Late Oligocene Sharks and Rays from the Chandler Bridge Formation, Dorchester County, South Carolina, USA

Authors: Cicimurri, David J., and Knight, James L.

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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

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.

David J. Cicimurri [dcheech@clemson.edu], Campbell Geology Museum, 140 Discovery Lane, Clemson, South Carolina 29634, USA;
James L. Knight [jim.knight@scmuseum.org], South Carolina State Museum, 301 Gervais Street, Columbia, South Carolina, 29202, USA.

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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 occur (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 lagoon environment. Bed 2 was thought to have formed in either an open shelf environment below wave
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 correlatable 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

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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).

**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.
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; Pfie1 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 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 Linnaeus, 1758, Recent, “European Seas”.

Squatina cf. S. angeloides van Beneden, 1873

Refereed specimens.—BCGM 9042 and 9043.

Comments.—Kent (1994) reported Squalus 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)

Refereed 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.
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:* *Rhincodon 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, 1938

Genus *Alopias* Rafinesque, 1810

*Type species:* *Alopias vulpinus* (Bonnet, 1788)

*Alopias* cf. *A. vulpinus* (Bonnet, 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 1993). 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

(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 1986), and other fossils reportedly from “Ashley phosphate beds” are definitively of Pleistocene age (Sanders 1986). Yabumoto and Uyeno (1994) assigned the *Nebrius* material reported by Müller (1999), is closer to the *N. serra* 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

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. delfortriei* 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
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 subseratata 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).
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 Carchariniformes 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-bato-morph 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). Oligocene C. gilmorei have variously been referred to in the literature as Sphyra 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 palatoquadrate (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-
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
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.

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 Sphyraena and even Physogaleus. Teeth of all of these taxa can have highly concave mesial cutting edges, as is the case with our specimen. Our specimens lack cusplets as seen on the distal blade of Physogaleus. Teeth of Sphyraena 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)

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) represent 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 morphological and histological differences with extant H. elongata (Kunzinger, 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: Scyliorhinus caniculus Springer, 1940

Bythaelurus sp.

Referred specimen.—BCGM 9074.
Comments.—Unfortunately, comparing this specimen to known scyliorhinid species is difficult because most of the root structure is 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 albigenis 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 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. caniculus
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 *Sphyrna*.

*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, Virginia, Maryland) and Europe.

*Family Triakidae Gray, 1851*

*Genus Galeorhinus* Blainville, 1816

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

*Galeorhinus* sp.

*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, Virginia, Maryland) and Europe.

*Family Rajidae Bonaparte, 1831*

*Genus Raja* Linneaus, 1758

*Type species:* *Raja batis* Linneaus, 1758, Recent, “European Seas”.

*Galeorhinus* sp.
Raja mccollumi sp. nov.

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 lateral 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 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...
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 mccoollumi* 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.
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)

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.

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). Additionally, 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).
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. eregodooodtenke (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 Pfeil, 1981 (see Case 1980: pl. 10: 2a–e). The former speci-
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 (Chat-tian), 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 api-co-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 polyaulacorhiz (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 Plithicus (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 ascertain if they are conspecific. Notabartolo di Sciarra (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 molubid 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 oligoecaera Leriche, 1910 from the French Rupelian (Baut and Génault 1999: pl. 7: 2, 4), and these remains may be conspecific. Myliobatis oligoecaera has been tentatively synonymized with Weissobatis micklichi Hovestadt and Hove-stadt-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. oligoecaera 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
ward and curve upward (Fig. 6E, F), the occlusal surface (Bor 1990). In contrast, the Chandler Bridge teeth slope in−
consists of anastomosing longitudinal ridges and grooves
the occlusal surface is flat, and the enameloid ornamentation
Cappetta 1987).

Cuvier, 1829 than

within the dentition was more similar to

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 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 re−

pects, the Chandler Bridge teeth are quite similar to Rhino−
ptera 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 For−
mation of North Carolina was identified as Rhinoptera aff. R. bonasus Mitchell, 1815 by Müller (1999: pl. 15: 7), but it
does not appear to be different than a tooth of R. studeri illus−
trated by Leriche (1927: pl. 6: 3). Other teeth from the Bel−
grade Formation were identified as Rhinoptera aff. R. brasi−
lienisi 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 pres−
ent during deposition of the Belgrade Formation. The North
Carolina and Chandler Bridge specimens appear to be con−
specific, but a larger sample is needed to make a more accu−
rate determination. Rhinoptera may have been more wide−
spread 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 attri−
butes as Chandler Bridge teeth we refer to Rhinoptera.

Stratigraphic and geographic range.—?Oligocene (Chat−
tian), 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 faunula. We re−
covered a variety of other elasmobranch remains from the
fossiliferous deposit, including individual and small aggre−
gates of calcified cartilage tesserae (BCGM 9132), and der−
mal denticles. Cartilage tesserae measure approximately 1
mm in diameter and less than 2 mm in thickness, and are
roughly cylindrical in shape with tuberculate vertical sur−
faces. 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 Dasylatis
Rafinesque, 1810 because of the similarity to denticles of ex−
tant D. centoura (Mitchill, 1815). Some denticles bear a
dorsoboventrally 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 be−
cause they are similar to ventral denticles of Mobula japon−
ica (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

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 premaxilar 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 pelucyopods (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), bryozoan (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 fauna 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 *Pliniticus* Cope, 1869 and *Sphyra* 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, *Sphyra*, *Parambula* Pfiel, 1981, *Pliniticus*, 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), *C. taurus* Leriche, 1908, *Physogaleus aduncus* (Agassiz, 1843), and *Alopias* cf. *A. vulpinus* (Bonnaterre, 1778), 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. subbarraculatus* (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. subbarraculatus* 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*...
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 *A glyptorhynchus* 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 (Notartolato 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). *Sphyraena 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 altogether 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 Semaey et al. 2004; Van Semaey and Vandenbergh 2006), and water depths reached 100 m during the lower part of this stage (De Man 2003). Occurrences of *Squalus alsatica* (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 Semaey 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 *Sphyraena* 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-

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 Simaëys 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 Simaëys 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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