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Two Shark-bitten Whale Skeletons from Coastal Plain Deposits of South Carolina

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Abstract - Two partial skeletons of baleen whales have been recovered from Coastal Plain deposits of South Carolina. One specimen, from the lower Pliocene Goose Creek Limestone, consists of a partial skull (including mandibles) and some incomplete ribs; the other was collected from Pleistocene–Holocene mud and includes numerous post-cranial elements in addition to fragmentary premaxillae and maxillae. These whale skeletons preserve compelling fossil/sub-fossil evidence, in the form of bite marks and shed/embedded teeth, that the elasmobranchs *Galeocerdo cuvier*, *Carcharhinus falciformis*, *C. longimanus*, *C. obscurus*, and *C. plumbeus* fed on cetacean carcasses.

Introduction

Although prey preferences of recent galeomorph sharks are generally well known (see Compagno 1984), published reports on prehistoric records of predation/scavenging by sharks on other vertebrates are limited. Many of these accounts have dealt with Cretaceous remains from North America, where the extinct shark genera *Cretoxyrhina* Agassiz (ginsu sharks) and *Squalicorax* Whitley (crow sharks) have been identified as primary consumers of large vertebrates, including mosasaurs, plesiosaurs, chelonioids, fishes, and dinosaurs (Everhart 1999, 2004; Everhart and Hamm 2005; Rothschild et al. 2005; Schwimmer 2004; Schwimmer et al. 1997; Shimada and Everhart 2004; Shimada and Hooks 2004). In addition to bite marks and shed teeth of *Squalicorax*, Dortangs et al. (2002) also reported teeth of *Plicatoscyllium* Case and Cappetta (extinct nurse shark) with a mosasaur skeleton from the Cretaceous of The Netherlands. Teeth associated with partial skeletons may provide indirect evidence that hybodont sharks consumed plesiosaurs (Cicimurri 2000, Wahl 2005).

Accounts for the Cenozoic are more limited, but include records of shark predation/scavenging on a pinniped by *Squalus* (Bigelow 1994), dolphin by *Carcharodon* (Cigala-Fulgosi 1990), mysticete whale by *Carcharodon* (Deméré and Cerutti 1982), and a desmostylian (Repenning and Packard 1990). Applegate (1965) reported a Miocene record of *Galeocerdo aduncus* Gibbes, previously considered an extinct Tiger Shark (= *Physogaleus aduncus* [Ward and Bonavia 2001]), with a concretion containing chelonioid bones. These records provide important paleobiological information regarding selachian usage of large vertebrate animals as food sources.

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Two partial skeletons of mysticete whales in the South Carolina State Museum (SC) have been recovered from Coastal Plain deposits of South Carolina. Both specimens exhibit shark bites to various bones, shed teeth of *Galeocerdo cuvier* Péron and Lesueur (Tiger Shark) and *Carcharhinus* sp. Blainville (requiem sharks) are associated with each, and several *Carcharhinus* sp. tooth fragments are also embedded in bones of SC 91.83. SC 91.83 was collected from mud along the shore of Port Royal Sound near Laurel Bay, Beaufort County (Fig. 1). The other specimen, SC 79.65, was recovered by divers from the Goose Creek Limestone exposed at the bottom of the Cooper River, near Charleston, Charleston County. More precise geographic information is not available for this specimen, and only a limited number of bones and surrounding matrix were recovered.

SC 79.65 and SC 91.83 are important because they preserve fossil evidence (shed teeth, bite marks, and embedded teeth) that Tiger Sharks, *Carcharhinus obscurus* (Lesueur) (Dusky Shark), *C. plumbeus* Nardo (Sandbar Shark), *C. longimanus* Poey (Oceanic Whitetip Shark), and *C. falciformis* Müller and Henle (Silky Shark) consumed carcasses of large cetaceans. The purpose of this report is to discuss the morphology of the bites and illustrate some of the more informative cuts. We have also utilized the

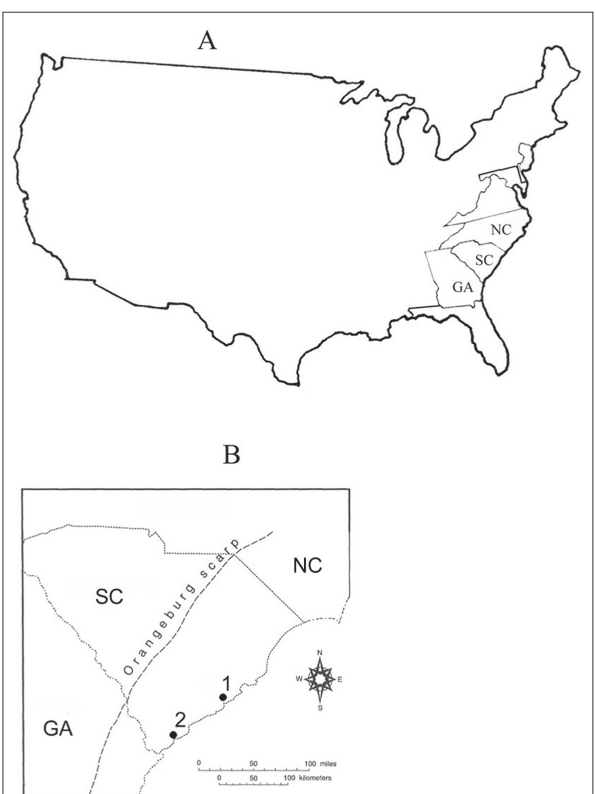

Figure 1. A. Geographic map showing outline of the contiguous United States and locations of some southeastern Atlantic Coastal states. B. Map of South Carolina showing maximum Pliocene sea level rise onto the state (Orangeburg Scarp). Abbreviations: GA = Georgia, NC = North Carolina, and SC = South Carolina. Closed circles in B indicate locations of the specimens discussed in the text: 1 = SC 79.65 and 2 = SC 91.83. A is modified from Case (1980), while B is adapted from Clandenin et al. (1999).

elasmobranch species (shed teeth) to formulate paleoecological interpretations for both cetacean occurrences.

Description of the Bite Marks

In addition to several ribs, SC 79.65 consists of a partial cranium, including the posterior portion of the skull, disarticulated right and left maxillae and petrosals, and right and left dentaries. Shark bite marks are preserved on several bones, including the distal ends of two ribs, the distal end of the left dentary, and most notably, the lateral edges of the right and left maxillae.

Many of the bite marks consist of isolated elongate (up to 4 cm), nearly straight grooves having V-shaped cross sections. The sides of the grooves may be the same height, indicating a tooth cut across the bone perpendicular to its surface. Other grooves have one side broader than the other, suggesting a low-angle cut as the tooth moved across the bone. Some grooves are wider at one end, indicating the direction in which a tooth punctured and then cut across the bone. These types of cuts are consistent with those described by Cigala-Fulgosi (1990), and several are preserved at the distal ends of ribs and the distal end of the left dentary of SC 79.65. In addition to the cut marks described above, one rib also exhibits two closely spaced deep cuts, as well as evidence of repeated bites where a series of short cuts are located. Small wedges of bone are missing, apparently removed as the teeth cut into the bone.

The most intriguing bite marks consist of parabolic arcs preserved on the dorsal and ventral surfaces of the right and left maxillae (Fig. 2A–B, G–H). Up to 10 rows of cuts are preserved on each side of the parabola, with the longest measuring approximately 10 cm in length. Individual cuts are arcuate, closely spaced, and parallel to each other. Some of the cuts are up to 11 mm deep (especially at the very edges of the bones), and it is obvious that bone was cut away from the outer margins of both maxillae (see esp. Fig. 2A).

SC 91.83 consists of the anteriormost 30 cm of the right and left premaxillae, anterior 39 cm of the left maxilla, partial right and left dentaries, nearly complete right forelimb, incomplete left forelimb, partial left scapula, lumbar and caudal vertebrae, some haemal arches, and numerous partial ribs. Most of the marks observed on the bones are considered to represent shark bites, but some shallow oval depressions (primarily on ribs) are interpreted as Holocene mollusk borings.

Three closely spaced cuts, oblique to the long axis of the bone and up to 40 mm long, are located on the ventromedial surface of the left premaxilla of SC 91.83. There are numerous bites to the ventromedial surface of the posterior half of the preserved left maxilla. The cuts are up to 1 mm deep and 30 mm long. There is a deep cut on the ventral margin located 26.5 cm from the anterior tip of the bone. Cuts on the inner surface of this bone are similar to those seen on the transverse processes of lumbar vertebrae (see below).

The right forelimb of SC 91.83 (Fig. 3A) is complete except for distal phalanges. No indisputable cuts were observed on the humerus or the inner

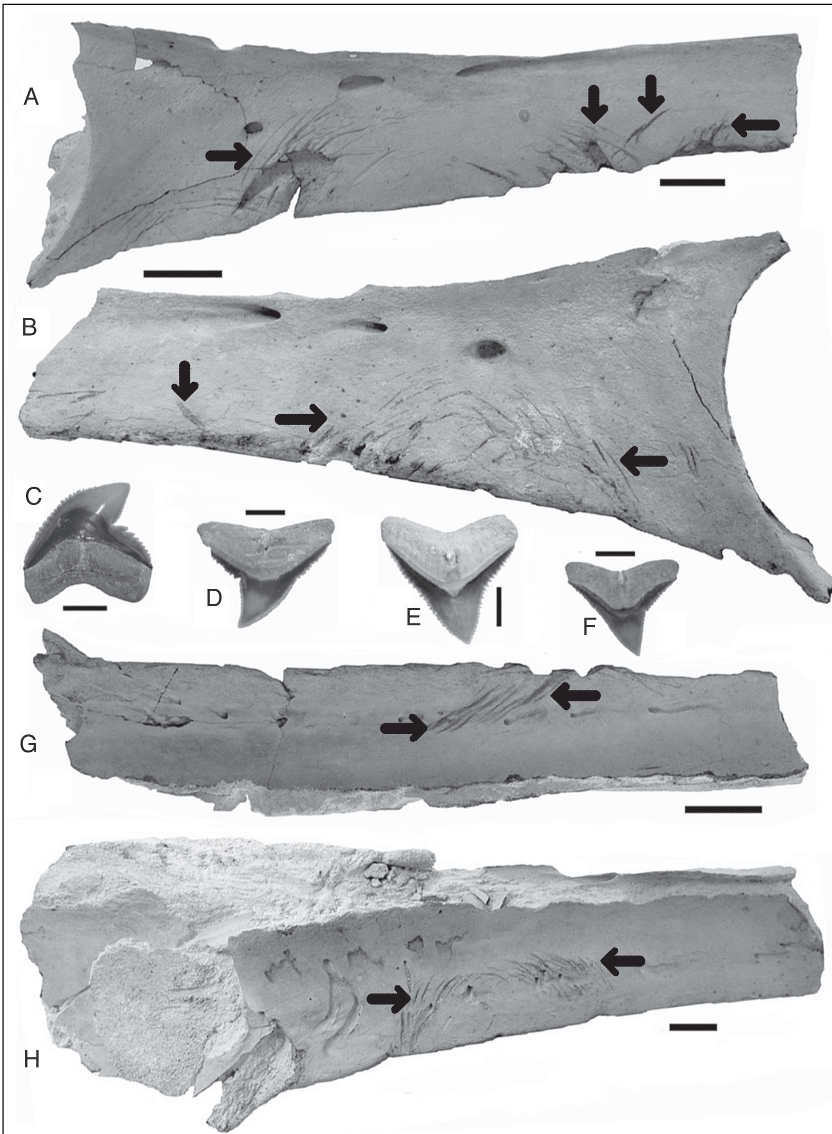

Figure 2. SC 79.65 (Goose Creek Limestone cetacean). A–B and G–H are photographs of the right and left maxillae showing bite marks to medial portions of outer margins of dorsal and ventral surfaces. A and G show right maxilla in dorsal and ventral views, respectively. B and H show left maxilla in dorsal and ventral views, respectively. C–F are lingual views of associated shark teeth: C = SC 79.65.9, Tiger Shark; D = SC 79.65.14, Silky Shark; E = SC 79.65.11, Oceanic Whitetip Shark; and F = SC 79.65.8, Sandbar Shark. Scale bars = 5 cm in A–B and G–H, 1 cm in C, and 5 mm in D–F. Image in G is slightly oblique from the inner margin. Outer margin of maxilla is at bottom in A, B, and H, and at top in G. Anterior is at right in A, G, and H, and at left in B. Arrows indicate locations of bite marks.

surfaces of the radius/ulna. At least seven cuts are preserved on the outer surface of the radius near its anterior margin, and an equal number of cuts are located on the outer surface of the ulna near its posterior margin (Fig. 3D). The cuts on both bones are up to 30 mm long and sub-perpendicular to the lengths of their shafts, although those on the ulna are relatively shallow (less than 1 mm) and those on the radius are up to 3 mm deep. The cuts on the ulna are located 10 cm from its distal articulation, and those on the radius are situated 13 cm from

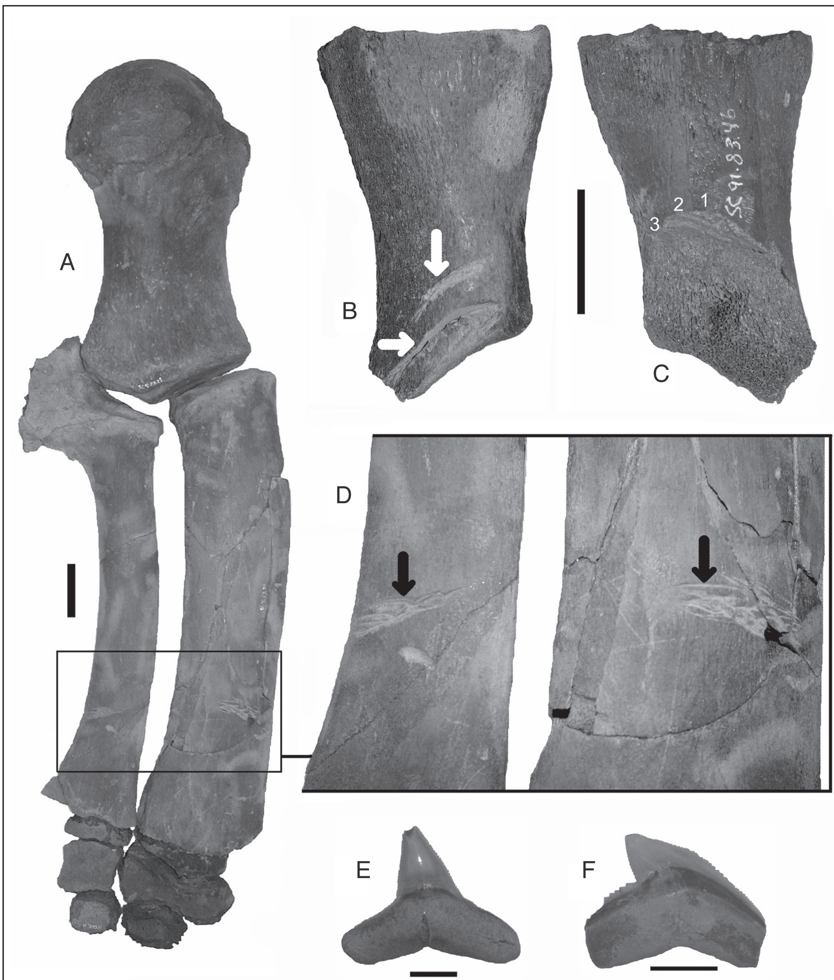

Figure 3. SC 91.83 (Laurel Bay cetacean). A–D show bite marks on various bones. A presents the outer view of right forelimb, while B and C present the outer and inner views, respectively, of carpal showing bite marks at distal end. D is a magnified view of the area within rectangle of A showing bites to radius and ulna. E–F are lingual views of associated shark teeth: E = Dusky Shark and F = Tiger Shark. Scale bars = 2.5 cm in A–C, 1 cm in E–F. In C, note the history of the cut made as a tooth sawed through the bone (indicated by 1, 2, 3). Arrows indicate locations of bite marks.

its distal articulation (Fig. 3A). The carpals are intact and bear no cuts, but the distal ends of medial phalanges are missing. The remaining portions of the phalanges preserve cuts to their inner and outer surfaces, with many penetrating completely through 4 mm of cortical bone (Fig. 3B and C).

The left forelimb of SC 91.83 (Fig. 4A) was also bitten, and there is a single 25-mm long cut to the outer surface of the left humerus, near the ulnar facet. At least 11 deep cuts are located on the neck of the olecranon process of the ulna (Fig. 4B). The cuts are sub-parallel to the humeral facet, up to 25 mm long, and some are over 2 mm in depth. The surface of each cut closer to the humeral facet is much broader than the opposite side, indicating oblique

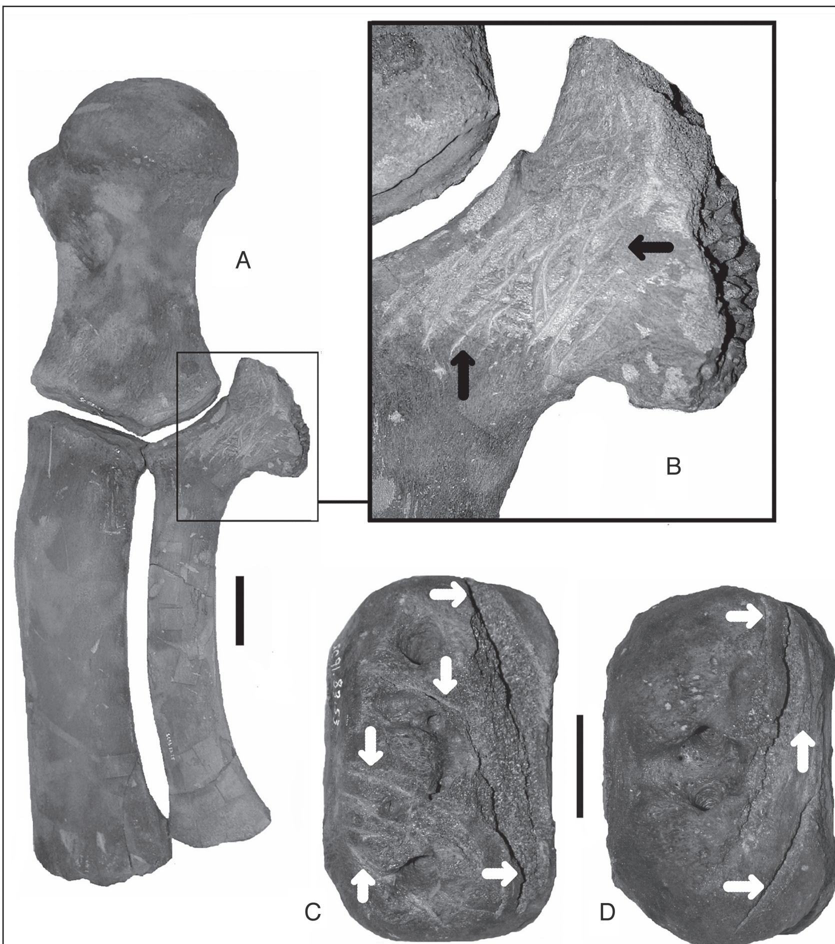

Figure 4. SC 91.83 (Laurel Bay cetacean). A–D show bite marks on various bones. A presents the outer view of left forelimb. B presents a magnified view of area within rectangle of A showing shark bites to olecranon process of ulna. C and D show dorsal and ventral views, respectively, of distal caudal vertebra. Cranial is at right in C and D. Scale bars = 2.5 cm. Arrows indicate locations of bite marks.

tooth impact with bone, and the broad surfaces often preserve wide parallel striae made by a coarsely serrated tooth. At least two cuts are located on the inner surface of the ulna at the epiphyseal margin of the olecranon process. Only the first carpal, which articulates primarily with the radius, is preserved in its entirety. The succeeding carpal is actually composed of two fused carpals (reflecting a previous pathologic condition?), and only its proximal portion is preserved. Two long (30 mm as preserved) and deep (6 mm) cuts are on the bone's outer surface near the articular facet for the preceding carpal. No other carpals or phalanges were recovered.

Seventeen lumbar vertebrae and eight caudal vertebrae are also part of SC 91.83. Bite marks are most abundant on the lumbar vertebrae, especially on the dorsal surfaces of the right and left transverse processes (Fig. 5A), but are much less common on the ventral surfaces of transverse processes and

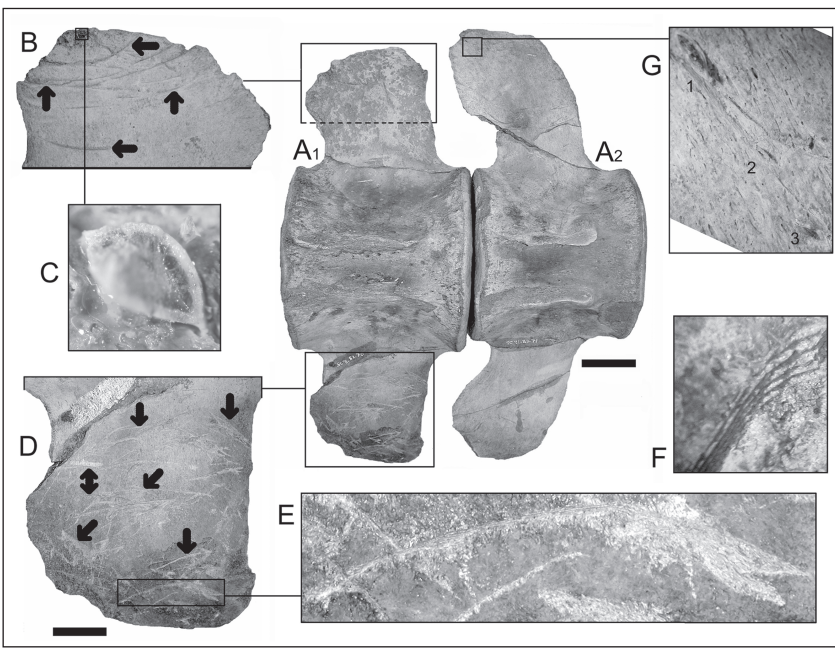

Figure 5. SC 91.83 (Laurel Bay cetacean). A–G are various views of two articulated lumbar vertebrae showing bite marks and embedded shark teeth. A (A_1 and A_2) shows dorsal view of the vertebrae (cranial at right); B is a magnified view of the ventral surface of area in rectangle of left transverse process of A1 showing cut marks and location of embedded shark tooth. C is a magnified view of area within square of B showing cross-sectional morphology of tooth tip (lower tooth - flatter labial face is at lower left). D is a magnified view of dorsal surface of right transverse process of A_1 showing bite marks. E is a magnified view of bite mark within rectangle of D. F is a magnified view of a portion of the cut shown in E. G is a magnified view in area within square of left transverse process of A_2 showing tips of three shark teeth (upper teeth - labial faces at lower left). Scale bars = 2.5 cm in A and D, 1 cm in G, 5 mm in B, and 1 mm in C and E. Arrows indicate locations of bite marks.

neural spines. The cuts to the transverse processes are straight to arcuate, up to 55 mm long and 1 mm deep (Fig. 5B and D). Small slivers of bone were removed at the edges of the processes or from areas where cuts are closely spaced. The side of the cut closer to the neural spine is broad and bears parallel striae (Fig. 5E and F). Its opposite edge is curled upwards and the fibrous bone texture distorted.

Short, shallow cuts are located on neural arches and transverse processes of most of the medially located caudal vertebrae. Two distal caudal vertebrae are heavily damaged, and one bears two massive cuts to the anterodorsal surface. The cuts are arcuate, approximately 6.5 cm long and nearly 1 cm deep, and bone has been sliced off from this region (Fig. 4C). A large portion of bone is also missing from the anteroventral part of the centrum, where two deep cuts span the width of the bone (Fig. 4D). These cuts are up to 7.5 cm long and 1.5 cm deep. At least five shallower cuts up to 3.6 cm long intersect the deeper ones. Only the ventral 25% of the second caudal vertebra (likely the succeeding centrum) is preserved, and deep cuts are on the outer surface.

The ribs of SC 91.83 were purposely and extensively damaged by a local resident, but up to 60 cm of the distal ends of several ribs were reconstructed. Cuts are generally short and shallow, oblique to the long axis of the bone, and one edge of the groove curls upwards, as described above on lumbar vertebrae. Small areas exhibit numerous parallel rows of striae that formed when the serated cutting edge of a tooth scraped across the bone.

Paleobiological Implications

The teeth of four shark species, Tiger Shark (Fig. 2C), Silky Shark (Fig. 2D), Oceanic Whitetip Shark (Fig. 2E), and Sandbar Shark (Fig. 2F), were found in the matrix recovered with SC 79.65. The teeth of six elasmobranch species, including Tiger Shark, Dusky Shark, *Rhizoprionodon* cf. *R. terraenovae* Richardson (Sharpnose Shark), *Rhinoptera* cf. *R. bonasus* Mitchill (Cownose Ray), *Rhinobatos* cf. *R. lentiginosus* Garman (Guitarfish), and "*Raja*" (skate) were found in matrix collected with SC 91.83. That teeth of multiple elasmobranch species were associated with SC 79.65 and SC 91.83 does not necessarily mean they were all shed as carcasses were eaten. Esperante et al. (2008) reported shed shark teeth associated with articulated whale skeletons, but no bite marks were observed on bones. This observation could indicate that the shed teeth were already on the sea floor when the carcasses came to rest, or became incorporated into the substrate after the carcass was reduced to bones. Cut marks on the bones of SC 79.65 and SC 91.83 leads us to the conclusion that at least some of the associated shark teeth were shed as sharks fed on the whale's flesh. None of the bite marks on SC 79.65 and SC 91.83 show signs of healing, and it is impossible to tell if the whales were already dead (scavenged) or killed and eaten (direct predation). In life, the right dentary of SC 91.83 was broken, and although there is a significant amount of bone remodeling, the two parts were not knitting together and remained as separate elements. We believe that this trauma hampered the ability of the whale to feed and contributed to its death.

Tiger Shark teeth bear very large, compound serrations and are capable of cutting through the shells of large chelonioids (Witzell 1987), and we believe that the widest, deepest cut marks on the bones of SC 79.65 (i.e., right maxilla) and SC 91.83 (i.e., left humerus and phalanges, caudal vertebrae) can be attributed to this taxon. The bites to the right maxilla of SC 79.65 (Fig. 2B) indicate a 42-cm bite width, which compares favorably to the estimated gape of SC 2000.120.10, the jaws of a 300-kg female Tiger Shark. The dimensions of the associated teeth, SC 79.65.9 and .10, are also identical to those in corresponding positions on SC 2000.120.10. In the case of SC 91.83, the forelimbs would have been easily accessible to Tiger Sharks, and the left elbow, which is near where the flipper emanates from the body, is heavily damaged. Cuts on the left scapular spine indicate that enough muscle was eventually removed to allow that bone to be exposed to a shark's teeth. The substantial trauma to the distal caudal vertebrae shows that the tail was also targeted.

The bite on the left maxilla of SC 79.65 measures approximately 10 cm across and represents a different individual (Fig. 2H) than the one that bit into the right maxilla. The size of this bite indicates a smaller shark or one with a narrower mouth, but we cannot be sure if an Oceanic Whitetip, Silky, Sandbar, or even a younger Tiger Shark was responsible. It is interesting to note that the cuts on lumbar vertebrae of SC 91.83 are much finer than those on the limb bones and caudal vertebrae. Five tooth tips embedded in the transverse processes of three lumbar vertebrae, as well as a single shed lower tooth (Fig. 2 C), are attributed to a Dusky Shark. Dusky Sharks exhibit dignathic heterodonty, the upper teeth being broadly triangular but labio-lingually thin, and lower teeth bearing a narrow cusp flanked by low shoulders. The cross sections of three tooth tips in the dorsal surface of a lumbar vertebra's left transverse process (SC 91.83.70) indicate these are from the upper dentition (Fig. 5G), whereas a tooth tip in the ventral surface of another transverse process (SC 91.83.65) is from the lower jaw (Fig. 5C). Long arcuate cuts formed as Dusky Shark teeth impacted bone and were drawn across surfaces, and teeth occasionally broke at the end of a cut. Small slivers of bone were also sliced away from the edges of some transverse processes (Fig. 5B).

SC 79.65 and SC 91.83 provide compelling fossil/sub-fossil evidence, in the form of shed teeth, bite marks, and teeth embedded in bones, that Tiger Sharks and Dusky Sharks fed on mysticete cetaceans. Whereas Tiger Sharks feed on a wide range of marine organisms, including cetaceans (Compagno 1984), the dietary preferences of Dusky Sharks are incompletely known, but include a variety of invertebrates and fish (Bass et al. 1973, Gelsleichter et al. 1999). Oceanic Whitetip and Sandbar Sharks also consume cetacean carcasses (Compagno 1984, Stillwell and Kohler 1993), and shed teeth associated with SC 79.65 (i.e., SC 79.65.11 and SC 79.65.8) provide circumstantial evidence of this feeding behavior. Atlantic Sharpnose Sharks feed primarily on small teleosts and crustaceans (Gelsleichter et al. 1999), but marine mammal remains have not been reported as gut contents. In the case of SC 91.83, perhaps Sharpnose Sharks, Guitarfish, Cownose Ray, and skates were drawn to the area to feed on scraps torn from the whale carcass by Tiger and Dusky Sharks.

Paleoecological Implications

The Goose Creek Limestone was deposited during the lower Pliocene and, based on calcareous nannofossils, is no younger than zone NN 15 of the uppermost Zanclean Stage (i.e., older than 3.6 Ma; Edwards et al. 2000, Weems et al. 1982). The shed Tiger, Oceanic Whitetip, Silky, and Sandbar Shark teeth associated with SC 79.65 shows that these species have inhabited South Carolina waters for at least the last 3.5 million years. The optimum preferred water temperature for Oceanic Whitetip, Silky, and Sandbar Sharks is between 23 and 28 °C (73 to 82 °F; Compagno 1984), and the latter two taxa, along with Tiger Sharks, venture into shallow South Carolina coastal waters during the late spring and summer months (Farmer 2004). These data suggest that water temperatures were comparable at the time the whale carcass was scavenged, and molluskan taxa occurring in the Goose Creek Limestone suggest water depths between 50 and 100 m (Campbell and Campbell 1995).

We cannot ascertain the stratigraphic position of SC 91.83 because of the nature of the exposure, and associated mollusks include taxa currently inhabiting the area. Although all of the whale bones and associated shark teeth are discolored through mineral infiltration, a precise age cannot be determined, and the bones could be hundreds to hundreds of thousands of years old. The shed shark teeth represent Tiger, Dusky, and Sharpnose sharks. Dusky Sharks enter shallow South Carolina coastal waters during the summer months, and Atlantic Sharpnose Sharks are the most abundant coastal shark from April through September, when water temperatures are between 9 and 29 °C (48 to 84 °F; Compagno 1984, Farmer 2004). Regardless of the age of the deposit, similar environmental conditions (i.e., water temperature, salinity) existed at the time the whale died.

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