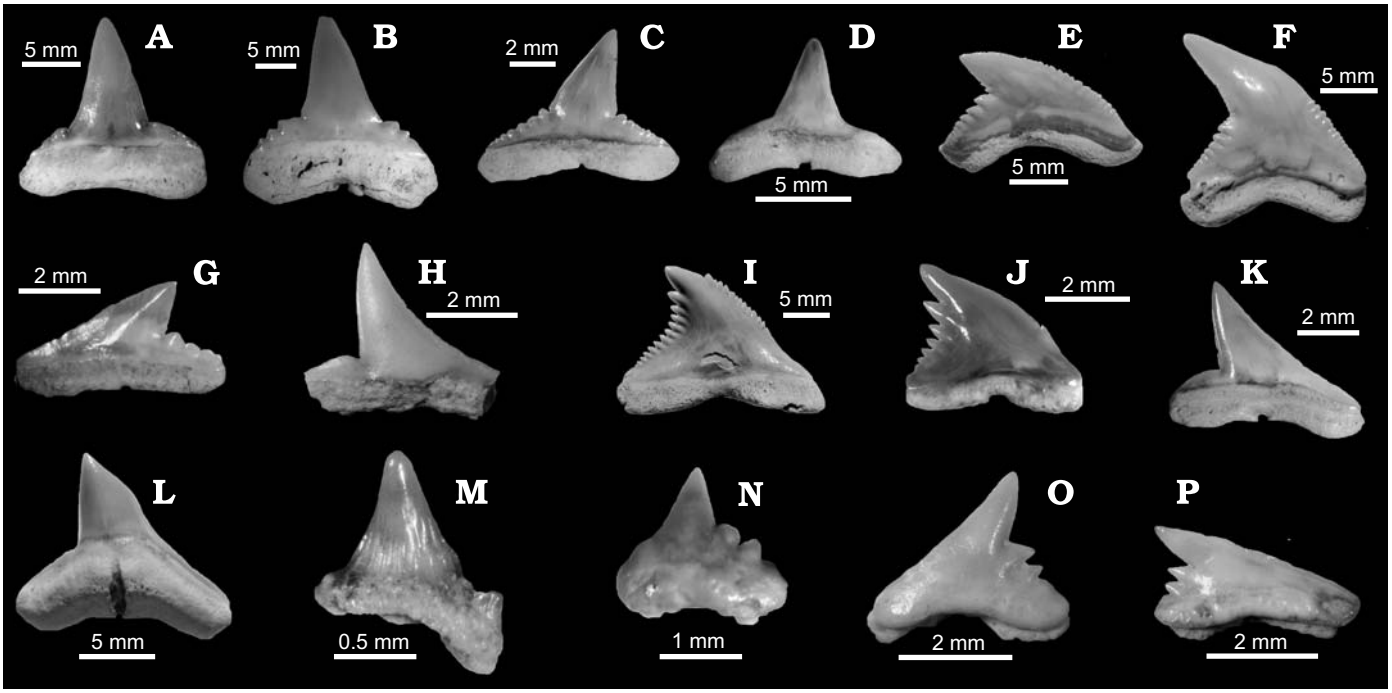


Fig. 5. Carcharhiniform sharks from Summerville, upper Chattian. **A**–**D**. *Carharhinus gibbesi* (Woodward, 1889). **A**. BCGM 9059, juvenile upper anterior tooth, labial view. **B**. BCGM 9060, adult upper anterior tooth, labial view. **C**. BCGM 9061, juvenile upper lateral tooth, labial view. **D**. BCGM 9058, adult lower anterior tooth, labial view. **E**, **F**. *Physogaleus aduncus* (Agassiz, 1835). **E**. BCGM 9064, upper lateral tooth, labial view. **F**. BCGM 9066, lower anterior tooth, labial view. **G**. *Physogaleus* sp., BCGM 9068, antero-lateral tooth, labial view. **H**. *Rhizoprionodon* sp., BCGM 9070, labial view. **I**, **J**. *Hemipristis serra* (Agassiz, 1835). **I**. BCGM 9073, adult upper lateral tooth, labial view. **J**. BCGM 9072, juvenile upper lateral tooth, labial view. **K**. *Sphyrna* cf. *S. media* Springer, 1940, BCGM 9077, lateral tooth, labial view. **L**. *Sphyrna zygaena* (Linneaus, 1758), BCGM 9079, lateral tooth, lingual view. **M**. *Bythaelurus* sp., BCGM 9074, labial view. **N**–**P**. *Galeorhinus* sp. **N**. BCGM 9081, parasymphyseal tooth, labial view. **O**. BCGM 9082, antero-lateral tooth, labial view. **P**. BCGM 9083, lateral tooth, labial view.

cies ("*G. aduncus*"), but they also believe these are sufficiently similar to another carcharhiniform shark, *Physogaleus* Cappetta, 1980, to warrant placement in that genus. Reinecke et al. (2005) assigned the *contortus* morphology to *Physogaleus*, but they referred the *G. aduncus* morphology to *Galeocerdo*, citing differences in tooth morphology and the paucity or complete lack of the *G. contortus* morphology in deposits yielding the *G. aduncus* morphology (see also Reinecke and Hoedemakers 2006). *Physogaleus* exhibits gynandric heterodonty (Cappetta 1987), and according to Ward and Bonavia's (2001) taxonomy the typical *G. aduncus* morphology represents teeth of females and upper teeth of males (Fig. 5E), whereas the *G. contortus* morphology represents teeth in the lower dentition of males (Fig. 5F). The taxonomic questions raised by the *G. contortus*/*G. aduncus* associations may not be answered without the aid of numerous crania with articulated dentitions (showing the range of gynandric/dignathic heterodonty).

Stratigraphic and geographic range.—Oligocene to Pliocene, Europe, USA (Atlantic Coastal Plain), Japan, Equador, Zaire.

Physogaleus sp.

Fig. 5G.

Referred specimens.—BCGM 9067 and 9068, SC 2009.18.8.

Comments.—Our specimens are broken and/or abraded, but the largest specimen would have measured approximately 8 mm in total width. All of our specimens appear to represent antero-lateral jaw positions. The mesial cutting edge is often medially convex but may be slightly sinuous, and it is smooth (some teeth exhibit very weak basal serration). Although the specimen illustrated shows four well differentiated cusplets, the distal heel is generally rather smooth except for one or two poorly differentiated cusplets. Teeth of Oligocene *Physogaleus latus* (Storms, 1894) are easily distinguished from our specimens in having large serrations on the basal half of the mesial edge (see Baut and Génault 1999; Reinecke et al. 2001, 2005), and individual cusplets on the distal blade are more numerous, much larger, and well differentiated from each other. The teeth of *P. maltzani* (Winkler, 1875) appear to have a narrower cusp that is also more elongated, the lower part of the mesial cutting edge is more consistently serrated, and the distal blade has three or four well differentiated cusplets (Reinecke et al. 2005). Teeth of *P. singularis* (Probst, 1878) also have a virtually smooth mesial cutting edge, but this species differs in having a narrower and more elongated cusp, and concave to weakly sinuous mesial cutting edge. Reinecke and Hoedemakers (2006: 4) suggested the possibility that *P. singularis* is synonymous with *P. latus*. Although *P. latus* reportedly survived at least into the early Miocene (Reinecke and Hoedemakers 2006), Haye et al. (2008) stated that the taxon was characteristic of the Rupelian, whereas *P. maltzani* occurs in the early Chattian, and

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P. singularis occurs in late Chattian to middle Miocene deposits. Miocene *P. hemmooriensis* Reinecke and Hoedemakers, 2006 differ from Oligocene species in having very narrow, more erect and sinuous cusps. The teeth in our sample appear to represent a new species, but this determination must await the discovery of a larger sample of complete teeth.

Genus *Rhizoprionodon* Whitley, 1929

Type species: *Carcharias* (*Scoliodon*) *crenidens* Klunzinger, 1880, Recent, Red Sea.

Rhizoprionodon sp.

Fig. 5H.

Referred specimens.—BCGM 9069 and 9070, SC 2009.18.9.

Comments.—These teeth are small (6 mm in total width) and imperfectly preserved, making it difficult to distinguish them from similarly toothed sharks like *Sphyrna* and even *Physogaleus*. Teeth of all of these taxa can have highly concave mesial cutting edges, as is the case with our specimens. Our specimens lack cusplets as seen on the distal blade of *Physogaleus*. Teeth of *Sphyrna media* Springer, 1940 can have concave mesial edges and convex distal heel, but we identify our specimens as *Rhizoprionodon* because the mesial edge is very concave, with the cusp being narrower and cusp apex more vertically oriented. Our teeth are similar to Oligocene specimens from North Carolina identified as *R. fischeuri* (Müller 1999: pl. 8: 2–4), but a larger sample is needed to accurately determine the identity of these Chandler Bridge teeth.

Family Hemigaleidae Hasse, 1879

Genus *Hemipristis* Agassiz, 1843

Type species: *Hemipristis serra* Agassiz, 1843, Miocene, Germany.

Hemipristis serra (Agassiz, 1835)

Fig. 5I, J.

Referred specimens.—BCGM 9071–9073, SC 2009.18.10.

Comments.—Dignathic heterodonty is strongly developed in the dentition of *Hemipristis serra*, with broad, recurved, very coarsely serrated upper teeth (Fig. 5I) and narrower lower lateral teeth. The largest upper lateral tooth is damaged but measures 18 mm in crown height. The crown of the largest complete upper lateral tooth measures 13 mm in height and 10.5 mm in width. The cutting edges of adult lower anterior teeth are poorly developed, with a few serrations located only at the crown foot. We see no appreciable difference between the Chandler Bridge sample and teeth we have personally observed from Mio-Pliocene deposits of South Carolina, North Carolina, Maryland, and Florida.

Adnet et al. (2007) hypothesized that specimens they identified as *Hemipristis* cf. *H. serra* (Rupelian of Pakistan) represented a transitional species between *H. curvatus* Dames, 1883 and *H. serra*, indicating a direct ancestor-descendant relationship between these taxa. Interestingly, Thomas et al. (1989) tentatively identified both of these species in Rupelian strata of Oman. We recovered several small (4 mm in basal width) upper teeth that lack serrations on the mesial cutting edge (Fig. 5J), identical to specimens Case (1980) identified as *H. wyattdurhami* White, 1956 (= *H. curvatus*), and we consider these to represent juvenile *H. serra* (see also Chandler et al. 2006). These data provide strong evidence that *H. serra* evolved directly from *H. curvatus* (see also Adnet et al. 2007). Based on histological differences with extant *H. elongata* (Klunzinger, 1871), Ward and Bonavia (2001) suggested that generic reassignment of the "*H. serra*" morphology is warranted.

Stratigraphic and geographic range.—Oligocene to Pliocene, Africa, Europe, USA, Java, India, Japan.

Family Scyliorhinidae Gill, 1862

Genus *Bythaelurus* Compagno, 1988

Type species: *Scyllium canescens* Gunther, 1988, Recent, "southwestern coast of South America".

Bythaelurus sp.

Fig. 5M.

Referred specimen.—BCGM 9074.

Comments.—Unfortunately, comparing this specimen to known scyliorhinid species is difficult because most of the root and the distal crown shoulder are missing. Isolated teeth referred to several scyliorhinid taxa have been reported from the Oligocene of the USA and Europe, including *Scyliorhinus dachiardi* (Lawley, 1876) (i.e., Baut 1993; Génault 1993; Reinecke et al. 2001), *S. distans* (Probst, 1879) (i.e., Case 1980), *S.* aff. *coupatezi* Herman, 1974 (i.e., Steurbaut and Herman 1978; Reinecke et al. 2001, 2005), and *Bythaelurus steurbauti* Hovestadt and Hovestadt-Euler, 1995 (see also Reinecke et al. 2005). Early Oligocene records of *S. dachiardi* were synonymized with *Pachyscyllium albigensis* Reinecke, Moths, Grant, and Breitkreutz, 2005, and these teeth differ from our specimen in that the enameloid is smooth and the labial crown foot is nearly flat. In fact, all species of *Pachyscyllium* Reinecke, Moths, Grant, and Breitkreutz, 2005 have smooth enameloid and straight or only slightly concave labial crown foot. The labial crown foot of *S. distans* is usually slightly concave and the lingual crown ornamentation is less extensive. Reinecke et al. (2001, 2005) adopted assignment of the "*S. distans*" morphology to *Premontreia* Cappetta, 1992 (see also Haye et al. 2008).

With respect to crown ornamentation, our specimen, *S.* aff. *coupatezi*, and *B. steurbauti* all bear labial and lingual longitudinal ridges. Steurbaut and Herman (1978) tentatively identified Belgian Oligocene teeth as *Scyliorhinus* aff. *coupatezi* because of the close similarity to Pliocene *S. coupatezi* (see Herman 1975). Hovestadt and Hovestadt-Euler (1995) later concluded that *S. coupatezi* was related to extant *Scyliorhinus* but Oligocene *S.* aff. *S. coupatezi* was more closely related to *Bythaelurus* Compagno, 1988. At 0.7 mm in height, our specimen is much smaller than the type specimens of *B. steurbauti* (3+ mm in height), but the crown ornamentation is similar. Comparison of our specimen to extant *B. canescens*

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Günther, 1878 shows that both species are in the same size range, exhibit similar crown ornamentation, and the labial crown foot is a shelf-like structure that overhangs the root as on lower teeth of *B. canescens* (Herman et al. 1990). For these reasons we assign our specimen to *Bythaelurus* sp., but a more specific identification must await the discovery of additional teeth.

Family Sphyrnidae Gill, 1872

Genus *Sphyrna* Rafinesque, 1810

Type species: *Squalus zygaena* Linneaus, 1758, Recent, "Europe, America".

Sphyrna cf. *S. media* Springer, 1940

Fig. 5K.

Referred specimens.—BCGM 9075–9077, SC 2009.18.11.

Comments.—Our sample compares favorably to material identified as *Sphyrna* cf. *S. media* by Purdy et al. (2001). We concur with Purdy et al. (2001) that *S. arambourgi* Cappetta, 1970 (pl. 19: 3–16) is indistinguishable from teeth they identify as *Sphyrna* cf. *S. media*. Based on overall size, cusp morphology, and elongated, low distal heel, we believe that specimens identified as *Scoliodon terraenovae* (Richardson, 1836) by Case (1980: pl. 7: 1, 2) are assignable to *Sphyrna* cf. *S. media*. The morphology and size of the tooth identified as *Rhizoprionodon* by Génault (1993: figs. 61, 62) also appears to be closer to *S. media*. Maximum tooth width of *Sphyrna* cf. *S. media* in our sample is approximately 10 mm, and they differ from those of *S. zygaena* (Linnaeus, 1758) in being smaller in size, having a much more gracile cusp, and mesial cutting edges are straight to concave.

Stratigraphic and geographic range.—Oligocene, USA (North and South Carolina), France(?); Miocene, USA (North Carolina), France.

Sphyrna zygaena (Linnaeus, 1758)

Fig. 5L.

Referred specimens.—BCGM 9078 and 9079, SC 2009.18.12.

Comments.—*Sphyrna zygaena* is the more common of the two Chandler Bridge hammerhead sharks, and the largest anterior tooth measures 14 mm in total width and 11 mm in total height. Purdy et al. (2001) synonymized *S. laevissima* (Cope, 1867) with *S. zygaena*, and Oligo-Miocene references to the former taxon should be emended accordingly (i.e., Leriche 1942; Kent 1994; Müller 1999). Some teeth of *S. zygaena* are similar to those of *Carcharhinus gibbesi*, but the cutting edges are completely smooth.

Stratigraphic and geographic range.—Oligocene to Miocene, USA (North and South Carolina, Virginia, Maryland) and Europe.

Family Triakidae Gray, 1851

Genus *Galeorhinus* Blainville, 1816

Type species: *Squalus galeus* Linneaus, 1758, Recent, "European Seas".

Galeorhinus sp.

Fig. 5N–P.

Referred specimens.—BCGM 9080–9083, SC 2009.18.13.

Comments.—These teeth can be distinguished from all other Chandler Bridge carcharhinids in that the labial crown foot is obviously thicker and clearly overhangs the root. Upper teeth of *Chaenogaleus* Gill, 1862 are distinguished from *Galeorhinus* Blainville, 1816 in having a labial crown foot that does not overhang the root (Cappetta 1987). Heterodonty is developed in our sample; parasymphyseal teeth are nearly symmetrical (Fig. 5N) and anterior teeth have a rather erect cusp, elongated and smooth mesial cutting edge, and two to four large cusplets on the distal heel (Fig. 5O). Teeth become smaller and the cusp more distally inclined towards the commissure (Fig. 5P). A specimen identified by Case (1980: pl. 7: 3) as *G. affinis* (Probst, 1878) is more appropriately referred to *Physogaleus*, and an additional specimen identified as *G. galeus* (Linnaeus, 1758) (see Case 1980: pl. 7: 6) may best be left in open nomenclature. This latter specimen differs from our material in having five obvious distal cusplets as opposed to three or four. Although of similar size, the Chandler Bridge *Galeorhinus* differs from extant *G. galeus* in having fewer cusplets on the distal blade, a more convex mesial cutting edge, and nodular ornamentation on the labial crown foot (see also Herman et al. 1988). A specimen from the Oligocene of North Carolina assigned to *G.* aff. *galeus* by Müller (1999: pl. 5: 1) is comparable to the Chandler Bridge *Galeorhinus*. Material documented from the German Oligocene (*Galeorhinus* sp.) is similar to the Chandler Bridge teeth (Reinecke et al. 2001, 2005).

Superorder Batomorphii Cappetta, 1980

Order Rajiformes Berg, 1940

Family Rhynchobatidae Garman, 1913

Genus *Rhynchobatus* Müller and Henle, 1837

Type species: *Rhinobatus laevis* Schneider, 1801, Recent, Japan.

Rhynchobatus pristinus (Probst, 1877)

Fig. 6A.

Referred specimens.—BCGM 9084–9086, SC 2009.18.14.

Comments.—Teeth of *Rhynchobatus* Müller and Henle, 1837 can be distinguished from *Rhinobatos* Link, 1790 in that crown enameloid has a granular texture, and the elongated medial lingual uvula is not flanked by lateral uvulae. Ontogentetic heterodonty in our *Rhynchobatus pristinus* sample is evident in that the enameloid of tiny teeth (~0.5 mm) is smooth and lacks the granular ornamentation seen on adult teeth.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Miocene, Europe and USA (North Carolina, Virginia).

Family Rajidae Bonaparte, 1831

Genus *Raja* Linneaus, 1758

Type species: *Raja batis* Linneaus, 1758, Recent, unknown.

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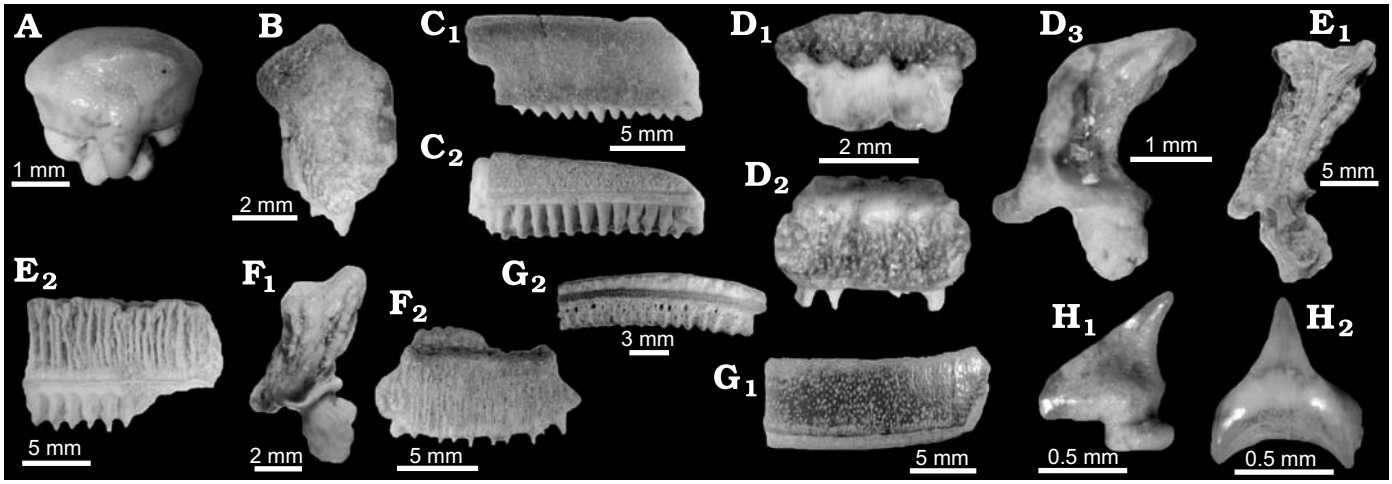


Fig. 6. Batoids from Summerville, upper Chattian. **A**. *Rhynchobatus pristinus* (Probst, 1877), BCGM 9085, occlusal view. **B**, **C**. Myliobatinae gen. indet. **B**. BCGM 9117, lateral tooth, occlusal view. **C**. BCGM 9116, partial medial tooth, occlusal (C_1) and lingual (C_2) view. **D**. *Paramobula fragilis* (Cappetta, 1970), BCGM 9113, anterolateral tooth, occlusal (D_1), labial (D_2), and lateral (D_3) view. **E**, **F**. *Plinthicus stenodon* Cope, 1869. **E**. BCGM 9120, partial anterior tooth, lateral (E_1) and lingual (E_2) view. **F**. BCGM 9121, lateral tooth, lateral (F_1) and labial (F_2) view. **G**. *Rhinoptera* cf. *R. studeri* (Agassiz, 1843), BCGM 9123, occlusal (G_1) and lingual (G_2) view. **H**. *Gymnura* sp., BCGM 9107, lateral (H_1) and labial (H_2) view.

Raja mccollumi sp. nov.

Fig. 7C, D, F–H.

Etymology: Species named in honor of Vance McCollum of Summerville, SC, for helping to increase our understanding of an upper Oligocene ecosystem, and for his efforts in broadening our knowledge of South Carolina vertebrate paleontology over the last two decades.

Type material: Holotype: BCGM 9093, male anterior tooth, Paratypes: BCGM 9199, male lateral tooth, BCGM 9200, female anterior tooth, 9201, female lateral tooth, BCGM 9202, female posterior tooth.

Type locality: Summerville, Dorchester County, South Carolina, USA.

Type horizon: marine facies of Katuna et al. (1997), Chandler Bridge Formation, upper Chattian (upper part of calcareous nannofossil zone NP 25), Oligocene.

Referred specimens.—BCGM 9090, SC 2009.18.15.

Diagnosis.—A fossil species in which male teeth bear a tall, narrow cusp; anterior teeth are symmetrical to weakly asymmetrical; the cusp is conical to slightly laterally compressed and lacks a labial cutting edge. In contrast, male anterior teeth of Oligo-Miocene *R. cecilae* Steurbaut and Herman, 1978 can be strongly asymmetrical, and the cusp is very laterally compressed with a conspicuous labial cutting edge (Hovestadt and Hovestadt-Euler 1995; Reinecke et al. 2005, 2008; Haye et al. 2008). The labial crown margin of *R. cecilae* is also narrower and more labio-basally directed. Female teeth of *R. mccollumi* sp. nov. differ from *R. cecilae* in that the labial face of *R. cecilae* is flat to weakly concave, and the root is larger (Hovestadt and Hovestadt-Euler 1995; Reinecke et al. 2005, 2008; Haye et al. 2008). Although of similar size, the cusp of male teeth of Miocene *Raja gentilli* Joleaud, 1912 has a broader base, and the marginal area is smaller (Ward and Bonavia 2001) than male *R. mccollumi* sp. nov. Male teeth of *R. mccollumi* sp. nov. are smaller than Oligo-Miocene *R. casieri* Steurbaut and Herman, 1978 and Miocene R. *olisiponensis* (Jonet, 1968), and lack the conspicuous mesial and distal cutting edges seen on male teeth of the latter two taxa. *Raja* sp. from the German Chattian differ from male *R. mccollumi* sp. nov. in having a wider cusp (Reinecke et al. 2005: pl. 53: 1, 3; Haye et al. 2008: pl. 9: 4). Teeth of *Raja* sp. 1 described by Müller (1999: 56, text-fig. 18, nos. 7–10) may be conspecific with *R. mccollumi* sp. nov., but this determination must await our examination of specimens from the Ashley Marl.

Description.—Male teeth are strongly cuspidate, especially in anterior positions. The cusp is lingually curved and conical to laterally compressed. The labial cusp face is very convex and lacks a cutting edge, whereas the lingual face is flatter and bears inconspicuous mesial and distal cutting edges, neither of which extend onto the crown base. The crown base is roughly circular in outline, with a rounded to slightly flattened labial margin. The lingual crown margin is formed into a basally directed uvula that is broadly concave. In labial view, the crown becomes asymmetrical towards the commissure in that the cusp is offset distally as well as more distally inclined. Additionally, the cusp is often more laterally compressed but still lacks a labial cutting edge, and the labial crown base is more irregular. Closer to the commissure, the cusp becomes lower and even more strongly directed lingually.

Female teeth are easily distinguished from males in that the lingually directed cusp is very low and the labial face is broadly triangular. The cusp is longest in anterior jaw positions, but it becomes reduced towards the commissure and is indistinct in posterior positions. In labial view, anterior teeth are slightly asymmetrical because the cusp is distally inclined, but towards the commissure the cusp becomes offset distally and more obviously distally inclined. In all jaw positions, mesial and distal cutting edges extend from the crown base to the cup apex, dividing the crown into a large labial face and much smaller lingual face. In lateral view, the outline of the labial face of anterior and antero-lateral teeth is sinuous because it is medially concave, and the labial crown

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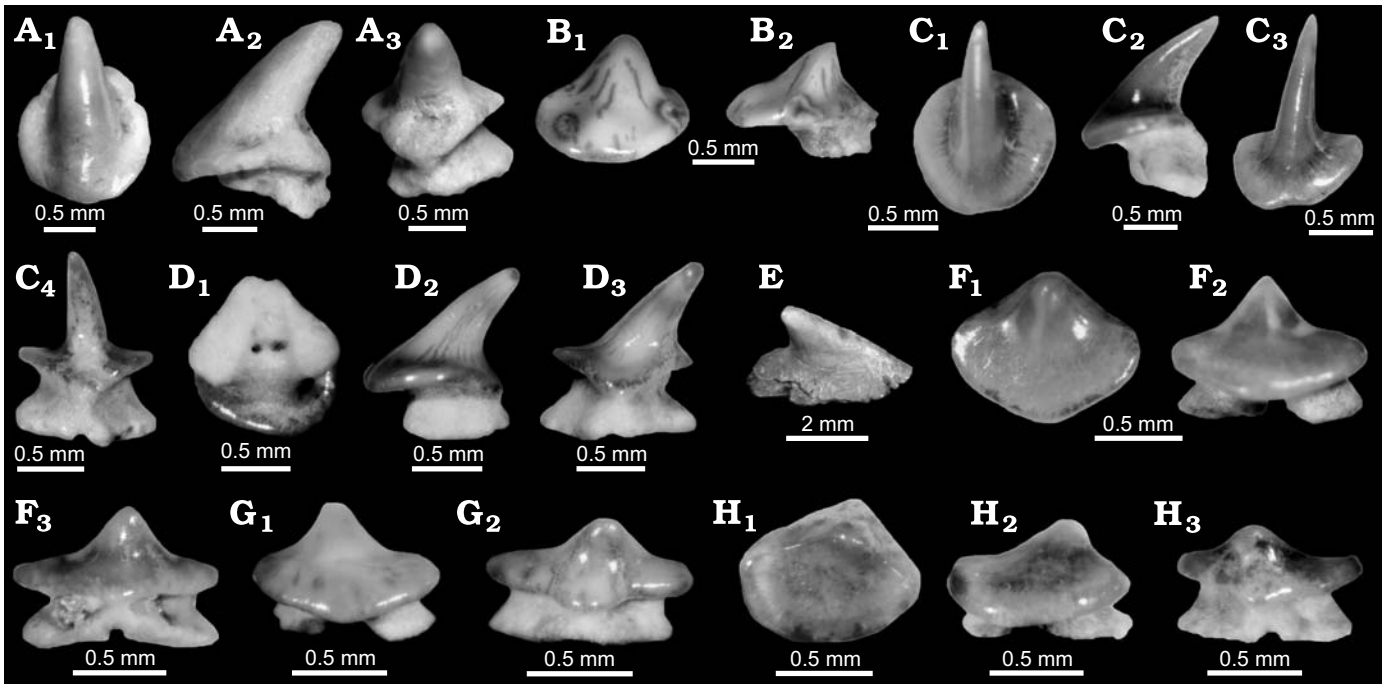


Fig. 7. Skates from Summerville, upper Chattian. **A**, **B**, *Raja* sp. **A**. BCGM 9088, male anterior tooth, occlusal (A_1), lateral (A_2), and lingual (A_3) view. **B**. BCGM 9089, female lateral tooth, labial (B_1) and lateral (B_2) view. **C**, **D**, *Raja mccollumi* sp. nov. **C**. BCGM 9093 (holotype), male anterior tooth, occlusal (C_1), lateral (C_2), labial (C_3), and lingual (C_4) view. **D**. BCGM 9199 (paratype), male lateral tooth, basal (D_1), lateral (D_2), lingual (D_3) view. **E**. BCGM 9095, *Raja* sp. denticle, lateral-oblique view. **F**–**H**, *R. mccollumi* sp. nov. **F**. BCGM 9200 (paratype), female anterior tooth, occlusal (F_1), labial (F_2), and lingual (F_3) view. **G**. BCGM 9201 (paratype), female lateral tooth, labial (G_1) and lingual (G_2) view. **H**. BCGM 9202 (paratype), female posterior tooth, occlusal (H_1), labial (H_2), lingual (H_3) view.

margin greatly overhangs the root. The labial face is flatter in more distal jaw positions, and the labial crown margin is not as pronounced. The lingual uvula is very small.

Tooth roots are rather low and bilobate. Root lobes flare outward from the base of the crown, and are separated by a deep nutritive groove. Basal attachment surfaces are triangular, flat, and may be narrow or broad.

Comments.—The morphological variation in our sample is interpreted to represent sexual (compare Fig. 7C and F) and monognathic (compare Fig. 7C and D, F and G) heterodonty. However, the monognathic heterodonty envisioned in male and female dentitions of *R. mccollumi* sp. nov. appears to have been gradational and similar to *R. laevis* Garman, 1913 (see Bigelow and Schroeder 1953), whereas monognathic heterodonty in *R. cecilae* is disjunct. Male and female teeth of *R. mccollumi* sp. nov. are nearly equally represented, and the taxon is the most common elasmobranch in our Chandler Bridge sample.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina).

Raja sp.

Fig. 7A, B.

Referred specimens.—BCGM 9087–9089, SC 2009.18.16.

Comments.—Male teeth are strongly cuspidate (Fig. 7A) but female teeth bear an indistinct cusp (Fig. 7B). These teeth are twice the size as those of *Raja mccollumi* sp. nov. but are much less common. Although the female morphotype in our sample is similar in size and overall morphology to the type *Raja casieri* Steurbaut and Herman, 1978 (a female tooth), the transverse cutting edge is less developed and the lingual uvula is not as pronounced (Hovestadt and Hovestadt-Euler 1995: pl. 2; Reinecke et al. 2005: pl. 56). The teeth of male *R. casieri* are comparable in size and morphology to the teeth in our sample, but our specimens lack cutting edges (Reinecke et al. 2005: pl. 55; Haye et al. 2008: pl. 9: 1, 2). Although the Chandler Bridge teeth are of similar size to *R. olisiponensis* (Jonet, 1968), the male teeth lack cutting edges and female teeth do not have the pyramidal appearance that has been described in the latter taxon (see Cappetta 1970; Antunes and Balbino 2007). The Chandler Bridge teeth differ from Pliocene *Raja* sp. of Purdy et al. (2001: fig. 9) in that the margin of the crown is thinner and does not curve apically, and the cusp lacks a labio-lingually oriented cutting edge.

Order Myliobatiformes Compagno, 1973

Family Dasyatidae Jordan, 1888

Genus *Dasyatis* Rafinesque, 1810

Type species: *Dasyatis ujo* Rafinesque, 1810, Recent, "European Seas".

Dasyatis cavernosa (Probst, 1877)

Fig. 8A, B.

Referred specimens.—BCGM 9096, 9097, and 9103, SC 2009.18.17.

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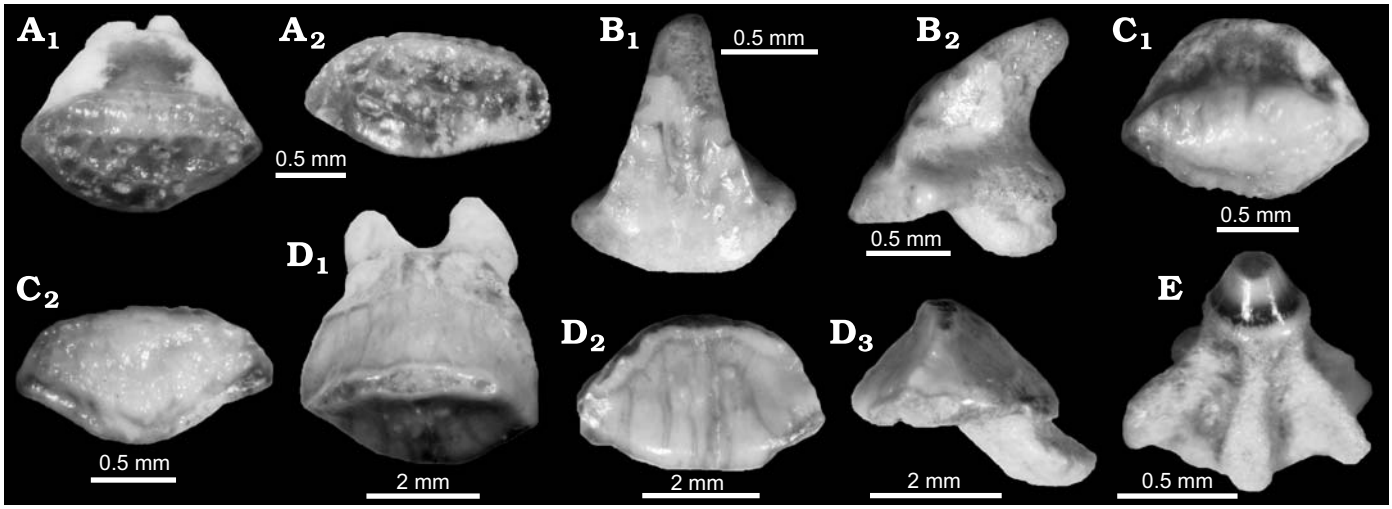


Fig. 8. Stingrays from Summerville, upper Chattian. **A**. *Dasyatis cavernosa* (Probst ,1877), BCGM 9097, occlusal (A_1) and labial (A_2) view. **B**. *D.* cf. *cavernosa*, BCGM 9103, male tooth, occlusal (B_1) and labial (B_2) view. **C**. *D. rugosa* (Probst, 1877), BCGM 9099, occlusal (C_1) and labial (C_2) view. **D**. Dasyatidae gen. et. sp. indet., BCGM 9101, occlusal (D_1), labial (D_2), and lateral (D_3) view. **E**. BCGM 9106, *Dasyatis* sp. denticle, lateral-oblique view.

Comments.—These teeth measure 2 mm in width and the majority are low-crowned. Labial ornamentation consists of large pits formed from highly irregular, interconnected ridges. The apical portion of the labial face is weakly concave, the transverse crest is sharp and distinct, and root lobes are rather gracile. Several male teeth are included in the sample, and these have higher crowns (more anterior teeth are highly cuspidate) and a concave labial face that is weakly ornamented with longitudinal ridges. The ornamentation of low-crowned teeth attributed to *D. cavernosa* is highly variable (see Leriche 1927: pl. 5: 20, 21, 24–28; Cappetta 1970; Case 1980; Bracher 2005; Müller 1999; Wienrich and Reinecke 2009). Teeth of *D. cavernosa* are comparable in size to *D. delfortriei* Cappetta, 1970, but the crown ornamentation of the latter species has an appearance similar to a honeycomb structure (i.e., Cappetta 1970; Reinecke et al. 2005, 2008).

It has been shown that development of gynandric heterodonty in extant *Dasyatis sabina* (Lesueur, 1824) is related to mating behavior and not diet (Kajiura and Tricas 1996). Male teeth of *D. sabina* are generally identical to those of females except during the mating season, when there is a transition to a high-crowned, cuspidate morphology that is used to grasp pectoral fins of females during copulation (Kajiura et al. 2000). If we assume that this form of gynandric heterodonty applies to all species of *Dasyatis* Rafinesque, 1810 and that it was occurring during the Oligocene, the limited development of cuspidate teeth in males (see Fig. 8B) could explain the high ratio (approximately 12:1) of low-crowned to high-crowned teeth in our sample.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (North and South Carolina); Miocene, Europe and USA (Maryland).

Dasyatis rugosa (Probst, 1877)

Fig. 8C.

Referred specimens.—BCGM 9098 and 9099, SC 2009.18.18.

Comments.—Although crown ornamentation is somewhat similar to *Dasyatis cavernosa*, *D. rugosa* is slightly larger (2.5 mm in width) and has a more convex labial face, wide but indistinct transverse crest, often sinuous labial crown margin (in basal view), and more robust root lobes (see also Cappetta 1970; Reinecke et al. 2005; Haye et al. 2008).

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Miocene, France, Germany, Portugal, Poland.

Dasyatidae gen. et sp. indet.

Fig. 8D.

Referred specimens.—BCGM 9100 and 9101, SC 2009.18.19.

Comments.—These teeth are very easily distinguished from *Dasyatis* in our sample, not just by their larger size (3.5 mm in width), but by the nearly complete absence of crown ornamentation. There is a sharp transverse crest that divides the crown into a small, weakly concave labial face and a much more lingually expanded lingual face, and the labial crown margin (in basal view) is virtually straight.

Although this morphology was not discussed by Purdy et al. (2001), we have personally observed identical teeth from North Carolina (Lee Creek). These teeth are comparable to *Dasyatis serralheiroi* Cappetta, 1970 from the French Miocene, as well as to smooth or weakly ornamented teeth from the German and Swiss Miocene thought to be female *D. cavernosa* (Probst, 1877) (i.e., Leriche 1927; Bracher 2005; Wienrich and Reinecke 2009). Additionaly, the morphology is akin to teeth of extant *Himantura* Müller and Henle, 1837 (see Compagno and Roberts 1982; Monkolprasit and Roberts 1990), a taxon known primarily from the Pacific realm in freshwater and marine environments (Bonfil and Abdallah 2004).

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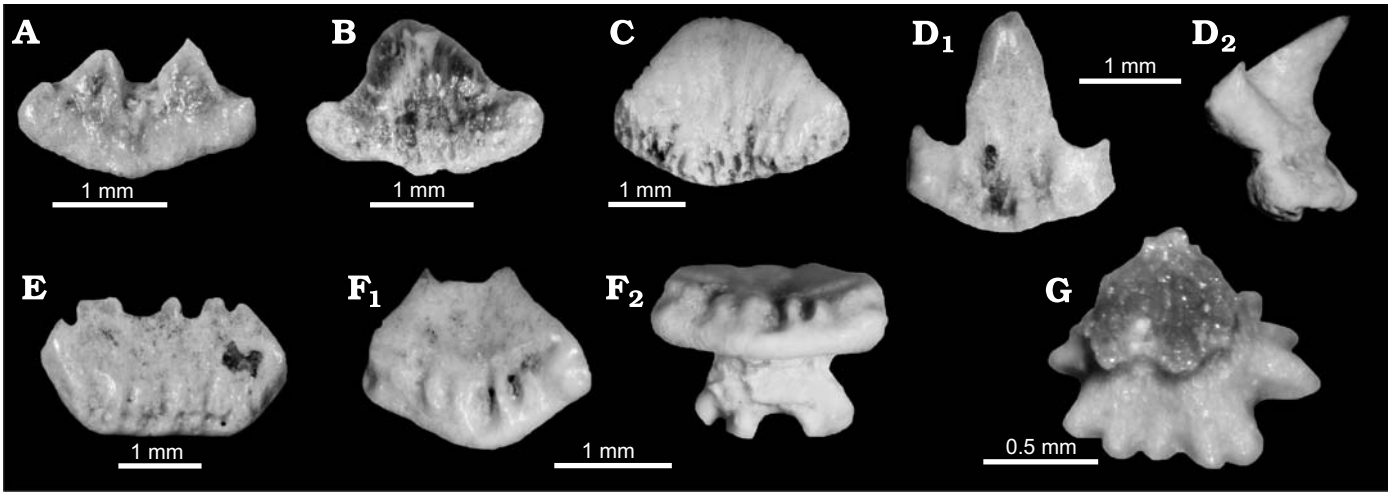


Fig. 9. Devil ray *Mobula* cf. *M. loupianensis* Cappetta, 1970, Summerville, upper Chattian. **A**. BCGM 9136, male (?) tooth, occlusal view. **B**. BCGM 9137, female (?) tooth, occlusal view. **C**. BCGM 9138, female tooth, occlusal view. **D**. BCGM 9141, male tooth, occlusal (D_1) and lateral (D_2) view. **E**. BCGM 9135, tooth, occlusal view. **F**. BCGM 9142, female (?) tooth, occlusal (F_1) and labial (F_2) view. **G**. BCGM 9109, denticle, anterior-oblique view.

Family Gymnuridae Fowler, 1934

Genus *Gymnura* van Hasselt, 1823

Type species: *Raja micrura* Schneider, 1801, Recent, Suriname.

Gymnura sp.

Fig. 8H.

Referred specimen.—BCGM 9107.

Comments.—Although crown size and morphology compares favorably to Rupelian *Gymnura hovestadti* Herman, 1984, root lobes of our specimen are not as robust. Reinecke et al. (2005) noted that their specimen (Chattian) was similar to *G. hovestadti*, but because morphological variation within the taxon is unknown (based on only three teeth) they chose not to assign the tooth to any species. *Gymnura* van Hasselt, 1823 is a rare component of the Chandler Bridge elasmobranch assemblage, being far outnumbered by comparably sized teeth of *Raja cecilae* Steurbaut and Herman, 1978 (ratio of 900:1).

Family Myliobatidae Bonaparte, 1838

Comments.—Recent phylogenetic analysis of Myliobatoidea (see González-Isáis and Domínguez 2004) show that Myliobatidae consists of Mobulinae, Myliobatinae, and Rhinopterinae.

Subfamily Mobulinae

Genus *Mobula* Rafinesque, 1810

Type species: *Mobula auriculata* Rafinesque, 1810, Recent, unknown.

Mobula cf. *M. loupianensis* Cappetta, 1970

Fig. 9.

Referred specimens.—BCGM 9133–9142, SC 2009.18.20.

Comments.—A variety of morphotypes are represented in our sample, and Notabartolo di Sciara (1987) reported that extant species of *Mobula* Rafinesque, 1810 can exhibit monognathic, dignathic, gynandric, and ontogenetic heterodonty. We regard the varied morphotypes in our sample to represent heterodonty within a single species. Purdy et al. (2001) described a number of *Mobula* tooth morphologies that were collected from the Miocene Pungo River Formation, and these teeth are quite similar to *M. loupianensis* reported from the middle Miocene of France (Cappetta 1970: 108–110, fig. 20). Regarding the specimens Cappetta (1970) illustrated, those in fig. 20A–D appear to be male teeth, whereas fig. 20F may represent a female. In Fig. 9, the teeth shown in A–D are equivalent to teeth illustrated by Cappetta (1970) in his fig. 20E, D, F, and B, respectively. Based on the work of Notabartolo di Sciara (1987), we believe that *M. pectinata* Cappetta, 1970 could be conspecific with *M. loupianensis* (see Fig. 9E).

The Chandler Bridge *Mobula* teeth differ from those of the extant species *M. eregoodootenkee* (Bleeker, 1859), *M. thurstoni* Lloyd, 1908, and *M. tarapacana* (Philippi, 1893) in that the occlusal surface is smooth, and teeth of *M. japonica* (Müller and Henle, 1841) are similar to those of *Manta* Bancroft, 1829 (see Notabartolo di Sciara 1987). Our sample contains morphologies attributed to *M. loupianensis* and *M. pectinata*, as well as to other Oligocene teeth identified as *M. irenae* Pfeil, 1981. The validity of these species is questionable because all are based on relatively few specimens (i.e., 15, 4, and 13 teeth, respectively), and the original reports provided no clear indication of morphological variation within each species. *Mobula pectinata*, *M. irenae*, and *M. loupianensis* exhibit some very close morphological similarities, and we consider it entirely possible that all of these represent heterodonty (monognathic, dignathic, ontogenetic, and gynantric) within the same taxon.

Manta melanyae Case, 1980 was described from the Trent Marl of North Carolina. However, of the two teeth originally illustrated, one specimen is referable to *Mobula* (Case 1980: pl. 10: 1a–e) and the other may be *Paramobula* Pfiel, 1981 (see Case 1980: pl. 10: 2a–e). The former speci-

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men does not differ appreciably from our *Mobula* sample, and morphologies illustrated by Müller (1999: pl. 15: 1–3) from the Old Church Formation also fall within the range of variation we observed. We consider *Manta melanyae* to be a nomen dubium, and Oligocene *Mobula* from the Atlantic Coastal Plain may be conspecific.

Stratigraphic and geographic range.—?Oligocene (Chattian), USA (North and South Carolina); Miocene, France.

Genus *Paramobula* Pfeil, 1981

Type species: *Manta fragilis* Cappetta, 1970, Miocene, France.

Paramobula fragilis (Cappetta, 1970)

Fig. 6D.

Referred specimens.—BCGM 9111–9113, SC 2009.18.21.

Comments.—Teeth of *Manta fragilis* Cappetta, 1970 (based on six isolated teeth) from the French Miocene differ significantly from extant *Manta* in having: mesio-distally wide, labio-lingually thin, and apico-basally high crowns; smooth, flat, often slightly labially sloping occlusal surfaces; there are numerous very narrow and closely spaced labial vertical ridges and grooves; wider and fewer lingual ridges and grooves; and the root is polyaulacorhize (Cappetta 1987). These *Mobula*-like characteristics led Pfeil (1981) to erect a new genus, *Paramobula*.

Although superficially similar to *Plinthicus stenodon* Cope, 1869, *Paramobula fragilis* is much smaller in size (up to 5 mm in width) and labio-lingually thinner (some Chandler Bridge specimens are partially translucent). Additionally, the occlusal surface of *Paramobula* is flat and smooth, whereas it is distinctly concave in *Plinthicus* Cope, 1869. We do not consider the *Paramobula* morphology to represent ontogenetic heterodonty in *Plinthicus* (i.e., juvenile individuals) because the smallest teeth in our *Plinthicus* sample possess the same characteristics as the largest teeth (see below).

Some of our *Mobula* teeth are mesio-distally wide like *Paramobula*, but the crowns are labio-lingually thicker. One characteristic we used to differentiate the two genera is crown height, with the labial face of *Mobula* teeth measuring 1 mm or less in height, whereas the vertical height of *Paramobula* teeth is 2 mm to 4.5 mm. These two genera occur together (see Cappetta 1970; Purdy et al. 2001), and admittedly we cannot acertain if they are conspecific. Notabartolo di Sciara (1987) noted that teeth of *Mobula* become wider as individuals mature, so the *Paramobula* morphology could represent ontogenetic heterodonty within *Mobula*. Cappetta and Stringer (2002) stated that *Paramobula* was synonymous with *Mobula* but provided no details for their reasoning. Controversies regarding the identification of isolated teeth may not be resolved without the benefit of at least one reasonably complete associated dentition, and for the purposes of this report we consider the morphologies distinct.

The degree of morphological variation in the dentition of *Paramobula* is inadequately known. Case (1980) assigned a suite of 13 teeth recovered from the Oligocene Trent Marl to a new species, *Manta melanyae*, based on comparison to the *P. fragilis* morphology. However, it is our opinion that the specimens illustrated by Case (1980: pl. 10), which were identified as belonging to lateral jaw positions, could be assignable to *Mobula* (pl. 10: 1) or *Paramobula* (pl. 10: 2). Müller (1999) but made no mention of *Paramobula*, and assigned all mobulid teeth from the Oligocene of North Carolina, Virginia, and South Carolina to *Mobula* sp. Although Case (1980) noted that *P. fragilis* occurs in Miocene deposits of North Carolina, Purdy et al. (2001) did not mention the taxon, even though one specimen they identified as *Mobula* sp. (fig. 14j–l) is morphologically similar to *P. fragilis*.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Miocene, France and USA (North Carolina).

Subfamily Myliobatinae

Myliobatinae gen. indet.

Fig. 6B, C.

Referred specimens.—BCGM 9114–9117, SC 2009.18.22.

Comments.—Our sample is represented by partial medial teeth and complete lateral teeth (i.e., Fig. 6B). The lingual ornamentation of each specimen is identical, and we believe that the fossils are conspecific. The preserved lateral margin on one medial tooth is weakly angular, indicating articulation with a lateral tooth (Fig. 6C). The dentition of *Aetobatus* Blainville, 1816 lacks lateral teeth and there is no indication of lateral angles on medial teeth (see Cappetta 1987).

The lingual crown ornamentation and morphology of lateral teeth in our sample are very similar to specimens identified as *Myliobatis* (sensu lato) sp. 2 from the Rupelian of Germany (Reinecke et al. 2001: pl. 57b, d) and as *Myliobatis oligocaena* Leriche, 1910 from the French Rupelian (Baut and Génault 1999: pl. 7: 2, 4), and these remains may be conspecific. *Myliobatis oligocaena* has been tentatively synonymized with *Weissobatis micklichi* Hovestadt and Hovestadt-Euler, 1999, a taxon from the German Rupelian known from partial skeletons and articulated dentitions. The crown ornamentation and morphology of the lingual transverse ridge at the crown/root junction is close to Miocene material identified as *Pteromylaeus* Garman, 1908 by Cappetta (1970), but our medial teeth do not appear to have been as highly curved and our lateral teeth are not nearly as mesio-distally narrow as in extant *Pteromylaeus* (see Hovestadt and Hovestadt-Euler 1999: 343). Lateral teeth of *Myliobatis* Cuvier, 1816 and *W. micklichi* have been described as being lozenge-shaped in occlusal view (Hovestadt and Hovestadt-Euler 1999: 343), and the lateral tooth of *M. oligocaena* illustrated by Baut and Génault (1999: pl. 7: 4) certainly appears to be so. Our two lateral teeth are less wide than long, but they appear to be within the range of the lateral-most row of teeth in *W. micklichi* (see Hovestadt and Hovestadt-Euler 1999: fig. 6). Hovestadt and Hovestadt-Euler (1999: 343) stated that attribution of isolated teeth to species of *Myliobatis* and *Weissobatis* Hovestadt and

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Hovestadt-Euler, 1999 should be avoided, and we follow this advice until more complete fossils are found.

Subfamily Rhinopterinae

Genus *Plinthicus* Cope, 1869

Type species: *Plinthicus stenodon* Cope, 1869, Miocene, New Jersey, USA.

Plinthicus stenodon Cope, 1869

Fig. 6E, F.

Referred specimens.—BCGM 9118–9121, SC 2009.18.23.

Comments.—Cappetta (1987) and Cappetta and Stringer (2002) assigned *Plinthicus* to Mobulinae because of dental similarities to *Mobula*. Purdy et al. (2001) studied a large sample of teeth and concluded that the arrangement of the teeth within the dentition was more similar to *Rhinoptera* Cuvier, 1829 than *Mobula* and placed *Plinthicus* within Rhinopterinae. Our analysis of Chandler Bridge *Plinthicus* shows that the mesial side of lateral teeth is lower than the distal side, a dental characteristic seen in *Rhinoptera* (see Cappetta 1987).

Plinthicus kruibekensis Bor, 1990 is based on a unique tooth recovered from Rupelian strata of Belgium. The tooth of *P. kruibekensis* slopes outwards and then curves inwards, the occlusal surface is flat, and the enameloid ornamentation consists of anastomosing longitudinal ridges and grooves (Bor 1990). In contrast, the Chandler Bridge teeth slope inward and curve upward (Fig. $6E_1$, $6F_1$), the occlusal surface is concave (Fig. $6F_2$), and the enameloid ornamentation consists of parallel ridges and grooves (Fig. $6E_2$). These features are identical to those we personally observed on Miocene *Plinthicus stenodon* from North and South Carolina, and the Chandler Bridge specimens constitute the oldest record of the species.

Stratigraphic and geographic range.—Oligocene (Chattian), USA (South Carolina); Miocene, USA (Atlantic Coastal Plain), France, Malta.

Genus *Rhinoptera* Cuvier, 1829

Type species: *Myliobatis marginata* Saint-Hillaire, 1817, Recent, Mediterranean Sea.

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

Fig. 6G.

Referred specimens.—BCGM 9122 and 9123, SC 2009.18.24.

Comments.—These teeth differ from those of Myliobatinae gen. indet. in having labial and lingual crown ornamentation consisting of fine vertical wrinkles (as opposed to having a granular texture), and the lingual basal ridge is thick and rounded (as opposed to rather narrow and sharp). In these respects, the Chandler Bridge teeth are quite similar to *Rhinoptera studeri* from the European Miocene (Leriche 1927; Cappetta 1970, 1987), but a specific assignment cannot be made with confidence because our sample size is small and the material incomplete. A specimen from the Belgrade Formation of North Carolina was identified as *Rhinoptera* aff. *R. bonasus* Mitchill, 1815 by Müller (1999: pl. 15: 7), but it does not appear to be different than a tooth of *R. studeri* illustrated by Leriche (1927: pl. 6: 3). Other teeth from the Belgrade Formation were identified as *Rhinoptera* aff. *R. brasiliensis* Müller, 1835 by Müller (1999: pl. 15: 4, 5), but the inter- and intraspecific variation in extant *Rhinoptera* (i.e., Cappetta 1987) suggests that only a single species was present during deposition of the Belgrade Formation. The North Carolina and Chandler Bridge specimens appear to be conspecific, but a larger sample is needed to make a more accurate determination. *Rhinoptera* may have been more widespread during the Oligocene than previously indicated, as Rupelian specimens identified as *Myliobatis* by Genault (1993: figs. 65, 66), Baut and Génault (1999: pl. 7: 3), and Reinecke et al. (2001: pl. 55: A, B) possess the same attributes as Chandler Bridge teeth we refer to *Rhinoptera*.

Stratigraphic and geographic range.—?Oligocene (Chattian), USA (North and South Carolina); Miocene, Europe.

Discussion

Other elasmobranch remains.—In addition to the taxa discussed above, we also personally observed large teeth of *Carcharocles angustidens* (Agassiz, 1843) and a single rostral spine of *Anoxypristis* White and Moy-Thomas, 1941. This material is currently housed in two private collections, but the occurrences are important to note because these taxa occur in the Chandler Bridge elasmobranch faunule. We recovered a variety of other elasmobranch remains from the fossiliferous deposit, including individual and small aggregates of calcified cartilage tesserae (BCGM 9132), and dermal denticles. Cartilage tesserrae measure approximately 1 mm in diameter and less than 2 mm in thickness, and are roughly cylindrical in shape with tuberculate vertical surfaces. Denticles consisting of a conical crown, covered with smooth enameloid, atop a convex base bearing numerous fingerlike marginal projections (BCGM 9105 and 9106, SC 2009.18.25; Fig. 8E) are tentatively assigned to *Dasyatis* Rafinesque, 1810 because of the similarity to denticles of extant *D. centroura* (Mitchill, 1815). Some denticles bear a dorso-ventrally flattened, posteriorly directed crown that has a teardrop shape (dorsal view), the dorsal surface of which bears granular ornamentation. The base of these denticles bears short finger-like projections that are better developed along the anterior margin (BCGM 9108 and 9109; Fig. 9G). We assign this morphology to *Mobula* Rafinesque, 1810 because they are similar to ventral denticles of *Mobula japonica* (Müller and Henle, 1841) (see Notabartolo di Sciara 1978: fig. 22C). Although similar to teeth of *Manta* Bancroft, 1829, the bases bear finger-like projections and lack nutritive grooves. Several denticles resemble the morphology of a rose thorn, consisting of an elliptical base (convex in profile view) that bears a small central spine, the leading margin of

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which may be covered with smooth enameloid (BCGM 9094 and 9095, SC 2009.18.26; Fig. 7E). We believe this type of denticle is referable to *Raja* (Linnaeus, 1758). Approximately 1,200 placoid scales are represented in our sample (BCGM 9124–9128, SC 2009.18.27), all having the same general morphology. These consist of a simple base capped by a flat crown bearing longitudinal ridges. The vast majority of the scale bases measure approximately 1 mm in height and are cylindrical or antero-posteriorly flattened. There is a good deal of morphological variation in the crown, which bears from three to eight ridges that originate at the anterior margin, and these may or may not extend to the posterior margin. Posterior margins are rounded or scalloped if ridges protrude a short distance past the main body of the crown. It is likely that more than one taxon is represented by these scales, but variations may also be related to locations on the body of an individual shark (i.e., Welton and Farish 1993: fig. 20A–G). A small sample of scales consist of a globular base located at the center of a thin, circular to oval crown that is devoid of ornamentation.

Other associated taxa.—A tooth of the large gavialosuchine crocodilian, *Gavialosuchus carolinensis* Erickson and Sawyer, 1996, was recovered (BCGM 9197), along with a premolar of the protocetid cetacean (BCGM 9198), *Squalodon* Grateloup, 1840. Osteichthyan remains are abundant and several taxa are represented by isolated teeth. Labridae (BCGM 9193 and 9194) dominate the sample (over 2,000 teeth), and Sphyraenidae (BCGM 9187), Scombridae (BCGM 9185), Trichiuridae (BCGM 9188), Sparidae (BCGM 9189), Albulidae (BCGM 9190), Diodontidae (BCGM 9182 and 9183), and possibly Lepisosteidae (BCGM 9186) are also present. Two isolated *Aglyptorhynchus* Casier, 1966 vertebral centra were found (BCGM 9192).

Katuna et al. (1997) noted that invertebrate microfossils and shells of macrofossils are rare in the Chandler Bridge Formation. Invertebrate fossils are uncommon in our sample, and with few exceptions they consist of phosphatic steinkerns. Species diversity is rather high and includes eight pelecypods (BCGM 9235–9242), eight gastropods (BCGM 9244–9251), a scaphopod (BCGM 9205), five ostracodes (BCGM 9211–9215), eight foraminifera (BCGM 9227–9234), a scleractinian coral (BCGM 9210), at least two crustaceans (BCGM 9224 and 9225), bryozoa (BCGM 9204), a cidaroid echinoderm (BCGM 9218), and two craniidinid brachiopods (BCGM 9208 and 9209). Peloids (BCGM 9203) are extremely abundant, and these may represent invertebrate feces.

Paleobiogeography.—The teeth of *Rhincodon* Smith, 1829 in the Chandler Bridge elasmobranch faunule represent the oldest record of this taxon, and the faunule also includes the first North American (western hemisphere) records of *Bythaelurus* Compagno, 1988 and *Dasyatis rugosa* (Probst, 1877). Although *Plinthicus* Cope, 1869 and *Sphyrna* Rafinesque, 1810 are known from the European Rupelian (Bor 1990; Génault 1993; Adnet et al. 2007), *P. stenodon* Cope, 1869 and *S. zygaena* (Linnaeus, 1758) are not known to occur until the Miocene (Leriche 1927; Cappetta 1970; Ward and Bonavia 2001). Comparison of the Chandler Bridge elasmobranchs to records from the German Chattian revealed a high degree of generic similarity between the two regions. Genera not reported from Germany include *Nebrius* Rüppel, 1837, *Rhincodon*, *Hemipristis* Agassiz, 1843, *Sphyrna*, *Paramobula* Pfiel, 1981, *Plinthicus*, and *Rhynchobatus* Müller and Henle, 1837, but hexanchoid, squaloid, and pristiophoroid sharks are present (Reinecke et al. 2005; Haye et al. 2008). Considering that both macroscopic and microscopic remains have been described in the reports cited above, we believe that these differences are related to environmental factors (not collecting bias).

Many of the Chandler Bridge species also occur in Germany. This may not be surprising considering that these include pelagic sharks like *Carcharias cuspidatus* (Agassiz, 1843), ?*Cetorhinus parvus* Leriche, 1908, *Physogaleus aduncus* (Agassiz, 1843), and *Alopias* cf. *A. vulpinus* (Bonnaterre, 1788), and extant representatives within these genera have circum-global distribution (Compagno et al. 2005). Teeth of *Carcharhinus gibbesi* (Woodward, 1889) are morphologically similar to *C. elongatus* (Leriche, 1910), and the two species likely occupied the same trophic niche. We only recovered a single complete tooth of *Carcharocles* Jordan and Hannibal, 1923. *Carcharocles angustidens* is the most widely reported taxon during the Oligocene (Yabumoto 1987; Baut and Génault 1999; Gottfried et al. 2001; Reinecke et al. 2005), and Chattian records of *C. subauriculatus* (Agassiz, 1839) from South Carolina (Purdy et al. 2001) would appear to be unique. However, teeth readily assignable to *C. angustidens* were recovered from the same stratum as our tooth (brought to our attention by Vance McCollum, personal communication 2008). We cannot discount the possibility that two coeval "mega-toothed" species inhabited the Oligocene Charleston Embayment, but we find this scenario unlikely and consider the prospect that the *C. angustidens*/*C. subauriculatus* morphologies represent a single species.

Paleoecology.—The Chandler Bridge elasmobranch assemblage is rather diverse and contains 29 taxa that inhabited a wide range of trophic niches. These niches include benthic predators (i.e., Myliobatidae, *Dasyatis*, *Rhynchobatus*, *Bythaelurus*), pelagic filter feeders (i.e., *Mobula*, *Rhincodon*, ?*Cetorhinus*), epipelagic predators of larger vertebrates (i.e., *Alopias*, *Carcharocles*), and pelagic/epibenthic carnivores (i.e., *Carcharhinus*, *Hemipristis*). Taxa of presumed benthic habits are nearly twice as numerous as those of presumed pelagic habit.

The nature of the collecting site and the patchy distribution of the Chandler Bridge Formation inhibit our ability to accurately determine the stratigraphic position of the fossiliferous deposit. However, the color, lithology, and general fossil content of the sediment are similar to the basal marine facies as described by Katuna et al. (1997). The occurrence of taxa like *Mobula*, *Rhincodon*, *Alopias*, and *Carcharocles*

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indicate open-ocean, normal salinity conditions, as opposed to bay/lagoon and fluvial/estuarine environments represented by other deposits within the formation (Sanders et al. 1982; Weems and Sanders 1986; Katuna et al. 1997).

The elasmobranchs and associated animal taxa we recovered provide a good indication of water temperature and the depth at which the Chandler Bridge deposit accumulated. *Leguminocythereis* aff. *L. copiosus* Butler, 1963, the most abundant ostracode in our sample (BCGM 9211), is indicative of relatively shallow water conditions (see also Elewa 2002). Miller (2000) stated that extant ostracodes that are closely related to extinct *Leguminocythereis* Howe, 1936 are most common in inner neritic environments. The corals we recovered appear to be *Flabellum* sp., and this genus has been identified in Oligocene strata that are believed to have been deposited in a neritic environment where water depth was between 40 and 120 m (Cape Roberts Science Team 2000; Stolarski and Taviani 2001). Of the foraminifera we collected, the most common genus is *Uvigerina* d'Orbigny, 1826 (BCGM 9226 and 9227), and Miller et al. (1999) considered *Uvigerina* biofacies to be characteristic of middle neritic (75+ m) depths. We occasionally observed glauconite grains (BCGM 9216) while sorting the screened concentrates, and modern sediments containing this material are found in current swept, open marine environments of the middle to outer shelf, with 200 m being the optimum depth for the formation of this mineral (Odin and Fullagar 1988).

Regarding the vertebrates, Purdy et al. (2001) reported *Aglyptorhynchus* from Miocene strata of North Carolina that formed in a warm-temperate to sub-tropical environment at a depth greater than 50 m, and the taxon has been reported from upper Oligocene strata of Oregon and Washington that were deposited at depths greater than 100 m and surface water temperature ranged from 20 to 24°C (Fierstine 2001, 2005). Extant *Rhincodon typus* (Smith, 1828) has circum-global distribution in tropical to warm-temperate environments (Compagno et al. 2005), preferring regions where surface temperatures are between 21 and 25°C (Compagno 1984). The occurrence of *Rhincodon* in the Chandler Bridge Formation is not necessarily an indication of coastal upwelling (Hazin et al. 2008). Species of *Mobula* inhabit tropical and sub-tropical waters (Notabartolo di Sciara 1987). Although extant *Alopias vulpinus* are found in tropical to cold-temperate seas and can occur far offshore at depths greater than 360 m, the species is most abundant in nearshore, temperate waters (Compagno et al. 2005). *Sphyrna zygaena* currently occupies coastal-pelagic and semi-oceanic habitats on continental and insular shelves (at least 20 m depth) in tropical and warm temperate zones (Compagno 1984; Southall and Sims 2005). This shark inhabits coastal waters of New York during the summer months, but individuals migrate southward once water temperatures drop below 19°C (Allen 1999). It has been suggested that the Charleston Embayment was used as a birthing area by *Carcharocles* (Purdy 1996; Purdy et al. 2001).

It is significant to note that taxa known to inhabit colder and/or deeper water (300+ m) are rare or absent altoghether from the Chandler Bridge elasmobranch assemblage. For instance, squaloid, pristiophoroid, and hexanchoid sharks, representatives of which have been documented in Oligocene strata of the northern Pacific (Welton 1979), the Albemarle (North Carolina) and Salisbury (Virginia) embayments (Case 1980; Müller 1999), and Europe (Steurbaut and Herman 1978; von der Hocht 1978a, b; van den Bosch 1980, 1981; Génault 1993; Baut and Génault 1999; Reinecke et al. 2001), and Oligo-Miocene deposits of New Zealand (Pfeil 1984). In the southern part of the North Sea Basin, foraminifera, ostracodes, and calcareous nannofossils indicate cold to cold-temperate conditions during the Rupelian (Van Semaeys et al. 2004; Van Semaeys and Vandenberghe 2006), and water depths reached 100 m during the lower part of this stage (De Man 2003). Occurrences of *Squalus alsaticus* (Andreae, 1892), often in very large numbers, in the European Rupelian may be an indication of coastal upwelling of cold water (Baut and Génault 1999). All extant species of *Bythaelurus* inhabit continental slope habitats where water depths are between 200 and 1000 m (Compagno et al. 2005), and this fact could explain the rarity of the genus in our sample (n = 1).

Although surface temperatures were between 14 and 19°C and inner shelf depth (~ 50 m) conditions had become established by the lower Chattian (De Man 2003; Van Semaeys et al. 2004), squaloid, pristiophoroid, and hexanchoid sharks persisted in the southern North Sea Basin (Reinecke et al. 2005; Haye et al. 2008). Further to the south, in the Mediterranean region, surface temperatures were slightly warmer, ranging from 19 to 20°C in the Rupelian and 19 to 21°C in the Chattian (Bosellini and Perrin 2008). Surface temperatures in the more southerly Charleston Embayment appear to have been between 20 and 25°C during the upper Chattian. Therefore, the absence of elasmobranchs like *Rhincodon*, *Hemipristis*, and *Sphyrna* from the German Chattian is likely a reflection of the colder water conditions existing in the North Sea Basin, whereas the absence of squaloids, pristiophoroids, and hexanchoids from the Chandler Bridge assemblage is a reflection of the warmer water conditions within the Charleston Embayment.

The locations within the Oligocene Albemarle and Salisbury embayments from which elasmobranchs are known to have been present are located approximately 400 km and 600 km (respectively) northeast of the Charleston Embayment locality. Species differences within these embayments reflect temporal, environmental and/or geographic separation. The strata exposed in these regions preserve a complex array of depositional environments that changed laterally (geographically) and vertically (temporally) within the embayments (see Rossbach and Carter 1991; Kier 1997; Katuna et al 1997). For example, elasmobranchs occurring within the lower part of the River Bend Formation (Rupelian, NP 21–NP 22) of North Carolina lived in a sub-tropical, inner neritic (10–20 m), open marine environment on the seaward side of a lagoonal or barrier island complex, whereas the upper part of the formation (Chattian, NP 25, equivalent to the Ashley or Chandler Bridge Formation) inhabited cooler wa-

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ter in the vicinity of barrier islands, backwater lagoons, and migrating inlets (Rossbach and Carter 1991). The mixture of tropical and cool-water mollusks in the Old Church Formation (Virginia, correlative to the Ashley Formation) indicate coastal upwelling of cold water adjacent to the Salisbury Embayment (Ward, 1992), and this could explain the occurrence of squaloid, pristiophoroid, and hexanchoid sharks (Müller, 1999) along with taxa also occurring in the Chandler Bridge Formation.

Conclusions

The Oligocene Epoch represents a time in earth history during which major climatic and oceanographic changes occurred. Deep-water temperatures show strong short-term fluctuations within a gradual climatic cooling trend (Miller et al. 1999; Van Simaeys et al. 2005; Pekar et al. 2006). Episodes of cooling and warming affected the expansion or retreat of polar ice sheets, which in turn affected global sea level fall/rise, and the strata deposited within the Oligocene Charleston (South Carolina), Albemarle (North Carolina), and Salisbury (Virginia) embayments preserve these environmental perturbations (Rossbach and Carter 1991; Ward, 1992; Katuna et al. 1997; Harris et al. 2000). Oligocene global temperatures rose to their highest levels during the upper Chattian (late Oligocene warming event of De Man and Van Simaeys 2004; late Oligocene climatic optimum of Flower and Chisholm 2006), and strata of the Chandler Bridge Formation accumulated during that time. The fossils we recovered during our study show that deposition of the fossiliferous deposit took place in a shallow inner to middle neritic environment where surface water temperatures were between 20 and 25°C.

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