SHARK-BITTEN PROTOSTEGID TURTLES FROM THE UPPER CRETACEOUS MOOREVILLE CHALK, ALABAMA

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INTRODUCTION

PROTOSTEGIDS ARE Cretaceous marine turtles. Fossil materials assignable to the family Protostegidae range from early Albian to Late Campanian in age and have been described from all continents except Antarctica (Hirayama, 1995). The group includes two gigantic forms, *Archelon* Wieland and *Protostega* Cope, that reached maximum carapace lengths in excess of 2 m and rank among the largest turtles that ever lived.

In this paper, we describe two specimens of *Protostega gigas* Cope housed in the Field Museum of Natural History (FMNH), Chicago, Illinois: FMNH P27452 and FMNH PR58. Both are from the Mooreville Chalk (Upper Santonian to Lower Campanian: Mancini et al., 1995) in Greene County, Alabama, and are noteworthy because they show tooth marks from at least one large shark. One of the specimens also exhibits five embedded teeth of the Late Cretaceous cretoxyrhinid shark *Cretoxyrhina mantelli* (Agassiz). This note constitutes the first report of protostegid turtles bitten by *C. mantelli*.

SPECIMEN DESCRIPTIONS

FMNH P27452.—The specimen consists of disarticulated bones of a partial skeleton. Two bones that exhibit evidence for shark biting are considered here: a nearly complete left humerus (Figs. 1.1, 2.1; also illustrated in Zangerl, 1953, fig. 49) and a left hyoplastron (Figs. 1.3, 2.2).

The head of the left humerus is largely missing, but the estimated length of the bone is 29.5 cm. On both dorsal and ventral surfaces, many curved grooves are present, and they are interpreted to be tooth marks of one or more sharks. Tooth marks are concentrated near the radial process region, but several of them, two of which are markedly deep and wide, are also present at the distal end of the bone. The depth of tooth marks ranges up to 9 mm, and the widest scrape measures 15 mm. Tooth marks lack serration grooves (note: a few tooth marks show more or less parallel stepwise "grooves," but the stepwise pattern is interpreted to be the result of a cut through concentrically deposited, cortical bony tissue at the shaft of the bone). Occurring along a few grooves on the ventral side are the tips of five broken teeth lodged into the bone (Figs. 1.1, 1.2, 2.1). All the tooth remains are fragmentary, but at least two of them (Fig. 1.2) are characterized by a dentine-filled, labiolingually thick crown, which has smooth labial and lingual surfaces without serrations on the cutting edge. The exact size of the teeth cannot be determined due to their fragmentary nature. However, the teeth are identified as those of *Cretoxyrhina mantelli* based on the observed dental characteristics (e.g., see Welton and Farish, 1993; Shimada, 1997a; Fig. 3.1, 3.2) combined with the fact that *C. mantelli* is one of the shark taxa known from the Mooreville Chalk of Alabama (for specimens from Greene County, see Applegate, 1970; for a summary of elasmobranch taxa, see Russell, 1988). Whether the five embedded teeth and the tooth marks are from one or multiple individuals cannot be ascertained.

The left hyoplastron measures 35 cm in length and 27 cm in width. It is a dome-shaped bone with a maximum thickness of about 26.5 mm. At the posterior half of the ventral surface are many gently arched grooves, which are also interpreted to be tooth marks of *Cretoxyrhina mantelli*. The depth of tooth marks measures up to 1.5 mm, and the cut surface lacks serration grooves. No tooth marks are found on the dorsal surface.

FMNH PR58.—The specimen consists of three peripheral bones. Two of the three bones show multiple grooves on their dorsal and ventral surfaces, which are up to 4 mm in depth. The characteristics of the grooves are identical to those on FMNH P27452 and thus tentatively identified as the bite marks of *Cretoxyrhina mantelli*. The exact position of each peripheral to one another is not certain due to damage along the articular edges. However, because the dorsal and ventral surfaces meet at angles of 65–70 degrees along their lateral edges, and because a depression for rib attachment is present on each bone, they probably represent fifth and sixth, or sixth and seventh, peripherals.

DISCUSSION

The two specimens noted here were initially described and referred to as *Protostega dixie* by Zangerl (1953). However, a recent osteological review (Hooks, 1998) suggests that *P. dixie* is a junior synonym of *P. gigas*. This taxonomic interpretation is followed in this paper.

The paleobiology of *Protostega gigas*, along with its sister taxon *Archelon ischyros* Wieland (Hooks, 1998), remains poorly understood, due primarily to the scarcity of comparative materials. Nevertheless, some general observations on *Protostega* give clues as to how it lived. The bones of the carapace and plastron are reduced, producing numerous fontanelles between the bones and reducing the weight of the shell. The limbs are modified to form large, relatively rigid paddles. The forelimbs are larger than the hind limbs and designed to move in a subaqueous flying motion typical of that used by modern marine turtles. *Protostega* also possesses relatively large eyes and large interorbital foramina. Such structures indicate the presence of large lachrymal glands, which are used by modern marine turtles and other marine reptiles for removal of salt (Hirayama, 1998). These characteristics are strong indicators that, while *Protostega* may have spent time in shallow bays or other nearshore environments, it was fully adapted for life in the open ocean. This interpretation is supported by the relatively common occurrence of *Protostega* in marine shelf deposits such as chalks (Hooks, personal observation).

The size of FMNH P27452 and PR58 are difficult to assess due to the fragmentary nature of the specimens. This is especially true of FMNH PR58. However, comparison of these specimens with relatively complete, reconstructed *Protostega gigas* specimens at the United States National Museum of Natural History (USNM 11651), Washington, D.C., and the Denver Museum of Natural History (DMNH 1663), Denver, Colorado, suggest that both FMNH P27452 and PR58 were small, probably juvenile, individuals with a carapace length of approximately 105 cm.
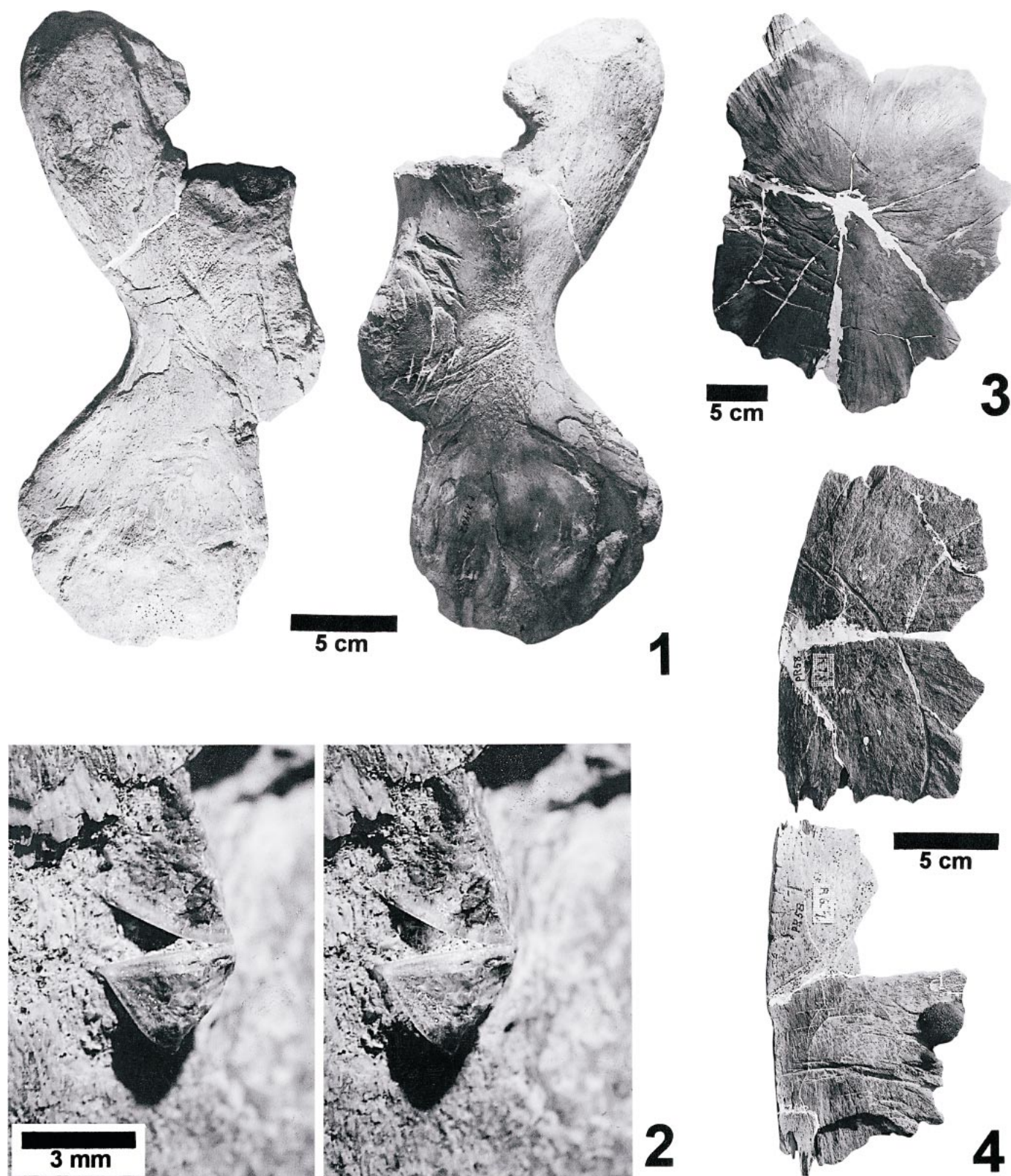
FIGURE 1—Photographs of two specimens of *Protostega gigas* with embedded *Cretoxyrhina mantelli* teeth and/or tooth marks from the Mooreville Chalk, Greene County, Alabama. *1,* Ventral (left) and dorsal (right) views of left humerus in FMNH P27452, (distal end oriented toward the bottom; cf. Fig. 2.1); *2,* close-up view (stereopair) of two tooth fragments of *C. mantelli* pierced in left humerus in FMNH P27452 (distal end of humerus oriented toward the bottom; see Fig. 2.1 for its location); *3,* ventral view of left hyoplastron in FMNH P27452 (anterior edge oriented toward the top; cf. Fig. 2.2); *4,* dorsal view of two peripheral bones in FMNH PR58 (exact arrangement of bones is uncertain; cf. Fig. 2.4).
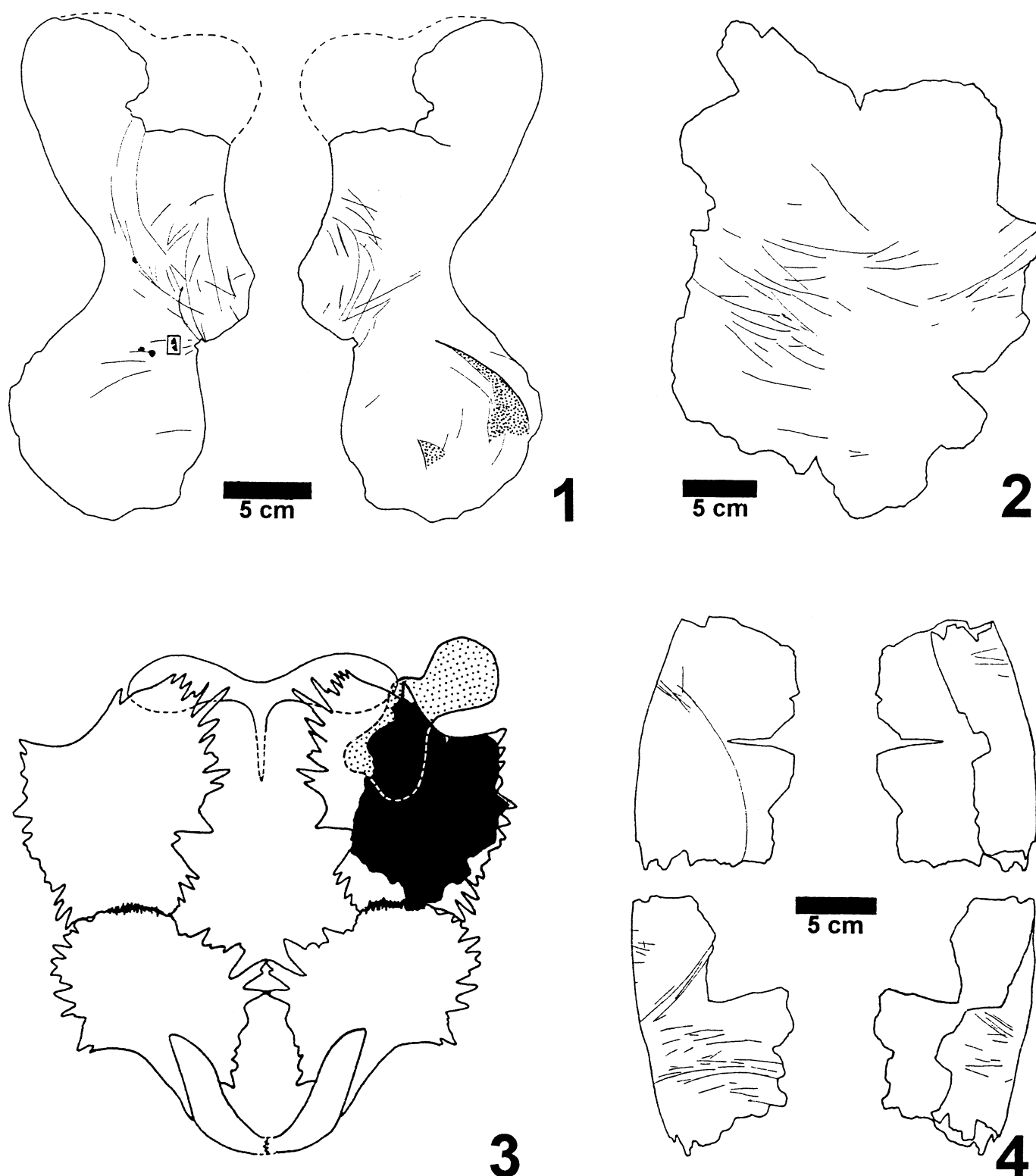
FIGURE 2—Line drawings of two specimens of *Protostega gigas* with embedded *Cretoxyrhina mantelli* teeth and/or tooth marks from Mooreville Chalk, Greene County, Alabama. *1,* Ventral (left) and dorsal (right) views of left humerus in FMNH P27452 (curved lines within bone outline = tooth marks; dotted area = wide tooth cut scarp; black specks = embedded teeth; rectangle = area illustrated in Fig. 1.2); *2,* ventral view of left hyoplastron in FMNH P27452 (curved lines within bone outline = tooth marks); *3,* reconstructed plastron of *P. gigas* in ventral view (anterior to the top; after Zangerl, 1953, fig. 18B) highlighting left hyoplastron represented in FMNH P27452 (solid black area; cf. Figs. 1.3 and 2.2) and showing the topological arrangement of left humerus (dotted element; cf. Figs. 1.1 and 2.1) in life; *4,* dorsal (left) and ventral (right) view of two peripheral bones in FMNH PR58 (exact arrangement of bones is uncertain; curved lines within bone outline = tooth marks).
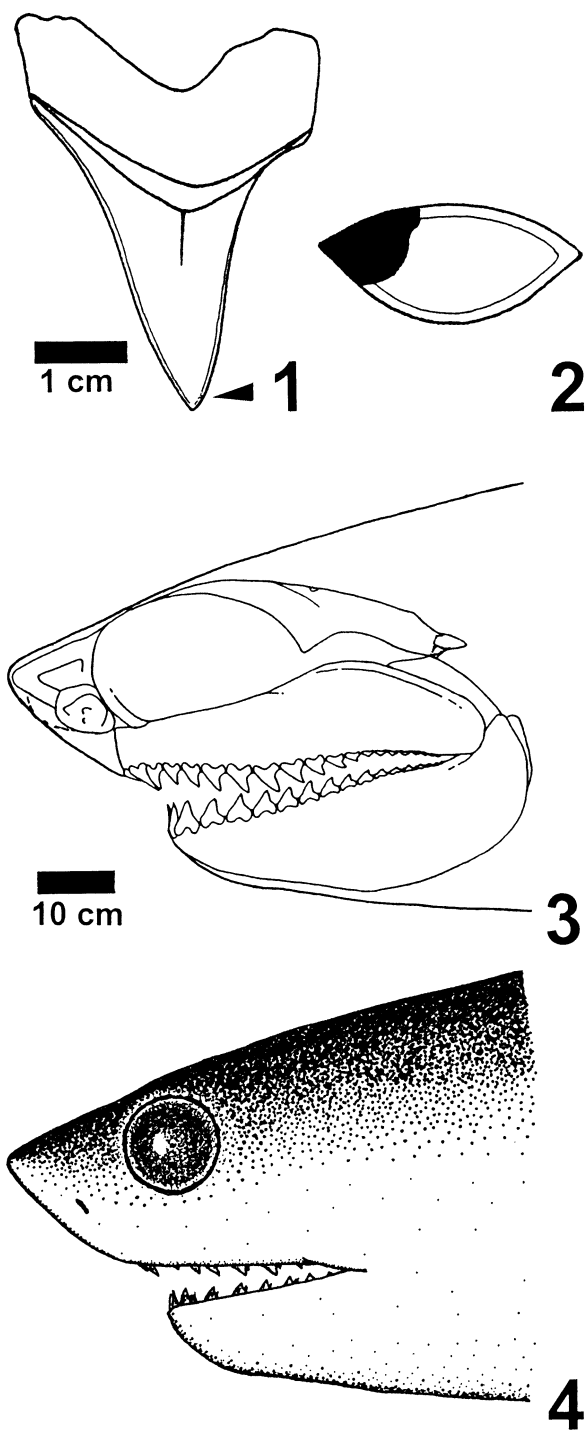
FIGURE 3—*Cretoxyrhina mantelli. 1,* Example of tooth from Mooreville Chalk of Alabama (anterior tooth in lingual view; after Applegate, 1970, fig. 178J: FMNH PF3512); *2,* inferred cross sectional view of crown tip at the level of arrow in Figure 3.1 (but not to scale) to show one interpretation of possible portion represented in one of two tooth fragments (bottom one) illustrated in Figure 1.2; *3,* reconstructed cranial skeleton of 5 m long individual based on material from Niobrara Chalk of western Kansas (lateral view; after Shimada, 1997b, fig. 11); *4,* tentative restoration of head (cf. Fig. 3.3).

Teeth of *Cretoxyrhina mantelli* (Lamniformes: Cretoxyrhinidae) occur in Cenomanian-Campanian marine deposits worldwide (e.g., Cappetta, 1987; Siverson, 1992, 1996). Based on skeletal remains from the Smoky Hill Chalk Member of the Niobrara Chalk in western Kansas (e.g., Fig. 3.3), large individuals of *C. mantelli* measured about 5 to 6 m in total length, possibly with a body form similar to the modern white shark, *Carcharodon carcharias* (Linnaeus) (Shimada, 1997b). The fossil record has demonstrated that *Cretoxyrhina mantelli* fed on active large marine vertebrates such as large teleosts (e.g., *Xiphactinus audax* Leidy which attained 5 m in total length), mosasaurs, and possibly plesiosaurs (Shimada, 1997c; Everhart, 1999; Shimada and Everhart, in press). A mosasaur specimen that showed bone healing over an embedded *Cretoxyrhina* tooth (i.e., postbite survival of the mosasaur) suggests that *C. mantelli* was an active shark (Shimada, 1997c). A recent discovery of a nodosaur (Dinosauria: Ankylosauridae) specimen with possible tooth marks of *C. mantelli* from the Niobrara Chalk of Kansas (Hamm and Everhart, 2001) suggests that *C. mantelli* possibly also scavenged "bloat-and-float" carcasses of fully terrestrial vertebrates that had washed out to sea.

Published records are scarce, but several modern sharks are known to feed on sea turtles, including bull [*Carcharhinus leucas* (Valenciennes)], white tip [*Carcharhinus longimanus* (Poey)], lemon [*Negaprion brevirostris* (Poey)], tiger [*Galeocerdo cuvier* (Peron and LeSueur)], hammerhead (*Sphyrna* sp.), and white sharks (*Carcharodon carcharis*) (Stancyk, 1981). The predation of sea turtles by tiger sharks (especially by larger individuals: ca. >3 m TL) is particularly common (Witzell, 1987; Heithaus, 2001; Simpfendorfer et al., 2001). For example, a tiger shark population along the Western Australia coast appears to consume at least several thousand sea turtles each year (Simpfendorfer et al., 2001). The feeding on sea turtles by the white shark, which is the largest modern shark known to feed on sea turtles, is limited (Fergusson et al., 2000). However, it is noteworthy that known prey turtle species include large forms, such as leatherback sea turtles [*Dermochelys coriacea* (Vandelli)], that have a total carapace length of approximately 1.6 m (Long, 1996).

Applegate (1965) noted the co-occurrence of a marine turtle with several teeth of an extinct tiger shark, *Galeocerdo aduncus* Agassiz, in a concretion from a Miocene bed. He suggested that the case may represent evidence for *Galeocerdo* feeding on a marine turtle in the fossil record. More convincing evidence for feeding on sea turtles by extinct sharks is known from the Late Cretaceous record. Druckenmiller et al. (1993) reported a skeleton of *Squalicorax falcatus* (Agassiz) that preserves probable stomach contents, including toxochelyid turtle elements. Schwimmer et al. (1997) documented a variety of examples of probable scavenging activities of *Squalicorax* spp., including tooth marks on humeri of *Toxochelys?* sp., *Desmatochelys lowii* Williston, and *Protostega gigas.*

A shark attack can be either nonpredatory (i.e., "grab-release": Fergusson et al., 2000) or predatory, but decisively identifying such behavioral scenarios is virtually impossible in the fossil record. Similarly, distinguishing attacks from scavenging activity by sharks is often difficult in the fossil record. The only compelling evidence for attacks in the fossil record is an indication of repaired tissue (e.g., healing or regrowth of bones) at the bitten region (Schwimmer et al., 1997; Shimada, 1997c). Bite marks without tissue repair (e.g., Cigala-Fulgosi, 1990; Everhart et al., 1995; this study) may or may not represent shark attacks. Likewise, a bone with embedded shark teeth does not necessarily indicate shark scavenging, except for the discovery of embedded teeth in remains of organisms that must have been already dead

at the time of the shark feeding (e.g., embedded teeth in a "decayed" bone and remains of fully terrestrial organisms with embedded shark teeth: Schwimmer et al., 1997; Schwimmer, 1997). A shark skeleton with stomach contents (e.g., Pollard, 1990; Druckenmiller et al., 1993; Shimada, 1997c) and cololitic/coprolitic masses (e.g., Williams, 1972; Stewart, 1978; Hattin, 1996) indicates the ingestion of food by the shark, but again does not provide a definitive answer to whether the shark attacked or scavenged the ingested organisms. Close association of shark teeth with a vertebrate skeleton is yet another type of fossil record that may indicate shark feeding (e.g., Cione and Medina, 1987; Repenning and Packard, 1990; Bigelow, 1994). However, such a case too indicates neither attack nor scavenging. The *Protostega* bones described here show embedded *Cretoxyrhina* teeth and/or putative *Cretoxyrhina* tooth marks without an indication of bone healing. Thus, whether the turtles were alive at the time of shark biting is uncertain.

More than one shark may feed on a single animal carcass in the modern seas. For example, Long and Jones (1996) reported a case of at least five individuals of *Carcharodon carcharias* scavenging a carcass of a blue whale, *Balaenoptera musculus* (Linnaeus) (but only one individual fed at a time). The exact number of *Cretoxyrhina* individuals involved in the feeding of FMNH P27452 or PR58 is uncertain. However, it is possible to consider that all the tooth marks (and embedded teeth in FMNH P27452) were left behind by a single *Cretoxyrhina* in each specimen, and the remaining discussion in this paper assumes this interpretation.

The embedded *Cretoxyrhina* teeth are fragmentary in FMNH P27452, so whether they represent upper teeth, lower teeth, or upper and lower teeth mixed cannot be ascertained. Therefore, the exact orientation of the turtle body with respect to the shark body as the shark bit is uncertain. Because of the well-preserved nature of the specimen, the turtle skeletal elements were most likely not disarticulated at the time of shark biting. When the left humerus and left hyoplastron are arranged in the original position (Fig. 2.3), the distribution of tooth marks and their curvature suggest that *Cretoxyrhina* intercepted the turtle more or less from the front and bit at least twice. This interpretation is supported by the fact that the lingual side of at least two embedded *Cretoxyrhina* teeth (Fig. 1.2) faces the distal side of the humerus, although the humerus appears to be shifted in angle with respect to the hyoplastron when the shark engaged in biting the latter bone. Based on the known *Cretoxyrhina* skeletal anatomy (Shimada, 1997b; Fig. 3.3; cf. Fig. 3.4), the size of *Cretoxyrhina* that fed on FMNH P27452 is considered to be approximately 5 m TL judging from the location of bite marks on the left hyoplastron.

The exact position of the peripheral bones in FMNH PR58 is uncertain. However, at least one of the two bones with putative *Cretoxyrhina* tooth marks clearly shows two different orientations of arched tooth marks (Figs. 1.4 and 2.4, bottom bone). Thus, the shark apparently bit the turtle at least twice from two different angles (e.g., once laterally and another posterolaterally). The exact body length of *Cretoxyrhina* that bit this turtle is too tenuous to assess primarily because of the anatomically peripheral nature of the bones.

Schwimmer et al. (1997, fig. 2F–G) illustrated another specimen of a left humerus of *Protostega gigas* from the Mooreville Chalk of Alabama that shows putative tooth marks of another Late Cretaceous shark, *Squalicorax* sp. Schwimmer et al. (1997, p. 78) described the tooth marks as "numerous bite marks on internal and external surfaces, concentrated on both ends and below the ulnar process ... No evidence of serration in bite marks." Equipped with serration along the cutting edges of each tooth, *Squalicorax* dentition has a function of cutting sensu stricto (sensu Cappetta, 1987) by showing monognathic heterodonty with only one functional dental series (Shimada, 1994). Thus, typical

Squalicorax tooth marks on a bone are characterized by the presence of serration grooves either along a relatively low-angled tooth cut scarp (e.g., Schwimmer et al., 1997, figs. 3A, 3C–D) or directly on the bone surface as scrapes (e.g., Schwimmer et al., 1997, figs. 2E, 3B, 3F–G). However, the tooth marks on the protostegid humerus illustrated by Schwimmer et al. (1997, fig. 2G) are characterized by numerous high-angled, nearly straight, groovelike cuts, and it must be noted that they are remarkably similar to the tooth marks found in FMNH P27452 and FMNH PR58 (Figs. 1, 2). Thus, we believe that the tooth marks on the protostegid humerus reported by Schwimmer et al. (1997) are attributable to *Cretoxyrhina*. If correct, this record concomitantly eliminates the only published record of putative *Squalicorax* biting on *Protostega gigas*. Unlike *Squalicorax*, the dentition of *Cretoxyrhina* consists of grasping and cutting teeth without serration (Shimada, 1997a, 2002), and the fact that *Cretoxyrhina* tooth marks are represented by puncture and cut marks without serration grooves is consistent with the functional interpretation of the teeth (Shimada, 1997c). In *Cretoxyrhina*, more than one tooth could have been functional in a tooth row (Shimada, 1997c), and the occurrence of numerous nearly straight, groovelike tooth marks may represent simultaneous cuts made by such multiple functional tooth series as the shark attempted to cut the bones through biting.

To paleontologists, deciphering any ecological dynamics in the fossil record (e.g., as simple as linking two organisms in the context of food chain) is a never-ending challenge. For example, despite the fact that one of the turtle specimens described here shows embedded teeth of an identifiable shark taxon, whether the shark attacked or scavenged the turtle is uncertain. Furthermore, even if it were an attack, whether the case was a predatory or nonpredatory attack cannot be ascertained. Nevertheless, documenting specimens with bite marks and/or embedded teeth, such as is the case in this report, is important 1) because such specimens represent solid evidence for the coexistence of the two organisms; and 2) because they provide a glimpse of their possible ecological interactions (e.g., in this case, *Cretoxyrhina mantelli* possibly feeding on *Protostega gigas*).

REFERENCES

APPLEGATE, S. P. 1965. A confirmation of the validity of *Notorhynchus pectinatus*; the second record of the Upper Cretaceous cowshark. Bulletin of Southern California Academy of Sciences, 64:122–126.

APPLEGATE, S. P. 1970. The vertebrate fauna of the Selma Formation in Alabama, Pt. VIII, the fishes. Fieldiana Geology Memoirs, 3:385–433.

BIGELOW, P. K. 1994. Occurrence of a squaloid shark (Chondrichthyes: Squaliformes) with the pinniped *Allodesmus* from the Upper Miocene of Washington. Journal of Paleontology, 68:680–684.

CAPPETTA, H. 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology. Volume 3B. Gustav Fischer Verlag, Stuttgart, 193 p.

CIGALA-FULGOSI, F. 1990. Predation (or possible scavenging) by a great white shark on an extinct species of bottlenose dolphin in the Italian Pliocene. Tertiary Research, 12:17–36.

CIONE, A. L., AND F. A. MEDINA. 1987. A record of *Notidanodon pectinatus* (Chondrichthyes, Hexanchiformes) in the Upper Cretaceous of the Antarctic Peninsula. Mesozoic Research, 1:79–88.

DRUCKENMILLER, P. S., A. J. DAUN, J. L. SKULAN, AND J. C. PLADZIEWICZ. 1993. Stomach contents in the Upper Cretaceous shark *Squalicorax*

falcatus. Journal of Vertebrate Paleontology, 13(supplement to Number 3):33A–34A.

EVERHART, M. J. 1999. Evidence of feeding on mosasaurs by the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*. Journal of Vertebrate Paleontology, 19(supplement to Number 3):43A–44A.

EVERHART, M. J., P. A. EVERHART, AND K. SHIMADA. 1995. A new specimen of shark bitten mosasaur vertebrae from the Smoky Hill Chalk (Upper Cretaceous) in western Kansas. Abstracts 129th Annual Meeting of Kansas Academy of Science, Pittsburg, 14:19.

FERGUSSON, I. K., L. J. V. COMPAGNO, AND M. A. MARKS. 2000. Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as stomach contents. Environmental Biology of Fishes, 58: 447–453.

HAMM, S. A., AND M. J. EVERHART. 2001. Notes on the occurrence of nodosaurs (Ankylosauridae) in the Smoky Hill Chalk (Upper Cretaceous) of western Kansas. Journal of Vertebrate Paleontology, 21(supplement to Number 3):58A.

HATTIN, D. E. 1996. Fossilized regurgitate from Smoky Hill Member of Niobrara Chalk (Upper Cretaceous) of Kansas, USA. Cretaceous Research, 17:443–450.

HEITHAUS, M. R. 2001. The biology of the tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: sex ratio, size distribution, diet, and seasonal changes in catch rates. Environmental Biology of Fishes, 61:25–36.

HIRAYAMA, R. 1995. Phylogenetic systematics of chelonioid sea turtles. The Island Arc, 3:270–284.

HIRAYAMA, R. 1998. Oldest known sea turtle. Nature, 392:705–708.

HOOKS, G. E., III. 1998. Systematic revision of the Protostegidae, with a redescription of *Calcarichelys gemma* Zangerl, 1953. Journal of Vertebrate Paleontology, 18:85–98.

LONG, D. J. 1996. Records of white shark-bitten leatherback sea turtles along the central California Coast, p. 317–319. *In* A. P. Klimley and D. G. Ainley (eds.), Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press, San Diego.

LONG, D. J., AND R. E. JONES. 1996. White shark predation and scavenging on cetaceans in the eastern North Pacific Ocean, p. 293–307. *In* A. P. Klimley and D. G. Ainley (eds.), Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press, San Diego.

MANCINI, E. A., T. M. PUCKETT, B. H. TEW, AND C. C. SMITH. 1995. Upper Cretaceous sequence stratigraphy of the Mississippi-Alabama area. Gulf Coast Association of Geological Societies Transactions, 45: 377–384.

POLLARD, J. E. 1990. Evidence for diet, p. 362–367. *In* D. E. G. Briggs and P. R. Crowther (eds.), Palaeobiology: A Synthesis. Blackwell Science, Oxford.

REPENNING, C. A., AND E. L. PACKARD. 1990. Locomotion of a desmostylian and evidence of ancient shark predation, p. 199–203. *In* A. J. Boucot (ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, New York.

RUSSELL, D. A. 1988. A check list of North American marine Cretaceous vertebrates including fresh water fishes. Royal Tyrrell Museum Palaeontology (Drumheller, Canada), Occasional Paper, 4:1–57.

SCHWIMMER, D. R. 1997. Late Cretaceous dinosaurs in eastern USA: a taphonomic and biogeographic model of occurrences. Dinofest International Proceedings, 203–211.

SCHWIMMER, D. R., J. D. STEWART, AND G. D. WILLIAMS. 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. Palaios, 12:71–83.

SHIMADA, K. 1994. Jaws of the Late Cretaceous shark, *Squalicorax kaupi*, from western Kansas. Journal of Morphology, 220:393.

SHIMADA, K. 1997a. Dentition of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk of Kansas. Journal of Vertebrate Paleontology, 17:269–279.

SHIMADA, K. 1997b. Skeletal anatomy of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk in Kansas. Journal of Vertebrate Paleontology, 17:642–652.

SHIMADA, K. 1997c. Paleoecological relationships of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). Journal of Paleontology, 71:926–933.

SHIMADA, K. 2002. Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). Journal of Morphology, 251:38–72.

SHIMADA, K., AND M. J. EVERHART. In press. Shark-bitten *Xiphactinus audax* (Teleostei: Ichthyodectiformes) from the Niobrara Chalk (Upper Cretaceous) of Kansas. The Mosasaur, 7.

SIMPFENDORFER, C. A., A. B. GOODREID, AND R. B. MCAULEY. 2001. Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environmental Biology of Fishes, 61:37–46.

SIVERSON, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. Palaeontology, 35:519–554.

SIVERSON, M. 1996. Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, western Australia. Palaeontology, 39:813–849.

STANCYK, S. E. 1981. Nonhuman predators of sea turtles and their control, p. 139–152. *In* K. A. Bjorndal (ed.), Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington, D.C.

STEWART, J. D. 1978. Enterospirae (fossil intestines) from the Upper Cretaceous Niobrara Formation of western Kansas. University of Kansas Paleontological Contributions, 89:9–16.

WELTON, B. J., AND R. F. FARISH. 1993. The Collector's Guide to Fossil Sharks and Rays from the Cretaceous of Texas. Before Time, Lewisville, Texas, 204 p.

WILLIAMS, M. E. 1972. The origin of "spiral coprolites." University of Kansas Paleontological Contributions, 59:1–19.

WITZELL, W. N. 1987. Selective predation on large cheloniid sea turtles by tiger sharks (*Galeocerdo cuvier*). Japanese Journal of Herpetology, 12:22–29.

ZANGERL, R. 1953. The vertebrate fauna of the Selma Formation in Alabama., Pt. VIII, the turtles of the family Protostegidae. Fieldiana Geology Memoirs, 3:37–133.