A Diagnosis of *Alligator mississippiensis* Bite Marks with Comparisons to Existing Crocodylian Datasets

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Crocodylians are known to consume and modify bones, but actualistic observations of their bite marks have been limited to forensic case studies and surveys of two taxa: *Crocodylus niloticus* and *Crocodylus porosus*. To further explore patterns of crocodylian bite mark expression, we conducted a survey of traces left by *Alligator mississippiensis*. We compared the results to pre-existing crocodylian datasets regarding the potentially diagnostic traits of bisected marks, hook scores, and a lack of furrows. Mark type did not correlate with vital statistics of the sampled animals or collections protocol. Bisected marks were found in rates similar to those seen in one previous survey of *C. niloticus*, and rates of hook scoring and bone breakage were higher. These traces were all present in higher rates than those reported in *C. porosus*. Unlike results seen in *Crocodylus*, furrows were identified in the *A. mississippiensis* samples. Hook scores were also identified, but recent surveys of non-crocodylian taxa have shown that these features are not unique to crocodylians and instead are related to inertial feeding strategies. The presence and rate of bisected marks found in this study bolster the interpretation that these traces are a clade-wide phenomenon and a useful diagnostic indicator for Crocodylia.

Keywords Tooth mark, Feeding trace, Trophic interaction, Crocodylia

INTRODUCTION

Crocodylians and their relatives long have been identified as active taphonomic agents, modifying and accumulating vertebrate remains (von Nopsca, 1902; Weigelt, 1927). Even though attributions of bite marks to crocodylians and their relatives are common in the paleontological literature (e.g., Davidson and Soloman, 1990; Carpenter and Lindsey, 1980; Erickson, 1984; Schwimmer, 2002, 2010; Forrest, 2003; Fuentes, 2003; Cisneros, 2005; Martin, 2013), actualistic studies of crocodylian bone-modifying behaviors and their diagnostic traces have only recently been performed (Njau and Blumenschine, 2006; Milàn et al., 2010; Westaway et al., 2011). Prior to those studies, most identifications and interpretations of crocodylian bite marks in the fossil record relied on comparisons of putative bite marks to the tooth and jaw morphology of the presumed tracemaker (e.g., Schwimmer, 2002; 2010; Cisneros, 2005; Mead et al., 2006; Steadman et al., 2007). Isolated observations of modern crocodylian feeding behavior also supported the association of specific crocodyliforms with bite marks in the fossil record (e.g., Davidson and Soloman, 1990; Forrest, 2003; Fuentes, 2003). Modern patterns of bite mark locations during intraspecific fighting in crocodylians (e.g., Webb and Manolis, 1983) have been compared with fossil examples to project that specific behavior onto extinct crocodyliforms (Buffetaut, 1983; Williamson, 1996; Avilla et al., 2004; Katsura, 2004). However, without identified diagnostic traces or novel patterns of marks, those identifications were sometimes considered equivocal (Brochu, 2003).

The first large-scale survey of crocodylian bite marks and bone modifications focused on captive and wild specimens of *Crocodylus niloticus*, the Nile crocodile (Njau and Blumenschine, 2006). Patterns of bite marks diverged strongly from more extensively studied mammalian marks in a number of ways. Crocodylians do not exhibit the same bone gnawing behaviors associated with many mammalian groups (Cleuren and deVree, 2000). Also, whereas bones often are ingested incidentally (Fisher, 1981), crocodylians do not actively seek out bone or marrow as a food source. Therefore, types of marks long associated with mammalian feeding strategies, such as the furrows, scalloped edges, and polishing caused during extensive gnawing (sensu Binford, 1981), were absent in the *C. niloticus* sample. Instead, large numbers of marks were often concentrated on grasping sites of bones, where the animal could find purchase before pulling and twisting away portions of the prey item whole for consumption (Njau and Blumenschine, 2006).

Two new types of bite marks were also identified in that *C. niloticus* sample: bisected marks and hook scores (Njau and
Blumenschine, 2006). Crocodylian teeth often have prominent carinae that wear down and chip away with use. When a relatively freshly erupted, unworn tooth is involved in a bite, the carina will often leave a distinct subcore in the mark, effectively “bisecting” it. This trace was also expressed as triangular notches on the margins of deeper punctures. These bisected marks had never been observed or described in any other group, and were therefore considered to be potentially diagnostic for crocodylians. Njau and Blumenschine (2006) then compared the modern bisected marks to traces occurring on bones found in the Plio-Pleistocene Olduvai Basin of Tanzania and determined that those fossilized marks could also be attributed to the crocodylians present at the site. Since the publication of this survey, bisected marks have also been found and attributed to other crocodylians and non-crocodylian crocodyliforms (Rivera-Sylva et al., 2009; Brochu et al., 2010; Noto et al., 2012; Boyd et al., 2013).

Hook scores were defined as L- or J-shaped tooth marks created when an impacting tooth changed direction abruptly during a single biting event (Njau and Blumenschine, 2006). Initially, this type of mark was tentatively associated with the death roll behavior of crocodylians, but it has since been found in non-crocodylians such as the Komodo dragon (Varanus komodoensis) and theropod dinosaurs that presumably did not exhibit death rolling behavior (D’Amore and Blumenschine, 2009). Hook scores now seem to be indicative of animals that exhibit an inertial feeding strategy rather than crocodylians alone.

While this C. niloticus survey represented a major step forward in crocodylian bite mark studies, a need was expressed for sampling of other extant crocodylians in order to independently verify the novelty of the identified marks and to determine how widely these traces occurred in the clade (Njau and Blumenschine, 2006, p. 17). A short study on Paleosuchus palpebrosus modifications of turtle shell by Milán and colleagues (2010) focused on patterns of shell breakage and behavior specific to chelonivory and not on detailed descriptions of the bite marks themselves. Forensic case studies covering attacks on humans provided potential sources of independent analyses of these groups (e.g., Hertner, 2006; Harding and Wolf, 2006; Sartain and Steele, 2009; Mendieta and Duarte, 2009; Cupal-Magaña et al., 2010; Haddad and Fonseca, 2011). Those studies focused more on patterns of soft tissue damage and, because most only covered one or a few attack events, the sample size was limited. Still, even though those studies are not directly comparable to the Njau and Blumenschine (2006) study, discussions of feeding strategy and bone modifications were largely consistent with the patterns described for C. niloticus.

Westaway and colleagues (2011) provided the first attempt to independently verify the patterns of modification described in C. niloticus. Three captive specimens of Crocodylus porosus, the salt water crocodile, were observed feeding on two feral pig (Sus scrofa) carcasses provided by the researchers. After feeding, the pig remains were cleaned and all bone modifications noted. Fracturing was common, if less so than in the C. niloticus survey, but identified bite marks were rare and only one potential bisected pit was noted by the authors. The scarcity of bite marks in the C. porosus study, particularly ones that exhibited the same novel morphologies as described in the larger C. niloticus survey, led the authors to question the applicability of the diagnostic marks identified by Njau and Blumenschine (2006) in C. niloticus to other crocodylian taxa. However, it was unclear if the differences in patterns between the Njau and Blumenschine (2006) and the Westaway et al. (2011) studies were the result of different sample collection protocols, the limited sample size from C. porosus, or differences in feeding ecology between the two species of Crocodylus.

A recent study by Baquedano and colleagues (2012) represented a second independent survey of modern crocodylian bite marks. The observed species was never identified by name in that paper, but two of the individuals are figured and are identifiable to C. niloticus (SKD, pers. obs.). Eight crocodiles were given 19 partial articulated limbs from pigs, boar, sheep, and cows. The rates of marked bones and marks per bone were significantly less than those seen by Njau and Blumenschine (2006). No hook scores were identified, and 43% of all marks were determined to be bisected (Baquedano et al., 2013). A number of possible explanations were provided for those differences in rate: collection protocols were not identical, different prey types were used, and only female crocodiles were observed. Most feeding events occurred in relative isolation with little interaction between individuals, and it was posited that females might be less inclined towards intraspecific conflict than males. Additionally, the definition of bisected, or carinated, marks seems to differ between the two studies—marks that exhibited marginal notches and discrete sub-grooves as bisections (sensu Njau and Blumenschine, 2006) were grouped by Baquedano et al. (2013) alongside marks that had a V-shaped profile in cross-section (contra Njau and Blumenschine, 2006).

To further explore how crocodylians modify prey bone and whether their traces can be positively diagnosed in the fossil record, we collected bite mark specimens of Alligator mississippiensis, the American alligator. Alligator mississippiensis is an ideal species for continuing actualistic research involving crocodylians. First, because of successful conservation efforts and the ensuing relative ease of access to members of this species to researchers, the anatomy, ecology, and behavior of A. mississippiensis has been extensively studied (Brochu, 1999). Second, because Alligator and Crocodylus last shared a common in the Late Cretaceous (Brochu, 1999, 2004a; Oaks, 2011), inclusion of Alligator increases our ability to identify commonalities and understand ranges of variation in bite mark type and frequency across Crocodylia. Information from two closely related species—C. niloticus and C. porosus, last shared a common ancestor in the middle to late Miocene (Brochu, 2000; Oaks, 2011; Meredith et al., 2011; Brochu and Storrs, 2012)—would only allow us to characterize features common to Crocodylus.
Variation in rates of mark types even within *C. niloticus*, as well as potentially inconsistent classification schemes, further complicate application of these actualistic datasets to the fossil record (Baquedano et al., 2012). It is unclear at present whether apparent differences between published analyses are based on actual biological variation between samples or on different analytical protocols. Our study attempts to explore and clarify this conflict between the existing crocodylian samples by broadening the phylogenetic reach of existing datasets.

**Crocodylian Feeding Behavior**

Interpretations of past crocodylian diets can vary substantially between species, and even age groups, based largely on factors such as snout shape and body size. However, the manner by which crocodylians obtain and consume their food is broadly similar (Cleurens and deVree, 2000). Prey is acquired utilizing the anterior portion of the jaw (Njau and Blumenschine, 2006) and most often involves a sideways, rotational motion of the head so that the angle of approach brings one side of the jaw into contact with the prey item (Cleurens and deVree, 2000).

Prey items are then dispatched in a number of ways. Smaller animals can be repositioned in the mouth until a single, powerful killing bite can be performed (Cleurens and deVree, 2000). This repositioning utilizes inertial feeding behavior. The head and neck are elevated and the hyolingual apparatus presses the prey item dorsally in the mouth. Then, the rapid opening of the jaws, partnered with further elevation of the open jaws, accelerates the prey item further into the mouth cavity. This can be partnered with lateral movement when shifting the prey item to one side or the other is desired. Rapid jaw closure, partnered with reversal of any lateral movement and a retraction of the hyolingual apparatus, thrusts the head forward. The prey item is then positioned further back in the toothrow. These types of bites can occur multiple times, shifting prey position in the mouth, until a killing or crushing bite can be applied (Cleurens and deVree, 2000). This phase can be particularly important when hard-bodied prey types, such as turtles, are involved, since careful positioning is required to effectively compromise the shell (Milán et al., 2010).

Larger prey items may require further effort. Jaw repositioning, similar to the inertial bites described above, can be used to achieve a better grasp on struggling prey. Subduing prey and retreating under water can lead to drowning (Njau and Blumenschine, 2006). “Death roll” behavior is also common, in which a crocodylian, having secured some portion of its prey in its jaws, initiates often violent rotation along the long axis of its body. Limbs are folded against the body, and the maneuver is accomplished through coordinated movements of head, trunk, and tail (Fish et al., 2007). Violent, lateral thrashing and repeated crushing bites can also cause further trauma, up to and including dismemberment (Davidson and Solomon, 1990).

Once smaller prey are dead, further inertial bites can be utilized to transport food items towards the throat, in preparation for swallowing (Cleurens and deVree, 2000). Larger prey may require further reduction before swallowing is possible. However, the conical teeth of most crocodylians, though useful for grasping prey, are not well adapted for cutting or tearing tissue on their own. Continued lateral thrashing can tear smaller portions off of a prey item, and crocodylians have been observed modifying this behavior to take advantage of a hard substrate, slamming prey items against rocks or fixtures in enclosures (Njau and Blumenschine, 2006; Drumheller, personal observation). Additional death rolling can twist away bite-sized portions of food (Fish et al., 2007), a technique that can become even more effective when two or more animals utilize it on the same prey item simultaneously, moving in opposition to one another (Njau and Blumenschine, 2006). Swallowing is accomplished through further inertial repositioning, until the prey item is positioned where muscles of the throat can take over food transport (Cleurens and deVree, 2000). Bones ingested during this phase are largely destroyed during digestion (Fisher, 1981).

Large prey reduction and defleshing can continue until the entire prey item is consumed. However, sections of carcases are often abandoned, particularly when large or durable prey items are involved. Violent dismemberment can scatter elements, which are then discarded (Davidson and Solomon, 1990). Remnants of turtle shell are often abandoned once the majority of soft tissues have been consumed (Milán et al., 2010). Though bite marks can be left at any of the stages of feeding described above, it is to these abandoned remnants of meals that taphonomists must turn (Njau and Blumenschine, 2006).

**MATERIALS AND METHODS**

**Bite Mark Sample Collection**

Partially butchered cow hind limbs and pig femora were obtained from meat packaging plants and transported to the St. Augustine Alligator Farm (SAAF) in St. Augustine, Florida (USA). Cow specimens consisted of articulated femora, tibiae, patellae, and varying amounts of tarsal bones, because the pes was partially severed as a part of initial processing. Though portions of muscle tissue had been removed previously from the midshaft regions of all limb elements, significant amounts of flesh remained, particularly surrounding the joints of the cow limbs. The pig femora had only small amounts of remaining flesh.

Two sets of bite mark samples were collected. The first sample (Group 1) consisted of specimens presented to 14 individual specimens of *A. mississippiensis* in isolation (Figure 1). Smaller animals were presented with the isolated pig femora while larger animals were given the partially butchered cow
hind limbs. Each animal was unrestrained while bite mark samples were collected, except in cases when handler and/or animal safety was a concern. In the event that restraint was deemed necessary by SAAF staff, individuals were held near the base of the skull by a handler seated on the animal’s back to limit movement. The animals were then given samples to bite from this position. Behaviors of note, such as death rolling or violent lateral thrashing, were recorded. Many samples were voluntarily abandoned, but some animals had to be induced to drop the limbs to facilitate retrieval once active biting ceased. Specimens were then labeled with each animal’s SAAF identification number or name for easy correlation to veterinary metadata (e.g., age, sex, length, weight) kept on site at the facility (Table 1). Animals whose bite marks were collected in this manner represented male and female, captive bred and wild caught individuals across a variety of ages (5–56 years in age) and sizes (122–402 cm in total length). Photographs and video footage were collected during the sampling events.

The second sample (Group 2) consisted of 27 partially butchered cow hind limbs placed in two enclosures containing adult A. mississippiensis (Figure 1). Feeding events were again photographed and video recorded using an Olympus® Stylus™ 760 camera (Olympus America, Center Valley, PA, USA). Most specimens were voluntarily abandoned by the animals within hours of introduction into the enclosures. However, some were kept for longer periods (up to several days) or abandoned in the water of the enclosures where immediate retrieval was problematic. Those samples were collected within a week of initial introduction when the water features for one of the enclosures was drained for regularly scheduled cleaning by the SAAF staff. During that time, the enclosures were thoroughly searched in order to avoid specimen loss not related to consumption. The remaining enclosure encompassed a natural section of swamp that could not be drained. Samples uncollected from that enclosure were considered lost and not necessarily consumed. Of the 27 limbs placed in the enclosures, 6 were never retrieved, with 4 being interpreted as wholly consumed and 2 recorded as lost. Animals were observed breaking and swallowing large sections of cow limbs, and many retrieved limbs were missing large fragments or had been disassociated from the other portions of the limb.

Samples from both groups were then cleaned and prepared by simmering each limb in water with an enzymatic detergent (Borax®, U.S. Borax Inc., Greenwood Village, CO, USA), then by successive rounds of rinsing and hand scrubbing with milder nonenzymatic detergents (Luminox®, Alconox, Inc., White Plains, NY, USA; and Dawn®, Procter & Gamble, Cincinnati, OH, USA), sponges, and soft plastic brushes until no more soft tissue remained and the bones were reasonably free of grease. These enzymatic and non-enzymatic detergents have proven to be highly successful at cleaning soft tissue and grease from bone in previous studies (e.g., Fenton et al., 2003; Mairs et al., 2004; Steadman et al., 2006).

**Bite Mark Identification and Classification**

Bite marks were identified and differentiated from the few butchering traces using a 10X hand lens following the method described in Blumenschine et al. (1996). Marks were then categorized according to Binford’s (1981) classification scheme, which divides all feeding traces into four broad groupings: pits, punctures, scores, and furrows. Pits are formed when a tooth contacts the surface of a bone, depressing but never fully piercing the cortical bone. When the tooth does break through the cortical bone, the bite marks is instead called a puncture. Similarly, when a tooth is dragged along the surface of a bone, leaving a groove that crushes and depresses the cortical bone without fully fracturing it, the mark is called a score. When the cortical bone is pierced as the tooth moves along the bone surface, the mark is instead called a furrow.

Diagnostic bite marks take the form of novel expressions of these general classes or statistically definable patterns of marks described in terms of preferential location, orientation, density, and other variables. Though a separate classification
scheme for bite marks specifically attributed to crocodylians has been suggested and ichnogenera erected by Mikulás and colleagues (2006), they were largely redundant with Binford’s (1981) earlier, more widely used nomenclature. Novel structures, including bisected pits, punctures, and scores, and hook scores as described by Njau and Blumenschine (2006), were recorded.

Other types of bone modifications were observed and recorded as well. Biting events often cause secondary alterations to bone in the form of fracturing patterns related to impact trauma (Byers, 2005). Depressed fractures occur when the bone surrounding a bite mark collapses under the force of the impacting tooth. This can impart an irregular, jagged margin to a bite mark, particularly a puncture or furrow. If the surrounding bone does not collapse under the force of a bite, due to differences in bone structure and bite strength, it may instead fracture in linear patterns radiating from the location of the impact. These secondary alterations are called fracture lines. If a bite is powerful enough to break a bone completely, these fractures often propagate in a spiral fashion around the circumference of the bone. These are called spiral fractures and often are expressed as diagonal breaks across the shafts of long bones. It is important to note that these types of marks are often associated with bite marks, but they can also be caused by other biotic and abiotic bone modifying agents involving impacting forces.

Each bone and its associated bite marks were photographed in detail with an Olympus Stylus 760 camera. As determined from blind inter-analyst tests, bite marks can be differentiated from other types of bone surface modifications using only a 10× hand lens for magnification (Blumenschine et al., 1996). However, the appearance of bisected marks as previously identified in the *C. niloticus* actualistic survey was believed to be affected by the relative wear of tooth carinae, and a spectrum of tooth morphologies and wear stages typically is present even within the mouth of a single individual (Njau and Blumenschine, 2006). Microscopic observation of marks, where more subtle bisections caused by incompletely worn carinae might still be visible, had been linked previously with higher rates of identified bisected marks (Baquedano et al., 2012). Therefore, specimens from the first group, representing bite marks from a single known animal, were sectioned into pieces small enough (<10 cm in maximum length) to fit in the stage of a Hitachi® S-3400N variable pressure scanning electron microscope (VP-SEM). Because this is a variable pressure SEM, further processing, such as gold sputter coating, was unnecessary. All bite marks and any tool marks created during the butchering process were imaged in the VP-SEM and the scale recorded. Any novel structures that had not been visible under the initial 10× hand lens survey were also recorded at this point.

To ensure that bite marks from only one identified individual were collected on each of these samples, the nature of Group 1’s collection was, of necessity, very limited. Animals were often physically isolated or restrained. Periods of feeding time were limited. Therefore, information on location, density, and orientation of these marks was not collected.

Since Group 2 bite marks were collected during more naturalistic feeding behavior and over longer periods of time than

### TABLE 1

| Accession number | Imaged | Sample | Sex | Age | Total length | Head length | Snout-vent length | Weight | Origin | Notes |
|------------------|--------|--------|-----|-----|--------------|-------------|-------------------|--------|--------|-------|
| 97062            | Y      | Pig    | M   | 22Y, 11M, 23D | 314 cm | 45 cm | 161 cm | 185.97 kg | C | Unrestrained |
| 99013            | N      | Cow    | M   | ~31Y | 296 cm | 41 cm | 151 cm | 143.6 kg | ? | Unrestrained |
| A05001           | N      | Cow    | M   | Adult | 244 cm | 31.5 cm | 120 cm | ? | ? | Unrestrained |
| A01025           | Y      | Cow    | M   | >56  | 402 cm | 57 cm | 193 cm | ? | W | Unrestrained |
| A00241           | N      | Pig    | ?   | 5Y, 11M, 5D | 122 cm | 15.25 cm | 62.25 cm | 7.8 kg | C | Restrained |
| 99106            | Y      | Pig    | ?   | 6Y, 10M, 9D | 185.5 cm | 25.5 cm | 95.25 cm | 25.4 kg | W | Restrained |
| A00268           | Y      | Pig    | ?   | 5Y, 11M, 5D | 146 cm | 19 cm | 73.5 cm | 12.6 kg | C | Restrained |
| 97103            | Y      | Cow    | M   | Adult | 304 cm | 41 cm | 158 cm | ? | ? | Unrestrained with 97064 |
| 97064            | Y      | Cow    | M   | 22Y, 11M, 24D | 353 cm | 45.5 cm | 169 cm | ? | C | Unrestrained |
| Fluffy           | Y      | Cow    | M   | Adult | ? | ? | ? | ? | ? | Unrestrained |
| Wally            | Y      | Cow    | M   | Adult | ? | ? | ? | ? | ? | Unrestrained |
| Mother           | Y      | Cow    | F   | Adult | ? | ? | ? | ? | ? | Unrestrained |
| 40264318         | Y      | Cow    | ?   | Adult | ? | ? | ? | ? | ? | Unrestrained |
| tt 00852         | N      | Pig    | ?   | Juvenile | 160 cm | 20.5 cm | 105.5 cm | 14.8 kg | ? | Restrained |

*Vital statistics were provided by the SAAF. Missing information is indicated with a ‘?’ Collection protocol information was recorded at the time of sampling. Under ‘Imaged,’ Y = yes and N = no. Under ‘Sex,’ M = male and F = female. Under ‘Origin,’ C = captive and W = wild.*
those of Group 1, these samples were inspected for presence or absence of marks as well as for preferences of mark location and orientation. Long bones from Group 2, representing long-term group feeding, were measured and marked delineating a proximal one-fourth, distal one-fourth, and central one-half of each bone. On broken long-bones, these delineations had to be estimated using references to landmarks on the remaining portions of the bones. Bite marks were identified and re-counted from each section. Then each specimen was oriented adjacent to a Skill® 8601-RL laser level (Robert Bosch, LLC, Farmington Hills, MI, USA) so that the laser level projected a laser line along the long dimension of the shaft. Measurements of the angle of individual bite marks found on each specimen in relation to the long dimension of the shaft were taken using the laser line and a protractor wherein the proximal end of the bone represented 0° along the laser line, and the distal end represented 180°. These angles were then entered into PAST 2.16 software (Hammer et al., 2001) to generate rose diagrams for better visualization of observed patterns.

Both legs of identified hook scores were measured in this manner, and the angle of the hook itself recorded. D’Amore and Blumenschine (2009) further refined the original definition of hook scores (Njau and Blumenschine, 2006), dividing the marks into groups based on the angle formed by two legs of the “hook.” Score curvature was grouped into three categories representing the angle one leg of the hook diverted from the initial direction of movement. Marks were grouped into <45°, 45–90°, and >90°, with only scores bending more than 90°, where the legs of the hook formed an acute angle, being called a true hook score (see D’Amore and Blumenschine, 2009, fig. 2). While hook score curvature was collected in a slightly different manner in the present study, the angle between the legs of each mark was measured instead of the angle at which each mark bent, categories were selected to make direct comparison between these two datasets possible (e.g., a hook mark that bends from the original bite trajectory >90° will have an angle between mark legs of <90°).

Bite marks on any remaining bones and bone fragments were also recorded. Mark counts were tallied and analyzed to calculate comparative statistics, such as percent of marks which exhibit bisects, percent of marked bones exhibiting bisected marks, and percent of specific mark types present on the different long bone sections (Appendix Table A1). These metrics were calculated using Microsoft® Excel® (Microsoft Corporation, Redmond, WA, USA) and PAST™ (Hammer et al., 2001).

In the absence of complete cow and pig carcasses, both sets of samples were unsuited to addressing questions of element choice and preference in crocodylians. As previously expressed (Njau and Blumenschine, 2006; Baquedano et al., 2012), actualistic observations of marks left on whole, living prey items, preferably from natural systems, are still required to adequately address this aspect of crocodylian predation and feeding traces.

RESULTS

Bite marks were present on every sample from both collected groups, though individual bones within the articulated cow limbs occasionally lacked feeding traces. Following Binford’s (1981) classification scheme, pits, punctures, scores, and furrows were all identified. Bisected marks and hook scores (Njau and Blumenschine, 2006) were identified in samples from both collected groups. Depressed fractures, fracture lines, and spiral fractures (Byers, 2005) were also found. A few individual bite marks were associated with flakes from the denser long-bone midshafts. Other bone surface modifications and any unusual structures, including cut marks related to butchering and pathologies, were identified and excluded from subsequent consideration.

Group 1 – Individual Feeding

At least one pit was present on every specimen collected for this group. Pits ranged from circular and ovoid, reflecting the shape of the individual tooth tip, to slightly teardrop-shaped, indicating a subtle drag-out structure from the end of the biting event. SEM images revealed obvious crushing damage to the
cortical bone inside the pits, indicative of the impact damage (Figure 2).

Only two punctures were identified on specimens created by SAAF A01025 and SAAF ‘Fluffy.’ Both individuals were large adult males, and SAAF A01025 was both the oldest (>56 years) and the largest (total length 402 cm) of the sampled animals (Table 1). SAAF A01025 was a wild-caught individual, whereas SAAF Fluffy’s origin, exact age, and other statistics were not available in the veterinary records. Both punctures were associated with secondary alterations, giving them irregular, fractured margins. Each puncture was located on the proximal end of the shaft of cow tibiae (Figure 2).

As with pits, scores were present on every sampled specimen. SEM images again revealed obvious crushing of cortical bone within the bite marks. Individual scores ranged from a few millimeters to several centimeters in length. Often one end was more rounded, indicating the point of tooth entry, and the other tapered to a point where the tooth pulled away from the surface of the bone. Some scores exhibited obvious microstriations (Baquedano et al., 2012), a feature possibly linked to the irregular surface of chipped, worn crocodylian teeth. In extreme cases, this would be expressed as a large puncture with a drag-out score exiting the mark (Figure 2). No furrows were identified among the bite marks collected from this group.

Seven specimens left bisected pits or scores on samples. SAAF 40264318 created one bisected pit that was only visible using the SEM. SAAF 99106 left two bisected pits and two bisected scores. However, only the pits’ bisections were identifiable with a 10X hand lens. SAAF “Fluffy” left two bisected pits and SAAF ‘Mother’ left three bisected scores, all of which were identifiable under a hand lens. The sample modified by SAAF A01025 had three bisected scores, of which only one was visible with a hand lens alone. SAAF 99013 left one bisected pit and SAAF t00852 left another bisected pit and one bisected score. These three marks were only identifiable under higher magnification in the SEM (e.g., Figure 3). The presence of bisected marks did not seem to be a function of animal age or size, with marks made by the largest, oldest specimen (SAAF A01025) and one of the smallest, youngest specimens (SAAF t00852). Though the majority of the sampled animals were male, the lone identified female, SAAF “Mother,” was one of the seven animals that left bisected marks, implying that sex was also not a factor. Similarly, neither the origin of the animals (captive bred or wild caught), nor the collection protocol (restrained or unrestrained), nor the type of prey item (pig femur or cow limb) could successfully predict presence or absence of bisected marks (Table 1).

While most identified scores had some degree of curvature, true hook scores (D’Amore and Blumenschine, 2009) were only present on samples taken from four individuals: SAAF A05001, SAAF 99013, SAAF t00852, and Mother. SAAF A05001 and SAAF 99013 created one hook score each, while SAAF t00852 left two, and SAAF Mother created three (Figure 3). Like the bisected marks, presence or absence of these marks was not restricted to a single size, age, sex, origin, or collection protocol. Contra Njau and Blumenschine’s (2006) interpretation that these marks were indicative of death-rolling behavior, none of the animals that created these marks exhibited this behavior during sample collection, which aligns well with D’Amore and Blumenschine’s (2009) findings. However, SAAF Mother in particular was noted for her violent attack on the cow limb, including powerful, repeated bites and lateral shaking of the sample. Handlers suggested that her behavior may have been less from an interest in feeding, and more in defense of her nest, which was nearby in the enclosure.

All bite marks exhibit some level of crushing damage, and a few marks exhibit further alteration and breakage meeting the criteria of secondary impact damage. Both identified punctures were associated with depressed fractures, giving them irregular, broken margins. A small number of fracture lines are also present radiating from the puncture created by specimen SAAF A01025 (Figure 2). The tibia from the cow limb presented to SAAF A01025 was broken, and roughly the distal half of the bone with all articulated distal elements were ingested immediately following the biting and fracturing event. The break on the recovered portion of the tibia is a spiral fracture. A large pit is present directly on the margin of the break, and the fracture was accomplished with a single, powerful bite to the tibia (Figure 3).

**Group 2 – Group Feeding**

Samples from this group represent bite marks made during prolonged group feeding (Figure 4). Twenty-seven articulated cow hind limbs were introduced during the collection of this
group. Of these, only 21 femora, 17 tibiae, and 23 other elements (e.g., patellae, astragali) representing 61 complete or partial bones were retrieved. On these bones, 3,831 individual marks were identified. Traces on long bones (i.e., femora and tibiae) were counted and organized by location on the element: proximal one-fourth, distal one-fourth, and central one-half. The results of this survey are presented in the Appendix (Table A1).

The density of bite marks on bone elements varied greatly, ranging from 1 (SKD12.3) to 378 (SKD14.1) individual marks identified per bone. Scores are by far the most common type of mark, representing 59.57% of all identified traces. Pits are the second most common, comprising 31.45% of the recorded marks. Punctures constitute 8.48% of the remaining bite marks, and furrows are represented by a mere 0.1% of marks. Of these, 10.37% of all pits, 9.95% of all scores, and 19.08% of all punctures exhibit bisections, representing 10.8% of all observed bite marks. Of the sampled bones, 83.61% exhibited at least one bisected mark. Hook scores constituted 6.18% of all observed scores, and were present on 62.5% of the observed bones.

Punctures and furrows were largely restricted to the proximal and distal ends of long bones. All six furrows were identified on proximal or distal portions of femora. Of the 309 total, identified punctures, 277 marks, comprising 89.64% of the subsample, were present on either the proximal or distal ends of the long bones, while a comparatively scant 32 marks, or 10.36% of punctures, were located on the denser long bone shafts. Three punctures were expressed as notches (Capaldo and Blumenschine, 1994) on the margin of spiral fractures. These notches, one on element SKD2 and two on SKD22, are associated with further alteration on the interior surface of the marrow cavity of both femora where the impact of the tooth created enough percussive force to flake away the surrounding bone. Other flakes have been identified in association with pits or scores on the exterior of the dense bone of the shaft (SKD5.2, SKD8.1, SKD21), along broken margins associated with spiral fractures (SKD17), and as the flaked away fragments themselves (SKD20).

Individual bite marks tended to be preferentially oriented perpendicular to the long axis of the bone, with very few marks falling in shallower, more parallel angles. A Rose diagram was generated with angle measurements taken from 1,688 individual bite marks (Figure 5). A random orientation of these marks was rejected using a Rao’s U test of uniform distribution ($p < 0.0001$). The diagram indicates a strong peak in orientations roughly perpendicular to the long axis of the bones, with a calculated mean of 90.6$^\circ$, a median of 91$^\circ$, and quartiles terminating at 73$^\circ$ and 109$^\circ$.
DISCUSSION

Bisected marks were identified in Group 1 samples from members of *Alligator mississippiensis* spanning all age and size classifications. These findings bolster the interpretation that bisected marks are a population-wide phenomenon. However, degree of prey bone damage, in terms of gross fracturing and more penetrative bite marks (i.e., punctures), does seem to be linked to body size in terms of both animal mass and length. This makes intuitive sense, because crocodylian bite force has been demonstrated to scale closely with animal size (Erickson et al., 2003, 2012).

Observed patterns of Group 2 *Alligator mississippiensis* bite mark type, location, and proportion are largely congruent with the Njau and Blumenschine (2006) *Crocodylus niloticus* study, though interesting differences are present. Identified marks were often (but not always) present in numbers per bone that exceeded that expected in similarly collected mammalian samples (378 individual marks per element in *A. mississippiensis*, 250 in *C. niloticus* from Njau and Blumenschine, 2006). These numbers surpass even captive mammalian-modified bones created during extensive “boredom gnawing” (Haynes, 1982). Both these numbers also far outstrip the density of marks per bone reported by Baquedano et al. (2012) at only 20. The animals in the present study were observed feeding collectively and competing for each sample, bolstering the interpretation that multiple participants increases the number of observed feeding trace density (Baquedano et al., 2012). However, the *A. mississippiensis* specimens observed included both male and female animals, indicating that this variable is probably not affecting the resulting bite mark types beyond the expected differences correlated with the range of body sizes and bite forces expected between the sexes (Erickson et al., 2003, 2012).

Types of bone modification associated with gnawing, such as extensive furrowing and concentrated damage at long bone ends (Binford, 1981), were largely absent in both collections. However, furrows, which were wholly absent in previous studies (Njau and Blumenschine, 2006; Westaway et al., 2011; Baquedano et al., 2012), were identified in this survey, which indicates that their absence should not be used as a diagnostic characteristic of crocodylian feeding traces. These marks were largely restricted to long bone ends, as were the punctures, and they also often occurred in isolation. This indicates that their presence was most likely a function of prey bone density and not focused attention by the animals in order to access the marrow cavity. This result is congruent with documented crocodylian feeding behaviors and inertial feeding strategies in general (Cleurens and deVree, 2000).

Bisected marks were identified at similar frequencies (10% of all observed bite marks in *C. niloticus*, 10.8% in *A. mississippiensis*) and were present on a similar percentage of individual marked bones (82.5% in *C. niloticus*, 83.61% in *A. mississippiensis*) to those presented by Njau and Blumenschine (2006). V-shaped marks were not identified as bisections (Njau and Blumenschine, 2006) and are therefore excluded from these statistics (contra Baquedano et al., 2012). Similar expression of bisected marks in the two samples reflects a broad similarity between tooth morphology and wear patterns in the two species. Though rare from the point of view of individual marks, the presence of at least one bisected mark on >80% of marked bones from both samples bolsters Njau and Blumenschine’s (2006) assertion that these marks are potentially strong diagnostic indicators of crocodylian feeding in the fossil record.

While Njau and Blumenschine (2006) described patterns of fracturing that seem to correlate well to depressed fractures and fracture lines (sensu Byers, 2005), wholesale bone breakage in the form of extensive spiral fractures ranged from rare (Baquedano et al., 2012) to only incomplete in the *C. niloticus* surveys. Among specimens of *A. mississippiensis*, 5 femora and 9 tibiae were not retrieved and are believed to have been consumed (26.92% of all initially introduced long bones), and 6 additional long bones exhibited complete spiral fracturing in which large portions of bone were consumed, representing 15.79% of the total femur and tibia samples. This is particularly interesting, because crocodylian bite force has been shown to scale linearly with animal size (Erickson et al., 2003, 2012). While captive specimens can be problematic to use in bite force studies (Erickson et al., 2004), similarly sized specimens of ecologically similar species (in this case, large semiaquatic ambush predators with unspecialized diets) would be expected to be capable of creating similar bite forces. The largest specimens sampled from both *C. niloticus* (Njau and Blumenschine, 2006) and *A. mississippiensis* were roughly 4 meters in length, and yet only the alligators caused extensive spiral fracturing.

It is possible that this difference and the presence of furrows, which are bone surface modifications created during particularly powerful bites, might be the result of some type of sampling artifact. Both taxa were presented with cow limbs, but smaller *A. mississippiensis* specimens from Group 1 were given isolated pig femora while some of the *C. niloticus* specimens were instead presented with sections of goat (Njau and Blumenschine, 2006) or sheep (Baquedano et al., 2012), which may have introduced some room for variation between the samples. Although specific details are not available for comparison, published images indicate that there may have been more remaining soft tissue on the initial samples used by Njau and Blumenschine (2006) and Baquedano and colleagues (2012) than in the current study, which could affect the animals’ ability to access and break bones. However, the presence of numerous punctures in the *C. niloticus* studies does not support the interpretation that the animals were hindered from accessing and heavily modifying their bones. Duration of feeding may have also contributed to this difference, but spiral fracturing was observed occurring even in the first few moments after sample introduction to specimens of *A. mississippiensis* (e.g. Group 1 – SAAF A01025), again.
implying that this factor may not have contributed to the differences.

It seems more likely that the differences in gross bone modification, in the form of bone breakage and wholesale consumption, represent actual differences in feeding strategy. Why this may be the case is less clear. Crocodylian snout shape has often been used as a guiding reference when interpreting feeding ecology, with more slender-snouted forms being interpreted as piscivorous (e.g., Iordansky, 1973; Langston, 1973; Busbey, 1995) or at least as small-prey specialists (McHenry et al., 2006), while boxier snouts with enlarged posterior teeth trended more towards durophagy, and broader, medium-length snouts indicating some kind of compromise between the two — an ecological generalist (e.g., Brochu, 2001). While these designations were largely qualitatively assigned at first (Busby, 1995; Brochu, 2001), more recent studies have applied quantitative techniques (Pierce et al., 2008; Sadleir and Makovicky, 2008). Though differences in these studies are present, both A. mississippiensis and C. niloticus are typically folded into groups interpreted to represent an ecologically generalist lifestyle. It seems that A. mississippiensis is simply a more violent feeder than C. niloticus, utilizing its ability to crush similar bones to greater effect.

The phylogenetic histories of these lineages suggest that broad ecological and morphological similarities between Alligator and Crocodylus were derived independently. The alligatorids and close alligatorid relatives were small (2–3m) and had short, robust snouts with globular teeth toward the back of the mouth (e.g., Norell et al., 1994; Brochu, 1999, 2004b) and are often interpreted as durophagous (Abel, 1928; Carpenter and Lindsey, 1980; Ösi, 2013). They arguably had a more specialized diet than their more generalized descendants. The lineage giving rise to Crocodylus, on the other hand, appears to have been dominated by generalized forms throughout the Cenozoic (e.g., Brochu, 2001, 2007; Delfino and Smith, 2009; Conrad et al., 2013). If the similar ecological roles filled by A. mississippiensis and C. niloticus were not inherited from a common ancestor, we might expect differences in how they fill these roles. It may be that this difference in feeding strategy can be traced to relict behaviors reflecting this evolutionary history rather than differences in the current morphology.

The presence of hook scores was elevated in the A. mississippiensis sample, constituting 6.18% of all observed scores (C. niloticus 0≤1%) and present on 52.46% of observed bones (C. niloticus 0≤27.5%). Death rolling and violent, lateral thrashing were observed during A. mississippiensis bite mark collection, particularly during Group 2 collection, as in the C. niloticus surveys (Njau and Blumenschine, 2006; Baquedano et al., 2012). It is unclear why the rate of hook scoring was so much higher in A. mississippiensis; it may be an artifact of the differences in collection methodology (i.e., feeding duration, group feeding, prey type, reported hook angle), but it may again reflect a more aggressive overall feeding strategy in A. mississippiensis relative to C. niloticus.

CONCLUSIONS

Bite marks in the fossil record provide direct evidence for a number of paleobiological subjects, such as determining the diet of extinct taxa (e.g., Schwimmer, 2002), feeding behaviors of individuals and species (e.g., Noto et al., 2012), and even the presence of intraspecific fighting (e.g., Avilla et al., 2004). However, the utility of these marks often is limited by whether they can be positively associated with a specific trace maker. Diagnostic marks or novel patterns of marks identified during actualistic surveys of extant groups are extremely useful in identifying these associations. Among crocodylians, potentially diagnostic bisected bite marks were identified in bones modified by C. niloticus (Njau and Blumenschine, 2006). Though similar research on C. porosus did not yield similar results (Westaway et al., 2011), production of bisected marks was also identified for a number of extinct crocodylians and their relatives (Rivera-Sylva et al., 2009; Brochu et al., 2010; Noto et al., 2012; Boyd et al., 2013), indicating that these traces might be fairly widespread throughout the clade. Faced with these contradicting conclusions, further actualistic observations involving other members of Crocodylia were warranted.

Bisected marks now have been identified for members of A. mississippiensis. Furthermore, the rate of bisected marks and the percentage of marked bones exhibiting bisections are nearly indistinguishable from those seen in C. niloticus (Njau and Blumenschine, 2006). While further studies of other crocodylian species are still needed, the presence and similarity of these bisected marks on both the Alligator and Crocodylus lineages supports their interpretation as diagnosable traces for other crocodylian taxa as well. However, both these taxa are relatively large bodied and exhibit generalized morphologies and feeding strategies (Brochu, 2001), indicating that further research on crocodylians with different body plans (e.g. tube-snouted forms like Gavialis, physically smaller forms like Alligator sinensis) is still required.

Other patterns of bite marks described in C. niloticus are less comparable to the A. mississippiensis survey. Specimens of A. mississippiensis created extensive bone fracturing and some furrowing, two features which were notably rare to absent among samples taken from C. niloticus (Njau and Blumenschine, 2006; Baquedano et al., 2012). The rate of hook scores and the percentage of marked bones exhibiting these marks were elevated in A. mississippiensis when compared to C. niloticus. This type of mark was also demonstrably not associated with death rolling behavior (contra Njau and Blumenschine, 2006), though violence of the feeding event did promote formation of hooked marks. Both of these trends seem to imply that as a group, A. mississippiensis exhibits a more aggressive style of feeding behavior that focuses more
on crushing and fracturing prey bone than do members of _C. niloticus_.

Similarities between bite marks identified in extinct and extant crocodylians and non-crocodylian crocodyliforms (Njau and Blumenschine, 2006; Rivera-Sylva et al., 2009; Brochu et al., 2010; Noto et al., 2012) indicate that the currently identified patterns and diagnostic types of bite marks are sufficient for broadly identifying the group as a whole. Species-level identifications can be more problematic, often relying on comparisons of mark types, size, spacing, and distribution to potential “contenders” present at a particular site (e.g., Davidson and Solomon, 1990; Noto et al., 2012). This study indicates significant differences in the level of hook scoring, bone fracturing, and consumption between members of _A. mississippiensis_ and the two sampled _Crocodylus_ species (Njau and Blumenschine, 2006; Westaway et al., 2011; Baquedano et al., 2012). The potential for more fine scale, species-level identifications will rely on further such surveys of traces made by other extant and extinct taxa.

**ACKNOWLEDGMENTS**

The Saint Augustine Alligator Farm and curator of reptiles David Kledzik provided access to animals. Southeastern Provisional and Swaggerty’s Farms provided the cow and pig samples. The Iowa Department of the State Archaeologist, the McClung Museum of Natural History and Culture, and Fred and Janet Drumheller provided storage space and equipment for sample processing and imaging. The University of Iowa Central Microscopy Research Laboratories provided training and access to scanning electron microscopes. This study represents part of a dissertation completed in partial fulfillment of a PhD at the University of Iowa. Committee members included Nancy Budd, Jim Enloe, Jonathan Adrain, Hallie Sims, and Walter Klippel. The following people also provided helpful discussion, feedback, and encouragement: Michelle Stocker, Colin Sumrall, Linda Kah, Troy Fadiga, Julia McHugh, Talia Karim, Jake Horton, Dorothy May, and the UI Paleontological Discussion Group.

**FUNDING**

Support for this study was provided though NSF DEB 0444133 and DEB 1257786-125748 to C. A. B. and the University of Iowa Department of Geosciences Littlefield Family Fund.

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**APPENDIX**

### TABLE A1

Bite mark types by specimen; associated bones indicated with decimal pointed identification numbers

| Number | Bone type | Bone section | Pits | Punctures | Scores | Furrows | Bisected pits | Bisected punctures | Bisected scores | Hook scores | Flakes | Notes |
|--------|-----------|--------------|------|-----------|--------|---------|---------------|-------------------|-----------------|-------------|--------|-------|
| SKD1   | tibia     | proximal     | 1    | 0         | 3      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
|        |           | midshaft     | 17   | 0         | 40     | 0       | 0             | 0                 | 6               | 8           | 0      |       |
|        |           | distal       | 2    | 0         | 1      | 0       | 0             | 0                 | 1               | 1           | 0      |       |
| SKD2   | femur     | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 1      | spiral fracture, proximal portion missing |
|        |           | midshaft     | 13   | 2         | 25     | 0       | 1             | 0                 | 0               | 0           | 0      |       |
|        |           | distal       | 0    | 10        | 0      | 1       | 0             | 4                 | 0               | 0           | 0      |       |
| SKD3   | femur     | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
|        |           | midshaft     | 35   | 0         | 230    | 0       | 6             | 0                 | 20              | 7           | 0      |       |
|        |           | distal       | 0    | 16        | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
| SKD4   | femur     | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
|        |           | midshaft     | 2    | 1         | 14     | 0       | 1             | 0                 | 1               | 1           | 0      |       |
|        |           | distal       | 3    | 15        | 0      | 0       | 0             | 4                 | 0               | 0           | 0      |       |
| SKD5.1 | femur     | proximal     | 11   | 5         | 16     | 0       | 0             | 3                 | 1               | 1           | 0      |       |
|        |           | midshaft     | 87   | 0         | 132    | 0       | 2             | 0                 | 11              | 10          | 0      |       |
|        |           | distal       | 0    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
| SKD5.2 | femur     | proximal     | 16   | 1         | 12     | 0       | 0             | 0                 | 2               | 0           | 0      |       |
|        |           | midshaft     | 67   | 1         | 90     | 0       | 10            | 0                 | 9               | 1           | 1      |       |
|        |           | distal       | 3    | 1         | 15     | 0       | 0             | 0                 | 4               | 0           | 0      |       |
| SKD5.3 | patella   | complete     | 1    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
| SKD6   | femur     | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
|        |           | midshaft     | 2    | 0         | 1      | 0       | 0             | 0                 | 0               | 0           | 0      |       |
|        |           | distal       | 0    | 8         | 0      | 0       | 0             | 3                 | 0               | 0           | 0      |       |

(Continued on next page)
| Number   | Type   | Bone section | Pits | Punctures | Scores | Furrows | Bisected pits | Bisected punctures | Bisected scores | Hook scores | Flakes | Notes |
|----------|--------|--------------|------|-----------|--------|---------|---------------|-------------------|----------------|-------------|--------|-------|
| SKD7.1   | femur  | proximal     | 0    | 1         | 3      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 4    | 0         | 19     | 0       | 2             | 0                 | 0              | 2           | 0      |       |
|          |        | distal       | 0    | 4         | 0      | 1       | 0             | 1                 | 0              | 0           | 0      |       |
| SKD7.2   | tibia  | proximal     | 2    | 0         | 0      | 1       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 27   | 1         | 22     | 0       | 1             | 1                 | 1              | 0           | 0      |       |
|          |        | distal       | 10   | 0         | 0      | 6       | 0             | 2                 | 0              | 0           | 0      |       |
| SKD8.1   | femur  | proximal     | 3    | 1         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 12   | 0         | 22     | 0       | 2             | 0                 | 3              | 1           | 1      |       |
|          |        | distal       | 0    | 11        | 0      | 0       | 0             | 5                 | 0              | 0           | 0      |       |
| SKD8.2   | tibia  | proximal     | 2    | 5         | 0      | 1       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 40   | 3         | 22     | 0       | 5             | 0                 | 2              | 0           | 0      |       |
|          |        | distal       | 8    | 3         | 3      | 0       | 0             | 0                 | 1              | 0           | 0      |       |
| SKD9.1   | femur  | proximal     | 3    | 1         | 1      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 14   | 0         | 29     | 0       | 1             | 0                 | 4              | 2           | 0      |       |
|          |        | distal       | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
| SKD9.2   | tibia  | proximal     | 5    | 4         | 6      | 0       | 0             | 0                 | 0              | 1           | 0      |       |
|          |        | midshaft     | 46   | 0         | 123    | 0       | 6             | 0                 | 15             | 5           | 0      |       |
|          |        | distal       | 10   | 1         | 18     | 0       | 3             | 0                 | 0              | 0           | 0      |       |
| SKD10.1  | femur  | proximal     | 0    | 2         | 2      | 0       | 1             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 19   | 1         | 48     | 0       | 1             | 0                 | 4              | 2           | 0      |       |
|          |        | distal       | 0    | 6         | 0      | 0       | 0             | 2                 | 0              | 0           | 0      |       |
| SKD10.2  | tibia  | proximal     | 5    | 0         | 4      | 0       | 0             | 0                 | 0              | 2           | 0      |       |
|          |        | midshaft     | 8    | 0         | 37     | 0       | 0             | 0                 | 0              | 2           | 0      |       |
|          |        | distal       | 2    | 0         | 2      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
| SKD11.1  | femur  | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 3    | 0         | 2      | 0       | 1             | 0                 | 0              | 0           | 0      |       |
|          |        | distal       | 0    | 1         | 0      | 0       | 0             | 0                 | 0              | 1           | 0      |       |
| SKD11.2  | tibia  | proximal     | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | distal       | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
| SKD12.1  | femur  | proximal     | 0    | 3         | 0      | 0      | 0             | 0                 | 1              | 0           | 0      |       |
|          |        | midshaft     | 31   | 4         | 33     | 0       | 4             | 1                 | 3              | 5           | 0      |       |
|          |        | distal       | 0    | 15        | 0      | 0      | 0             | 5                 | 0              | 0           | 0      |       |
| SKD12.2  | tibia  | proximal     | 0    | 1         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 15   | 3         | 17     | 0       | 1             | 0                 | 0              | 2           | 0      |       |
|          |        | distal       | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
| SKD12.3  | calcaneus|              | 1    | 0         | 0      | 0      | 0             | 0                 | 0              | 0           | 0      |       |
| SKD13    | femur  | proximal     | 6    | 0         | 20     | 1      | 5             | 0                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 0    | 4         | 46     | 0      | 0             | 0                 | 5              | 3           | 0      |       |
|          |        | distal       | 0    | 0         | 0      | 0       | 0             | 0                 | 0              | 0           | 0      |       |
| SKD14.1  | femur  | proximal     | 3    | 13        | 6      | 0      | 0             | 2                 | 0              | 0           | 0      |       |
|          |        | midshaft     | 95   | 0         | 228    | 0      | 4             | 0                 | 4              | 17          | 0      |       |
|          |        | distal       | 3    | 16        | 10     | 4      | 0             | 0                 | 0              | 0           | 0      |       |
| SKD14.2  | tibia  | proximal     | 4    | 13        | 13     | 0      | 0             | 1                 | 0              | 3           | 0      |       |
|          |        | midshaft     | 58   | 2         | 100    | 0      | 0             | 0                 | 2              | 3           | 0      |       |
|          |        | distal       | 8    | 4         | 23     | 0      | 0             | 0                 | 1              | 0           | 0      |       |

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| Number | Bone type | Bone section | Pits | Punctures | Scores | Furrows | Bisected pits | Bisected punctures | Bisected scores | Hook scores | Flakes | Notes |
|--------|-----------|--------------|------|-----------|--------|---------|---------------|-------------------|----------------|------------|--------|-------|
| SKD14.3 | astragalus | proximal | 0 | 3 | 13 | 0 | 1 | 0 | 1 | 0 | 0 | |
| SKD14.3 | astragalus | midshaft | 20 | 0 | 76 | 0 | 3 | 0 | 4 | 6 | 0 | |
| SKD14.3 | astragalus | distal | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | |
| SKD15.1 | femur | proximal | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD15.1 | femur | midshaft | 32 | 0 | 43 | 0 | 4 | 0 | 7 | 3 | 0 | |
| SKD15.1 | femur | distal | 12 | 1 | 9 | 0 | 3 | 0 | 4 | 2 | 0 | |
| SKD15.2 | tibia | proximal | 0 | 0 | 41 | 0 | 4 | 0 | 4 | 3 | 0 | |
| SKD15.2 | tibia | midshaft | 20 | 0 | 76 | 0 | 3 | 0 | 4 | 6 | 0 | |
| SKD15.2 | tibia | distal | 0 | 2 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | |
| SKD15.3 | calcaneus | proximal | 0 | 4 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | |
| SKD15.3 | calcaneus | midshaft | 7 | 0 | 16 | 0 | 1 | 0 | 1 | 3 | 0 | |
| SKD15.3 | calcaneus | distal | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD16 | femur | proximal | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD16 | femur | midshaft | 10 | 22 | 11 | 2 | 0 | 4 | 5 | 1 | 0 | |
| SKD17 | femur | proximal | 2 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | |
| SKD17 | femur | midshaft | 41 | 1 | 26 | 0 | 3 | 0 | 4 | 3 | 0 | |
| SKD17 | femur | distal | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKLD18 | tibia | proximal | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKLD18 | tibia | midshaft | 7 | 0 | 16 | 0 | 1 | 0 | 1 | 3 | 0 | |
| SKLD18 | tibia | distal | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD19 | tibia | proximal | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD19 | tibia | midshaft | 16 | 0 | 20 | 0 | 1 | 0 | 3 | 2 | 0 | |
| SKD19 | tibia | distal | 3 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | |
| SKD20 | flake | proximal | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD21 | tibia | proximal | 1 | 1 | 8 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD21 | tibia | midshaft | 28 | 2 | 30 | 0 | 3 | 0 | 6 | 1 | 0 | |
| SKD21 | tibia | distal | 8 | 1 | 4 | 0 | 2 | 1 | 0 | 1 | 0 | |
| SKD22 | femur | proximal | 1 | 2 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD22 | femur | midshaft | 45 | 4 | 26 | 0 | 12 | 2 | 1 | 0 | 0 | |
| SKD22 | femur | distal | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD23 | calcaneus | proximal | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD23 | calcaneus | midshaft | 14 | 1 | 8 | 1 | 3 | 1 | 3 | 0 | 0 | |
| SKD23 | calcaneus | distal | 3 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | |
| SKD24 | calcaneus | proximal | 5 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD24 | calcaneus | midshaft | 14 | 1 | 8 | 1 | 3 | 1 | 3 | 0 | 0 | |
| SKD24 | calcaneus | distal | 3 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | |
| SKD25 | calcaneus | proximal | 1 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | |
| SKD25 | calcaneus | midshaft | 7 | 2 | 9 | 0 | 0 | 2 | 3 | 1 | 0 | |
| SKD25 | calcaneus | distal | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD26 | calcaneus | proximal | 2 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | |
| SKD26 | calcaneus | midshaft | 6 | 0 | 7 | 0 | 1 | 0 | 2 | 0 | 0 | |
| SKD26 | calcaneus | distal | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD27 | calcaneus | proximal | 5 | 10 | 2 | 0 | 0 | 3 | 0 | 1 | 0 | |
| SKD27 | calcaneus | midshaft | 32 | 0 | 50 | 0 | 1 | 0 | 4 | 3 | 0 | |
| SKD27 | calcaneus | distal | 1 | 16 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | |
| SKD28 | calcaneus | proximal | 3 | 3 | 9 | 0 | 1 | 2 | 5 | 0 | 0 | |
| SKD28 | calcaneus | midshaft | 13 | 0 | 27 | 0 | 4 | 0 | 6 | 2 | 0 | |
| SKD28 | calcaneus | distal | 2 | 0 | 16 | 0 | 0 | 0 | 3 | 1 | 0 | |
| SKD29 | calcaneus | proximal | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| SKD29 | calcaneus | midshaft | 45 | 4 | 26 | 0 | 12 | 2 | 1 | 0 | 0 | |
| SKD29 | calcaneus | distal | 2 | 12 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | |
| SKD30.1 | femur | proximal | 8 | 1 | 4 | 0 | 3 | 0 | 0 | 0 | 0 | |
| SKD30.1 | femur | midshaft | 35 | 2 | 44 | 0 | 2 | 0 | 7 | 2 | 0 | |
| SKD30.1 | femur | distal | 4 | 0 | 8 | 0 | 0 | 0 | 2 | 1 | 0 | |

(Continued on next page)
| Number | Bone type | Bone type | Bone section | Pits | Punctures | Scores | Furrows | Bisected pits | Bisected punctures | Bisected scores | Hook scores | Flakes | Notes |
|--------|-----------|-----------|--------------|------|-----------|--------|---------|---------------|-------------------|----------------|------------|--------|-------|
| SKD32  | patella   |          |              | 1    | 0         | 2      | 0       | 0             | 0                 | 0             | 0         | 0      |       |
| SKD33  | patella   |          |              | 2    | 0         | 1      | 0       | 0             | 0                 | 0             | 0         | 0      |       |
| SKD34  | patella   |          |              | 0    | 1         | 0      | 0       | 0             | 0                 | 0             | 0         | 0      |       |
| SKD35  | astragalus|          |              | 2    | 0         | 0      | 1       | 0             | 0                 | 0             | 0         | 0      |       |
| SKD36  | astragalus|          |              | 2    | 0         | 0      | 1       | 0             | 0                 | 0             | 0         | 0      |       |
| SKD37  | navicular |          |              | 0    | 0         | 3      | 0       | 0             | 0                 | 0             | 3         | 0      |       |
| SKD38  | femur     |          | proximal     | 0    | 6         | 0      | 0       | 1             | 0                 | 0             | 0         | 0      |       |
|        |           |          | midshaft     | 15   | 1         | 54     | 0       | 2             | 0                 | 9             | 3         | 0      |       |
|        |           |          | distal       | 0    | 11        | 0      | 2       | 0             | 1                 | 0             | 0         | 0      |       |
| SKD38  | tibia     |          | proximal     | 0    | 3         | 0      | 1       | 0             | 0                 | 0             | 0         | 0      |       |
|        |           |          | midshaft     | 8    | 0         | 53     | 0       | 5             | 0                 | 17            | 0          | 0      |       |
|        |           |          | distal       | 5    | 0         | 35     | 0       | 0             | 0                 | 0             | 6         | 0      |       |
| SKD38  | calcaneus |          | proximal     | 3    | 1         | 7      | 0       | 0             | 0                 | 1             | 0         | 0      |       |
| SKD39  | femur     |          | proximal     | 0    | 5         | 1      | 2       | 0             | 1                 | 0             | 1         | 0      |       |
|        |           |          | midshaft     | 12   | 0         | 55     | 0       | 1             | 0                 | 1             | 9         | 0      |       |
|        |           |          | distal       | 0    | 10        | 0      | 0       | 0             | 1                 | 0             | 0         | 0      |       |
| SKD39  | tibia     |          | proximal     | 2    | 1         | 3      | 0       | 0             | 0                 | 0             | 0         | 0      |       |
|        |           |          | midshaft     | 41   | 0         | 55     | 0       | 4             | 0                 | 4             | 7         | 0      |       |
|        |           |          | distal       | 6    | 1         | 15     | 0       | 0             | 0                 | 3             | 1         | 0      |       |
| SKD39  | patella   |          |              | 1    | 1         | 0      | 0       | 1             | 0                 | 0             | 0         | 0      |       |
| SKD39  | calcaneus |          |              | 0    | 1         | 0      | 0       | 0             | 0                 | 0             | 0         | 0      |       |
| TOTAL  |           |          |              | 1205 | 325       | 2282   | 19       | 125           | 62                | 227           | 141        | 3       |       |