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FEEDING TRACES AND PALEOBIOLOGY OF A CRETACEOUS (CENOMANIAN) CROCODYLIFORM: EXAMPLE FROM THE WOODBINE FORMATION OF TEXAS

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ABSTRACT

Direct evidence of behavior in extinct tetrapods is rare. However, these traces can inform a variety of research questions touching on paleoecology, taphonomy, and functional morphology. Here we present fossil specimens from the Upper Cretaceous (Cenomanian) Woodbine Formation that exhibit tooth marks consistent with predation by a new taxon of large crocodyliform currently under study. Collected from the recently discovered Arlington Archosaur Site, the marked bones were largely found in a single peat horizon and in close association with the new crocodyliform. The feeding traces themselves consist of pits, scores, and punctures that occur on multiple turtle shell fragments and two dinosaur limb bones. The pattern of marks and the breakage on turtle carapaces and plastra suggest that they were crushed, whereas the marks on dinosaur bones indicate possible dismemberment. These interpretations and the association with a crocodyliform trace maker are based on observations of feeding behaviors and accompanying, diagnostic bite mark patterns made by extant crocodylians. The morphology of the new crocodyliform taxon and the distribution of bite marks indicates it was likely a generalist: an opportunistic predator that fed on a variety of prey, including turtles and dinosaurs. Given this evidence and the paleoenvironmental setting, the ecology of the large crocodyliform from the Woodbine Formation was likely most similar to that of fossil and living crocodylians inhabiting delta-plain environments. Not only were these crocodyliforms likely significant predators in the Woodbine paleoecosystem, they also played an important taphonomic role in the assembly of vertebrate remains from the surrounding community.

INTRODUCTION

In the study of vertebrate paleobiology, inferences regarding behavior must often rely on skeletal material. Direct evidence of behavior in the vertebrate fossil record is exceedingly rare (e.g., Hasiotis et al., 2007 and references therein), especially for interspecific interactions like predation (e.g., Carpenter, 1998; Varricchio, 2001). In terrestrial ecosystems, the most abundant evidence of behavior consists of such ichnofossils as trackways (Lockley, 1986, 1998; Lockley and Hunt, 1995; Hasiotis et al., 2007) and coprolites (Hunt et al., 1994; Richter and Baszio, 2001; Chin, 2007). Tooth marks, when attributable to a particular taxon, can provide direct evidence of carnivore feeding behavior and information on the trophic structure of the community (Fiorillo, 1991a; Chure et al., 1998; Schwimmer, 2002; Rogers et al., 2003; Jennings and Hasiotis, 2006; Reisz and Tsuji, 2006).

Here we describe tooth marks and bone breakage patterns on the fossil remains of turtles and ornithopod dinosaurs that are consistent with feeding by a large crocodyliform. These marks differ substantially from those produced by other potential carnivores and are attributed to a new taxon of crocodyliform from the same locality. The presence of large, predatory crocodyliforms in the extinct biota has important paleoecological and taphonomic implications for the fossil locality and our understanding of this ancient ecosystem.

FOSSIL LOCALITY

All fossil material was recovered from a productive new locality in north-central Texas dubbed the Arlington Archosaur Site (AAS; Fig. 1) and is currently housed in the Earth and Environmental Sciences Department at the University of Texas at Arlington (UTA). The AAS is from the uppermost Woodbine Formation (Dodge, 1952, 1968, 1969; Oliver, 1971; Johnson, 1974; Main, 2005) and is Cenomanian in age (ca. 90–100 Ma) (Kennedy and Cobban, 1990). Woodbine Formation exposures in Texas extend from Lake Texoma on the Red River to the Edwards Plateau near Austin and occur as an irregular and narrow north-south band (Hill, 1901; Bergquist, 1949; Oliver, 1971; Johnson, 1974). Deposits primarily preserve nearshore continental and shallow marine depositional systems, and include fluvial, deltaic, and shelf deposits (Dodge, 1952; Oliver, 1971; Main, 2005). The AAS represents a coastal ecosystem from a delta plain along the southeastern margin of the Western Interior Seaway. The diverse biota recovered so far includes lungfish, gar, shark, ray, turtle, amphibian, mammal, dinosaur (ornithopod and theropod), and crocodyliform remains along with numerous carbonized logs (Main, 2009). The fossils primarily occur within a 1 m section of organic-rich deposit with prominent carbonized wood remains (Main, 2009). The crocodyliform remains represent a new taxon, distinguished from the Woodbine crocodyliform *Woodbinesuchus byersmauricei* primarily by its wide, A-shaped skull and occurrence in much younger strata than the latter. Description of the new Woodbine taxon is in progress.

MATERIALS AND METHODS

Taphonomic Analysis

As part of ongoing work at the AAS, a preliminary taphonomic analysis was done, focusing on the sedimentary environments represented, quality of macrofossil preservation, and spatial distribution of fossils recovered so far. Because the quarry remains active, with new fossils recovered on a weekly basis, more detailed taphonomic analyses (e.g., MNI, taxonomic diversity and evenness) remain to be completed. Sedimentological analysis consisted of detailed study of vertical and horizontal changes in lithology throughout the entire exposure forming the walls and floors of the quarry. A large proportion of material removed from the quarry has been screenwashed for microfossils following generally practiced methods (McKenna, 1962; Jamniczky et al., 2003). The identities of microfossil taxa from continental, brackish, and marine environments were used to help determine the proximity of the AAS to the paleocoastline. Preservation quality was assessed through a survey of over 100 bones. Bone surface features and breakage patterns were noted and compared to published features for identification (Behrensmeyer, 1978; Fiorillo, 1991b; Fiorillo et al., 2000; Bader et al., 2009).

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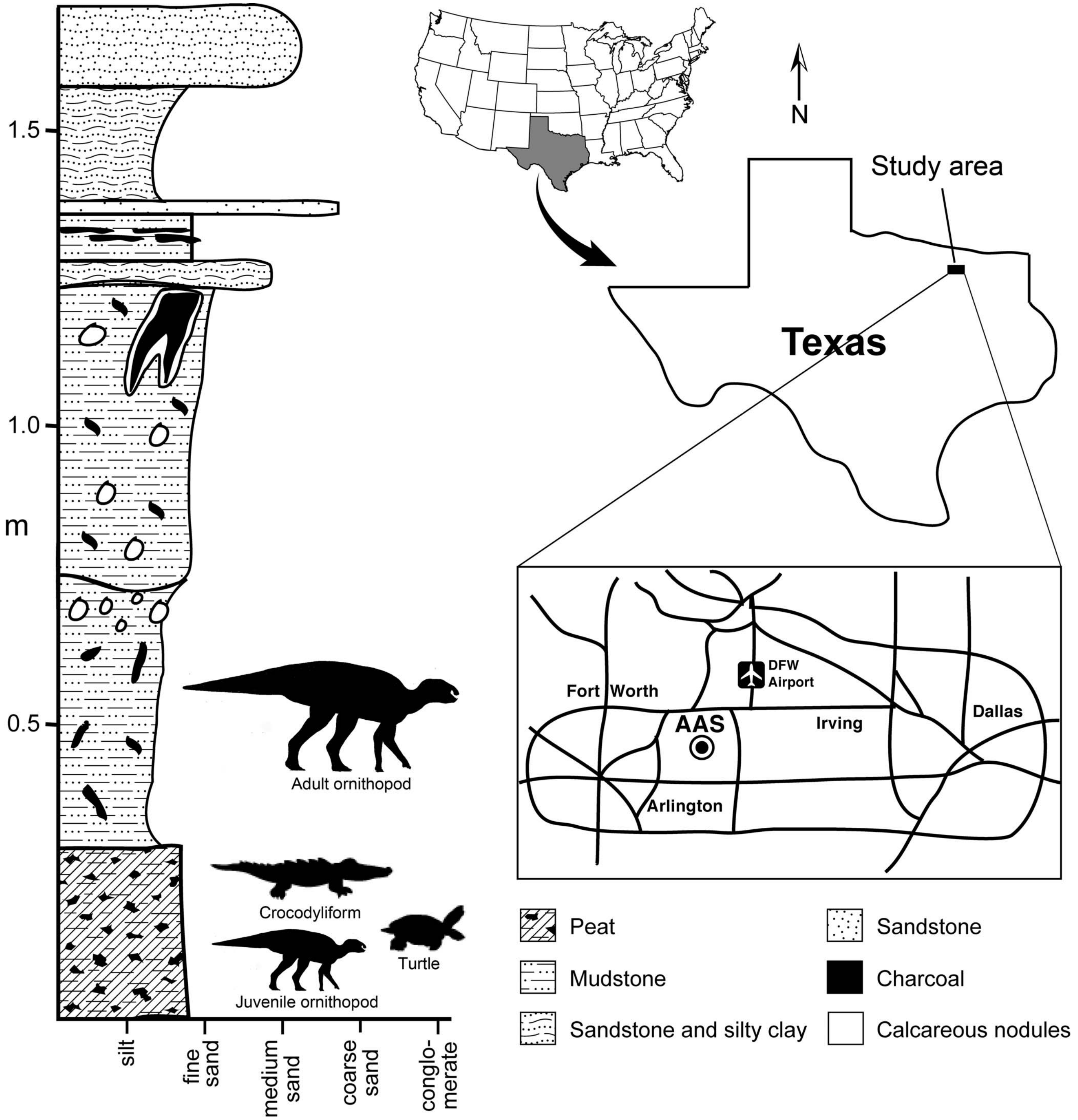

FIGURE 1—Location of the Arlington Archosaur Site (AAS). At left is a composite stratigraphic column for the site. The lowermost horizon represents the peat bed containing the crocodyliform, turtle, and juvenile ornithopod remains. The horizon immediately above contained the bitten adult ornithopod bone in a paleosol complex, which also contains carbonate nodules and charcoal fragments.

Fossil Specimens and Documentation

Over two hundred dinosaur bones and 29 turtle shell fragments were examined for tooth marks. The specimens described here include 17 fragments of turtle shell and two partial dinosaur limb bones (Table 1). Turtle shell fragments include pieces of carapace and plastron referable to at least two individuals and smaller fragments of several others. All represent relatively large individuals (35–45+ cm carapace length), and include at least two different taxa. The turtle material was found in close association to the remains of a large adult crocodyliform and in a nearby concentration that produced numerous juvenile remains. Dinosaur bones are the proximal ends of femora from one adult and one juvenile ornithopod. Note that the adult bone was recovered from the paleosol layer directly overlying the peat bed (see Fig. 1).

Most specimens required modest preparation with hand tools due to the relatively friable matrix. Probable tooth marks were examined with a 10X hand lens or microscope, photographed, and measured with digital calipers. Marks were identified following the criteria of Binford (1981) and include pits, scores, and punctures. Special attention was paid to features diagnostic of crocodyliforms (Njau and Blumenschine, 2006). When multiple bone fragments are attributed to the same individual, the count assumes that each bite mark on each fragment is

TABLE 1—Fossil specimens from the Arlington Archosaur site demonstrating crocodyliform bite marks. Each Field ID# corresponds to a fossil fragment that is grouped by individual. The columns show the number of identifiable and questionable marks of each type, respectively, separated by a forward slash. The first number refers to confidently identifiable marks, whereas those with a '?' are questionable.

Taxon	Field ID#	Pits/?	Punctures/?	Scores/?	Notes
Adult ornithopod	UTA-AASO-125	3/0	0/0	0/0	One pit associated with a flake.
Juvenile ornithopod	UTA-AASO-201	0/6	0/0	0/0	
Turtle 1 "crushed turtle"	UTA-AASTL-001	6/2	0/1	1/0	
	UTA-AASTL-002	12/0	0/0	2/0	One of the scores is bisected.
	UTA-AASTL-003	1/2	0/0	0/0	
	UTA-AASTL-008	4/0	0/0	1/0	
	UTA-AASTL-012	2/0	0/0	5/1	
	UTA-AASTL-013	6/0	0/0	0/0	
	UTA-AASTL-014	0/1	0/0	2/2	
	UTA-AASTL-015	4/0	0/0	1/0	
	UTA-AASTL-016	2/0	0/0	0/0	
	UTA-AASTL-020	0/0	0/0	0/1	
	UTA-AASTL-025	5/0	0/0	1/2	
Turtle 1(?)/2	no number	0/5	0/0	0/1	Associated with 012.
Turtle 3	UTA-AASTL-007	0/0	0/0	4/0	One of the scores is hooked.
	UTA-AASTL-009	1/0	0/0	1/0	
Turtle 4	UTA-AASTL-005	3/0	0/0	3/0	
Turtle 5	UTA-AASTL-006	2/0	0/0	2/0	Scores are bisected.
Turtle 6	UTA-AASTL-024	3/0	0/0	3/0	

unique. Some marks run off the edge of the fragments, however, and thus there is the possibility that one tooth mark was counted multiple times as it tracked across multiple fragments. Measurements of alveoli and isolated teeth were taken from four adult and two juvenile jaw elements recovered from the site and compared to the marks as well as visually assessing the congruence between spacing of jaw elements, teeth, and bite marks (after Rogers et al., 2003).

RESULTS

Paleoenvironment and Taphonomy

Fossils in the AAS are derived almost exclusively from the two lowest layers exposed in the quarry (Fig. 1). The lowermost layer is a carbonaceous silty shale (peat) with occasional fine sand mixed in the matrix. Pyrite growths and siderite nodules are common throughout the layer. Some clay is present, as shown by the presence of occasional slickensides. Plant remains are abundant, including coalified plant parts 10–40 cm long, most likely the remains of large branches. Some faint rhizoliths are also visible. Turtles, dinosaurs, and crocodyliforms are the most common macrovertebrates. Because all but one of the specimens used in this study come from the peat bed we will focus on the taphonomy of this layer. Bones are mainly disarticulated and unassociated, with the remains of several species and individuals mixed throughout the exposed area, although some associated bones do occur. The distribution of skeletal elements and variety of sizes indicate many individuals of varying ontogenetic stage. Bones appear to show no preferred horizontal orientation and occur at a variety of vertical angles within the layer, most likely from shrink-swell cycles and or bioturbation. The survey of more than 200 bones from this layer shows that most fall within weathering stages 0 or 1 (Behrensmeyer, 1978) with little evidence of sediment abrasion from aqueous transport or surface pitting from acidic soil conditions. Many bones are complete or nearly complete. Incomplete bones are often separated at growth plates, or, if broken, exhibit transverse fracturing associated with breakage after fossilization (Fiorillo et al., 2000). A diverse vertebrate microfossil assemblage has been recovered, including *Hybodus*, *Lepisosteus*, *Onchopristis*, *Cretodus*, an amphibian, pycnodonts, semionotids, three different chelonian shell morphotypes, and a new species of lungfish (Main et al., in press). All represent mainly aquatic or semi-aquatic taxa known to have freshwater, brackish, or marine distributions (McNulty and Slaughter, 1968; Russell, 1988; Cumbaa et al., 2010).

The layer above the carbonaceous shale represents a thick, well-developed paleosol, though its exact type has yet to be determined. The upper horizons are well drained and consist of red-gray mottles, carbonate nodules, and charcoalified plant remains (Fig. 1). The lower horizon is a gray siltstone where the majority of the ornithopod dinosaur remains were recovered.

Tooth Marks

A total of 31 bone fragments exhibited tooth marks (2 ornithopod, 29 turtle). Eighty definitive tooth marks were identified along with numerous possible marks (Table 1). Nearly 60% of turtle fragments showed tooth marks (17 of 29), while only 1% of ornithopod bones were similarly marked (2 of 202).

Pits.—A total of 54 pits were observed on 16 different fragments (52% of fragments). Pits appeared as bowl-shaped or irregular depressions in the bone surface and varied in diameter from 1–11 mm (Fig. 2 and Table 1). Few bisected pits were observed as described in Njau and Blumenshine (2006). This is likely due to varying states of wear between teeth when the bite took place (Njau and Blumenschine, 2006). Only one pit was observed to have a small notch that potentially represents a partial bisect (Fig. 2B). Pits were observed on carapace and plastron fragments from both turtle taxa, some of which led into scores. At least two pits sit at the center of a 40 mm wide concave oval with edges cracked and depressed towards the center, likely representing bone failure (Fig. 2D). Two pits were identified on the adult dinosaur femur and six smaller, questionable pits on the juvenile femur (Fig. 3). On both femora pits appear oriented transversely across the greater trochanter. Pits on the adult specimen are about twice the size of those on the juvenile. In addition, a large flake (30 mm long by 25 mm wide) and associated pit are present on the lateral side of the broken end of the adult femur (Fig. 3B).

Scores.—Twenty-six scores were observed on 12 fragments (39% of fragments), ranging from 6 to 94 mm long and 2 to 20 mm wide (Fig. 4). Multiple score marks are present on most turtle specimens, but absent from the dinosaur bones. Score shapes vary substantially. Many are shallow and U-shaped in cross section, whereas a few are deeply bisected. They are singular or occur as serial tooth marks. One large score is significantly hooked, which may be diagnostic of inertial feeding behavior (Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009). Some marks end at fractured edges or bone margins. A small subset of scores exhibits bisections along their length. These bisected scores tend to be narrow (≤4 mm) and elongate. One

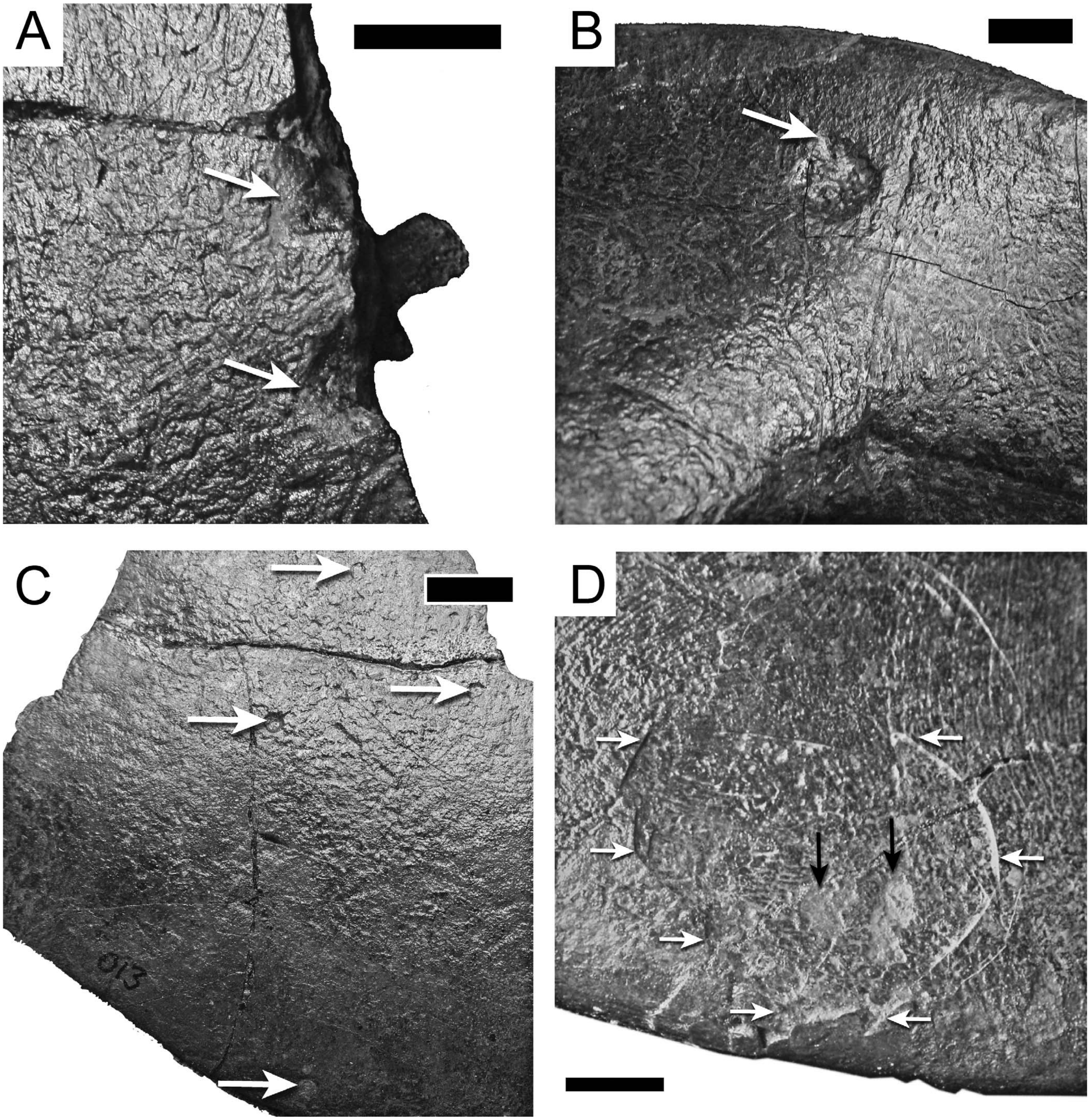

FIGURE 2—Examples of pit marks on AAS specimens. A) Two pits along broken edge of turtle shell UTA-AASTL-012 (arrows). B) Pit on underside of turtle carapace piece UTA-AASTL-003. Arrow points to possible partial bisect. C) Turtle shell with small circular pits (arrows). D) Pits (black arrows) on turtle carapace section UTA-AASTL-001. White arrows are arranged along fractured edges. All scale bars equal 1 cm.

exception occurs on the underside of one turtle specimen (UTA-AASTL-006) where two large, bisected scores have crushed and distorted the underlying bone, with the larger (20 mm wide) leading into a fractured edge.

Punctures.—Only one potential puncture mark was observed on a turtle specimen (UTA-AASTL-001). It is oval in shape and ~3 mm wide.

Distribution Patterns and Comparisons

All three types of bite marks were observed on the turtle specimens, although there is no specific pattern in their distribution. Pits were by far the most commonly observed traces, followed by scores, with punctures the least prevalent (or absent). In the most complete associated turtle specimen, most visible pits and scores surround the edges and sides of the carapace and plastron; the center of each is largely missing (Fig. 5).

The width of the large bisected scores on the underside of turtle specimen UTA-AASTL-006 closely matches the diameter of the largest crocodyliform teeth collected from the site, which range from 19 to 24 mm. Furthermore, the distance between the start of both marks is nearly identical to the distance between the centers of the two largest dental alveoli, about 31–32 mm (Fig. 6).

Only pits but no scores were observed on the dinosaur bones. Although the femora are incomplete these pits appear to be

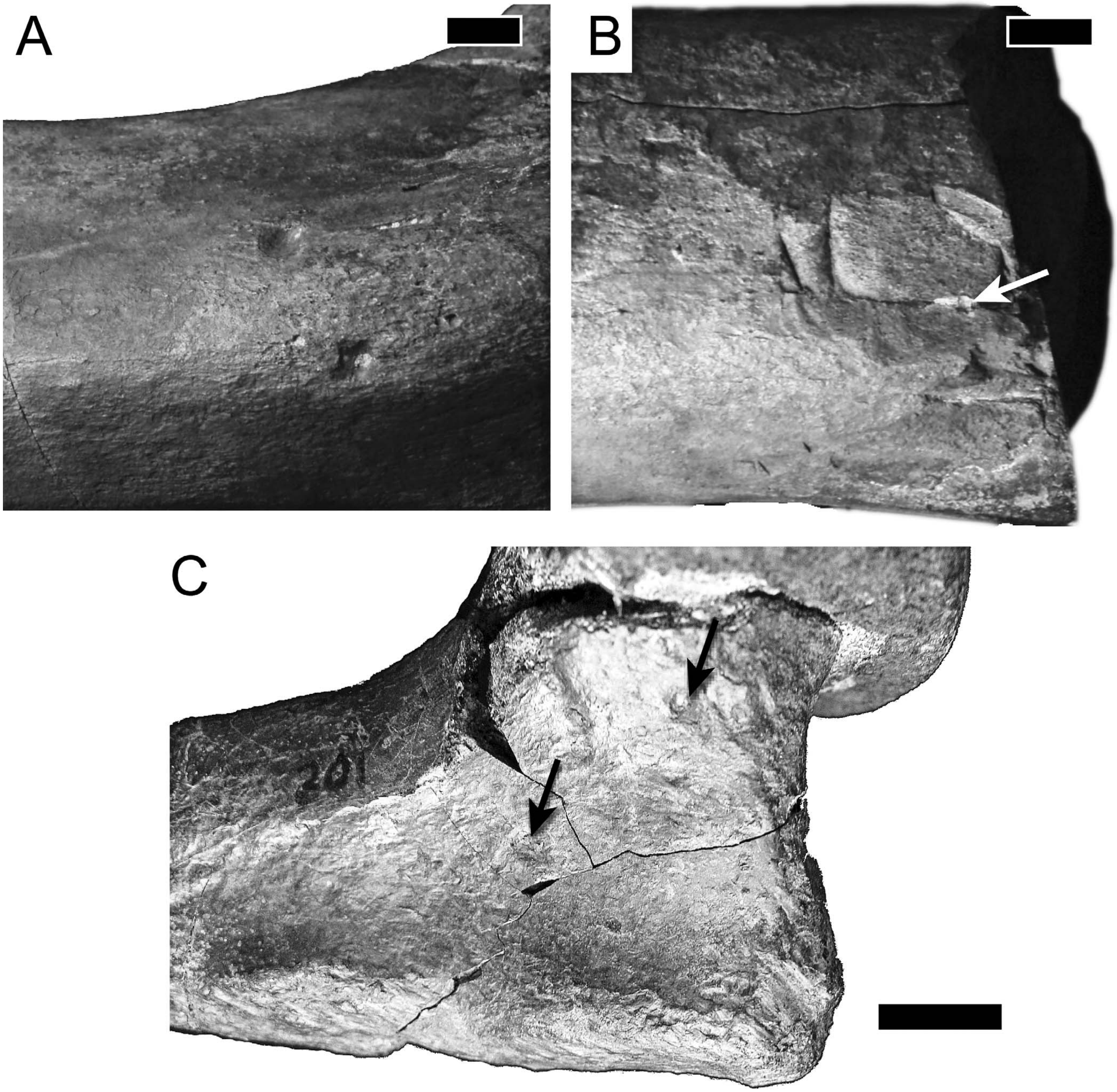

FIGURE 3—A) Proximal end of adult ornithopod femur UTA-AASO-125 showing two pit marks. B) Large flake in broken distal end of same adult ornithopod femur. Arrow points to pit along midline of flake. C) Proximal end of juvenile ornithopod femur UTA-AASO-201 showing two potential pits (arrows). All scale bars equal 1 cm.

concentrated proximally, nearer the femoral head. The large flake and associated single pit are the only other identifiable marks on the broken distal end of the larger femur.

DISCUSSION

Taphonomy and Paleoenvironment

The taphonomy of the lowermost carbonaceous layer indicates it is an attritional assemblage formed in a low-energy environment. The sedimentary matrix is extremely fine grained with no evidence of aqueous sorting. The macrofossils appear to corroborate this interpretation: the lack of surface modification (i.e., abrasion), size disparity between sediment particles and bones, and relatively random orientation of bones suggests they underwent little, if any, aqueous transport (Fiorillo et al., 2000). The nearly complete absence of association among bones, coupled with evidence of remains from multiple individuals or different sizes and ontogenetic stage, strongly suggests attritional formation. The extremely disassociated nature of the macrovertebrate assemblage is likely a combination of decay and disarticulation at the surface prior to burial and or the shrink-swell cycles and bioturbation of the sediment following burial. As such, the macrovertebrate remains at the AAS are most likely parautochthonous, and are representative of dominant taxa from the surrounding area. On the other hand, the mixed terrestrial, freshwater, brackish, and marine nature of the microfossil assemblage suggests a largely allochthonous origin and indicates the close proximity of the AAS to the paleocoastline.

Most bones were likely buried within a few years of deposition as indicated by the minimal amounts of weathering and breakage. The

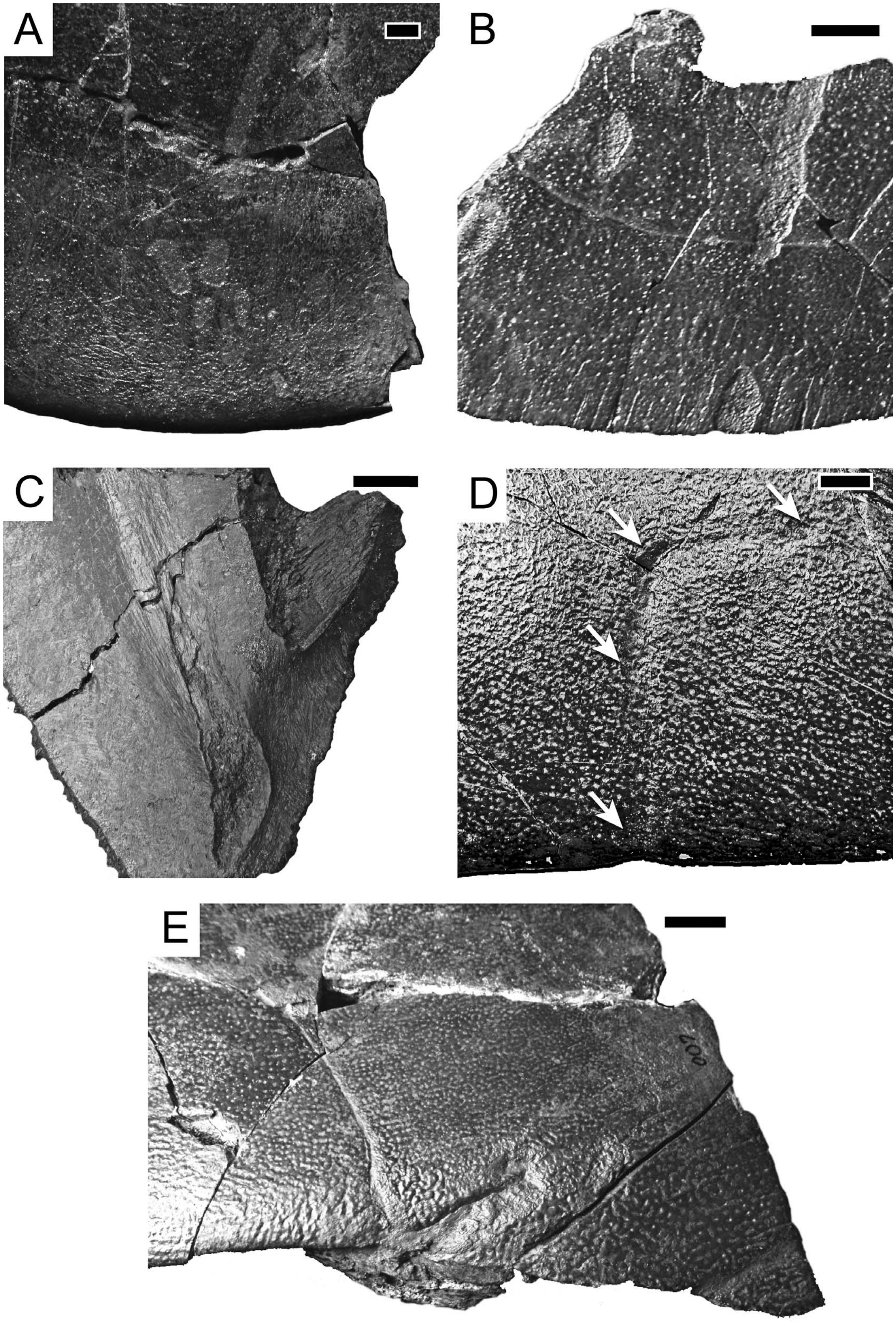

FIGURE 4—Examples of score marks on AAS turtle specimens. A) Carapace section UTA-AASTL-002 with multiple scores. B) Carapace section UTA-AASTL-006 with serial scores. C) Underside of specimen in B, showing two deep bisected scores. D) Carapace section UTA-AASTL-007 with hook score (arrows). E) Bisected scores along edge of same specimen as in D. All scale bars equal 1 cm.

moist conditions, however, would have further delayed surface weathering as seen in similar environments, allowing bones to accumulate for a period of years before complete burial without developing noticeable weathering features (e.g., Behrensmeyer et al., 1979; Lyman and Fox, 1989; Tappen, 1994). Estimating the time of formation for a fossil assemblage is difficult. Comparisons with the weathering profiles of similar assemblages may provide some insight. The nearly homogenous surface condition of the bones (weathering

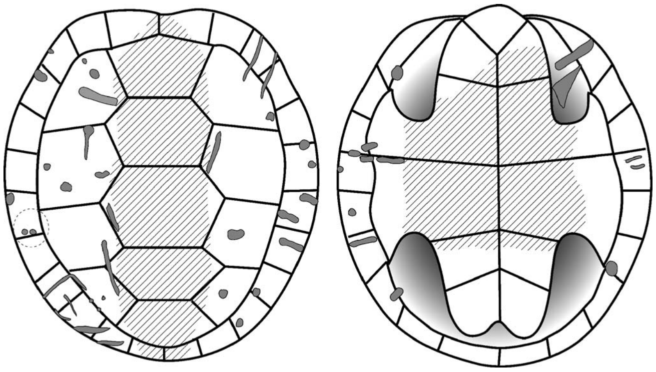

FIGURE 5—Distribution of tooth marks from multiple shell fragments and individuals placed on a generalized turtle shell. Hatched area represents missing portions of shell material recovered so far. In some cases, exact placement of marks on shell can only be estimated.

stage 0–1) and low incidence of breakage are similar to those described from waterhole assemblages in the Miocene of Nebraska (Fiorillo, 1988) and the Late Triassic of Arizona (Fiorillo et al., 2000). Both studies concluded that their respective assemblages formed in relatively short periods of time, on the order of decades. The effect of a moist environment in delaying the onset of weathering may, however, underestimate this time frame (Lyman and Fox, 1989). The remains constituting the AAS assemblage may have accumulated over a period of decades based on this comparison, but the uncertainty created by delayed weathering in a moist environment could potentially extend that estimate up to a century (or more). More work in moist environments will be necessary to understand such fundamental processes such as the time for assemblage formation.

Following burial, organic preservation was enhanced by a locally high water table, which promoted anoxic and reducing conditions, as shown by widespread siderite and pyrite formation. The data as a whole indicates a coastal, possibly seasonal, marsh that was periodically influenced by marine incursions.

Diagnosis of Crocodyliform Tooth Marks

Theropod feeding traces are fairly common in the literature (e.g., Carpenter, 1998; Fiorillo, 1991a; Horner and Lessem, 1993; Erickson and Olson, 1996; Chure et al., 1998; Jacobsen, 2001; Fowler and Sullivan, 2006; Jennings and Hasiotis, 2006), the morphology of which is considered closely related to the ziphodont dentition of the clade. The pronounced denticles on theropod teeth often leave striations in bite marks (Figs. 7A–B). The laterally compressed shape of ziphodont teeth tends to create marks that are more deeply V-shaped in cross section than the more conical teeth of crocodyliforms. Edge marks, where the recurved surface of the posterior tooth edge contacts a sharp surface on the prey bones, are also present. All of these traces have been found through actualistic work with modern komodo dragons (*Varanus komodoensis*), a group that, while only distantly related to theropod dinosaurs, has similar ziphodont dentition (D'Amore and Blumenschine, 2009).

Paleontological examples of bite marks attributed to crocodylian and non-crocodylian crocodyliforms, particularly on turtles (e.g., Fuentes, 2003; Mead et al., 2006; Steadman et al., 2007) and dinosaurs (e.g., Schwimmer, 2002; Rivera-Sylva et al., 2009), are well documented.

FIGURE 6—Visual alignment of AAS crocodilian jaw elements and tooth marks. Isolated teeth were fitted into the two largest maxillary alveoli with clay, then positioned over the score marks shown in Fig. 4C.

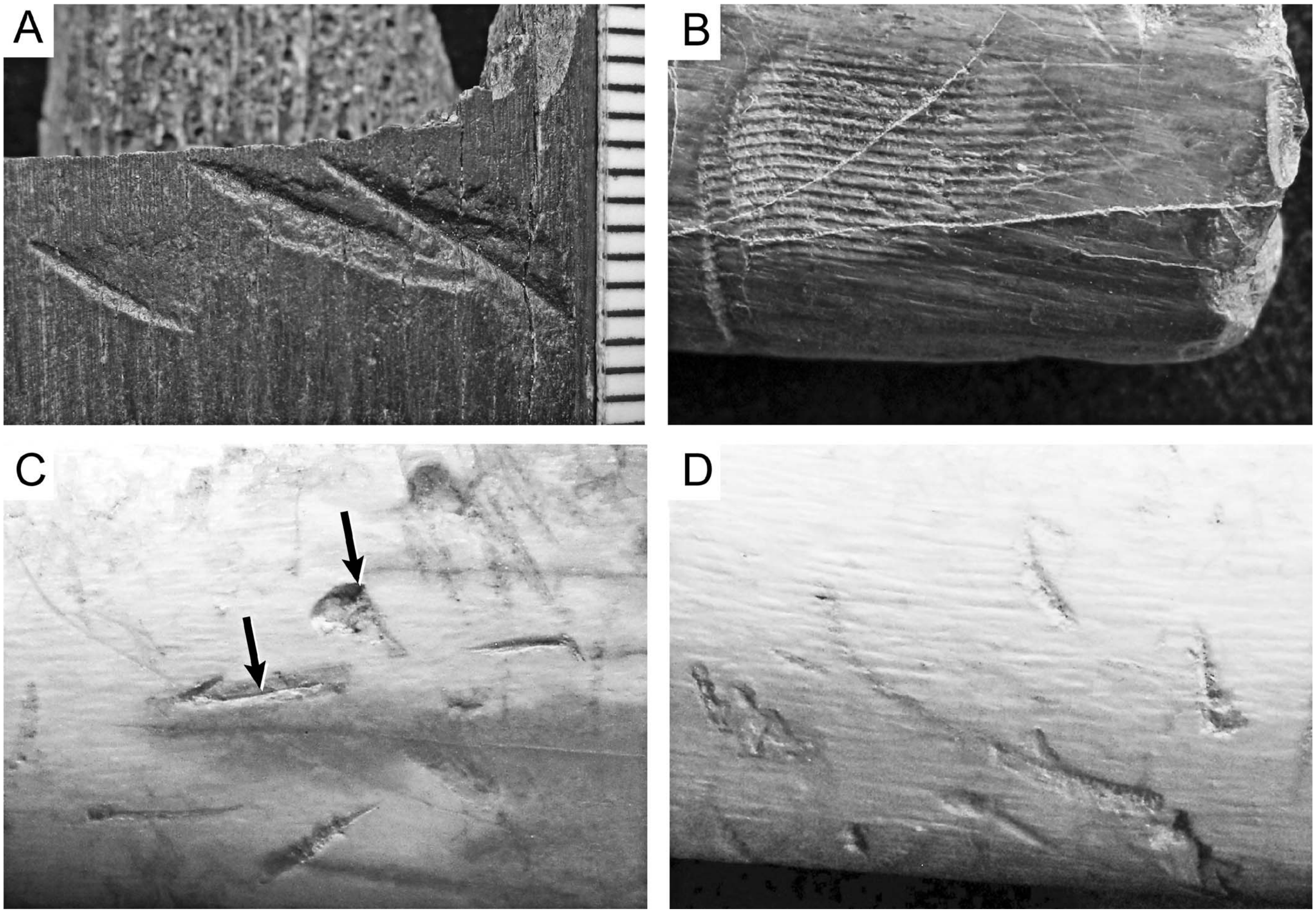

FIGURE 7—Comparison of theropod tooth marks exhibiting ziphodont condition (A, B) and tooth marks produced by a crocodylian (C, D). A) Dinosaur bone fragment with theropod tooth marks. B) Distal ceratopsian rib fragment with striated score from denticles of theropod tooth. C) Bisected score and pit on cow bone. Bisects denoted with arrow. D) Multiple wide, U-shaped scores. Lowermost score is leading from a pit.

Actualistic experiments focusing on members of *Crocodylus niloticus* have revealed a number of novel bite marks and feeding patterns (Njau and Blumenschine, 2006). A variety of tooth mark morphologies may be created, even by a single individual depending on the age of the tooth (Njau and Blumenschine, 2006). Tooth shape varies depending on ontogenetic stage of the individual and eruption age of the tooth. As tooth roots are resorbed and shed, each successive tooth grows larger than its predecessor, with replacement slowing through life (Poole, 1961; Lubkin, 1997; Njau and Blumenschine, 2006). Teeth possess anterior and posterior carina that may have small denticles. Newly erupted teeth are typically more pointed and sharp, becoming rounded and blunt with age and use. The tips of new teeth are easily chipped, creating unusual surfaces.

Tooth marks created by crocodylians tend to be wide and oval or U-shaped in cross section. A lack of extensive furrows or scalloped edges, which have been associated with mammalian-style chewing or gnawing (Binford, 1981), and the presence of hook scores, which are L- or J-shaped structures (Njau and Blumenschine, 2006) both have been associated with animals which exhibit inertial feeding behavior (D'Amore and Blumenschine, 2009). Bisected pits, scores, and punctures, which are caused by the prominent carina present in relatively newly erupted, unworn crocodyliform teeth, were first identified among specimens of *C. niloticus* (Njau and Blumenschine, 2006), but have since been observed in many extant (Drumheller, 2007) and extinct (Rivera-Sylva et al., 2009; Brochu et al., 2010) crocodylians. These marks, identified by subscores within the body of the bite mark and or notches on the margin of pits and punctures, are considered to be diagnostic of crocodyliforms (Figs. 7C–D). Pathological sources of these marks, such as shell disease, can be excluded due to secondary alterations, i.e., fracturing and crushing, related to impact damage (Byers, 2005; Hernandez-Divers et al., 2009).

The traces discovered at the AAS closely match the above morphologies and are, therefore, attributed to a crocodyliform agent. Most important are the presence of bisections, a diagnostic trait of crocodyliform feeding. In addition, the size and spacing of many marks closely matches the skull and dental morphology of AAS crocodyliform fossil remains. All tooth marks lack features created by ziphodont teeth. The few theropod teeth found at the AAS demonstrate no features that could have produced the observed tooth mark morphology. Theropod dinosaurs may, therefore, be excluded as the source of the tooth marks present at this locality. Furthermore, no fossil evidence of any other crocodyliform taxa, such as the goniopholidid *Woodbinesuchus*, has yet been recovered from the site. The new crocodyliform taxon discovered at the AAS is thus inferred to be the primary trace-maker.

Tooth marks and related damage inflicted on bone are traces of feeding behavior (Njau and Blumenschine, 2006). Numerous studies exist on bone modification by extant mammals, but comparatively little actualistic work has been done on reptiles. Crocodyliform feeding traces have been documented on a variety of recent vertebrates, including turtle, cow, horse, small mammal, and human remains (Fisher, 1981; Davidson and Solomon, 1990; Mead et al., 2006; Njau and Blumenschine, 2006; Steadman et al., 2007). There is a growing record of fossil crocodyliform feeding traces from the Mesozoic and early-mid Cenozoic (Fisher, 1981; Schwimmer, 2002; Forrest, 2003; Mikuláš et al., 2006; Hua et al., 2007; Bader et al., 2009; Rivera-Sylva et al., 2009; Schwimmer and Harrell, 2010). The feeding traces described

FIGURE 8—Two examples of feeding behavior by the American alligator, *Alligator mississippiensis*, on turtles. In both cases the shell is being crushed transversely, shattering the shell along the midline. Photos by Jessie Dickson, used with permission.

here, in the context of the AAS, provide important data on the paleobiology of a large Cretaceous crocodyliform and give insight into their role in forming this unique fossil assemblage.

Feeding Behavior and Ecology

The pattern of bite marks and damage to turtle shell and dinosaur bone specimens suggests that the AAS crocodyliform fed in a manner very similar to living, generalist representatives (Cleuren and De Vree, 2000). Based on personal and published observations of crocodylian feeding behavior, the AAS crocodyliform likely fed in the following manner: the entire turtle body is grasped in the mouth, then quick inertial motions of the head and jaws position the turtle either parallel or perpendicular to the jaws, at which point the shell is rotated to one side, where it is crushed between the jaws (Fig. 8). This pattern of feeding takes advantage of potential weak points in the turtle shell where bone is thinnest, targeting the hinges laterally and the mid-sagittal axis of the shell. Such behavior potentially obliterates the central portions of the shell while leaving thicker marginal portions relatively intact. Continuing motion of the jaws may then be used to further fragment the shell before ingestion (Cleuren and De Vree, 2000). In some cases the body of the turtle can be consumed while leaving the carapace and plastron intact (Milàn et al., 2010). The abundance of shell remains and paucity of other turtle skeletal material at the AAS may imply this feeding behavior, although preservation bias in favor of robust shell elements cannot be discounted.

Living crocodylians are known to consume turtles, which have been found to make up the majority of stomach contents in some large alligators and crocodiles (Cott, 1961; Delany and Abercrombie, 1986; Milàn et al., 2010). Multiple healed bite marks on turtle and mammal bones are known from the recent fossil record of the Bahamas and Costa Rica (Mead et al., 2006; Steadman et al., 2007). Weigelt (1989) discussed the feeding grounds of crocodylians and noted the presence of turtle remains occurring with them in the Gosau Formation of Austria as well as the German Weald. The preponderance of both marked and unmarked turtle remains suggest turtles were both plentiful and diverse in the ecosystem, and likely formed a portion of the AAS crocodyliform's diet.

The AAS crocodyliform skull is mostly complete, with at least one element represented from most skull bones, including the frontal, nasal, maxilla, premaxilla, angular, dentary, and quadrate. These bones show that the skull was broad and triangular in shape with a laterally expanded and overhanging premaxilla similar to *Sarcosuchus*. The rostrum is tall and robustly built with a large dentary symphysis, blunt or rounded teeth, and a flat superior alveolar margin. These last three features are shared with the Late Cretaceous alligatoroid *Brachychampsa montana*, which is thought to have included turtles as part of its diet (Carpenter and Lindsey, 1980; Sullivan and Lucas, 2003). The extremely blunt posterior teeth of *Brachychamspa* and related alligatoroids suggest turtle consumption was likely common among crocodyliforms, but the lack of correlation between tooth morphology and chelonivory in living crocodylians implies these taxa were not specialized turtle predators (Sullivan and Lucas, 2003).

Living crocodylians will take a variety of prey, depending on availability, body size, and ontogenetic stage of the individual (Erickson et al., 2003; Njau and Blumenschine, 2006; Milàn et al., 2010). Bitten remains likely resulted from a combination of predation and scavenging. The transverse or oblique orientation of pits to the long axis of both femora is consistent with crocodyliform feeding behavior (Njau and Blumenschine, 2006). The proximal position of pits and large flake associated with a break on the adult dinosaur femur suggest the AAS crocodyliform dismembered larger prey (such as dinosaurs) in a manner similar to living crocodiles: by grasping the limb near the joint and shaking, pulling, or death rolling to separate it from the socket (Njau and Blumenschine, 2006).

Tooth-marked remains occur with the bones of adult and juvenile crocodiles, including numerous teeth, in a single, well mapped horizon (except for the adult ornithopod femur). All bones are well-preserved and lacked any pitting or etching that would indicate they had passed through a crocodile's digestive system. Crocodylians are notorious for their strong stomach acids, which can completely dissolve bone (Fisher, 1981). Small fragments of etched turtle shell were described by Carpenter and Lindsey (1980) as possible scat remnants of *Brachychampsa*, but the large size and good condition of the remains described here precludes a digestive- or scat-residue origin. Instead, we propose that a portion of the fossil bones in this large accumulation were produced during feeding by resident AAS crocodyliforms (Njau, 2006). Some of the associated skeletal remains may even represent preserved caches; however a conclusive determination remains difficult. This site was part of an active feeding area for an extended time as shown by the over 300 isolated crocodyliform teeth and numerous feeding traces recovered to date, a feature typical of localities with intense crocodylian activity (Njau, 2006).

In modern ecosystems crocodylians are known to feed upon a diversity of prey from the surrounding community (Nopsca, 1902; Cott, 1961; Delany and Abercrombie, 1986; Weigelt, 1989). Living crocodylians usually attack prey in water or at the water's edge, dragging the carcass into water to be consumed (Cott, 1961; Weigelt, 1989; Njau and Blumenschine, 2006). They may even travel inland to capture or scavenge prey. Remains too large to swallow may simply be ignored, dismembered, or cached for later consumption (Cott, 1961). Such activities introduce vertebrate remains into an active depositional environment, thus enhancing their preservation potential. As opportunistic predators, crocodylians act as wide samplers of the surrounding fauna, especially smaller and or juvenile individuals (Cott, 1961; Delany and Abercrombie, 1986; Weigelt, 1989). This vertebrate material may be aggregated into relatively small areas (Weigelt, 1989; Njau, 2006), possibly forming bone beds that eventually attract the attention of paleontologists (Nopsca, 1902). In many ways then, crocodyliforms play a positive role in the formation of the vertebrate record of the areas they inhabit.

The bite marks described from the AAS provide additional evidence of crocodyliform predation on dinosaurs and represent the best evidence for this behavior among Late Cretaceous communities (Schwimmer, 2002; Rivera-Sylva et al., 2009; Schwimmer and Harrell, 2010). Crocodyliforms may have killed unwary dinosaurs that journeyed too close to the water's edge and scavenged their carcasses when available, possibly even dragging them to the water from further inland (Cott, 1961; Delany and Abercrombie, 1986; Weigelt, 1989). This is not unlike the paleoecology reconstructed for other, much larger, Cretaceous crocodyliforms (Sereno et al., 2001; Schwimmer, 2002; Rivera-Sylva et al., 2009; Schwimmer and Harrell, 2010). The addition of evidence for similar predatory behavior from the AAS shows that crocodyliforms remained dominant large predators in and around aquatic ecosystems throughout the Cretaceous.

CONCLUSIONS

Fossil turtle and dinosaur specimens from the Upper Cretaceous Woodbine Formation at the AAS show clear evidence of tooth marks consistent with predation by a large crocodyliform. These feeding traces are attributed to a crocodyliform based on (1) the presence of bisected score marks and hook scores and lack of diagnostic marks from ziphodont teeth (such as those of theropods); (2) similar size ranges of feeding traces and crocodyliform teeth recovered from the same bed; (3) the spacing between marks, which is consistent with the distance between the largest dental alveoli on cranial material from the same bed; (4) the location and orientation of bite marks, which follows patterns of feeding behavior observed in living crocodylians (Njau and Blumenschine, 2006; Drumheller, 2007); and (5) an abundance of the crocodyliform taxon and paucity of material from other predatory taxa (including *Woodbinesuchus* and theropod dinosaurs) from the AAS and vicinity. The position of tooth marks and patterns of damage on turtle and dinosaur remains are consistent with feeding behavior observed in living crocodylians (Njau and Blumenschine, 2006; Milàn et al., 2010). Furthermore, the data collected here suggests that crocodyliforms were likely important predators of the AAS coastal ecosystem and their behavior may have contributed to the formation of this unique fossil assemblage.

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