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Scavenging by Sharks of the Genus *Squalicorax* in the Late Cretaceous of North America

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*Diverse sources and types of evidence indicate that common Cretaceous selachians of the genus *Squalicorax* were the preeminent scavengers of vertebrate carcasses during Santonian and Campanian ages of the Late Cretaceous. Evidence considered comes from the eastern Gulf Coastal Plain and Western Interior of the United States. Direct, material evidence of scavenging includes a decayed mosasaur vertebral centrum and a hadrosaurian dinosaur metatarsal, each containing a *Squalicorax* tooth evidently embedded after the host's death. Abundant implicit evidence of scavenging includes *Squalicorax* bite marks and *Squalicorax* teeth associated with numerous marine tetrapod and fish remains, and at least one additional dinosaur. Many of these bite marks and tooth associations are with predaceous tetrapod taxa, well beyond the reasonable prey size of *Squalicorax* species.*

*Inference of scavenging by *Squalicorax* is also based on comparative counts of selachian teeth in Upper Cretaceous deposits in the eastern Gulf of Mexico. Typical shark-tooth assemblages are dominated by lamnoid teeth, but at two well-studied localities containing the associated remains of large vertebrate carcasses, few shark teeth are found except those of *Squalicorax*, implying that these were shed during scavenging activity. Although it is not definitively proven that *Squalicorax* was an obligate scavenger, the longevity and cosmopolitan distribution of the genus may relate to this primary feeding strategy.*

INTRODUCTION

All living neoselachians are carnivores (Cappetta, 1987), with teleostean fish as their typical prey; however, the larger, characteristically fast-swimming galeomorph sharks (Compagno, 1973) may prey on virtually any and all available mollusks, crustaceans, and vertebrates within their habitats (Springer, 1961; Budker, 1971). There is substantial documentation of Recent shark predation on marine tetrapods (e.g., Arnold, 1972; Ames and Morejohn, 1980; Tricas and McCosker, 1984; McCosker, 1985) and on humans (e.g., Schultz and Malin, 1963; Baldrige, 1974; Miller and Collier, 1980; Lea and Miller, 1985).

Although literature on ancient shark predatory activity is limited, one may infer from comparative fossil and recent tooth morphology that feeding behavior among galeomorph selachians has changed little since at least the Early Cretaceous, and that large sharks have always been largely predatory. Paleontological studies specifically documenting attacks by sharks on live marine animals (i.e., predatory attacks) include evidence of attacks on Tertiary marine mammals by species of white sharks (Deméré and Cerutti, 1982; Cigala-Fulgosì, 1990) and evidence of predation on a Late Cretaceous mosasaur by the large lamnoid shark *Cretoxyrhina mantelli* (Martin and Rothschild, 1989). The primary indications that a fossil situation represents predatory attack are signs of either healing or necrotic tissue around bite marks, or regrowth of an apparently damaged bitten region, any of which demonstrates that the presumptive prey animal was alive subsequent to attack.

The few remaining reports of sharks feeding on Late Cretaceous vertebrates are moot as to whether the host animal was alive or carrion at the time of attack. These reports include bite marks without evidence of healing on elasmosaurid plesiosaurs (Williston and Moodie, 1917; Welles, 1943), and mosasaurs (Hawkins, 1990; Everhart et al., 1995).

Recent sharks are commonly observed or assumed to facultatively scavenge the carcasses of a variety of animals (Applegate, 1965a; Carey et al., 1982; Cigala-Fulgosi, 1990); indeed, dead fish and other carrion are used as bait by shark fishermen to attract a wide range of sharks. One may postdict similar facultative scavenging among similar selachian guilds back to at least the Jurassic. It is nevertheless difficult to positively identify a specific ancient shark taxon as a scavenger, since most associations in the fossil record are ambiguous as to whether shark teeth or tooth marks in or on another organism indicate predation, scavenging, or happenstance (Applegate, 1965a; Cione and Medina, 1987).

Observations reported here from Upper Cretaceous localities in the eastern Gulf of Mexico Coastal Plain and the U.S. Western Interior provide multiple sources of evidence that species of the common and widespread genus *Squalicorax* were frequently (and perhaps preferentially) scavenging vertebrate remains in the nearshore marine realm. These sources include explicit discoveries of *Squalicorax* teeth embedded in remains of organisms which could not have been alive at the time of the shark's feeding, and much implicit evidence of scavenging based on bite-marks and teeth of *Squalicorax* in situations where scavenging is the parsimonious interpretation.

ON *SQUALICORAX*

North American Upper Cretaceous Species

A brief, systematic summary of *Squalicorax* within the Euselachii (Cappetta, 1987) is as follows:

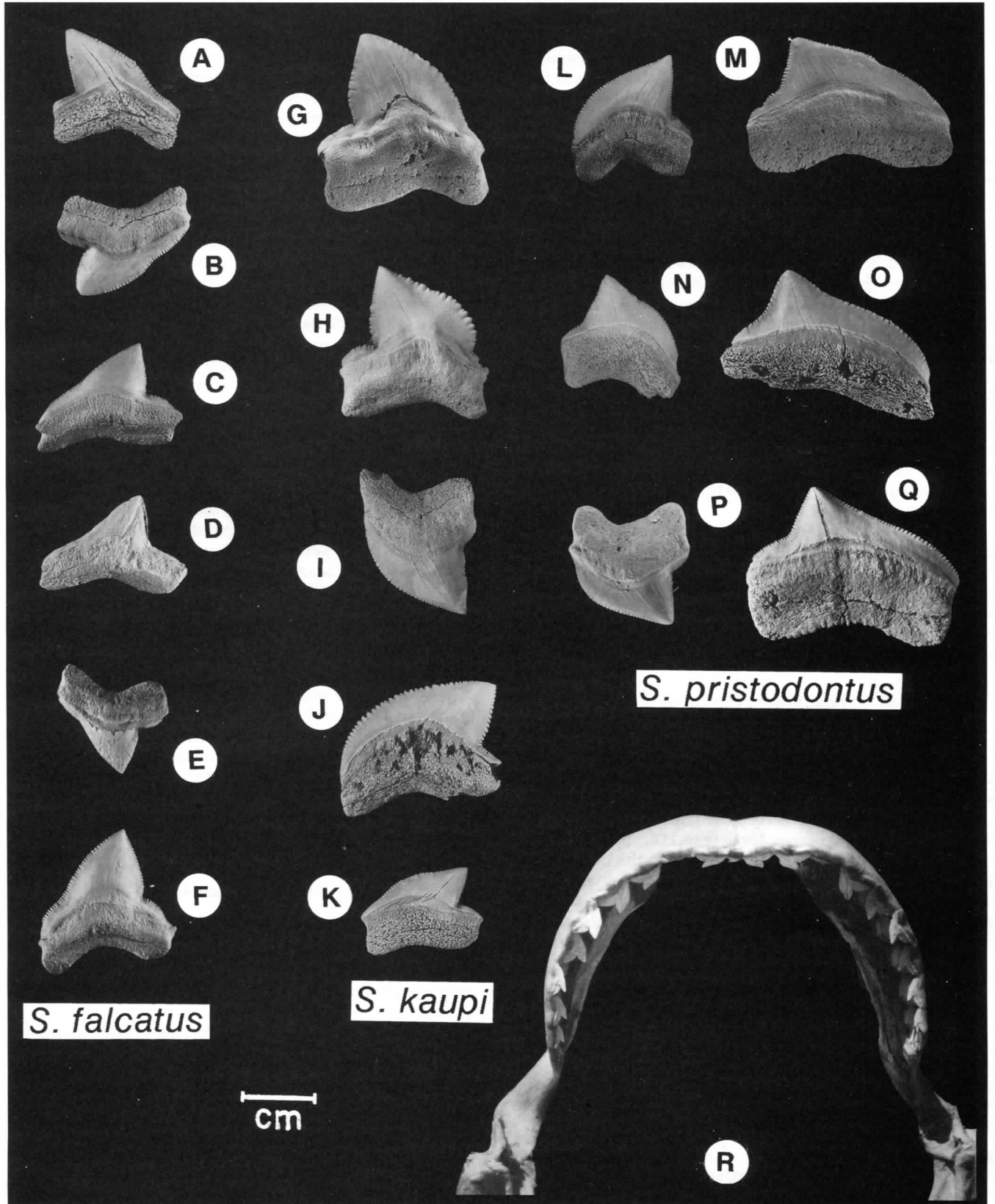
Subcohort: Neoselachii Compagno, 1977
 Superorder: Galeomorpha Compagno, 1973
 Order: Lamniformes Berg, 1958
 Family: Anacoracidae Casier, 1947
 Genus: *Squalicorax* Whitley, 1939.

Squalicorax species are known only from Cretaceous fossils, and the assignment to family, as well as the higher assignment of the Family Anacoracidae, is uncertain (S.P.

Applegate, pers. comm. 1994). Many species of *Squalicorax* have been erected. Meyer (1974) cited at least 19 species, with uncertainty about many specific differential diagnoses. *Squalicorax* species range chronologically from the Albian to the Maastrichtian and geographically to virtually all regions containing Upper Cretaceous marine deposits. Although most *Squalicorax* occurrences are isolated teeth, a few Konservat Lagerstätten, notably several members of the Niobrara Formation in Kansas, preserve vertebrae, associated dentitions, and other body parts. Shimada (1994) described a *S. kaupi* specimen from Kansas with associated teeth, and Meckel's and palatoquadrate cartilages. Among the Kansas Niobrara *S. falcatus* specimens is an individual with associated putative stomach contents (Druckenmiller et al., 1993), and it is noteworthy for the discussion that follows that this shark's ostensible stomach contents included remains from a mosasaur larger than itself. An incomplete associated dentition, attributed by the authors to *S. falcatus*, was also described from Saskatchewan (Case et al., 1990). This locality was assigned by the authors to the Niobrara Formation, but subsequent pollen data and other associated vertebrate remains suggest the dentition occurs in beds of Cenomanian age (S. Cumbaa, pers. comm., 1994), where typical *Squalicorax* teeth are *S. curvatus*.

In North America, four widespread, common *Squalicorax* species range chronologically from Cenomanian through latest Maastrichtian ages: *S. curvatus*, *S. falcatus*, *S. kaupi*, and *S. pristodontus* (Meyer, 1974; Cappetta, 1987; Welton and Farish, 1993). The precise chronological ranges of these species has been uncertain (Cappetta, 1987; Siverson, 1992) because the tooth morphologies appear to overlap, particularly in the lateral and posterolateral regions. Nevertheless, given good samples representing varied tooth positions, we believe these species can be accurately discriminated morphologically and temporally. *Squalicorax curvatus* is primarily found in the Cenomanian of Texas, Kansas, and adjacent parts of the American Western Interior where Cenomanian fossiliferous strata occur. *Squalicorax falcatus* is present in a wide variety of strata in North America from the Turonian through the late Santonian. *Squalicorax kaupi* was the sole species present in North America, and probably globally, through the early and middle Campanian. *Squalicorax pristodontus* also has nearly global distribution, from the latest Campanian through the late Maastrichtian, possibly over-

FIGURE 1—*Squalicorax* and *Galeocerdo* tooth morphology, showing typical variations within the Turonian to Maastrichtian specimens of *Squalicorax falcatus*, *S. kaupi*, and *S. pristodontus*. One centimeter scale bar for all teeth. (A–F) *Squalicorax falcatus*: A and B, from the Eutaw Fm. (middle Santonian), Chattahoochee Co., GA; C–F, from the Carlile Sh. (Turonian), Ellis Co., KS. (G–K) *Squalicorax kaupi*: G, from lower Blufftown Fm. (early Campanian), Russell Co., Alabama; H, I, K, from upper Blufftown Fm. (middle Campanian), Stewart Co., GA; J, from upper Blufftown Fm. (middle Campanian), Barbour Co., AL. (L–Q) *Squalicorax pristodontus*: L and M, from Demopolis Fm., (late Campanian or early Maastrichtian), Bullock Co., AL; N and O, from Ripley Fm. (early Maastrichtian), Stewart Co., GA; P and Q, from Ripley Fm. (early Maastrichtian), Barbour Co., AL. Note apparently overlapping morphologies between species in some tooth positions (e.g., C and K, I and P); however, morphologies A, B and F are specific for *falcatus*, G, H and ?J are specific for *kaupi*, and M, O, and Q are specific for *pristodontus*. (R) Upper jaw of Recent *Galeocerdo cuveri*, showing characteristic arrangement of "cutting-type" teeth; width of jaw at hinge 51.0 cm.



lapping with *S. kaupi* during the latest Campanian (which is currently under study).

These four species may be distinguished most easily by the morphology of anterior and anterolateral teeth (Fig. 1). Specific distinction among teeth is based on tooth size (Glückman and Shvazaite, 1971; Glückman, 1980) and apical cusp angles, both increasing through time, and on subtle configurations of the accessory (posterior) cusp which is subtended by constriction of the posterior margin of the tooth (Cappetta, 1987). However, the identity of a given tooth within the chronological overlap of two species is commonly uncertain and the concepts of the various species need better definition (Siverson, 1992). Siverson also observed that *Squalicorax kaupi* teeth from the Campanian of Sweden are characteristically one and one-half times larger (and, thus, the sharks may have been considerably longer and heavier) than *S. kaupi* reported from the Campanian of Montana (Case, 1978). However, this size difference may be an artifact of incorrect scale notation in Case (1978). We observe that typical *S. kaupi* teeth from Georgia and Alabama (Fig. 1) are morphologically identical with specimens illustrated by Case, yet they are considerably larger than the proportions he showed and are, in fact, co-equal or larger in size than specimens illustrated by Siverson (1992).

The ages of scavenged materials to be considered here are Turonian through middle Campanian. Thus, the *Squalicorax* species represented are probably *S. falcatus* and *S. kaupi*. Nevertheless, one cannot be absolutely certain which *Squalicorax* species is involved in a given situation represented by few or a single tooth or tooth marks, especially at or near the limits of species' ranges.

Squalicorax Dentition

Squalicorax species possessed dentitions typical of the "cutting-type" (Cappetta, 1987). Cusps form a nearly continuous cutting blade across the entire jaw and slant progressively from symphysis to the jaw hinge, providing a uniform cutting surface across the gape. The characteristic serration of *Squalicorax* teeth (Fig. 1) amplifies the cutting morphology. *Squalicorax* species are the only known Late Cretaceous selachians that have serrate teeth. Tooth serration generally increases in coarseness from *S. falcatus* to *S. kaupi*, but decreases in coarseness (yet, with increased overall tooth size) in *S. pristodontus*. There is typ-

ically great variation in serration within species, especially notable within *S. kaupi*.

Because of the obvious physical constraints within the cutting-type morphology, variations among individual dentitions are relatively limited. That is, *Squalicorax* heterodonty was of the monognathic type (i.e., upper and lower jaws match; Compagno, 1973) and there was limited heterodonty within jaws (see Applegate, 1965b on shark tooth terminology, and Shimada, 1994). *Squalicorax* tooth morphology is superficially similar to that of the Cenozoic tiger shark *Galeocerdo* (Fig. 1R), but the genera are not closely related (Case, 1978). The similarity in tooth form is almost certainly convergent, reflecting function rather than phylogenetic relationship. Nevertheless, modern tiger sharks are noted for dietary variety (Budker, 1971; Siverson, 1992; Wilson, 1992) and are known as both scavengers and man-eaters. The "cutting-type" dentition of *Galeocerdo* serves admirably in predation but also seems to be efficient in processing a range of available food sources, including harder materials such as marine turtle shells (Springer, 1961), and for gnawing tissue from tetrapod bones.

Associated with *Squalicorax* teeth in most Late Cretaceous deposits are abundant teeth from a variety of other lamnoid sharks (e.g., *Scapanorhynchus texanus*, *S. raphiodon*, *Cretolamna appendiculata*, *Cretoxyrhina mantelli*). These taxa generally show contrasting selachian dentitions of the "tearing-type" (Cappetta, 1987), featuring relatively long, slender cusps and commonly sizeable spaces between teeth. Such dentition would seem best adapted to capturing and killing live fish (Springer, 1961), and would be disadvantageous in gnawing, cutting, and (especially) durophagous feeding strategies.

Therefore, were other kinds of evidence not available, the dental morphology of *Squalicorax* species would still reflect relatively diverse feeding strategies compared with their contemporaries, and that would imply scavenging, mixed prey (including invertebrates) and/or another, non-piscivorous habit. The discussion below will provide evidence that scavenging was the preferred feeding habit.

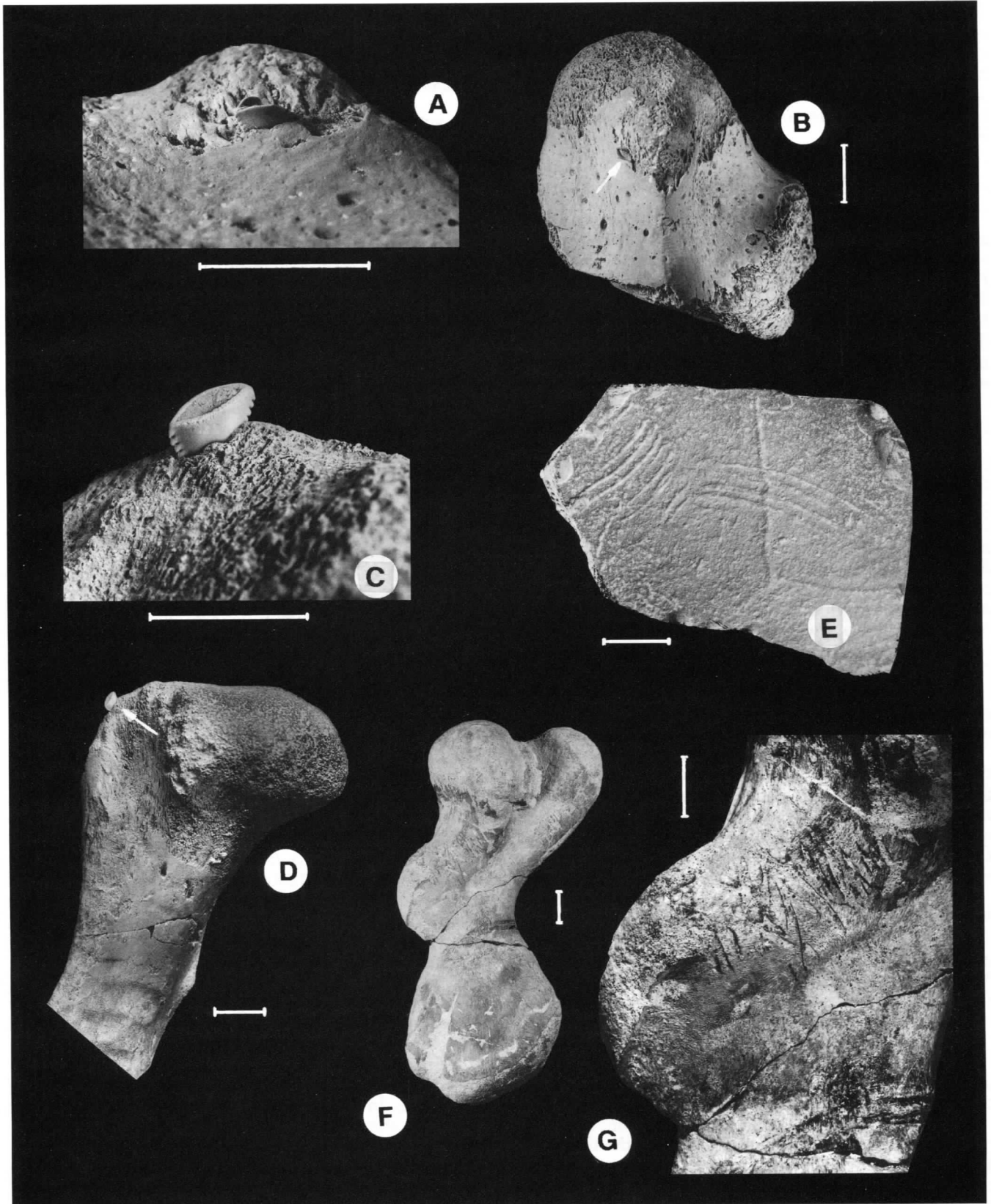
EVIDENCE OF SCAVENGING BY *SQUALICORAX*

Direct Evidence

As previously stated, shark teeth embedded in tetrapod or fish bones do not necessarily identify the nature of the

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FIGURE 2—Tetrapod bones with embedded *Squalicorax* teeth, and shark-bite traces in marine turtle bones from the eastern Gulf Coastal Plain. Note serration of both tooth specimens, which is diagnostic for *Squalicorax* in Late Cretaceous strata. Collection abbreviations as in Table 1. (A and B) *Squalicorax kaupi* tooth tip embedded in *Platecarpus centrum*, CSUK 94-1-1, Blufftown Fm. (early Campanian), Russell Co., AL: A, closeup of tooth and surrounding bone showing erosion of vertebral surfaces proximal to the tooth tip; B, the centrum with arrow showing position of *Squalicorax* tooth. (C-D) Hadrosauridae, genus and sp. indet., juvenile right metatarsal II, ALAM PV993.1.2.2, with *Squalicorax kaupi* tooth embedded in posterolateral surface, Mooreville Formation (early Campanian), Dallas Co., AL: C, closeup of insertion site; D, overall view of metatarsal (distal end upward), with *Squalicorax* tooth site shown by arrow. (E) *Bothremys barberi*, costal fragment CSUK 90-17-3, upper Blufftown Formation (middle Campanian), Stewart Co., GA, showing two sets of parallel scape marks attributed to *Squalicorax kaupi*. (F-G) left humerus of *Protostega gigas*, ALAM PV985.10.2, from the Mooreville Formation (early Campanian), Dallas Co., AL: F, overall view showing numerous bite marks concentrated around the ulnar process and toward both ends; G, closeup view of bite marks on the ulnar process region. All scale bars = 1.0 cm.



feeding activity; i.e., differentiating predation from scavenging. The presence of Mesozoic fossil bones with embedded or associated shark teeth, including *Squalicorax* teeth, has been occasionally cited (Welles, 1943, Applegate, 1965; Martin and Rothschild, 1989). However, the following specimens offer rare situations where scavenging is indicated explicitly.

Squalicorax Tooth in a Decayed Mosasaur Vertebra

Columbus State University [CSUK] 94-1-1 is an ablated mosasaur vertebral centrum, probably from the anterior dorsal series (Fig. 2A, B), from a partial skeleton of *Platecarpus* sp. It was collected from the lower Blufftown Formation (early Campanian) in Russell County, Alabama. A shark-tooth tip is embedded in the right anterodorsal region of the vertebra. The tooth is readily identifiable as a *Squalicorax* by its generally triangular outline and the serration. Given the age of the occurrence and associated *Squalicorax* teeth, the embedded tooth is most probably from *S. kaupi*.

This association is explicitly attributed to scavenging because of two conditions: the significant relief between the vertebra and the tooth fragment, and their relative states of erosion. The *Squalicorax* tooth tip, apparently from a smaller individual, extends approximately 2.0 mm above the vertebral surface, which otherwise shows significant ablation adjacent to the site. The tooth fragment is lodged in a relatively flat, exposed region of the vertebra, and is quite thin in cross section at the interface; therefore, any significant weathering and mechanical ablation after the tooth was embedded should have worn the tooth down to the bone's surface. Given the ablation of the vertebra adjacent to the tooth and surrounding the insertion site, it is concluded that the tooth was lodged in decayed and, therefore, clearly dead, bone.

This specimen indicates feeding by *Squalicorax* after the mosasaur carcass had undergone post-mortem decay to the degree that bone deterioration occurred. It is also noteworthy that the associated mosasaur remains indicate an animal having a total length of at least 5.0 m and, thus, was significantly larger than any known *Squalicorax kaupi*.

In an analogous, but contrasting example of tooth insertion during predation, Martin and Rothschild (1989) described a diseased (osteomyelitic) mosasaur centrum encapsulating a shark tooth [the shark taxon attributed by Martin and Rothschild (1989) was *Cretolamna*; however, this tooth was subsequently identified by one of us (JDS) to be from *Cretoxyrhina mantelli*]. Martin and Rothschild (1989) argued that the mosasaur was evidently alive at the time of insertion and, indeed, survived the attack to develop the diseased tissue observed in the vertebra. Since the shark involved, *C. mantelli*, was a relatively large species, with lengths estimated at 5.0 m (Siverson, 1992; Shimada, 1993), it is credible in this case that the live mosasaur was indeed predated upon by the shark. A similar case of apparent predation on a mosasaur by a large *C. mantelli* was reported by Everhart et al. (1995), who based

their assumption of an unsuccessful predatory attack on signs of healing around some bite marks.

Squalicorax Tooth in Juvenile Hadrosaur Metatarsal

A small, right metatarsal II, Alabama State Museum (ALAM) PV993.1.2.2, contains the embedded tip from a *Squalicorax* tooth (Figs. 2C-2D). In addition, the metatarsal also includes many apparent bite marks across the shaft. The dinosaur bone comes from the Mooreville Formation in Dallas County, Alabama, and is of late, early Campanian age. The *Squalicorax* tooth tip is preserved sufficiently to show that the apical cusp angle is small, indicating that, given the age, this is most likely a lateral or posterior tooth from *S. kaupi*.

At the collecting locality the Mooreville Formation is a muddy chalk, deposited on the open marine shelf (Russell and Keady, 1983). Langston (1960) discussed the occurrence of another juvenile hadrosaur in the Mooreville, the type specimen of *Lophorothon atopus*, with consideration of means by which a presumably shore-dwelling duck-billed dinosaur might be transported onto the marine shelf. The dinosaur remains may have arrived in the marine strata as a bloat-and-float beach carcass, a fluvially-transported floating carcass, or (as a novel alternative) as a crocodile kill. Giant crocodiles (~10 m) are relatively common in penecontemporaneous deposits in the Southeastern United States (Schwimmer et al., 1993a). Regardless of the means by which the dead hadrosaur entered the marine shelf environment, association of a dinosaur anklebone and a *Squalicorax kaupi* tooth is explicitly the result of scavenging, given that hadrosaurs were not marine inhabitants.

Indirect Evidence

Bite Mark Associations With Larger Marine Species

Squalicorax falcatus and *S. kaupi* were generally modest-sized sharks, at least in North America during Santonian and Campanian times. Associated head and vertebral remains of *Squalicorax falcatus* from the Niobrara Formation (e.g., LACM 120090) indicate body lengths to a maximum around 3.5 m. Assuming that sharks of this size would not prey (at least, individually) on predatory marine vertebrates of equal or larger size, associations of *Squalicorax* teeth with such larger vertebrate's remains leads to a primary interpretation of scavenging behavior.

A plausible alternative hypothesis is that *Squalicorax* hunted larger predators in packs, an argument supported by the excellent olfactory prey location and "feeding frenzy" behavior of modern sharks. This hypothesis is, however, counterindicated by the lack of multiple occurrences of *Squalicorax* in the fossil record: One would presume that schooling sharks would occasionally be preserved in groups, but this phenomenon has never been recorded.

It was noted previously that Druckenmiller et al. (1993) reported a *Squalicorax falcatus* from the Niobrara Formation in Kansas that contains possible gut contents, in-

TABLE 1—Additional Upper Cretaceous shark bite and shark tooth associations.

[Data are compiled from museum materials and publications. Not all occurrences are attributable to specific localities, ages, nature of serration in bite marks, states of healing, etc. Taxonomic summary is given for each new genus listed.] Abbreviations: ALAM: Alabama State Museum, Tuscaloosa, Alabama. AMNH: American Museum of Natural History, New York. AUMP: Auburn University Museum of Paleontology, Auburn, Alabama. CSUK: Columbus State University Cretaceous Research Collections, Columbus, Georgia. DMNH: Dallas Museum of Natural History, Dallas, Texas. FHSM: Fort Hays State University Museum, Hays, Kansas. KUVV: University of Kansas Vertebrate Paleontology Museum, Lawrence, Kansas. LACM: Natural History Museum of Los Angeles County, Los Angeles, California. SDNHM: San Diego Natural History Museum, San Diego, California.

Catalog number, locality, age	Prey/scavenged species, remains preserved	Feeding evidences
ASSOCIATIONS WITH OTHER FISH		
KUVV 59041 Niobrara Fm. Gove Co., KS late Santonian	<i>Ptychodus mortoni</i> (Selachii, Ptychodontidae) approximately 50 vertebrae and partial chondrocranium	six <i>Squalicorax falcatus</i> teeth in immediate association (Stewart, 1980)
KUVV 36243 Niobrara Fm. Trego Co., KS late Coniacian	<i>Lepisosteus</i> sp. (Actinopterygii, Lepisosteidae) partial skeleton	numerous <i>Squalicorax falcatus</i> teeth in association (Wiley and Stewart, 1977)
LACM 133270 Niobrara Fm. Gove Co., KS late Coniacian	<i>Protosphyraena nitida</i> (Actinopterygii, Pachycormidae) pectoral fin, complete)	unhealed bite and scrape marks on dorsal and ventral surfaces; indications of serration in bite marks in anteroventral margin
LACM 135837 Niobrara Fm. Graham Co., KS late Coniacian	<i>Protosphyraena tenuis</i> pectoral fin, proximal end truncated (prior to preservation)	pectoral fin with numerous bite marks and scrapes on dorsal and ventral surfaces
KUVV 49514 Niobrara Fm. Gove Co., KS late Coniacian	<i>Protosphyraena nitida</i> pectoral fin	bite marks on both sides, most near proximal end; four show serration
KUVV 433 Niobrara Fm. Kansas, no loc. late Coniacian	<i>Protosphyraena tenuis</i> pectoral fin	one serrate graze on each side
KUVV 125302 Niobrara Fm. Gove Co., KS late Coniacian	<i>Protosphyraena nitida</i> pectoral fin and girdle	bite marks on fin and cleithrum, two marks showing evidence of serration, none healed
KUVV 125303 Niobrara Fm. Gove Co., KS late Coniacian	<i>Protosphyraena tenuis</i> pectoral fin and girdle	cleithrum showing three serrated scrape marks, none healed. Fin with four or more bites along anterior edge, two marks showing serration
KUVV 60692 Niobrara Fm. Logan Co., KS Campanian	<i>Protosphyraena gladius</i> pectoral girdle and additional skeletal parts	bite marks with serration on cleithrum, none healed
AMNH 1849 Niobrara Fm. "Logan River, KS" Senonian	<i>Protosphyraena gladius</i> (holotype), pectoral fin	bite marks with slight evidence of serration
FHSM VP-10266 Niobrara Fm. Kansas, no loc. age unknown	<i>Protosphyraena pernicosa</i> pectoral fin	several cuts with serration

TABLE 1—Continued.

Catalog number, locality, age	Prey/scavenged species, remains preserved	Feeding evidences
FHSM VP-12059 Niobrara Fm. Kansas, no loc. Coniacian	<i>Protosphyraena pernicosa</i> pectoral fin base	bite marks on proximal end.
LACM 132705 Niobrara Fm. Lane Co., KS early Santonian	<i>Pachyrhizodus caninus</i> (Actinopterygii, Pachyrhizidae) partial maxilla	at least 31 bite marks, 13 showing serration, along labial margin none healed
ASSOCIATIONS WITH MARINE TETRAPODS		
LACM 50974 Niobrara Fm. Logan Co. Campanian	<i>Toxochelys?</i> sp. (Chelonia, Toxochelyidae) humerus	numerous bite marks on dorsal and dorsoventral surfaces of distal end, showing serration, none healed.
KUVP 32401 Carlile Fm. Ellis Co., KS middle Turonian	<i>Desmatochelys lowii</i> (Chelonia, Cheloniidae) humerus	three parallel arcuate cuts one showing serration
KUVP 32405 Carlile Fm. Ellis Co., KS middle Turonian	<i>Desmatochelys lowii</i> humerus	numerous cut marks, three showing serration
ALAM PV985.10.2 Mooreville Fm. Dallas Co., AL early Campanian	<i>Protostega dixie</i> (=gigas) (Chelonia, Protostegidae) small left humerus	numerous bite marks on internal and external surfaces, concentrated on both ends and below the ulnar process (Fig. 2g-2h). No evidence of serration in bite marks.
LACM 131156 Niobrara Fm. Harlan Co., NB Campanian	<i>Platecarpus ictericus</i> (Squamata, Mosasauridae) partial skeleton	at least 19 cuts on ribs, 17 with serration, none healed.
KUVP 84803 Niobrara Fm. Rooks Co., KS late Coniacian	<i>Platecarpus</i> sp. cervical vertebrae	associated teeth of <i>Squalicorax falcatus</i> and <i>Pseudocorax laevis</i>
KUVP 86656 Niobrara Fm. Gove Co., KS Senonian	<i>Platecarpus</i> sp. pubis and ischium	both bones with at least two cut marks, each with serrations
FHSM VP-3 Niobrara Fm. Logan Co., KS Senonian	<i>Tylosaurus proriger</i> (Squamata, Mosasauridae) associated skeleton	left mandible with bite marks showing serrations
FHSM VP-2156 Niobrara Fm. Kansas, no loc. Senonian	Mosasauridae, indet. ilium	cut with serrations
KUVP 1117 Niobrara Fm. Kansas, no loc. Senonian	Mosasauridae, indet. radius or ulna	both serrated and non-serrated bite marks
DMNH (no catalog number given) Taylor Gp. Fannin Co., TX Campanian	Mosasauridae, indet. vertebra	numerous shark-bite marks on neural spine, attributed to <i>Squalicorax</i> (Welton and Farish, 1993, p. 35-36)

TABLE 1—Continued.

Catalog number, locality, age	Prey/scavenged species, remains preserved	Feeding evidences
FHSM VP 12059 Carlile Sh. Ellis Co., KS middle Turonian	<i>Dolichorhynchops</i> sp. (Plesiosauria, Polycotylidae) pectoral girdle	serrate bite marks on both surfaces of left coracoid, not healed
KUVP 5070 Greenhorn Fm. Cloud Co., KS early Turonian	<i>Trinacromerum willistoni</i> (Plesiosauria, Polycotylidae) holotype (Riggs, 1944)	bite marks on left pubis
FHSM (unnumbered) Carlile Sh. Russell Co., KS Turonian	<i>Brachauchenius lucasi</i> (Plesiosauria, Pliosauridae) partial skeleton	one rib with serrate tooth marks, another rib with embedded <i>Squalicorax</i> tooth, no evidence of healing
ASSOCIATIONS WITH TERRESTRIAL TETRAPODS		
SDNHM 33909	Nodosauridae indet. (Ornithischia, Nodosauridae)	<i>Squalicorax kaupi</i> teeth (SDNHM 33916, 32301, 34060) in immediate association.

cluding a limb fragment from an undetermined mosasaur species. Other mosasaur remains in the Niobrara Formation show *Squalicorax* bite marks (Table 1), which are easily identified among other possible shark feeding traces by the signs of tooth serration (Fig. 3; See: Deméré and Cerutti, 1982, and Cigala-Fulgosi, 1990, concerning similar traces left by serrate *Carcharodon* teeth). As discussed, it is unlikely that the sharks would feed on any species of mosasaur unless it were already dead. A similar argument can be made concerning *Squalicorax* bite marks on sauropterygian bones. Welles (1943) and Williston and Moodie (1917) described Late Cretaceous elasmosaurid plesiosaur remains bearing evidence of shark feeding. The specimen described by Welles (1943) comes from the Maastrichtian Moreno Formation in California. Table 1 includes additional, unpublished occurrences of plesiosaur fossils showing evidence of *Squalicorax* tooth marks, which we interpret as scavenging traces.

Squalicorax bite marks, as well as bites from indeterminate Cretaceous sharks (lacking evidence of serration), are also found abundantly on larger fish remains from the Niobrara Formation (Fig. 3). Such traces are especially common on the large, bony pectoral fins of the pachycormid teleosts of the genus *Protosphyraena*, in which the durability of the fins probably helped preserved bite marks (Fig. 3B). It seems improbable that sharks would preferentially feed on large, swift, predaceous fish such as *Protosphyraena* species while they were alive; therefore, scavenging seems the logical explanation for the abundance of *Squalicorax falcatus* feeding traces on *Protosphyraena* pectoral fins. Table 1 lists numerous additional predaceous fish fossils with shark-bite marks, many with the evidence of serration characteristic of *Squalicorax* species. These, too, are most parsimoniously interpreted as scavenging activity.

A costal fragment, CSUK 90-17-3, from the large pleurodire turtle *Bothremys barberi* (Schmidt, 1940), shows two overlapping sets of parallel scrape-marks on the dorsal surface (Fig. 2E), proximal to the suture with the adjacent neural bone. The specimen was collected from the mid-Campanian Blufftown Formation in western Georgia. The marks are well-incised in the dense compact bone of the costal, implying they resulted from very strong jaw pressures. The spacing of scrapes is indicative of two sets of oblique, raking shark bites that incorporate the tips of several tooth rows. These scrapes almost certainly testify to scavenging, rather than predation, because of the relatively large size of the turtle (with a carapace width minimally 0.7 m), and the location of the scrapes near the proximal end of the costal. It is unlikely that the shark could have bitten the intact turtle nearly to the midline, and it is unlikely that any shark would have disarticulated the shell of a large, hard-shelled marine turtle during predation. Thus, the costal must have been separated from other parts of the shell prior to the action which caused the scrapes. It is not as clearly argued that *Squalicorax kaupi* produced the scrape marks, but among selachians in the associated fauna, this species alone has dentition likely to have withstood biting into such dense bone.

Relative Abundances of Selachian Teeth

As with bite marks and embedded teeth, simple association of an organism's remains with shark teeth does not differentiate scavenging from predation. However, the following field observations imply that scavenging produced many associations of *Squalicorax* teeth with other fossil remains.

Collections of shark teeth from early and mid-Campanian strata in eastern Alabama and western Georgia (Case

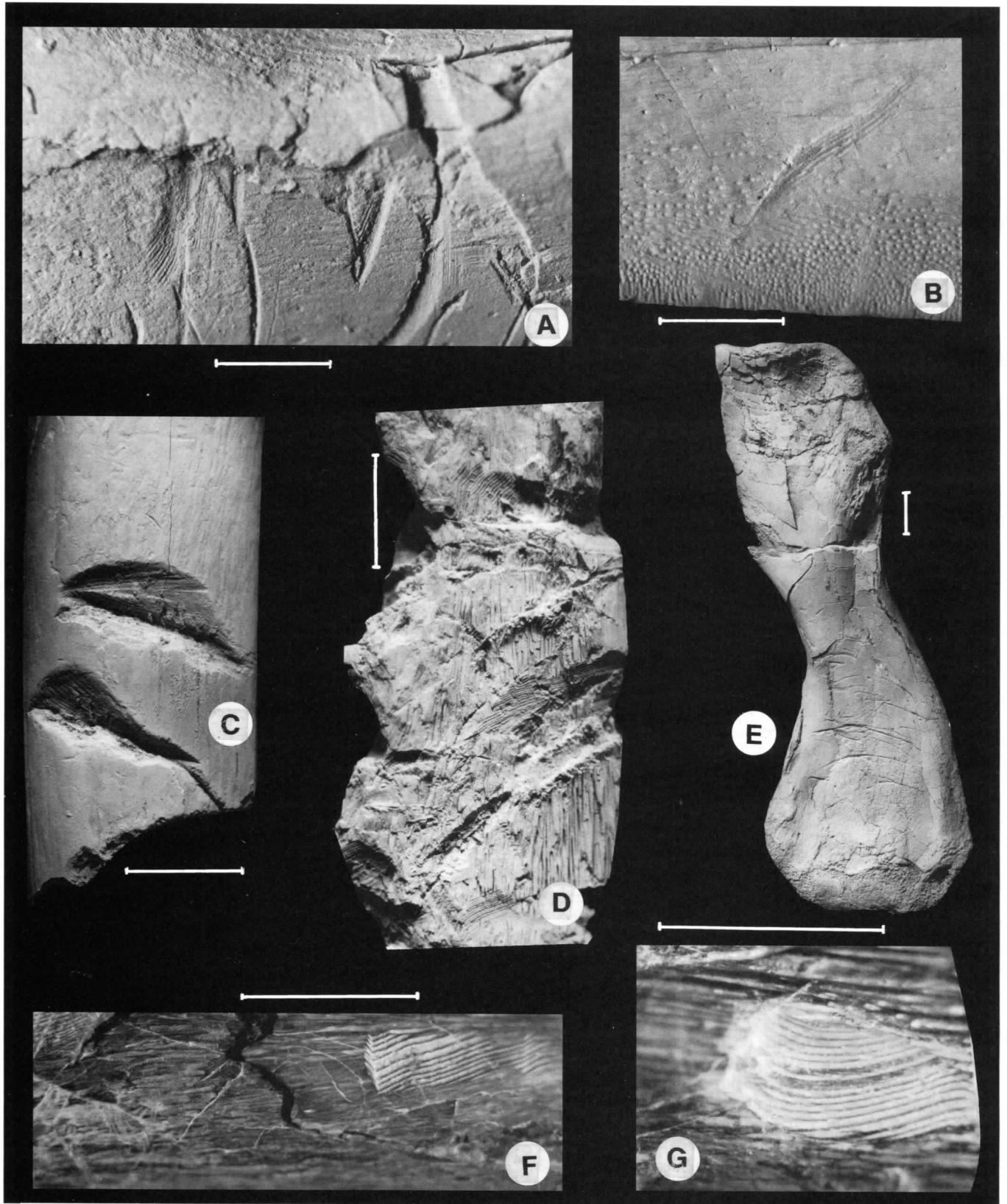


TABLE 2—Relative abundances of common shark species in field collections from western Georgia and eastern Alabama. Data expressed as percentages of selachian fauna in combined collections. (Percentages may be less than 100 where unlisted selachian species are present). Collection abbreviations as in Table 1.

	<i>Scapanorhynchus texanus</i>	<i>Creto-lamna appen-diculata</i>	<i>Squali-corax falcatus/kaupi</i>
CSUK 82-1 Upper Eutaw Fm. Chattahoochee Co., GA	65	20	10
CSUK 93-17-9 Lower Blufftown Fm. Hatchechubbee Cr. Russell Co., AL	60	18	10
CSUK 87-20 Lower Blufftown Fm. Hatchechubbee Cr. (hadrosaur matrix) Russell Co., AL	0	0	100
CSUK 88-20 Lower Blufftown Fm. (coelacanth matrix) Cowikee Cr. Barbour Co., AL	0	0	100
CSUK 94-6-1 Upper Blufftown Fm. Bullock Co., AL	85	2	8
CSUK 79-10 Upper Blufftown Fm. Stewart Co., GA	80	1	15

and Schwimmer, 1988) contain great abundances of teeth from the goblin shark *Scapanorhynchus texanus* (Table 2). In the lowermost Campanian deposits, the lamnoid *Creto-lamna appendiculata* is of secondary abundance and a small number of other neoselachian taxa are present, including *Cretoxyrhina mantelli*. All of the above-named species have dentitions of the "tearing type" of Cappetta (1987), contrasting with the "cutting type" dentition of *Squalicorax kaupi*, which is the contemporaneous *Squalicorax* species. Tooth counts taken in the field and in cataloged collections, including thousands of specimens, show

local occurrence ratios generally with 2 and 5 times as many *Scapanorhynchus* and other "tearing" teeth as *Squalicorax* teeth.

In these same regional Upper Cretaceous strata, bones of larger vertebrates are typically isolated and fragmentary (Schwimmer, 1986). However, at two sites in eastern Alabama, each yielding associated large vertebrate remains, we have recorded a great abundance of *Squalicorax kaupi* teeth in enclosing matrix, to the near exclusion of other selachian teeth. One site contains ten lower leg bones from an adult hadrosaur dinosaur (Schwimmer et al., 1993b); the other contains the skull, mandibles, pectorals and branchials of a giant coelacanth fish (Schwimmer et al., 1994). Matrix enclosing both sets of associated remains is sedimentologically distinct from that of adjacent areas, suggesting the influence of decomposition products, and it is in this enclosing matrix that *Squalicorax kaupi* teeth are the only selachian teeth found.

It is obvious that *Squalicorax kaupi* was not preying on an adult hadrosaur and, therefore, the fossil association at that site must be the result of scavenging. Schwimmer et al. (1993b) observed that this dinosaur material, like all other known eastern Alabama and western Georgia dinosaur occurrences, consists of distal elements (here, the leg from the tibia downward; at other regional localities, the typical preserved materials are distal tailbones and limbs). The taphonomic model that best explains these occurrences is a bloat-and-float dinosaur carcass having its dangling elements (limbs and tail) scavenged by *Squalicorax kaupi*, with the severed portions of the dinosaur settling on the nearshore sea bottom, at which time scavenging continued to an undeterminable state.

In the case of the giant coelacanth site, the evidence for scavenging is not quite as compelling, but we note that this coelacanth fish was approximately 3.5 m in overall length, and relatively heavy-bodied. The *Squalicorax* teeth associated with the remains are among the smaller *S. kaupi* specimens (typical for the early Campanian), of 1.2 cm and lesser widths, reflecting feeding by sharks less than 3.0 m in length. Scavenging, again, is the parsimonious explanation for these associations by virtue of the sheer size of the ostensible prey.

DISCUSSION

The very abundant bite traces and tooth associations of *Squalicorax* species with apparently scavenged fossils amply document their frequency of scavenging. It remains difficult to determine and, further, to prove whether or not

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FIGURE 3—Shark-bite traces in marine vertebrate bones from the Smoky Hill Member, Niobrara Formation. (A and E) *Toxochelyidae*, gen. and sp. indet., LACM 50974, Logan Co., KS, (early Campanian), left humerus showing numerous bite marks, many with evidence of serrations: A, (proximal end to right) closeup of ventral mid-shaft region with evident serrate bite marks; E, overall ventral view of humerus. (B) *Protosphyraena nitida*, LACM 133270, Lane Co., KS, (Coniacian), dorsal side of anterior edge of pectoral fin, showing a single bite mark with serrate impressions. (C,F,G) *Platecarpus ictericus*, LACM 131156, Harlan Co., NB, (early Campanian), three ribs: C, two deeply incised bite marks showing serrate impressions; F and G, additional serrate bite marks on ribs. (D) *Pachyrhizodus caninus*, LACM 132705, Lane Co., KS, (early Santonian), left maxilla showing numerous bite marks with serrate impressions. All scale bars = 1.0 cm.

Squalicorax sp. were obligate scavengers as opposed to opportunistic or facultative frequent scavengers. We argue that the absence of any known *Squalicorax* tooth associations with healed injuries in marine vertebrates (contrasting with the examples of *Cretoxyrhina mantelli* associations in Martin and Rothschild, 1989, and Everhart et al., 1995) offers modest evidence for scavenging and against predation; but, it is admittedly very modest evidence because healed-over shark bites and encapsulated shark teeth are very rare in the fossil record.

It is evident that the large number of *Squalicorax* teeth found in association with vertebrate remains in eastern Gulf Coastal Plain Upper Cretaceous deposits contrasts markedly with more typical great abundances of lamnoid teeth (especially *Creto lamna appendiculata* and *Scapanorhynchus texanus*) in the same strata. We note, too, that although *Squalicorax* species were generally less abundant than lamnoids during the Late Cretaceous, the clade was long-lived, widespread, and common in selective (scavenging) situations. We deduce from these observations that the relative success of *Squalicorax* derives from the specialization for scavenging. This deduction may not provide adequate evidence for an exclusive scavenging role, but it does suggest that it was the characteristic behavior.

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