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Alligator (*alligator mississippiensis*) taphonomy: analysis of gnawed and digested bone

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Thesis

**ALLIGATOR (*ALLIGATOR MISSISSIPPIENSIS*) TAPHONOMY: ANALYSIS OF
GNAWED AND DIGESTED BONE**

by

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ABSTRACT

Understanding the tooth mark morphology and behavior of animal scavenging is essential in forensic analysis during recovery of remains in an outdoor setting. Scavengers are part of the natural process of disarticulation; therefore, further research on these taphonomic agents can aid in the analysis of various postmortem bone modifications. The present study focuses on the classifiable morphologies of American alligator (*Alligator mississippiensis*) bite marks on bone as a method of clearly distinguishing bite marks from other scavengers, specifically canids.

Based on previous research, the bite marks of American alligators include punctures, pits, and scoring; however, American alligators also have potentially diagnostic bite marks including bisected mark and hook scores.

The sample for the present study consisted of feeding five adult American alligators, aged at least fifty years old, and four nine-year-old American alligators located at the Edisto Island Serpentarium in Edisto Island, South Carolina. The bones fed to the alligators included: thirty-three commercially available white-tailed deer (*Odocoileus virginianus*) partially fleshed long bones, which included articulated radii and ulnae, femora, tibiae, and humeri; fifteen pounds of partially fleshed white-tailed deer back ribs; and twenty-five pounds of mostly fleshed white-tailed deer neck bones. Additionally, six

articulated pig (*Sus scrofa*) fully fleshed hind limbs were included in the present study. The alligators were typically fed three days a week during the duration of the study.

Once the bones were gnawed on by the alligators and left alone in their enclosures, the bones were collected by the serpentarium personnel and stored for analysis. After bones were macerated, the author observed and measured the morphologies of the tooth marks on the bone surface and observed each tooth mark.

There was a total of 412 tooth marks observed on all bones. The most frequent tooth mark observed on all bones were pits, followed by punctures, scores, furrows, hook scores, and bisected marks. The results indicate that American alligators have the potential to leave identifiable marks; however, crocodylian species also leave some tooth marks that are morphologically indistinguishable from other mammalian carnivores. The patterns of tooth marks were distinguished from other mammalian carnivores based upon previously published literature, such as Njau and Blumenschine (2006), Drumheller *et al.* (2014), Delaney-Rivera *et al.* (2009), Dominguez-Rodrigo and Piqueras (2003), and Pobiner (2007). A paired t-test was run to statistically compare the frequencies of tooth marks from previous crocodylian studies and descriptive statistics are provided to analyze the tooth mark measurements. The present research demonstrates the potential of tooth marks to identify the activity of American alligators.

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LIST OF ABBREVIATIONS

BUSM.....	Boston University School of Medicine
C.A.P.H.I.L.....	Cicero Addison Pound Human Identification Laboratory
CNN.....	Cable News Network
F.B.I.....	Federal Bureau of Investigation
OH.....	Olduvai Hominid

CHAPTER ONE: INTRODUCTION

Forensic taphonomy relates to the study of postmortem changes to human remains and focuses on the environmental effects, such as decomposition in soil and water and interaction with plants, insects, and other animals. Forensic taphonomy allows researchers to differentiate natural damage to bone from deliberate trauma and pathological changes, assists in interpretation of skeletal recovery patterns, estimated the postmortem interval, and interprets past events (Haglund and Sorg 1997, 2002; Martin 1999; Micozzi 1991; Pokines and Symes 2014; Pokines and Tersigni-Tarrant 2013; Ubelaker and Adams 1995).

Knowledge of animal scavenging and dispersal patterns is necessary for forensic analysis when recovering remains in an outdoor environment. Animals will consume and disperse remains that could potentially disrupt the decomposition process and postmortem estimation (Alexander 1956; Berryman 2002; Brain 1980; Carson et al. 2000; Crader 1983; Haglund 1997a; Haglund et al. 1988, 1989; Moraitis and Spiliopoulou 2010; Morton and Lord 2006; Pickering 2001; Pokines 2014; Steadman and Worne 2007; Willey and Snyder 1989). Animal scavenging on human remains occurs regularly due to the nutritional value and minerals in bone, especially in the marrow cavity. Mammalian terrestrial taxa gnaw on bone for a multitude of reasons, including as a byproduct of predation, dismembering prey, the presence of exterior soft tissue, the marrow and grease content of bones, and the nutrients from the mineral content in bones (Pokines 2014).

The examination of tooth marks by predators on bone can illustrate the ecology, behavior, and morphology of the taxa that produced them (Pobiner 2008). Tooth marks can be used to identify extinct taxa along with their killing and feeding behaviors, their prey, and biomechanical capabilities. Tooth marks on bones produced from mammalian carnivores have been observed at Plio-Pleistocene archaeological sites, especially tooth marks produced by hyenas (Binford 1981; Cruz-Urbe and Klein 1994). Njau and Blumenschine (2006) identified and described modern and fossil crocodile bone modification. A large number of marks made by crocodylians were concentrated on the grasping sites, where the animal would pull and twist limbs from the prey item (Njau and Blumenschine 2006). To diagnose specific carnivore taxa, there are two types of tooth mark data to take into consideration: 1) the frequency and patterning of tooth markings on bones, and 2) tooth mark morphology (Pobiner 2007). Additionally, length and width measurements of tooth marks from an entire sample can be used to statistically distinguish between the relative size of the carnivore.

Zooarchaeologists have developed quantitative methods to identify specific carnivore actors that produced tooth marks on archaeofaunas by measuring carnivore tooth pits (Andrews-Fernandez-Jalvo 1997; Baquedano *et al.* 2012; Delaney-Rivera *et al.* 2009; Dominquez-Rodrigo and Piqueras 2003; Parkison *et al.* 2015; Pickering *et al.* 2004; Pobiner 2007; Sala and Arsuaga 2013; Sala *et al.* 2014; Selvaggio and Wilder 2001; Yravedra *et al.* 2017). Classifying and identifying bone surface modifications inflicted by carnivores remains forensically relevant because of the present existence of these carnivore species. Specifically, comparison of canid tooth marks is important

because canids remain a common and significant scavenger of remains (Sala *et al.* 2014; Steadman and Worne 2007; Yravedra *et al.* 2017). Tooth marks of canids, such as punctures, pits, and scores (described in further detail below) could potentially be morphologically similar to that of crocodylians; however, certain traits make canids and crocodylians distinguishable. The identification of tooth marks forensically has the potential to reveal the identity of carnivores, their killing and feeding behaviors, the degree of competition for a carcass or assemblage of carcasses, and their biomechanical capabilities (Pobiner 2007).

Teeth of modern carnivores evolved for different functions. Broad, low-cusped molars crack and grind; blade-like carnassial slice flesh and soft tissues; pointed premolars pierce; and knife-like canines stab (Pobiner 2007; Van Valkenburgh 1996). The differences among dental morphologies in carnivore species will also affect the feeding behavior and vice versa. For instance, felids utilize their anterior teeth, incisors and canines, while feeding rather than the posterior teeth. Even among the felids, there are differences; cheetahs (*Acionyx jubatus*) have larger premolars, while lions (*Panthera leo*) have more massive canines. Spotted hyenas (*Crocuta crocuta*) have massive premolars with felid-like carnassials and moderately developed canines. Wild dogs (*Lycaon pictus*) have molars posterior to the carnassial and four premolars that are not expanded mediolaterally (Biknevicius and Ruff 1992; Van Valkenburgh 1996). Lions and hyenas use their premolars for bone gnawing, while wild dogs use their postcarnassial molars. This is supported by work done on differential mandibular cortical thickness in these species. The mandibles in hyenas are most robust the premolars, and in wild dogs

they are most robust beneath the carcassials and molars (Biknevičius and Ruff 1992; Pobiner 2007).

The differences in dental morphology in carnivores may allow the identification of different tooth marks created by various species. However, there are numerous difficulties distinguishing between carnivore bone gnawers; for example, dental size among these taxa overlaps, and an individual bone gnawer can create punctures of different diameters because tooth size can vary and different carnivores use different bite forces at different times. Additionally, repeated damage to bone occurs when new gnawing damage overlaps with, obscures, or destroys previous gnawing damage. The proximal and distal portions of the gnawed bone (that best preserve a tooth puncture and could potentially identify the carnivore) are the least durable and least likely to survive continued gnawing and other postmortem damage (Delaney-Rivera et al. 2009; Dominguez-Rodrigo and Piqueras 2003; Pokines 2014; Pobiner 2007, 2008).

There are numerous reasons for common terrestrial taxa to scavenge bone in their natural habitats. The consumption of bone and remains for scavengers has proven to be valuable for scavengers and their ecosystem (Barton et al. 2013; Cantu 2014; DeVault *et al.* 2003). The consumption of remains is based primarily on foraging strategies, access to remains, and selective pressures within an ecosystem (Cantu 2014; DeVault *et al.* 2003). When food sources become scarce or when an ecosystem alters, animals will scavenge for any available nutrients (Barton *et al.* 2013; Rippley *et al.* 2012). Bones are a valuable source of fat and provides scavengers with a nutrient rich-food for consumers who are able to break into them to consume within-bone nutrients. Fleshed remains containing

nutrients and minerals and bone marrow attract multiple species (DeVault *et al.* 2003; DeVault *et al.* 2004; Wilson and Wolkovich 2011).

Reptile Taphonomy

Taphonomic research regarding modern reptiles includes studies involving swallowed digested bones and scats of crocodiles and bone surface modifications of crocodiles and alligators (Drumheller *et al.* 2014; Fisher 1981; Njau and Blumenschine 2006; Pobiner 2008). In comparison to mammalian terrestrial taxa, crocodylians often swallow whole parts of mammal carcasses, leaving tooth marks on bones that they were unable to digest (Njau and Blumenschine 2006; Pobiner 2008).

Crocodylian taphonomy is also relevant to paleoanthropology research. Davidson and Solomon (1990), for instance, argue that there was possible crocodile inflicted damage to OH 7, which is an Olduvai hominin from the species *Homo habilis*. OH 7 consisted of juvenile bones: a mandible with the third molar unerupted, left and right parietals, occipital fragments, and fragments of a temporal, phalanges, and carpals scattered over a wide area of the site. OH 7 presented 8 marks that could be classified as tooth marks, possibly from the Nile crocodile (*Crocodylus niloticus*) or the saltwater crocodile (*Crocodylus porosus*). Nile crocodiles prey on large mammals and are successful human predators (Davidson and Solomon 1990).

Research on crocodile damage to bone is scarce in the forensic anthropological field. The majority of research is attributions to crocodylians and their relatives in paleontological literature (Botfalvai *et al.* 2014; Baquendano *et al.* 2012; Joyce 2000;

Meyer 1994; Nifong *et al.* 2011; Njau and Blumenschine 2006; Pobiner 2008). There is a lack of forensic research on crocodylian taphonomy and more specifically a lack of research of crocodylian bite marks on gnawed and digested bones in areas where crocodylians are prominent.

Fatal alligator attacks on humans are uncommon in the United States. In Florida, there have been 384 attacks recorded since 1948. Of those 384 attacks, 126 were minor, requiring no treatment other than first aid, and 258 attacks were major, requiring medical attention. Of those 258 major attacks, only 24 were fatal (Florida Fish and Wildlife Conservation Commission 2018). Most American alligators (*Alligator mississippiensis*) attack smaller animals rather than humans because of their natural fear of humans; however, when alligators do attack humans, it is most likely because the animal has been desensitized through, for example, illegal feeding or discarding food into a body of water populated by alligators (Harding 2006).

While fatal alligator or crocodile attacks on humans are rare, alligator-inflicted postmortem injuries are a potentially important taphonomic effect, especially in locations where alligators are prevalent. There are documented cases where human remains have been found with alligator-inflicted postmortem injuries, but these cases lack the forensic research used to identify postmortem tooth marks on bone and digested bone. Marshlands in Louisiana, for instance, are a popular area of body disposal. The Los Angeles Times (1995) reported an incident of a law enforcement officer involved in at least two of 24 serial killings in the New Orleans area. His victims were disposed of throughout New Orleans and the nearby swamps infested with alligators. Furthermore, the New York

Times reported that between 2005 and 2009, eight women from Jennings Louisiana were victims of homicide and disposed on in swamps in the surrounding area. All remains were found in such an advanced stage of decomposition that cause of death was difficult to determine (Robertson 2010).

Saltwater and freshwater crocodiles prey on humans in Zimbabwe and southern Mozambique. Of the 43 investigated crocodile attacks, 23 of them were fatal (Hart and Sussman 2009). If the victims escaped the attack, death often followed due to infection. Research in southwestern Madagascar along the Mongoky River details how crocodiles are known to kill people in a regular basis (Hart and Sussman 2009). In Northern Australia, 12 fatalities were attributed to crocodiles between 1975 and 1988.

There are forensic case studies covering attacks on humans, but these focused more on soft tissue damage than bone modification (Cupal-Magana et al. 2010; Haddad and Fonseca 2011; Harding and Wolf 2006; Mendieta and Duarte 2009). Mendieta and Duarte (2009) described two cases of shark and alligator attacks in Panama, examining the pattern of bite injuries and the vulnerable anatomical areas affected. Davidson and Solomon (1990) further examined the remains of a man killed by a saltwater crocodile; portions of the body were not consumed, and there were observable damage and tooth marks on the lower limbs of the individual. The legs of the victim had been torn off from the torso and were found ten meters from the bank of a river. The bones were still articulated except for the left tibia and fibula and had approximately 20 tooth marks distributed over both upper and lower legs. More tooth marks could have been identified;

however, due to immersion in water and putrefaction, there was difficulty differentiating between tooth marks and decomposing flesh (Davidson and Solomon 1990).

The C.A. Pound Human Identification Laboratory in Florida, U.S.A., identified nine cases that list possible alligator inflicted postmortem damage; however, none are confirmed as alligator damage due to difficulty distinguishing between alligator marks and other carnivore damage (Katie Rubin, personal communication, C.A.P.H.I.L).

In southwest Florida, reports of alligator attacks were described by Harding and Wolf (2006). Their report included the description of three out of nine fatal cases in southwest Florida that were a result of an alligator attack. The other six cases were excluded from the research by Harding and Wolf (2006), because the alligator-inflicted injuries were determined to be postmortem. Sinton and Byard (2016) discuss pathological findings of fatal crocodile cases in Northern Australia but left out cases of crocodile inflicted postmortem injuries (Sinton and Byard 2016).

More recently in Florida, it was reported by CNN that a fisherman sighted alligators eating human remains which were disposed in a body of water. The alligators reportedly gnawed on the remains but were not the cause of death (Acevedo 2016). In 2009, a teenage girl was murdered after travelling to McClellanville area from Myrtle Beach in April 2009 and her body was fed to alligators. The FBI conducted a detailed search through several alligator ponds, but the victims' remains have yet to be found (Dickerson 2017).

The present study examined gnawed and digested bone from American alligators to determine classifiable bite marks observed on bone. Based on previous studies of

crocodilian digestion and bite force, it was hypothesized the alligators would make distinctive marks on the bone, both gnawed and digested, that could be clearly distinguished from other scavengers, including canids. These differences in tooth marks could lead to predictions of tooth mark morphologies created by these different species; which, for instance, could help forensically identify and differentiate carnivore tooth marks observed on human remains.

CHAPTER TWO: PREVIOUS RESEARCH

Hominins have long been the prey of other predators (Brain 1980; Corbett 1944; Hart 2002; Hart and Sussman 2008; Kerbis Peterhans and Gnoske 2001; Kruuk 2002; Patterson 1996; Treves and Naughton-Treves 1999). Though there is variation between the anatomy and body mass of humans and other prey species, some, but not all, predators follow a similar pattern when it comes to scavenging and dispersing mammal carcasses (Pokines 2014). This pattern includes dispersing the remains away from the initial deposition site. Dispersal is a direct result of feeding behavior by carnivores: as a body is consumed, bones disarticulate and move a short distance as limbs are detached from the axial skeleton, ribs are broken and removed, and the skull is removed over time (Hudson 1993; Kent 1981; Mech 1970; Pokines 2014; Willey and Snyder 1989).

Along with soft tissue, bone offers valuable resources for scavengers. Remains are typically dispersed and transported from the primary deposition site and even further moved to secondary locations. Dispersal of remains ranges from those still intact on the surface or buried to few traces of remains at their initial deposition. Advanced dispersal of remains is likely the result of mammalian scavengers. Secondary dispersal locations is defined as occurring when remains have been moved from the initial deposition location (Haynes 1982; Hill 1979; Moraitis and Spiliopoulou 2010; Pokines 2014). Additionally, remains are rarely only scavenged by a single species (Andrés *et al.* 2012; Fisher 1995; Haglund 1992; Haynes 1982; Murad 1997), therefore, bone surface modifications and movement are indicators of the behavior of various scavengers.

Carnivore Scavenging

There has been much research on the sequence in which animals scavenge remains. The process of disarticulation can occur after a body has been exposed to the environment for an extended period of time (Cantu 2014). Hill (1979) addressed natural disarticulation and noted the correlation between the various stages of disarticulation and decomposition. Natural disarticulation of bones depends on the rate in which joints holding the bones together disintegrate (Hill 1979). Additionally, natural disarticulation varies based on environmental conditions, such as regions of mixed temperate forest and humid or arid regions.

Animal scavenging also has an effect on the disarticulation of remains (Cantu 2014; Hill 1979, 1984). Similar natural disarticulation patterns are evident cross-environmentally regardless of specific species and taxa in various regions. Large scavengers, however, will discover fresh remains, consume and penetrate the paunch, followed by the upper hindquarters, ribs/vertebrae, upper forelegs/shoulders, throat and face and disarticulate the limbs of the remains (see below; Haynes 1980b). Predators such as coyotes (*Canis latrans*) and wild other canids will disarticulate portions of the body to transport remains away from the primary deposition site (Hill 1984; O'Brien *et al.* 2010).

Using a sample of 46 partially skeletonized remains, Haglund (1989) developed a model of the sequence in which animals scavenge human remains. The sequence begins with the removal of the face and neck region followed by the destruction of the ventral thorax, the upper extremities, and finally the lower extremities, leaving the head and the vertebral column the last elements to be scavenged (Haglund 1989).

Wiley and Snyder (1989) conducted a wolf scavenging study that provided a detailed description of damage done by scavengers. They noted a pattern of complete long bone destruction based on accessibility and bone density. Wolves and other canids tend to destroy bones that are more porous due to their fragility and to access the marrow cavity and grease (Cantu 2014; Parkinson *et al.* 2014; Wiley and Snyder 1989).

Canid scavenging is a part of the natural sequencing process of disarticulation, rate of decomposition, and destruction of the remains (Domínguez- Rodrigo and Piqueras 2003; Haglund 1989, 1997a; Haglund and Sorg 1997; Haynes 1980, 1982; Kjørlien 2009; Klippel and Synstelién 2007; Rippley *et al.* 2012; Wiley and Snyder 1989). The most common canid scavengers in North America include dogs, coyotes, and wolves (Haglund 1997a; Klippel and Synstelién 2007). Generally, the highest yield/least effort portions of the remains will be consumed first followed by decreasing yield/least effort portions. These portions include the thoracic cavity followed by the upper hindquarters/rump area (Cantu 2014; Pokines 2014; Wiley and Snyder 1989).

Gnawing causes extensive damage to bones and can distinctive tooth marks. The main types of scavenging marks produced by carnivores include tooth pits, tooth punctures, tooth scores or striations, tooth furrows, crenulated margins, and edge polish (Binford 1981; Pobiner 2007, 2008; Pokines 2014). These marks are caused by continual tearing of flesh from the bone and chewing and scooping at the proximal and distal ends of long bones for the grease and marrow.

Tooth pits are circular or irregular shaped depressions in cortical bone that do not penetrate the cancellous bone or marrow cavity (Figure 2.3). The maximum length of

tooth pits is no more than three times their maximum width (Binford 1981; Lyman 1994:205-214; Pobiner 2007; Pokines and Kerbis Peterhans 2007).

Tooth punctures are deep depressions that penetrate into cancellous bone or marrow cavities (Figure 2.4). Punctures occur when the bone collapses under the tooth, leaving an imprint. The puncture margin will typically be more broken than tooth pits; this is due to full penetration of the cortical bone (Cantu 2014; Pobiner 2007; Pokines 2014). The distinct shape of the puncture preserved in the tooth may be used for identifying the species or the size of the species that gnawed on the remains (Pobiner 2007, 2008; Pokines 2014).

Tooth scores or striations are similar to tooth pits, but tooth scores are at least three times longer in length than wide (Figure 2.6). Scores usually occur on random places, especially along the diaphysis of long bones, because they are usually where the bone was gripped for transport or repositioning by the carnivore. Scores can be termed as gripping marks if they are on the diaphysis of long bones (Binford 1981; Lyman 1994:205-214; Njau and Blumenschine 2006; Pokines and Kerbis Peterhans 2007).

Tooth furrows are similar to tooth punctures, but furrows are at least three times longer in length than wide (Figure 2.5). Tooth furrows can be identified in cancellous bone if it has been exposed by previous gnawing. This forms a secondary stage usually caused by carnivores dragging their teeth through it. The secondary furrows are typically destroyed by continual gnawing of carnivores, because the cancellous bone inhibits access to the marrow cavity (Binford 1981; Lyman 1994:205-214; Njau and Blumenschine 2006; Pobiner 2007; Pokines and Kerbis Peterhans 2007).

Crenulated margins, common in mammalian carnivore feeding, are bone margins that are jagged or scalloped by repetitive bites (Figure 2.3) (Binford 1981; Njau and Blumenschine 2006).

Edge polish damage is defined as the gnawing consumption on the exposed edges of bones, leaving behind a polished or worn surface (Figure 2.3). Edge polish is typically accompanied by tooth marks, along the consumed margins or elsewhere on the bone (Pokines and Kerbis Peterhans 2007). This type of damage is located along the epiphyses of long bones, allowing for consumption and access to the marrow cavity, and results in the formation of a bone cylinder, where only a hollow portion of the diaphysis remains.

Pits and punctures are formed by direct tooth pressure and striations/scores and furrows are formed by teeth dragging across the surface of remains (Pobiner 2007; Pokines 2014). Scores and furrows can be V- or U-shaped depending on the shape and angle of the tooth. Tooth marks can occur on any part of a bone as isolated or in clusters; however, mammalian carnivore tooth marks are typically found in clusters of 2-5 marks. Tooth marks are possibly located in denser concentrations along gnawed margins or fracture edges and occur on the thickness or internal surface of fragmented bone (Njau and Blumenschine 2006). Furthermore, bones taken by mammalian carnivores from an original kill site to their den have also been shown to have more gnawing damage at den sites (Haynes 1983). Besides hyenas, canids tend to be the most destructive to skeletal remains due to their pack behavior. In addition, Steadman and Worne (2007) state that canid scavenging of human remains in an indoor setting over a period of time can leave few identifiable osseous remains behind.

Gnawing Damage

There has been much research that has attempted to differentiate bone damage caused by large carnivore families such as canids, ursids, felids, and hyaenids (Andres *et al.* 2012; Carson *et al.* 2000; Delany-Rivera *et al.* 2009; Dominguez-Rodrigo and Piqueras 2003; Drumheller *et al.* 2014; Haglund *et al.* 1988; Haynes 1983; Murmann *et al.* 2006; Payne 1983; Pobiner 2007, 2008; Pobiner and Blumenschine 2003; Pokines and Kerbis Peterhans 2007; Richardson 1980). The difficulties in differentiating between bone damage caused by specific taxa includes a general dental size overlap, diameters of punctures, congruencies in dental morphology, repeated damage to the bone's surface, and the possibility that more than one scavenging species gnawed on the bone. However, using markers such as footprints, feces, and indoor/outdoor environments can help in identifying the specific taxa that may have interacted with the remains (Pokines 2014).

Hyaenids cause the most skeletal damage to bone and disperse remains in a terrestrial environment (Pobiner 2007, 2008; Pokines and Kerbis Peterhans 2007). Wolves, however, can cause the same amount of damage to remains but over a longer period of time. Large scavenging carnivores typically take more time to gnaw on the remains until they have lost interest due to the time between death and discovery.

Crocodylian Species, Physiology, and Feeding Behavior

Of the twenty-three species of crocodylians in the world, two are native to the United States (Table 2.1; Figure 2.7). American alligators (*Alligator mississippiensis*), family Alligatoridae, inhabit the southeastern United States, and American crocodiles

(*Crocodylus acutus*), family Crocodylidae, inhabit coastal areas of south Florida as well as parts of Central America (National Park Service 2008). There are twenty-three species of crocodilians in the world today spanning 90 countries. Crocodilians are generally found in tropical regions, but the American alligator and Chinese alligator (*Alligator sinensis*) are cold-tolerant and will be found in the highest elevations and latitudes of any crocodilian species. Family Alligatoridae has eight species found around the globe: the American alligator (*Alligator mississippiensis*), Chinese alligator (*Alligator sinensis*), spectacled caiman (*Caiman crocodilus*), broad-snouted caiman (*Caiman latirostris*), Yacare caiman (*Caiman yacare*), black caiman (*Melanosuchus niger*), Cuvier's dwarf caiman (*Paleosuchus palpebrosus*), and smooth-fronted caiman (*Paleosuchus trigonatus*) (Crocodilian Species List 2012).

Family Crocodylidae has fifteen species found around the world: American crocodile (*Crocodylus acutus*), lender-snouted crocodile (*Crocodylus cataphractus*), Orinoco crocodile (*Crocodylus intermedius*), freshwater crocodile (*Crocodylus johnstoni*), Philippine crocodile (*Crocodylus mindorensis*), Morelet's crocodile (*Crocodylus moreletii*), Nile Crocodile (*Crocodylus niloticus*), New Guinea crocodile (*Crocodylus novaeguineae*), mugger crocodile (*Crocodylus palustris*), saltwater crocodile (*Crocodylus porosus*), Cuban crocodile (*Crocodylus rhombifer*), Siamese crocodile (*Crocodylus siamensis*), dwarf crocodile (*Osteolaemus tetraspis*), false gharial (*Tomistoma schlegelii*). The gharial (*Gavialis gangeticus*), a fish eating crocodile, comes from the family Gavialidae (Crocodilian Species List 2012). The locations and environments of these species can be found in Table 2.1.

American alligators are found as far north as North Carolina in freshwater marshes and rivers and as far south as the Florida Keys (Lance 2003). Climate, in addition, affects the growth cycle of an alligators. For instance, in southwest Louisiana, alligators stop feeding in October and do not resume feeding until late March or early April. Additionally, the varying annual thermal cycle affects the physiology of American alligators. During the warmer season, captive alligators can grow about 150 cm a year and reach sexual maturity in six years, while wild alligators on average grow 30 cm a year and reach sexual maturity in ten years.

American alligators are carnivorous, with teeth strong enough to crack a turtle shell. Americans alligators forage opportunistically, exhibiting a varied diet, ranging from small insects and crustaceans to large vertebrates. Their prey consists of fish, snails, birds, frogs, and mammals that come near the water's edge (Smithsonian's National Zoo and Conservation Biology Institute 2016). Their diet varies by specific geographic location, habitat, prey encountered, and prey size (Rice 2004). Furthermore, as an American alligator increases in size, its diet becomes more diverse; juveniles tend to prey on invertebrates, whereas large adults prey on vertebrates. (Wallace *et al.* 2008; Saalfeld *et al.* 2011). Fish, however, are the most prevalent vertebrates in the diet of adult alligators.

The diets between crocodylian taxa vary due to factors such as snout shape and body size; however, these variations in body size and snout shape are caused by diet. Alligators have between 74 to 80 teeth in their mouth at a time and as the teeth wear

down, they are replaced. An alligator can go through 3,000 teeth in a lifetime (Smithsonian 2016).

The manner in which crocodylians consume their food is similar throughout all species (Cleurens and deVree 2000). Crocodylians secure prey through the anterior portion of the jaw and rotate the head sideways so that the angle of approach brings one side of the jaw into contact with the prey (Cleurens and deVree 2000).

Small animals are repositioned in the mouth of a crocodylian in such a way that one powerful killing bite can be performed. The repositioning of the prey indicates inertial feeding behavior, a stereotypic form of prey transport which is utilized to move large food items from the jaw tips into, and through the oral cavity. The head and neck are elevated, and the hyolingual apparatus presses the prey into the mouth. The expansive opening of the jaw draws the prey farther into the mouth cavity. These bites can occur multiple times until the prey is killed or crushed (Cleurens and deVree 2000).

If the prey is larger, further effort is required from the crocodylian. Repositioning the jaw is used to achieve a better grasp on the prey. Bringing the prey underwater can lead to drowning. “Death roll” behavior is common for crocodylians. It entails securing a portion of the prey in its jaws and initiating a violent rotation along the long axis of its body (Drumheller *et al.* 2014; Smithsonian’s National Zoo and Conservation Biology Institute 2016). Limbs are folded against the body, and the movement is accomplished through motions of the head, trunk, and tail (Fish *et al.* 2007).

Further bites are utilized to transport food into the throat once smaller prey are dead. For larger prey, crocodylians may require further reduction before swallowing is

possible. Though the conical teeth of crocodylians are important for grasping prey, they are not well adapted to cut or tear into soft tissue. Lateral thrashing has been observed in crocodylians as a means to tear smaller portions off of a prey item (Drumheller *et al.* 2014). Large prey reduction and defleshing can continue until an entire prey is consumed. However, there are instances where parts of a carcass are abandoned. Dismemberment can scatter elements which are then discarded (Davidson and Solomon 1990). Turtle shell remnants are often abandoned once the majority of soft tissues have been consumed (Milàn *et al.* 2010).

Digestive Processes

Since alligators and crocodiles gulp their food in large pieces, their digestive system is complex. Deifenbach (1975a) observed the rate of gastric function of *Caiman crocodilus* relative to temperature. Sixteen small, medium, and large crocodiles were used. The animals were fed at 15°, 20°, 25°, and 30°C (Deifenbach 1975a). It took four to five days for crocodiles to completely digest their food at 30°C, but at 15°C it took more than fourteen days.

The digestive system of crocodylians, including American alligators, is highly acidic. Fisher (1981) conducted an experiment on crocodylia scatology, microvertebrate concentrations, and enamel-less teeth. Previous research (Gadow 1901; McIlhenny 1935; Cott 1961; Neill 1971; Skoczylas 1978) stated that there was absolutely no trace of mineralized tissue left in feces, but Fisher (1981) found traces of teeth and bones in excrement of crocodiles. Fisher (1981) conducted feeding experiments that involved four

individuals each of two species, *Alligator mississippiensis* and *Caiman crocodilus*, that were fed rats and mice. He found teeth recovered from feces are usually isolated and enamel-less due to decalcification. Features of bones are subdued and more difficult to recognize. Preserved organic matrices may retain their histologic structure, though signs of bacterial decomposition may begin to show (Fisher 1981).

Crocodylian Bite Marks and Bite Force

Identifications and interpretations of crocodylian bite marks previously relied on comparisons of presumed bite marks to the tooth and jaw morphology of the assumed crocodylian (Cisneros 2005; Mead *et al.* 2006; Schwimmer 2010; Steadman *et al.* 2007). Isolated observations of modern crocodylian feeding behavior supported the classifications of specific crocodylians with bite marks in the fossil record.

Recently, studies of crocodylian bone-modifying behaviors and their diagnostic traces have been conducted (e.g. Milàn *et al.* 2010; Njau and Blumenschine 2006; Westaway *et al.* 2011). Njau and Gilbert (2016) attempted to standardize terms for bite marks on bone surfaces resulting from crocodile feeding behavior (Table 2.2; Figure 2.1). Many marks produced by crocodiles are individually indistinguishable from mammalian carnivores (Figure 2.2). Crocodile feeding behaviors leave some specific bone modifications that are distinctive relative to other sources. Bisected pits, rounded pits, and jagged pits are associated with crushing, grasping, and holding between teeth. Anterior crocodile teeth tend to leave bisected pits and posterior teeth are more rounded and frequently worn (Njau and Gilbert 2016). Crocodylian teeth have prominent carinae,

the sharp ridges of conical teeth, that wear down and chip away. When an erupted, unworn tooth is involved in a bite, the carina will leave a “bisected” mark (Drumheller *et al.* 2014). These bite marks had not been identified in any mammalian group and were considered to be potentially diagnostic for crocodylians. The diameter of bisected marks typically ranges from 1.4-4.0 mm (Dominguez-Rodrigo and Piqueras 2003; Njau and Blumenschine 2006). Bisected marks have been found in other crocodylians and non-crocodylians by Njau and Blumenschine (2006), Boyd *et al.* (2013), Brochu *et al.* (2010), Noto *et al.* (2012) and Rivera-Sylva *et al.* (2013).

Rounded pits are often left behind due to teeth imposing extreme compressive force. Jagged pits lack typically lack morphology that can be related to tooth position (Njau and Gilbert 2016). The diameters of the pits range from 0.1 mm to over 6.0 mm (Njau and Blumenschine 2006). Some pits in crocodylians are partly or entirely bisected by a sharp linear depression that can exceed the diameter of the pit, resulting in a V-shaped cross-section.

Hook scores, pivoted-drag-snags, striation pivots, and striations of various orientations and depths are associated with torsional forces applied against incompletely gripped bones that slip on clasped jaws during side-to-side head movements and death rolls (Figure 2.2). Hook scores are L- or J-shaped tooth marks with various depths created when an impacting tooth changed direction abruptly during a single biting event (Njau and Blumenschine 2006). Hook scores range from 3.5-55.0 mm in length. The average length for scores of mammalian carnivores is 3.0-13.0 mm, and hook scores are generally not observed (Njau and Blumenschine 2006). Hook score tooth mark modifications often

contain internal parallel and sun-parallel striations within the main mark and are unique to crocodile-modified assemblages. Tooth marks identified in the *C. niloticus* sample included bisected marks and hook scores. While it was thought that the tooth marks were caused by the death roll of crocodylians, it has been found on bones fed upon by non-crocodylian reptiles such as the Komodo dragon (*Varanus komodoensis*) and theropod dinosaurs (D'Amore and Blumenschine 2009). Hook scores are common among crocodylians, but, these marks can also be produced by Komodo dragons and avian scavengers (D'Amore and Blumenschine 2009; Fetner and Soltysiak 2013; Njau and Gilbert 2016). Hook scores are associated with animals that exhibit an inertial feeding pattern, such as crocodylian species.

The above descriptions of the crocodile-induced tooth mark morphologies are usually observed as combinations of these overlapping modification types. A combination of bisected pits, rounded pits, hook scores, and striations on an individual bone is characteristic of crocodylian activity and has not been observed in mammalian carnivores.

The bite force of crocodylians is over three times stronger than the spotted hyena, *Crocuta crocuta* (Erickson *et al.* 2012). Erickson *et al.* (2004) compared bite force between wild and captive American alligators and found captive alligators to bite more forcefully than wild alligators. Captive alligators are generally larger in size, with broader heads, shortened jaws, and greater body masses, which contributes to a more forceful bite. The bite force attained by sharp anterior teeth is sufficient to create deep punctures and V-shaped traces, such as hook scores on the bone surface.

Punctures penetrate through thick cortical bone, may be associated with chipping and shallow to deep cracks coming from opposite sides of punctures, that run along the long axis of the bone. Serial puncturing is observed occasionally (Njau and Blumenschine 2006). Punctures observed in crocodylians are sometimes bisected, similar to pits (Dominguez-Rodrigo and Piqueras 2003; Njau and Blumenschine 2006). Bisected punctures are generally not observed in mammalian carnivores. The average diameter of crocodile punctures is 2.5-7.5mm (Dominguez-Rodrigo and Piqueras 2003; Njau and Blumenschine 2006; Selvaggio and Wilder 2001). Additionally, pits created by crocodylians can also mimic tooth pits produced by mammalian carnivores (Njau and Gilbert 2016; Sala and Arsuaga 2013; Sala *et al.* 2014).

“Drag-snap” is a term used to describe tooth mark patterns created by crocodylians that produce long, arching, curving, or pivoting marks with deep grooves or striae. The bite force in unison with torsional force gives crocodile marks a plowed appearance, where adjacent bone has been compressed, crumpled, or flaked-off (Njau and Gilbert 2016). Crocodylian tooth marks can occur anywhere on any bone, though the marks are commonly observed on limb bone parts unprotected by overlying soft tissue. Most affected bones from crocodile assemblages typically have only one or a few tooth marks visible. However, without context, isolated crocodile modifications are frequently indistinguishable from those made by other agents (Njau and Gilbert 2016; Sala and Arsuaga 2013; Sala *et al.* 2014).

Njau and Blumenschine (2006) conducted a large-scale survey of crocodylian bite marks and bone modifications focused on captive and wild specimens of *Crocodylus*

niloticus, the Nile crocodile, and compared the identified marks to bones found in Olduvai Basin, Tanzania. The bite mark morphology diverged from previously studied mammalian marks (Table 2.3). Crocodylians do not present common gnawing behaviors associated with other carnivores (Cleurens and deVree, 2000). The interior morphology of pits, scores, and furrows show crushing in both crocodylians and mammalian carnivores; however, in crocodylians, pits are circular to oval while mammalian carnivores are circular to angular (see above). Furrows are rarely observed in crocodylians, nor anywhere else (Drumheller *et al.* 2014; Njau and Blumenschine 2006; Njau and Gilbert 2016); however, furrows are occasionally observed in mammalian carnivore assemblages and are linear with an average length ranging from 13.0-24.0 mm (Dominguez-Rodrigo and Piqueras 2003; Njau and Blumenschine 2006). Mammalian carnivores create semicircular tooth notches that commonly occur at fracture edges (Drumheller *et al.* 2014; Njau and Blumenschine 2006). Edge polish and crenulated edges are characteristic of mammalian carnivores (Pokines 2014; Pokines and Kerbis Peterhans 2007; Pokines and Tersigni-Tarrant 2013) and not observed on crocodylian tooth mark morphology. Though bones are typically ingested, crocodylians do not seek out bone marrow as a source of nutrition as other carnivores do (Fisher 1981; Pobiner 2008).

Milàn *et al.* (2010) conducted a study on the Dwarf caiman (*Paleosuchus palpebrosus*) bite modifications on Red-eared slider (*Trachemys scripta*) shells. They focused on patterns of shell breakage and behavior specific to chelonivory and not on bite identification specifically. The caiman was observed manipulating the turtle into an

upright position before applying jaw pressure, so the shell could be opened and emptied. This movement left several bite traces in the shells, including round punctures, often arranged in rows, elongated scores from the teeth scraping along the shell, and large crushed areas from the repeated bites applied to the same area.

In an attempt to verify the patterns of modification described in the Nile crocodiles (*Crocodylus niloticus*), Westaway *et al.* (2011) conducted a study with three captive salt water crocodiles, *Crocodylus porosus*. The specimens were observed feeding on two pig carcasses provided by the researchers. The pigs were then cleaned and examined for modifications. Fracturing was frequent; however, teeth marks were infrequent and only one bisected pit was noted.

Baquendano *et al.* (2012) conducted a study on modern crocodylian bite marks. Eight crocodiles were fed 19 partial articulated limbs from pigs, sheep (*Ovis aris*), and cows (*Bos taurus*). Marked bones and marks per bone were less frequent than those seen by Njau and Blumenschine (2006). Baquendano *et al.* (2012) did not observe any hook scores, and less than half of the marks were determined to be bisected marks.

Observations between these two studies varied because the collection protocols were not identical, the definition of bisected marks differed, and the conditions of the captive crocodiles used differed. The sample used by Njau and Blumenschine (2006) contained a higher number of males, which are highly competitive, while Baquendano *et al.* (2012) used a sample that contained only females, which may explain the minimal competition over carcasses.

Drumheller *et al.* (2014) observed tooth marks of American alligators (*Alligator mississippiensis*) and compared the results to existing crocodylian (*Crocodylus niloticus* and *Crocodylus porosus*) datasets to observe the potentially diagnostic traits of bisected marks, hook scores, and a lack of furrows (Figure 2.8). Drumheller *et al.* (2014) fed groups of captive alligators partially butchered cow hind limbs and pig femora. They found scores to be the most common types of mark, representing 59.6% of all identified traces. Pits were the second most common marks, representing 31.5% of the recorded marks. Punctures comprised 8.5% of the remaining bite marks, and furrows represented only 0.1% of marks. Of these marks, 10.4% of all pits, 9.9% of all scores, and 19.1% of all punctures exhibited bisections, representing 10.8% of all recorded marks. From the sampled bones, 83.6% exhibited at least one bisected mark. Bisected marks made by American alligators were found in rates similar to *C. niloticus* (10% of all observed bite marks in *C. niloticus* and 10.8% in American alligators; 82.5% of individual marks bones in *C. niloticus* and 83.6% in American alligators) (Drumheller *et al.* 2014). Hook scores comprised 6.2% of all observed scores, and were present on 62.5% of the observed bones. Hook scores were found at a higher rate in American alligators. Furrows, unique to American alligators, were identified. Bone fracturing and furrowing created extensively by American alligators are notably rare or absent among *C. niloticus* and *C. porosus* (Figure 2.5 and 2.6). American alligators exhibited a more aggressive style of feeding, focusing more on crushing and fracturing prey (Drumheller *et al.* 2014).

Conclusion

Animal scavenging will typically follow a similar pattern including dispersal of the remains from the initial deposition site and disarticulating the remains over time. Since remains are scavenged by more than a single species, bone surface modifications are indicators of the behavior of various scavengers. Gnawing by mammalian carnivores and crocodylians causes extensive damage to the bones and leaves distinctive tooth marks. Tooth punctures, tooth pits, and tooth scores are observed in both mammalian carnivores and crocodylians; however, the morphology of the tooth marks differ. Additionally, because of the forceful bite of crocodylians, hook scores and bisected marks are tooth marks distinctively observed in crocodylians tooth mark morphology. Finally, the digestive processes of crocodylians is highly acidic, indicating that remains found in feces will be highly decalcified and features of bones will not be recognizable.

Table 2.1. List of Crocodylian Species

Species	Binomial Name	Location	Environment
American alligator	<i>Alligator mississippiensis</i>	Southeastern United States	Freshwater (marshes, swamps, and rivers)
Chinese alligator	<i>Alligator sinensis</i>	China around the lower Yangtze River	Slow-moving freshwater rivers and streams
Spectacled caiman	<i>Caiman crocodilus</i>	Central and South America	All lowlands, wetlands, and riverine systems
Broad-snouted caiman	<i>Caiman latirostris</i>	Northern Argentina, Bolivia, southeastern Brazil, Paraguay, Uruguay	Freshwater and brackish mangroves, marshes, and swamps
Yacare caiman	<i>Caiman yacare</i>	Northern Argentina, southern Brazil, southern Bolivia Paraguay	Wetlands, rivers, and lakes
Black caiman	<i>Melanosuchus niger</i>	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam, Venezuela	Freshwater riverine systems
Cuvier's dwarf caiman	<i>Paleosuchus palpebrosus</i>	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam, Venezuela	Freshwater forested ravine systems and flooded forests around larger lakes.
Smooth-fronted caiman	<i>Paleosuchus trigonatus</i>	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Surinam, Venezuela	Freshwater riverine systems
American crocodile	<i>Crocodylus acutus</i>	Central and South America; extreme south of Florida	Freshwater and brackish coastal habitats

Species	Binomial Name	Location	Environment
Slender-snouted crocodiles	<i>Crocodylus cataphractus</i>	Africa	Riverine habitats with dense vegetation cover
Orinoco crocodile	<i>Crocodylus intermedius</i>	Colombia and Venezuela	Freshwater riverine systems
Freshwater crocodile	<i>Crocodylus johnstoni</i>	Northern Australia	Freshwater (lakes and swamps)
Philippine crocodile	<i>Crocodylus mindorensis</i>	Philippines	Freshwater
Morelet's crocodile	<i>Crocodylus moreletii</i>	Belize, Guatemala, Mexico	Freshwater swamps and marshes in forested area
Nile crocodile	<i>Crocodylus niloticus</i>	Africa	Lakes, rivers, freshwater swamps, and brackish water
New Guinea crocodile	<i>Crocodylus novaeguineae</i>	Indonesia and Papua New Guinea	Freshwater swamps, lakes, and rivers
Mugger crocodile	<i>Crocodylus palustris</i>	Bangladesh, India, Islamic Republic of Iran, Nepal, Pakistan, Sri Lanka	Freshwater lakes, rivers, and marshes
Saltwater crocodile	<i>Crocodylus porosus</i>	Australia, Myanmar, Cambodia, China, India, Indonesia, Papua New Guinea, Singapore, Thailand, Vietnam, and surrounding countries	Brackish waters around coastal areas and in rivers
Cuban crocodile	<i>Crocodylus rhombifer</i>	Cuba	Freshwater swamps
Siamese crocodile	<i>Crocodylus siamensis</i>	Cambodia, Indonesia, Laos, Malaysia, Myanmar, Thailand, Vietnam	Slow-moving freshwater swamps, lakes, and marshes
Dwarf crocodile	<i>Osteolaemus tetraspis</i>	Africa	Permanent pools in swamps and areas of slow-moving

			freshwater in rain forests
False gharial	<i>Tomistoma schlegelli</i>	Indonesia, Malaysia, and possibly Vietnam	Freshwater lakes, rivers, and swamps
Gharial	<i>Gavialis gangeticus</i>	India and Nepal	Riverine systems

Table 2.2. Crocodylian modifications compared to other agents of bone modification that leave similar marks. (Njau and Gilbert 2016, 3). Y = present; NR = not reported.

Crocodylian modifications	Mammalian Carnivores	Stone Tools	Reptiles	Trampling	Avian carnivores
Shoulder marks	NR	Y	NR	Y	NR
Multiple, fine, parallel striations within main groove	NR	Y	Y	Y	NR
V-shape cross section cross	NR	Y	Y	Y	Y
Periosteal crushing/subcambial spawling, sometimes associated striations and/or V-shape cross section mark	Y	Y	NR	NR	NR
Bone flake removal usually associated with deep pit and/or fracture on midshaft	NR	Y	NR	NR	NR
Multiple fine parallel striations across broad area of bone	NR	Y	Y	Y	NR
Drag-snags	NR	Y	NR	NR	NR
Pivoted V-shape cross section mark	NR	NR	NR	NR	NR
Pivoted V-shape cross section mark	NR	NR	Y	NR	Y
Hook marks (scores)	NR	NR	Y	NR	NR
Pits	Y	Y	Y	Y	NR
Bisected pits or marks	NR	NR	NR	NR	NR
Striation pivots	NR	NR	Y	NR	Y

Table 2.3. Tooth mark morphology comparison between mammalian carnivores and crocodylians (Dominguez-Rodrigo and Piqueras (2003), Njau and Blumenschine 2006; Selvaggio and Wilder 2001)

Tooth Mark	Mammalian Carnivores	Crocodylians
Pits	Circular to angular and range from around 1.5-4.0mm.	Circular to angular and some pits are bisected by a sharp linear depression. Pit diameters can range from 0.1-6.0mm or more
Scores	Linear, angulating from a well-defined pit and lengths range from 3.0-13.0mm	Linear, superficial to deep and lengths range from 3.5-55.0mm
Punctures	Circular to oval, semicircular notches at fracture edges and diameter ranges from 2.5-7.5mm	Circular to oval, serial puncturing, and diameters range from 1.0-11.0mm
Furrows	Linear with average length from 13.0-24.0mm	Furrows occasionally observed in American alligator assemblages

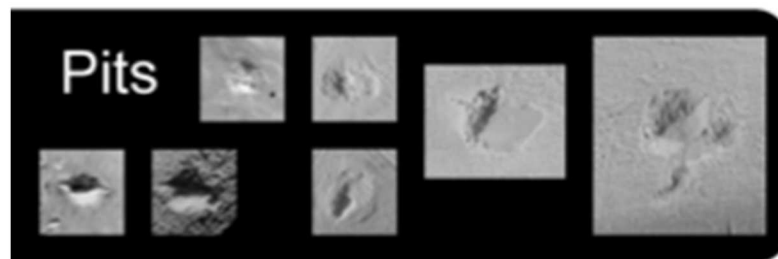
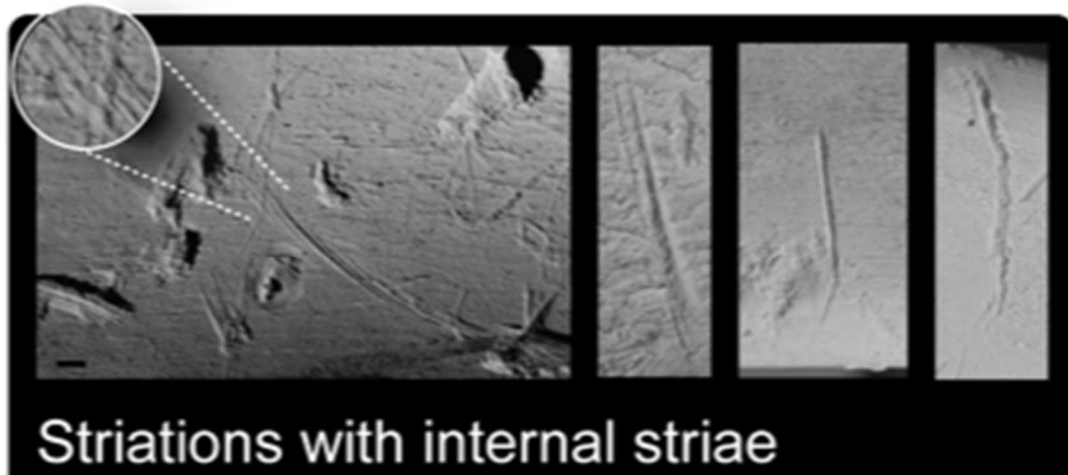
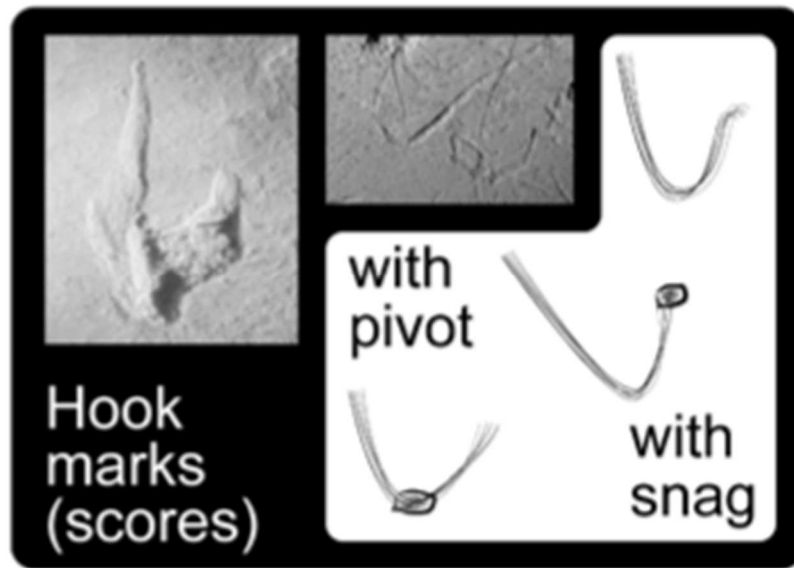


Figure 2.1. Example of hook scores (top), striations (middle) and pits (bottom) from crocodile (Njau and Gilbert 2016: 6).

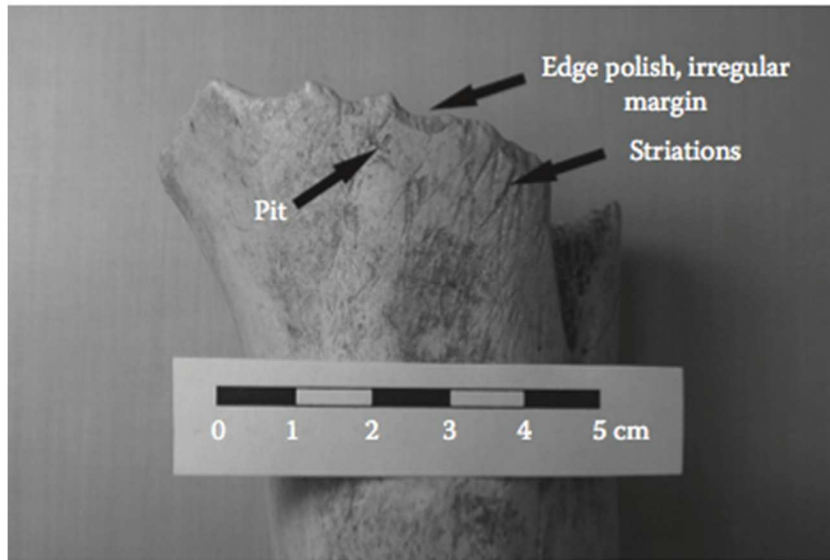


Figure 2.2. Example of tooth pit, striations, edge polish, and irregular margins from carnivore (Pokines 2014: 211).



Figure 2.3. Example of a puncture inflicted by a lion (Pobiner 2008: 375).

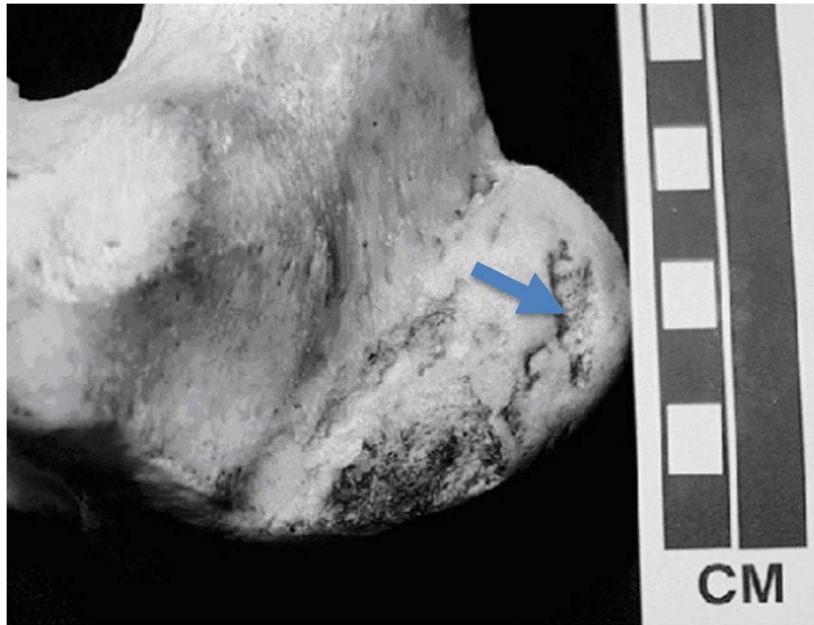


Figure 2.4. Example of tooth furrows inflicted by a lion (Pobiner 2008: 376).

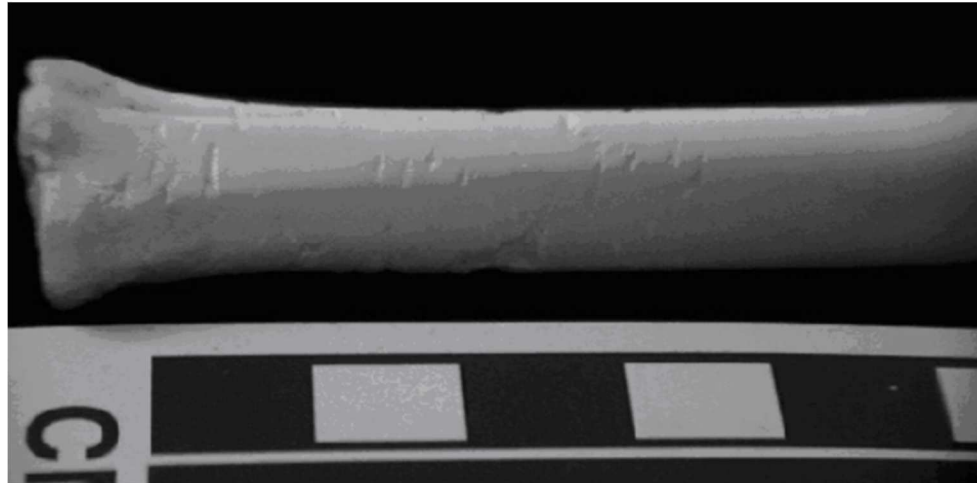


Figure 2.5. Example of tooth scoring inflicted by a lion (Pobiner 2008: 375).

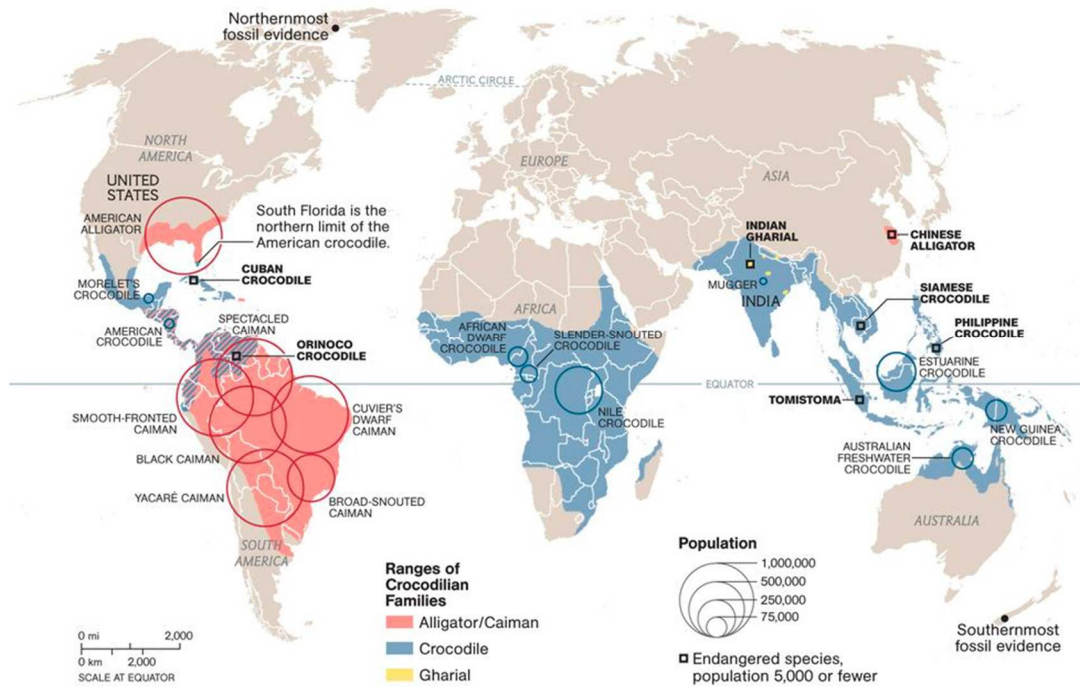


Figure 2.6. Geographical locations of crocodylians (<https://www.nationalgeographic.org/maps/crocodylian-ranges/>).

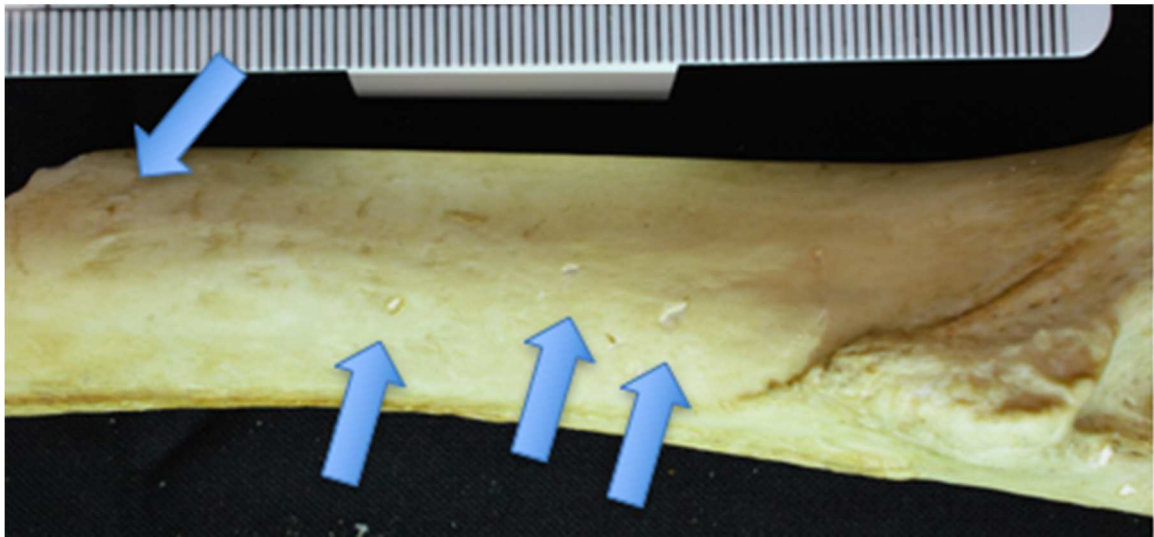


Figure 2.7. Top: punctures. Bottom: pitting (photographs by the author)

CHAPTER THREE: MATERIALS AND METHODS

The sample for the present study consisted of thirty-three commercially available fleshed white-tailed deer (*Odocoileus virginianus*) long bones (radii, ulnae, femora, tibiae, and humeri), seven kilograms of back ribs of white-tailed deer, and eleven kilograms of fleshed neck bones of white-tailed deer. Six fully fleshed articulated pig hind-limbs were also utilized in the present study. In addition, any feces from the adult alligators were collected in order to observe any identifiable bone fragments. White-tailed deer and pig are used as a proxy for human long bones due to the anatomical similarities, availability to have a larger sample size, and less research restrictions (Huculak and Rogers 2009; Jagers and Rogers 2009; Komar 1999; Pokines 2014). The white-tailed deer bones were purchased from elkusa.com and shipped directly to Edisto Island Serpentarium in South Carolina. Edisto Island Serpentarium is an indoor and outdoor facility dedicated to the recognition, preservation, and study of reptiles. The articulated pig hind-limbs were purchased from Burbage Meats, a local butchery located in Ravenel, South Carolina. Once the bones were obtained, they were stored in a freezer at the Edisto Island Serpentarium until the processing of the bones began.

The bones that were fed to the alligators were chosen at random and were set out to thaw the night before the animals were fed. Initially, five adult alligators were exclusively fed the white-tailed deer bones; however, four nine-year-old alligators were added to increase data collection. The adult alligators were all males of at least 50 years of age. Additionally, the adult alligators were all housed in the same enclosure. When

their feeding time comes around, typically three days a week at noon, the alligators will congregate in the pond housed within their enclosure and wait to be fed from the serpentarium personnel, who stand on an elevated platform.

The nine-year-old alligators were housed in the same enclosure that was much smaller than the adult alligator enclosure but also contained a small pond. The sex of the nine-year-old alligators included one female and three males. The nine-year-old alligators were more aggressive and active during feeding than the adult alligators. The nine-year-old alligators had to be trained to forage for their food in the pond rather than being fed with tongs, as they previously were during their younger age: the food was thrown into the pond and the nine-year-old alligators had to actively forage for their food.

The bones obtained from elkusa.com were pre-butchered by the meat company. The femoral heads were sawn off at an angle. The bones were disarticulated except for the radii and ulnae. The articulated pig hind-limbs from Burbage Meats were more heavily fleshed and had feet still attached. The hind-limbs, which were predominantly fed to the adult alligators, were not defleshed in order to keep the alligators interested in consuming the bones.

Data Collection

The author spent two weeks at the research site and fed the alligators for a total of seven nonconsecutive days. The alligators were fed three to four times a week due to their usual dietary habits in captivity. Initially, the five adult alligators were exclusively being fed; however, the adults swallowed the white-tailed deer bones whole and did not

leave any portions of bone behind. By day three, the author adjusted the methods in response and fed the nine-year-old alligators in order to increase the amount of data. While being housed at the serpentarium since 1999, the captive alligators have only been fed boneless chicken meat, never pork or white-tailed deer. A black vulture (*Coragyps atratus*) was present around the alligator enclosure and would hover and peck at the remains held in the alligators' mouth. The vulture would actively try to, and at times successfully, scavenge bits of meat that remained in the mouth of the alligator; however, scavenging marks from the vulture were not visible on the remains. The alligators never made any attempt to move away from the vulture.

Day 1

On 17 May 2017, four white-tailed deer ulnae/radii, one white-tailed deer femur, and fifteen white-tailed deer neck bones were fed to the adult alligators during the afternoon. To feed the alligators, the author stood on a platform above the enclosure and dropped the bones into the alligators' pond. The alligators were fed while they were wading in the pond of their enclosure. The alligators actively made an effort to obtain the bones that sank to the bottom of the pond. The alligators swallowed the bones whole and did not leave any bone portions or fragments in the enclosure.

Day 2

On 18 May 2017, four white-tailed deer humeri, two white-tailed deer articulated ulnae and radii, and sixteen white-tailed deer back ribs were fed to the five adult

alligators. The bones which were caught directly by the alligators were maneuvered in such a way until the alligators could swallow the bone whole. The elements that sank to the bottom of the pond were actively retrieved by the alligators (diving underwater to obtain it). The adult alligators again did not leave any bone portion or fragment in their enclosure. Additionally, there was not yet any excrement to be retrieved from the enclosure.

Day 3

On 20 May 2017, the nine-year old alligators were fed in addition to the regular feeding of the adult alligators. The adult alligators were continually fed to increase the chance of obtaining excrement. The adult alligators were fed 4 white-tailed deer humeri, 4 white-tailed deer femora with the head sawn off from butchery, 1 articulated white-tailed deer radius and ulna, ten white-tailed deer neck bones, and eight white-tailed deer back ribs. Once again, the alligators did not leave any part of the element behind and made an effort to retrieve the bones that sank to the bottom of the pond. The 4 nine-year-old alligators were fed 5 white-tailed deer femora, 2 white-tailed deer ulnae, 1 white-tailed deer humerus, white-tailed deer neck bones and white-tailed deer back ribs. Due to the smaller size of the nine-year-old alligators, the long bones could not be swallowed whole. Occasionally, once the bones were in the mouths of the nine-year-old alligators, the alligators would maneuver the bone to the side of their mouth in order to create enough force to break the bone in half into more manageable pieces. At other

times, the nine-year-olds simply kept the bone in their mouth. The nine-year-old alligators ate the back ribs without a problem due to the smaller size of the elements.

This same day, five bones were retrieved from the nine-year-old alligators' enclosure. Two of the bones were fragmented, and three of the bones were whole bones that the alligators gnawed on but lost interest in. The bones collected were left at the serpentarium to dry and prepare for maceration.

Day 4

On 24 May 2017, the adult alligators were not fed due to flooding in the enclosure from a thunderstorm the night before. The adult alligator left excrement on the surface in their enclosure, and it was collected by the lead administrator of the serpentarium and stored in a freezer. The nine-year-old alligators were fed 3 white-tailed deer radii and ulnae, 2 white-tailed deer humeri, and 8 white-tailed deer back ribs. The nine-year-olds consumed the ribs with no trouble due to the small size of the elements; however, they had difficulty gnawing and crushing the long bones. They gnawed on the long bones for a small amount of time, held them in their mouths, and eventually lost interest and dropped the bone onto the ground. One nine-year-old alligator cracked a long bone but did not swallow it. The remaining bones were collected later the same day.

Day 5

On 25 May 2017, the adult alligators were fed a single articulated pig hind-limb as well as two femora and three articulated ulnae and radii. The author fed the adult

alligators from the platform above the pond in the enclosure. One alligator obtained the whole pig leg, left the pond, and sat with the limb in its mouth on the terrestrial surface. Since the alligator had never had an element that large before, it sat with it in its mouth for a substantial amount of time before consuming the limb. The nine-year-old alligators were fed 1 white-tailed deer tibia, 3 articulated white-tailed deer ulnae and radii, and one rack of white-tailed deer back ribs. The nine-year-olds consumed the ribs with no difficulty. They gnawed on the long bones for some time, cracking some of the bones. The nine-year-old alligators did not actively make an effort to obtain the bones that sank to the bottom of their shallow pond. The long bones remaining at the bottom of the pond were collected by the lead administrator by the end of the day.

Day 6

The articulated pig hind-limb fed to the alligators on Day 5 was consumed whole by an adult alligator; there was no whole or fragmented bone left behind in their enclosure.

Day 7

On 27 May 2017, the adult alligators were fed 2 white-tailed deer necks and 8 white-tailed deer back ribs. The entire elements were swallowed whole, and there were no bone fragments or portions left behind. The nine-year-old alligators were fed 3 white-tailed deer radii and ulnae, 1 white-tailed deer femur, 3 white-tailed deer necks, and 8 white-tailed deer back ribs. The long bones were gnawed on, but the alligators lost

interest quickly. The necks and ribs were consumed whole with no difficulty by the nine-year-old alligators.

Day 10

Three fully fleshed articulated pig legs were fed to the adult alligators, and two additional fully fleshed articulated pig legs were fed to the nine-year-olds. The adult alligators obtained the hind-limbs while in the pond, swam to the terrestrial surface, and three alligators sat with a limb in its mouth. Occasionally, the black vulture would come around and try to scavenge pieces of the carcass. The alligators did not seem bothered but did eventually move once the vulture was present. Excrement was collected from the adult alligator enclosure. The nine-year-olds appeared excited about the hind-limbs likely due to the excessive amount of flesh present. In one instance, one of the nine-year-old alligators' death rolled with the pig hind-limb in an attempt to break apart the limb into smaller, more manageable pieces.

Day 11

The remaining elements were collected on this day, 1 June 2017. From the nine-year-old enclosure, a radius and ulna were found, but likely from an earlier feeding, not from the day before. A half-eaten whole leg was found in the enclosure of the nine-year-olds as well as parts of the pig pelvis. One whole pig leg was missing from the nine-year-

old enclosure and therefore it is assumed that the alligators completely consumed the pig leg.

The only bone collected from the adult alligators' enclosure was a small fragment of pig pelvis left over from the hind-limb. All other remains were fully consumed. The author decided to keep feeding the adult alligators obtain more feces.

Processing Collected Data

The remains and feces were prepared for shipment and shipped to Boston University School of Medicine (BUSM) for analysis. Once the bones arrived at BUSM, the remains were set out on trays and put under a fume hood to thaw. The bones were analyzed for the variation of the tooth marks between the bones, the frequency of the marks, the maximum diameters of the marks, and the morphological differences between the alligator tooth marks and carnivore tooth marks. The maximum diameter of each puncture and pit and the length of scores and furrows were measured to the nearest tenth of a mm using digital calipers and documented by the author. The feces were sifted through, using a water hose with low pressure and a 2mm screen, to identify surviving bone fragments; however, there were no remaining fragments of bone to identify. If there was any bone identifiable in the feces, it was analyzed under a light microscope provided by BUSM. The frequency of the bite marks on the bones were tabulated. The maximum breadth of hook scores was measured using digital calipers and rounded to the nearest tenth of a mm. I present descriptive statistics, including 95% confidence intervals for the lengths of pits and scores. The morphological differences between alligator bite marks

and other terrestrial carnivore bite marks were compared using previously published literature, including Pobiner (2007), Njau and Blumenschine (2006), Delaney-Riveria *et al.* (2009), and Drumheller *et al.* (2014) and a paired t-Test was used determine the statistical significance of the results.

Table 3.1. Feeding chart including days and total number of each bone fed to the alligators.

Day	Femora (white-tailed deer)	Radii/Ulnae (white-tailed deer)	Humeri (white-tailed deer)	Tibiae (white-tailed deer)	Back Ribs (white-tailed deer)	Neck bones (white-tailed deer)	Pig hind- limbs
Day 1	1	4	0	0	0	15	0
Day 2	0	2	4	0	16	0	0
Day 3	9	3	5	0	16	15	0
Day 4	0	3	2	0	8	0	0
Day 5	0	3	0	1	8	0	1
Day 7	0	3	0	0	16	5	0
Day 10	0	0	0	0	0	0	5



Figure 3.1. Nine-year-old alligator gnawing on a white-tailed deer bone.



Figure 3.2. White-tailed deer long bones recovered from nine-year-old alligator enclosure.



Figure 3.3. Nine-year-old alligator with fully fleshed pig hindlimb.



Figure 3.4. Adult alligator with fully fleshed pig hindlimb and vulture scavenging part of the carcass.

CHAPTER FOUR: RESULTS

All tooth marks on the bones were analyzed and documented. The only bone retrieved from the enclosure of the adult alligators was a left innominate from the fully articulated pig leg. The remaining bones were retrieved from the enclosure of the nine-year-old alligators. The number of each tooth mark was documented.

A total of 412 tooth marks were observed on all bones (Table 4.3). A total of 189 pits (46.0%), 55 punctures (13.3%), 136 scores (33.0%), 4 furrows (1.0%), 18 hook scores (4.3%), and 10 bisected marks (2.4%) were observed and measured on all bones (Figure 4.1). Pitting was the most frequent morphology observed on all bones, typically identified on the proximal (n=41) and midshaft (n=135) portion of bones. Scores were frequently identified on the midshaft (n=60) region of the bones. Punctures were observed often on the proximal (n=22) and distal (n=19) ends of the bones. Hook scores (n=14) and bisected marks (n=9) were observed most frequently on the midshaft portion of the bones. Furrows, typically uncommon in bones altered by crocodylian species, were observed on the distal ends (n=2) of the bones. Edge polish, commonly observed in mammalian carnivore-altered samples, was not observed in the present study (Binford 1981; Njau and Blumenschine 2006; Pokines 2014). The edges of all of the proximal portions of the innominate were gnawed and crushed by the alligators, creating crenulated edges, also commonly observed in mammalian carnivore gnawing (Pokines and Kerbis Peterhans 2007).

Four furrows were observed in the present study, and Drumheller *et al.* (2014) observed 19 furrows out of a total of 4,386 tooth marks (Table 4.2; 4.3). Njau and

Blumenschine (2006) found bisected marks to be uncommon, accounting for about 10.2% of the total number of tooth marks produced during the captive feeding trials; however, at least one bisected mark occurred on 82.5% of their tooth-marked bone specimens. In the present study, bisected marks accounted for 2.0% of the total number of tooth marks produced (Table 4.3). Drumheller *et al.* (2014) observed 414 bisected marks out of 4,386, whereas the present study found 10 bisected marks out of 412 tooth marks (Table 4.2). Drumheller *et al.* (2014), however, observed a total of 61 bones consisting of partially butchered cow limbs and isolated pig femora, and fed 14 American alligators. Njau and Blumenschine (2006) found hook scores to be less common than bisected pits, occurring on 27.5% of marked specimens from their feeding trials and accounting for less than 1.0% of the total number of tooth marks. In contrast, hook scores observed in the present study accounted for 4.0% of the total number of tooth marks produced (Table 4.1; 4.3).

Table. 4.1. Hook scores and bisected mark frequencies compared between present study and Njau and Blumenschine (2006).

Tooth marks	Present study	Njau and Blumenschine (2006)
Hook Scores	4.4%	<1.0%
Bisected marks	2.4%	10.2%

Table 4.2. Number and percentage of observed tooth marks compared between present study (n=37) and Drumheller (2014) (n=61).

	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected marks
Drumheller (2014)	1205/27.4%	325/7.4%	2282/52.1%	19/0.4%	141/3.2%	414/9.4%
Present study	189/46.0%	55/13.3%	136/33.0%	4/1.0%	18/4.4%	10/2.4%

Scores, in both crocodylians and mammalian carnivores, are usually oriented transversely or diagonally to the long axis of a cylindrical bone. Mammalian carnivores produce shallower and smaller tooth marks along the diaphysis of bones and larger tooth marks along the gnawed margins of soft bone portions. Crocodylians can inflict a high density of tooth marks on bone relative to that observed for mammalian carnivores. Njau and Blumenschine (2006) observed an average of 50 marks of all types inflicted on bones in their crocodile control sample, with a maximum number of 230 marks on one bone. In the present study, an average of 60 marks were inflicted on bones in the American alligator sample, with a maximum number of 67 marks on one bone. Serial pitting, scoring, and puncturing also provide an indication of crocodylian feeding and were observed in both the present sample and in the crocodylian sample by Njau and Blumenschine (2006).

Mammalian carnivores, such as canids, generally inflict tooth marks on a higher proportion of specimens than crocodiles and alligators. The size of pits and scores observed in small canids are bigger on cancellous bone tissue than on dense cortical surfaces. The maximum length of pits observed in dogs, from cancellous bone (from

epiphyseal sections) and dense cortical bone (from mid-diaphyseal sections), measured between 1.84 mm to 9.88 mm (Dominguez-Rodrigo and Piqueras 2003). The lengths of pits are more useful than tooth score sizes for distinguishing between carnivores, such as among small canids. However, tooth mark sizes alone are not reliable enough to identify specific carnivore taxa in bone assemblages (Dominguez-Rodrigo and Piqueras 2003).

Canids, such as coyotes (*Canis latrans*) or dogs (*Canis familiaris*) spend an extensive amount of time gnawing on the bone, including the destruction of weaker elements, swallowing small elements whole, and the destruction of long bone epiphyses through incremental gnawing to access the marrow spaces (Hudson 1993).

The comparison of tooth pits and scores has been used to determine the types of carnivores that have modified bone surfaces (Andrews and Fernandez Jalvo 1997; Delaney-Riviera 2009; Dominguez and Piqueras 2003; Njau and Blumenschine 2006; Pobiner 2007; Selvaggio and Wilder 2001). Unless the analysis of the tooth pits and scores considers their distribution and variation in large samples and other variables, such as the location according to bone section, tooth marks alone can not be used to differentiate among species. However, species-specific carnivore bone damage can only be confidently identified when comparing small-sized versus large-sized carnivores.

Domínguez-Rodrigo and Piqueras (2003) found pits and scores under 4 mm were observed in all carnivores but lions. Samples with pits and scores smaller than 4 mm are usually from small canids, such as jackals and middle-sized felids (Dominguez-Rodrigo and Piqueras 2003). Pits and scores between 4-6 mm are made by middle-sized and large-sized carnivores except felids other than lions. The mean percentage of tooth marks in

this size category belongs to mammalian carnivores such as dogs and bears. Marks above 6 mm are made by large carnivores, such as lions and hyenas (Dominguez-Rodrigo and Piqueras 2003).

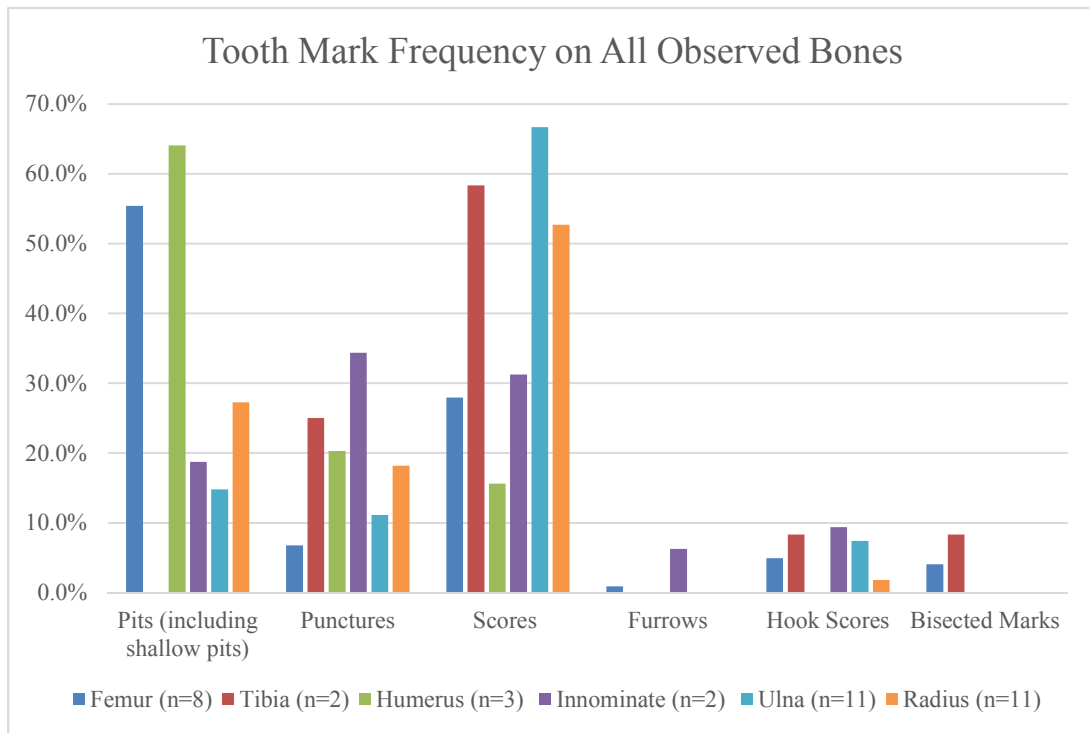
Delaney-Rivera *et al.* (2009) observed tooth marks on a varied sample of taxa and included comparative data from Dominguez-Rodrigo and Piqueras (2003), Selvaggio and Wilder (2001), and Pobiner (2007). Their study suggested that only limited number of inferences about taxa and body size could be made based upon the tooth pit dimensions and location.

Table 4.3. All bones and tooth marks observed in the present study (consumed elements included: 5 white-tailed deer neck bones (177mm), 7 white-tailed deer back ribs (305mm), and 4 fleshed articulated pig legs (914mm)).

	Bone portions	Femur (n=8)	Tibia (n=2)	Humerus (n=3)	Innominate (n=2)	Ulna (n=11)	Radius (n=11)
Maximum length of bone		241mm	279mm	254mm	*fragmented	267mm	229mm
Pits (including shallow pits)	Proximal	14	3	11	4	0	9
	Midshaft	86	0	41	0	7	0
	Distal	23	0	0	2	0	2
Punctures	Proximal	5	0	8	10	2	3
	Midshaft	0	0	0	0	0	0
	Distal	10	0	0	1	1	7
Scores	Proximal	1	5	0	7	16	0
	Midshaft	45	1	7	1	0	3
	Distal	6	1	3	2	3	26
Furrows	Proximal	0	0	0	1	0	0
	Midshaft	0	0	0	1	0	0
	Distal	2	0	0	0	0	0
Hooks Scores	Proximal	0	1	0	0	0	0
	Midshaft	9	0	0	3	2	0
	Distal	1	0	0	0	0	1
Bisected marks	Proximal	0	1	0	0	0	0
	Midshaft	9	0	0	0	0	0
	Distal	0	0	0	0	0	0

Observations of All Bones

Figure 4.1. Percentages of tooth mark frequency on all observed bones. N=number of samples from which the data were collected.



A total of 82 tooth marks were observed on ulnae and radii D-K (Table 4.2).

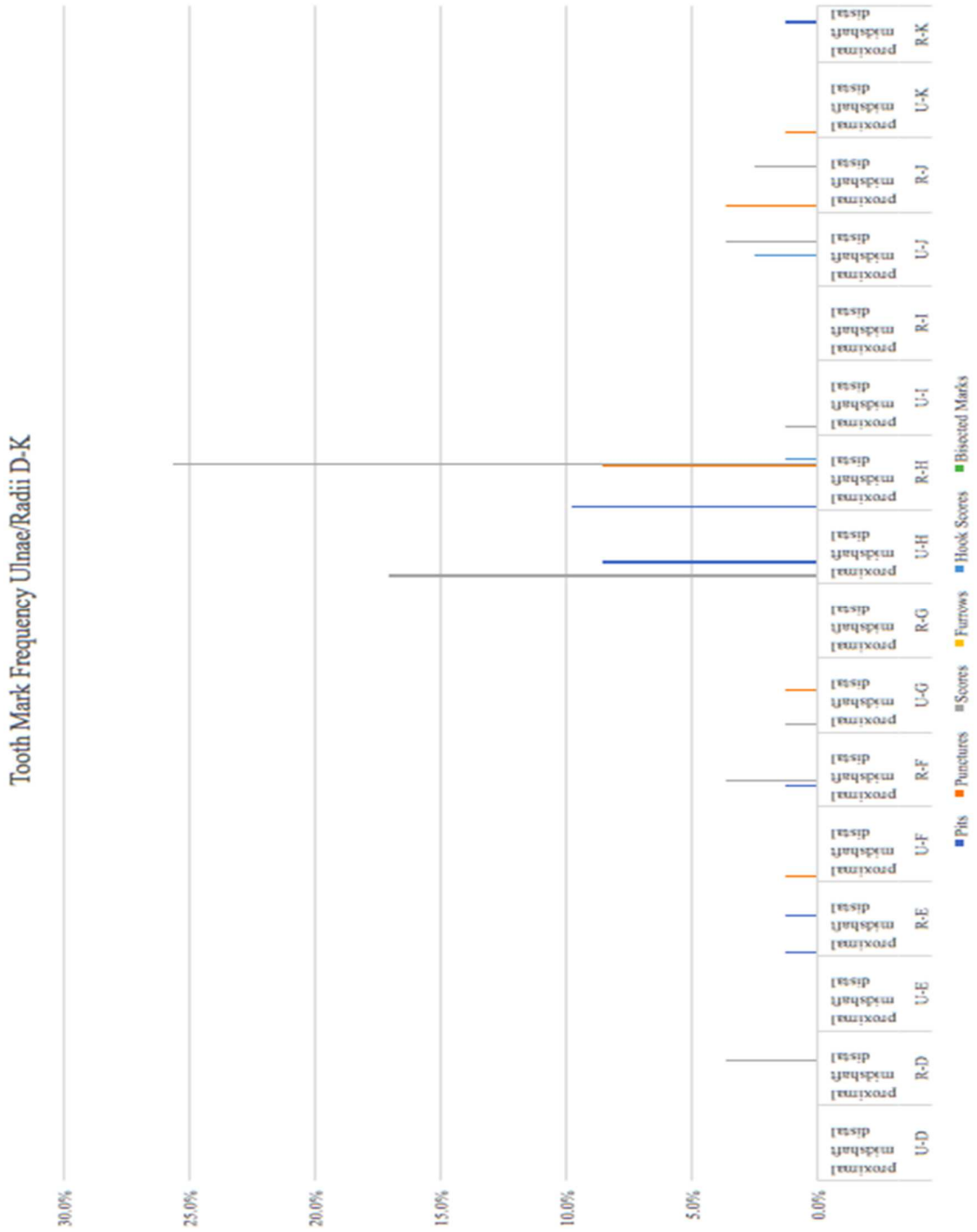
Ulnae and Radii A-C presented no visible damage. A total of 18 pits (23%), 13 punctures (7%), 48 scores (59%), and 3 hook scores (3%) were observed and measured on ulnae and radii D-K (Figure 4.2; Appendix A). Scores were the most frequent tooth marks observed, typically identified on the proximal (n=16) and distal (n=19) portions of the bone. Pits were most prevalent on the proximal (n=9) and midshaft (n=8) portions of the bone. Punctures were observed mostly on the proximal (n=5) and distal (n=8) ends. Hook scores were observed on the midshaft (n=2) portions of the bone. No furrows or bisected marks were observed.

Table 4.4 All tooth marks observed on Ulnae/Radii D-K.

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
Ulna D	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius D	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	3	0	0	0
Ulna E	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius E	Proximal	1	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	1	0	0	0	0	0
Ulna F	Proximal	0	1	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius F	Proximal	0	0	0	0	0	0
	Midshaft	0	0	3	0	0	0
	Distal	0	0	0	0	0	0
Ulna G	Proximal	0	0	1	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	1	0	0	0	0
Radius G	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Ulna H	Proximal	0	0	14	0	0	0
	Midshaft	7	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius H	Proximal	8	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	7	21	0	1	0
Ulna I	Proximal	0	0	1	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius I	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Ulna J	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	2	0

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
	Distal	0	0	3	0	0	0
Radius J	Proximal	0	3	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	2	0	0	0
Ulna K	Proximal	0	1	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Radius K	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	1	0	0	0	0	0

Figure 4.2. Percentages of tooth mark frequencies on the ulnae and radii. U= Ulna; R= Radius.

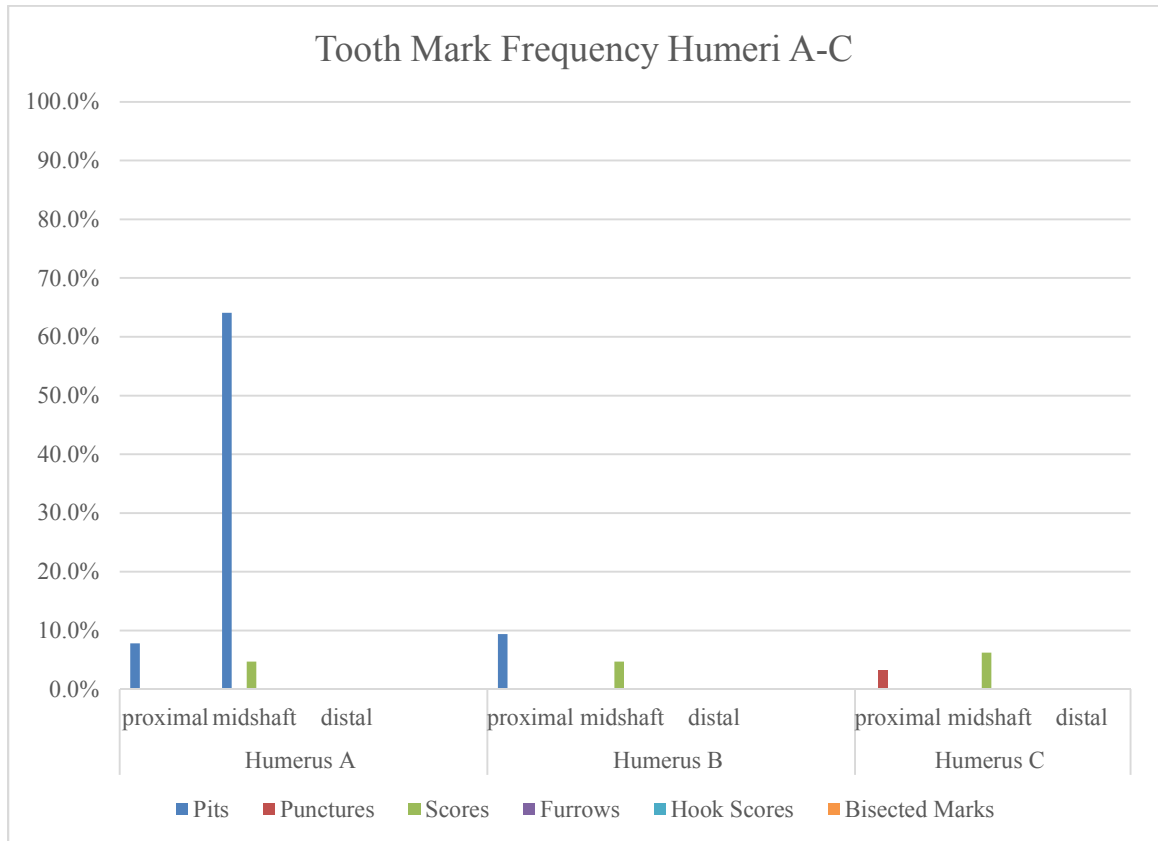


A total of 70 tooth marks were observed on the humeri (Table 4.6). A total of 52 pits (72%), 8 punctures (3%), and 10 scores (16%), were observed and measured on the humeri (Table 4.3; Appendix B). Pits were the most frequent tooth marks observed, often identified on the midshaft (n=41). Scores were most prevalent on the midshaft (n=10). Punctures were observed on the proximal ends (n=2). The punctures are circular, but the edges around the puncture are getting wider and fanning out, differing from mammalian carnivore punctures which typically more even and sharp. Hook scores, bisected marks, and furrows were not observed. Crenulated edges were observed on the humeral heads (cancellous bone was exposed on the humeral heads from crushing by the alligators).

Table 4.5 All tooth marks observed on the humeri.

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
Humerus A	Proximal	5	6	0	0	0	0
	Midshaft	41	0	0	0	0	0
	Distal	0	0	3	0	0	0
Humerus B	Proximal	6	0	0	0	0	0
	Midshaft	0	0	3	0	0	0
	Distal	0	0	0	0	0	0
Humerus C	Proximal	0	2	0	0	0	0
	Midshaft	0	0	4	0	0	0
	Distal	0	0	0	0	0	0

Figure 4.3. Percentages of tooth mark frequencies on the humeri.



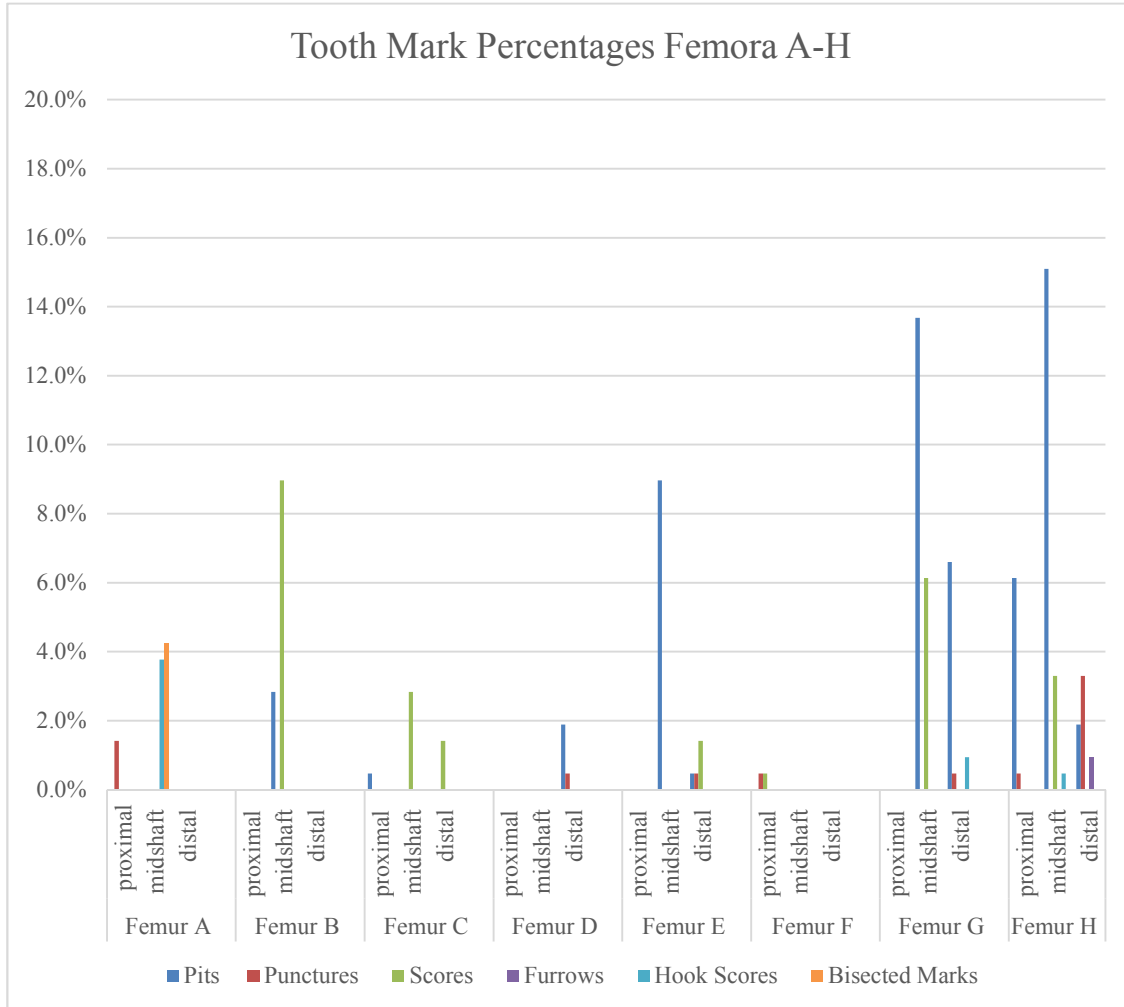
A total of 212 tooth marks were observed on the femora (Table 4.4). A total of 123 pits (58.0%), 15 punctures (7.0%), 52 scores (24.5%), 2 furrows (0.9%), 11 hook scores (5.2%), and 9 bisected marks (4.3%) were observed and measured on the femora (Figure 4.4; Appendix A). Pits were the most frequent tooth marks observed, typically identified on the distal (n=23) and midshaft (n=86) portions of the bone. Scores were most prevalent on the midshaft (n=45) of the bone. Punctures were observed on the proximal (n=5) and distal ends (n=10). The edges of punctures were crushed and fanning out, unlike canid punctures. The crushing of the ends of the punctures is likely caused by

the conical shape of the alligator teeth. Hook scores (n=9) and bisected marks (n=9) were present on the midshaft and furrows were observed on the distal ends (n=2).

Table 4.6. All tooth marks observed on the femora.

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
Femur A	Proximal	0	3	0	0	0	0
	Midshaft	0	0	0	0	8	9
	Distal	0	0	0	0	0	0
Femur B	Proximal	0	0	0	0	0	0
	Midshaft	6	0	19	0	0	0
	Distal	0	0	0	0	0	0
Femur C	Proximal	1	0	0	0	0	0
	Midshaft	0	0	6	0	0	0
	Distal	0	0	3	0	0	0
Femur D	Proximal	0	0	0	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	4	1	0	0	0	0
Femur E	Proximal	0	0	0	0	0	0
	Midshaft	19	0	0	0	0	0
	Distal	1	1	3	0	0	0
Femur F	Proximal	0	1	1	0	0	0
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0
Femur G	Proximal	0	0	0	0	0	0
	Midshaft	29	0	13	0	0	0
	Distal	14	1	0	0	2	0
Femur H	Proximal	13	1	0	0	0	0
	Midshaft	32	0	7	0	1	0
	Distal	4	7	0	2	0	0

Figure 4.4 Percentages of tooth mark frequencies on the femora.

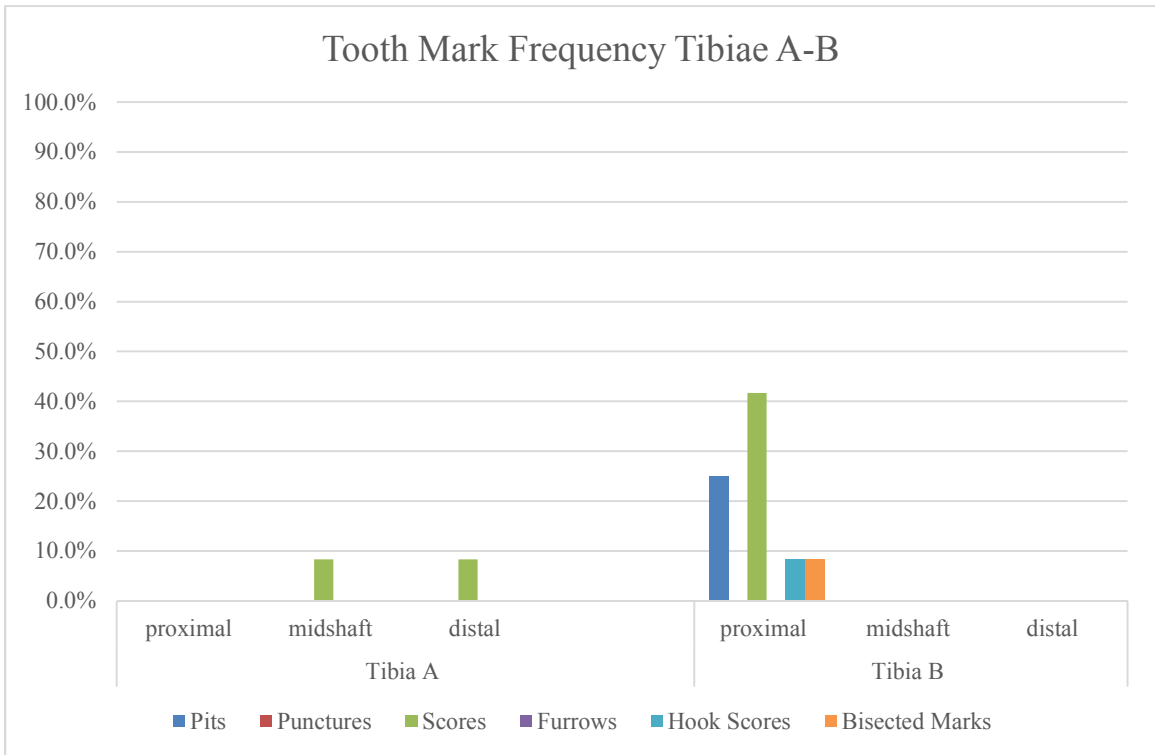


A total of 12 tooth marks were observed on the tibiae (Table 4.5). A total of 3 pits (25%), 10 scores (58%), 1 hook score (8%), and 1 bisected mark (8%) were observed and measured on the tibiae (Figure 4.15; Appendix A). Punctures and furrows were not observed on the tibiae. Scores were the most frequent tooth marks observed, identified on the proximal (n=5), midshaft (n=1), and distal (n=1) portions of the bone. Pits (n=3), hook score (n=1), and a bisected mark (n=1) were identified on the proximal ends.

Table 4.7 All tooth marks observed on the tibiae.

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
Tibia A	Proximal	0	0	0	0	0	0
	Midshaft	0	0	1	0	0	0
	Distal	0	0	1	0	0	0
Tibia B	Proximal	3	0	5	0	1	1
	Midshaft	0	0	0	0	0	0
	Distal	0	0	0	0	0	0

Figure. 4.5. Percentages of tooth mark frequencies on the tibiae.



A total of 32 tooth marks were observed on the innominates (Table 4.6). A total of 6 pits (19%), 11 punctures (34%), 10 scores (31%), 2 furrows (6%), and 3 hook scores (9%) were observed and measured on the innominates (Figure 4.6, Appendix A).

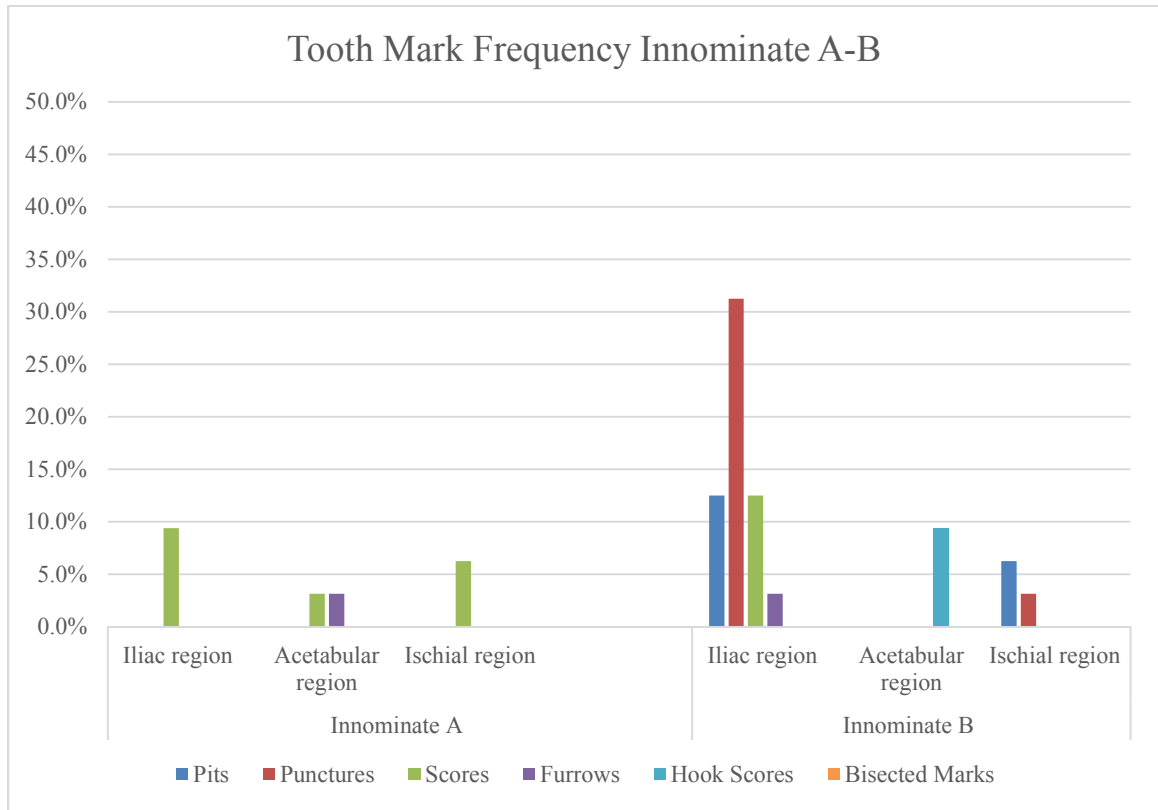
Bisected marks were not observed on the innominates. Punctures were the most frequent

tooth marks observed, identified on the iliac regions (n=10). Scores were identified on the iliac (n=7), acetabular (n=1), and ischial (n=2) regions. Pits were identified on the iliac (n=4) and ischial (n=2) regions. Furrows were identified on the ischial (n=1) and acetabular (n=1) regions. Hook scores were identified on the acetabular (n=3) regions. The edges of the innominates are crushed from gnawing and majority of punctures are irregular in shape, opposed to the standard circular punctures made by canids. All carcass parts were from pigs.

Table 4.8 All tooth marks observed on the innominate.

	Bone Section	Pits	Punctures	Scores	Furrows	Hook Scores	Bisected Marks
Innominate A	Iliac Region	0	0	3	0	0	0
	Acetabular Region	0	0	1	1	0	0
	Ischial Region	0	0	2	0	0	0
Innominate B	Iliac Region	4	10	4	1	0	0
	Acetabular Region	0	0	0	0	3	0
	Ischial Region	2	1	0	0	0	0

Figure 4.6. Percentages of tooth mark frequencies on the innominate.



Statistical Analysis

A paired t-Test was applied and compared to the frequency of tooth marks observed by Drumheller *et al.* (2014) (Table 4.2) and to the observed hook scores and bisected marks by Njau and Blumenschine (2006) (Table 4.1) to indicate if there is any statistical significance in the observations. For the comparison between this study and Drumheller *et al.* (2014), the t-stat is occurring at 2.01 standard deviation from the mean and the p-value (two-tail) is 0.100. The mean difference is at 662.33 and the 95% confidence interval of the mean difference between tooth marks found is between -184.66 and 1509.32 (Table 4.9, 4.10), indicating that the differences in in results are statistically significant.

Table 4.9. Statistical comparison between the frequency of tooth marks observed between Drumheller *et al.* (2014) (n=61) and the present study (n=37).

t-Test: Paired Two Sample for Means		
	<i>Drumheller et al. (2014)</i>	<i>Present Study</i>
Mean	731	68.66666667
Variance	750129.2	5878.266667
Observations	6	6
Pearson Correlation	0.787768633	
Hypothesized Mean Difference	0	
df	5	
t Stat	2.010171318	
P(T<=t) one-tail	0.050312155	
t Critical one-tail	2.015048373	
P(T<=t) two-tail	0.10062431	
t Critical two-tail	2.570581836	

Table 4.10. Incidence of tooth marks observed between Drumheller et al. (2014) and the present study.

Mean Difference	662.33
Standard Dev. Of Difference	807.08
Standard Error of Difference	329.49
T alpha half 95% CI	2.57
Lower Confidence Interval	-184.66
Upper Confidence Interval	1509.32

For the comparison between this study and Njau and Blumenschine (2006), the t-stat is occurring at 0.45 standard deviations from the mean and the p-value (two-tail) = 0.73. The mean difference is at 0.03 and the 95% confidence interval of the mean difference between hook scores and bisected marks found is between -0.67 and 0.72 (Table 4.11, 4.12). The mean difference between the present study and Njau and Blumenschine (2006) is 0.03, indicating the differences in results are not statistically significant.

Table 4.11 Statistical comparison between the frequency of hook marks and bisected marks observed between Njau and Blumenschine (2006) and the present study.

t-Test: Paired Two Sample for Means		
	<i>Njau and Blumenschine (2006)</i>	<i>Present Study</i>
Mean	0.055	0.03
Variance	0.00405	0.0002
Observations	2	2
Pearson Correlation	-1	
Hypothesized Mean Difference	0	
df	1	
t Stat	0.454545455	
P(T<=t) one-tail	0.364200251	
t Critical one-tail	6.313751515	
P(T<=t) two-tail	0.728400502	
t Critical two-tail	12.70620474	

Table 4.12. Incidence of hook scores and bisected marks observed between Njau and Blumenschine (2006) and the present study.

Mean Difference	0.03
Standard Dev. Of Difference	0.08
Standard Error of Difference	0.06
T alpha half 95% CI	12.71
Lower Confidence Interval	-0.67
Upper Confidence Interval	0.72

Descriptive statistics are provided for the comparative analysis of pits and scores by canids (dogs, coyotes, and black-backed jackals (*Canis mesomelas*) and American alligators (Table 4.13, 4.14), provided by Delaney-Rivera *et al.* (2009) and Domínguez-Piqueras and Rodrigo (2003).

Table 4.13. Sample size and distribution of pit and score marks analyzed, including standard deviation (s.d) and 95% confidence interval (C.I.). Comparative data are provided by Delaney-Rivera *et al.* (2009) and Domínguez-Piqueras and Rodrigo (2003). American alligator data is from the present study. “X” indicates no data recorded.

	N	Mean	s.d.	95% C.I.
Epiphyses				
(A) Pits				
<i>Canis latrans</i>	10	2.76	1.18	1.25-5.19
<i>Canis familiaris</i>	23	4.93	2.02	1.84-9.88
<i>Canis mesomelas</i>	40	3.5	0.7	2.80-4.20
<i>Alligator mississippiensis</i>	66	2.21	0.96	0.5-4.20
Epiphyses				
(B) Scores				
<i>Canis latrans</i>	X	X	X	X
<i>Canis familiaris</i>	12	12.8	4.65	6.26-21.48
<i>Canis mesomelas</i>	X	X	X	X
<i>Alligator mississippiensis</i>	67	3.9	1.61	1.4-10.4
Diaphyses				
(A) Pits				
<i>Canis latrans</i>	3	1.39	0.63	0.66-1.80
<i>Canis familiaris</i>	16	3.87	1.47	1.96-6.32
<i>Canis mesomelas</i>	40	1.45	0.75	0.51-3.67
<i>Alligator mississippiensis</i>	117	2.61	1.20	1.0-10.3
Diaphyses				
(B) Scores				
<i>Canis latrans</i>	X	X	X	X
<i>Canis familiaris</i>	23	12.8	6.12	4.95-26.55
<i>Canis mesomelas</i>	40	3.35	1.09	1.88-5.67
<i>Alligator mississippiensis</i>	72	5.36	3.87	2.0-28.0

Table 4.14. Descriptive statistics provided to the analysis of the maximum length in mm of pits and scores observed from the present study. Standard deviation and a 95% confidence interval (C.I.) are included.

<i>Pits(n=202)</i>		<i>Scores (n=124)</i>	
Mean	2.47	Mean	4.66
Standard Error	0.08	Standard Error	0.26
Median	2.50	Median	4.00
Standard Deviation	1.14	Standard Deviation	3.08
Range	9.80	Range	26.60
Minimum	0.50	Minimum	1.40
Maximum	10.30	Maximum	28.00
95% C.I.	0.16	95% C.I.	0.51



Figure 4.7. Pig femur with hook scoring.



Figure 4.8. Multiple punctures on the white-tailed deer femoral head.



Figure 4.9. Multiple punctures on the proximal end of the white-tailed deer femur.



Figure 4.10. Linear scoring on the proximal end of the white-tailed deer femur.

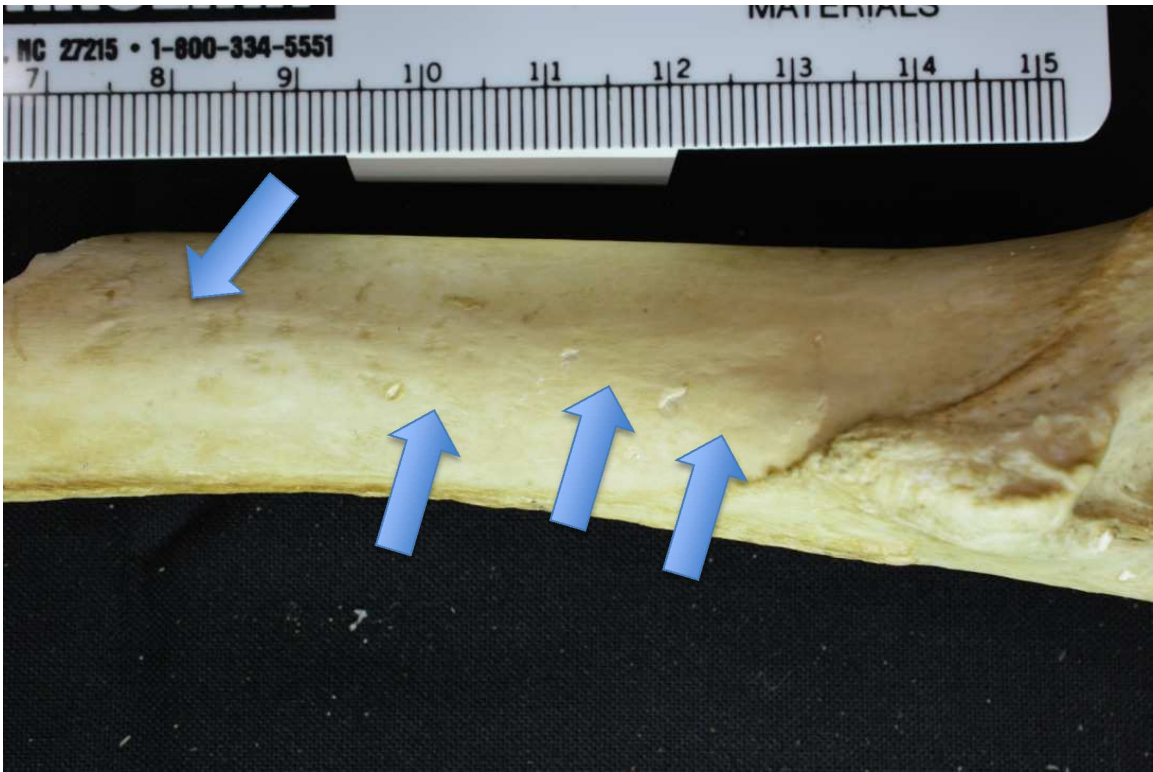


Figure 4.11. Multiple pits on the white-tailed deer femur.

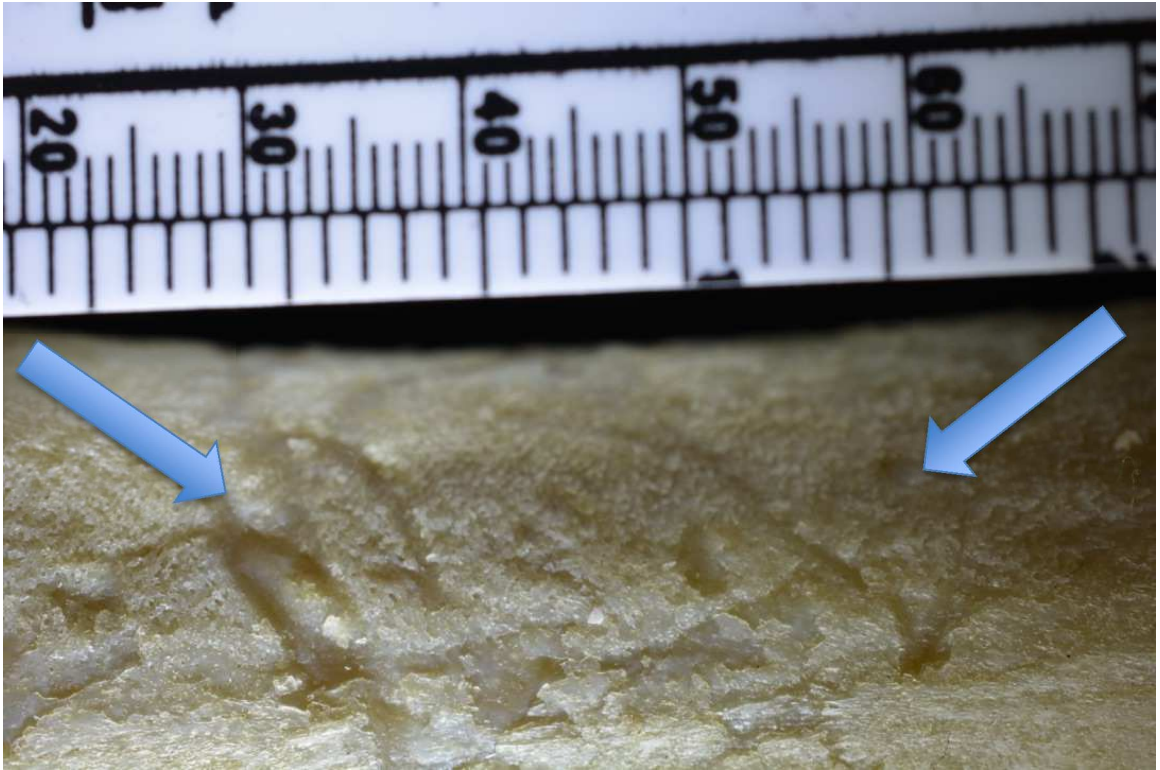


Figure 4.12. Damaged pig femur with hook scoring.



Figure 4.13. Damaged pig innominate from the nine-year-old alligator enclosure; crushed edges on proximal end and furrows near acetabular region (indicated by arrows).

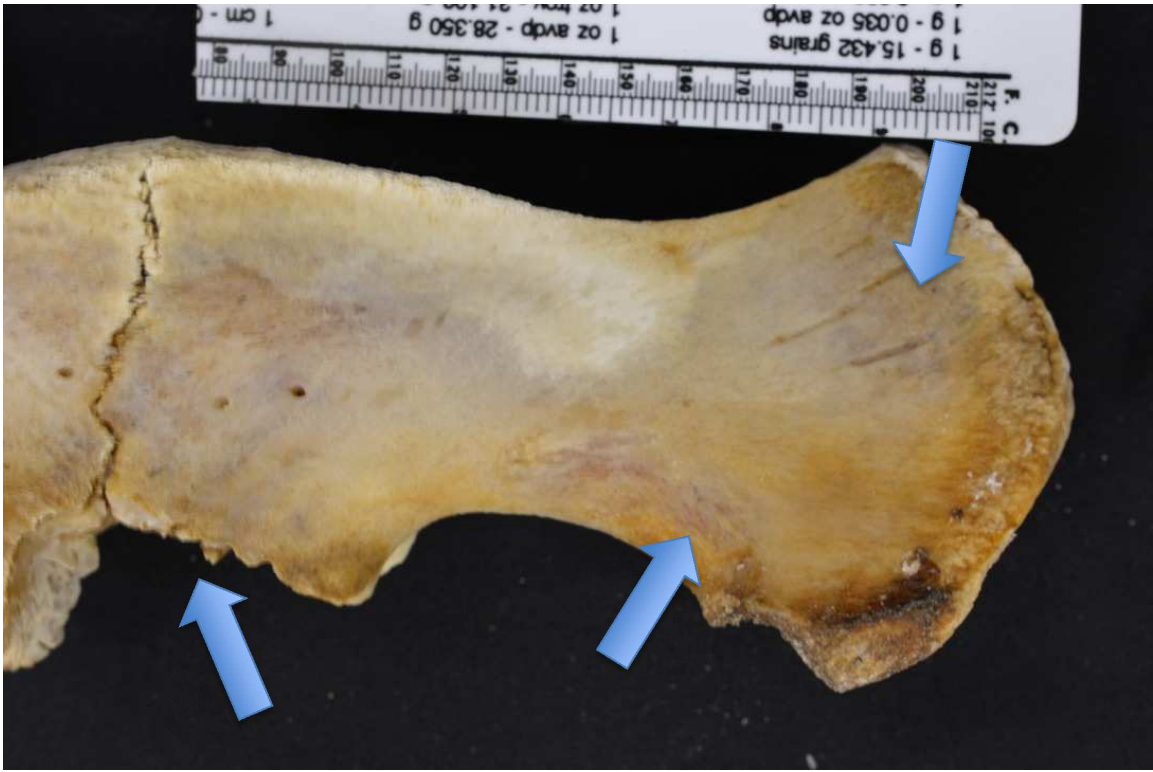


Figure 4.14. Damaged pig innominate from the nine-year-old alligator enclosure; linear scoring on the proximal end and crushed edges near acetabular region (indicated by arrows).



Figure 4.15. Pig innominate recovered from the adult alligator enclosure. Multiple punctures on the surface of the innominate (indicated by arrows).

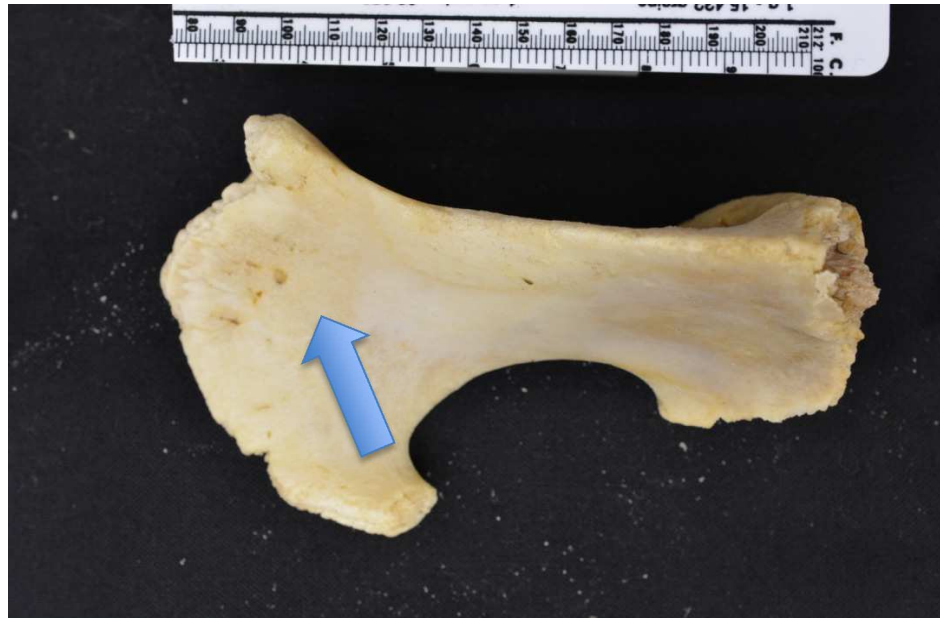


Figure 4.16. Proximal portion of the pig innominate from the adult alligator enclosure. Punctures are visible on the most proximal end. Top: proximal portion of innominate; Bottom: close-up of punctures.



Figure 4.17. Multiple punctures penetrating into bone (arrows) on the proximal portion of the innominate from the adult alligator enclosure.



Figure 4.18. Puncture (arrow) on the distal end of the innominate recovered from the adult alligator enclosure.



Figure 4.19. Proximal portion of the pig femur with a puncture (arrow) recovered from the nine-year-old alligator enclosure.



Figure 4.20. Puncture (arrow) on the distal end of the white-tailed deer femur.



Figure 4.21. Punctures (arrows) on the distal end of the white-tailed deer femur.



Figure 4.22. Multiple pits (left and middle arrows) and scores (top right arrow) on the diaphysis of the white-tailed deer femur.



Figure 4.23. Puncture (arrow) on the distal end of the white-tailed deer femur.

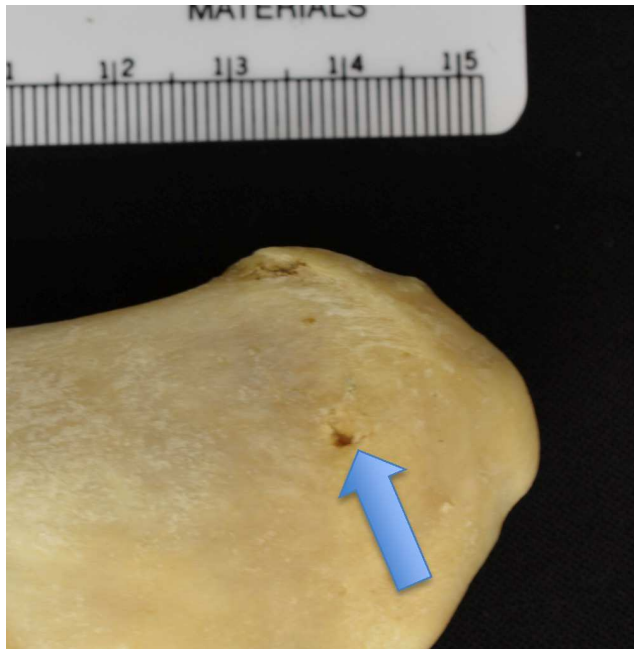


Figure 4.24. Small puncture (arrow) on the proximal end of the ulna. This mark is classified as a puncture due to the depth of the mark into the bone and the circular crushed edges.

CHAPTER FIVE: DISCUSSION

It was hypothesized that the alligators would make distinctive marks on the bone, both gnawed and digested, that could be clearly distinguished from other scavengers, including canids. While data from the adult American alligators were not able to be collected, data were collected from the nine-year-old alligators and classifiable bite marks were visible. The variations and patterns of the tooth marks were present between the samples and compared to other carnivore bite marks, such as canids, which are discussed in more detail below.

Punctures and pits were identified in majority of the sample from the nine-year-old American alligators. These findings do not support previous observations that bisected marks and hook scores are prevalent among this crocodylian species. The degree of damage on the bone is related, however, to the body size in terms of both animal mass and length. This is because crocodylian bite force scales closely with animal size (Erickson *et al.* 2003; 2012).

The total number of tooth marks identified in the present study was 412. Pits (including shallow pits), accounting for 46.0% of total tooth marks, followed by scores (including shallow scores) (33.0%), punctures (13.3%), hook scores (4.3%), bisected marks (2.4%), and furrows (1.0%). The most frequent tooth mark observed on the femora was pits (55.6%) of tooth marks observed, followed by scores (23.5%), punctures (6.8%) hook scores (5.0%), bisected marks (4.1%), and furrows (1.0%). The most frequent tooth mark observed on the tibiae were scores, accounting for (58.2%) of tooth marks observed, followed by pits (35.1%), and hook scores and bisected marks (8.2%).

Punctures and furrows were not observed on the tibiae. The most frequent tooth mark observed on the humeri were pits (81.0%) of tooth marks observed, followed by scores (16.0%), and punctures (3.0%). Furrows, hook scores, and bisected marks were not observed on the humeri. The most frequent tooth mark observed on the innominate were scores (86.0%) of tooth marks observed, followed by furrows (14.0%). Pits, punctures, hook scores, and bisected marks were not observed on the innominate recovered from the nine-year-old alligator enclosure. Finally, the most frequent tooth marks observed on the ulnae and radii were scores, accounting for (59.0%) of tooth marks observed, followed by pits (23.0%) punctures (7.0%), and hook scores (3.0%). Bisected marks and furrows were not observed on the ulnae and radii.

Observed patterns of the nine-year-old American alligator tooth type, mark, location, and proportion present differences with the Njau and Blumenschine (2006) Nile crocodile study. Identified marks were present in numbers per bone that exceeded the expected in similarly collected mammalian samples (an average of 69 marks per bone in the present study compared to an average of 378 individual marks per element in American alligator from Drumheller *et al.* (2014) and 250 in Nile crocodile from Njau and Blumenschine (2006). The elements observed in Drumheller *et al.* (2014) and Njau and Blumenschine (2006) were not the same elements involved in the present study, which could be a contributing factor to differences in individual marks per bone. A paired samples t-Test was used to statistically compare the frequencies of observed tooth marks from the present study and Drumheller *et al.* (2014) and Njau and Blumenschine (2006). When compared to the results of Drumheller *et al.* (2014), the p-value (0.10) is less than

t-alpha (2.01) indicating that there is significant difference in the means of each sample. Drumheller *et al.* (2014) had a higher sample size and used large cow limbs, while the present study had a slightly smaller sample size and used mostly white-tailed deer elements and pig hind limbs. When compared to Njau and Blumenschine (2006), the p-value (0.73) is slightly higher than the t alpha (0.45), indicating that there is no significant difference in the means of each sample. The frequency of hook scores and bisected marks observed by this study and Njau and Blumenschine (2006) had a mean difference of 0.03, a very slight difference between the samples.

The animals in the present study were observed feeding collectively and competing for each sample, which amplifies the interpretation that multiple participants increases the number of observed feeding trace density (Baquedano *et al.* 2012). The present study, however, did not observe the feeding behavior and competition between males and females. This variable is probably not affecting the resulting tooth mark types beyond the expected differences correlated with the range of body sizes and bite forces between the sexes (Erickson *et al.* 2003; 2012). A variable that is likely affecting the resulting bite marks is the age and size difference between the American alligators studied. The adult alligators have a stronger bite force and when consuming their prey, they did not perform any maneuvers such as “death rolls”, and consumed the remains whole. The young alligators demonstrated more difficulty with maneuvering the remains into their mouths and could not swallow anything whole. When fed the whole pig leg, the young alligators demonstrated maneuvers such as the “death roll” in order to break apart the leg into more manageable pieces. Furthermore, the young alligators also had

difficulty swallowing the white-tailed deer bones due to their size but could manage swallowing the neck bones and ribs whole.

Bone modification associated with gnawing, such as extensive furrowing, was largely absent on the bones in this study. Concentrated damage at long bone ends (Binford 1981) was present on a fair amount of bones but not as much expected. Furrows were completely absent in previous studies (Njau and Blumenschine 2006; Westaway *et al.* 2011; Baquedano *et al.* 2012) were identified occasionally in the present study, which indicates that the absence of such furrows should not be used as a diagnostic characteristic of crocodylian feeding traces. The furrows, and punctures, were restricted to long bone ends, and mostly occurred in isolation. This is an indication that the presence of this type of bone modification was likely a function of prey bone density and a distracted 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 a much lower frequency of all observed bite marks in American alligators than previous studies had reported (less than 20.0% in the present study) and were not as present on individual marked bones (only observed on the humerus, radius, and tibia). Previous research reported bisected marks of all observed bite marks present at 10.8% in American alligators and were present on individual marked bones at 83.6% in American alligators (Njau and Blumenschine 2006; Drumheller *et al.* 2014). Likewise, bisected marks in the present sample reflects a similarity between tooth morphology and wear patterns of American alligators.

Njau and Blumenschine (2006) described fracture patterns (*sensu* Byers 2005) and whole bone breakage presenting spiral fractures which range from rare (Baquedano *et al.* 2012) to incomplete (Drumheller 2014) in the Nile crocodile surveys. Among the data collected from the American alligators, all bones fed to the adults were fully consumed, and all bones from the young alligators' enclosure were collected, aside from one articulated pig leg that was completely consumed. Only one femur presented complete spiral fracturing, in which large portions of the bone was consumed. This is significant, because crocodylian bite force has been shown to scale linearly with animal size (Erickson *et al.* 2003; 2012). Captive animals are problematic to use in bite force studies due to their specialized diets and size but are still expected to be capable of creating similar bite forces of wild species. Though both the Nile crocodiles, sampled by Njau and Blumenschine (2006), and American alligators, sampled by Drumheller *et al.* (2014) measured around 4 meters in length, the American alligators caused more extensive damage. In the present study, the sizes between the nine-year-old and adult alligators were vastly different. Upon observation, the damage inflicted by the adult alligators was much more extensive than damaged inflicted by the young alligators.

The similarities and differences between the tooth marks might be the result of some type of sampling artifact. The American alligators were presented with white-tailed deer long bones, ribs, and necks and fully articulated pig legs. This is different from previous studies where cow (*Bos taurus*) limbs, significantly larger than white-railed deer limbs, were presented to both Nile crocodiles and American alligators (Drumheller *et al.* 2014), and Nile crocodiles were presented with sections of goat (Njau and Blumenschine

2006) or sheep (Baquedano et al. 2012). This factor could have been the reason why there was variation in between the samples. Published images indicate that there is likely more adhering soft tissue on the initial samples used by Njau and Blumenschine (2006) and Baquedano *et al.* 2012 than in the present study, which could potentially affect the animal's ability to access and break bones. The presence of numerous punctures in the Nile crocodile studies do not support the interpretation that the animals were hindered from accessing and heavily modifying their bones.

The differences in gross bone modification may represent actual differences in feeding strategies. For instance, the crocodylian snout has been used as a guiding reference when interpreting feeding ecology, with more slender-snouted forms being interpreted as piscivorous (Iordansky 1973; Langston 1973; Busbey 1995). Boxier snouts with enlarged posterior teeth trended more towards durophagy, the eating behavior of animals that can consume hard-shelled organisms. Broader, medium-length snouts indicates a compromise between the piscivorous and durophagy (Brochu 2001). American alligators are typically folded into groups interpreted to represent an ecologically generalist lifestyle (Drumheller 2014). American alligators are also more violent feeders, utilizing their ability to crush bones to a greater degree than other carnivores.

Hook scores in the American alligator specimens were the third-most observed tooth mark, constituting almost 20.0% of all observed scores and present on over 50.0% of observed bones. Death rolling and violent, lateral thrashing were only observed during the last day of feeding. In previous studies, death rolling maneuvers were also observed

during the feeding of American alligators and Nile crocodiles (Drumheller *et al.* 2014; Njau and Blumenschine 2006; Baquedano *et al.* 2012). The presence of hook scoring may be an artifact of the difference in collection methodology, including feeding duration, group feeding, prey type, and reported hook angle, but it also may reflect a more aggressive overall feeding strategy of the American alligators. In addition, the nine-year-old alligators were much more aggressive when being fed than the adult alligators.

Mammalian carnivores, such as canids, tend to gnaw more frequently on bone and for an extensive amount of time, leaving multiple punctures, pits, and furrows on bone. Canids will gnaw and break bones in order to access the marrow and grease. Tooth marks are then left behind during defleshing, gnawing, and fragmentation. American alligators will either swallow the carcass whole to access nutrients or break bones to reduce the size sufficiently, which may result in bear tooth marks. Tooth mark size alone cannot be used to identify specific carnivore taxa in bone assemblages; however, taking into consideration the variation and distribution of the marks can be used, accordingly, to distinguish between groups of carnivores. Tooth pit size, considered with other bone destruction processes, can yield information regarding the type of carnivore modification. Descriptive statistics were provided to compare the tooth pit and score sizes of canids (coyotes, Black-backed jackals, and dogs) and American alligators. The maximum length of pits of canids range from 2.76-4.93mm while the mean of pits of American alligators range from 1.70-2.27mm. The maximum width of scores of canids range from 3.35-12.8mm while the mean of scores of American alligators range from 1.86-4.66. The tooth marks of the American alligators are smaller in size; however, since most of the tooth

marks were made by young alligators in the present study, it could be assumed that they would produce smaller pits and scores than the canids, especially since canids continually gnaw on bones to access the marrow cavity, while American alligators do not actively try to access marrow.

CHAPTER SIX: CONCLUSIONS

The examination of bite marks by predators on bone provides evidence into the ecology, behavior, and morphology of the taxa that produced them (Pobiner 2008). Recognizing and understanding these taphonomic alterations is beneficial for forensic analysis and forensic cases; as previously discussed, there have been recent cases of body disposal in swamp regions in the southern region of the United States. Tooth marks of American alligators on bone remains a significant topic of study within forensic anthropological and law enforcement cases, especially in areas where body disposal in swamps is prevalent, for instance in Florida and Louisiana. Crocodylian taphonomic alterations to bone are also significant in paleontological research. Identifying bite marks in the fossil record could provide direct evidence for determining the diet of extinct taxa (Schwimmer 2002), feeding behavior of individuals and species (Noto *et al.* 2012), and the presence of intraspecific fighting (Avilla *et al.* 2004). Among crocodylians, potentially species-specific bite mark patterns included bisected marks, identified in bones modified by Nile crocodiles (Njau and Blumenschine 2006). Bisected marks were subsequently 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); however, similar research on *C. porosus* did not yield similar results (Westaway *et al.* 2011). This could be an indication that bisected marks are widespread throughout the crocodylian species. Further research on American alligator feeding can address a number of questions regarding evidence of feeding traces of crocodylian species on bone and

digested bone as well as the amount of time it would take for the species to fully consume an individual and what is left behind, if anything.

The purpose of the present research was to examine gnawed and digested bone from American alligators and determine classifiable bite marks observed on bone. It was hypothesized that alligators make distinctive bite marks on bone, both gnawed and digested, that could be clearly distinguished from other scavengers, including canids.

The results presented in this study indicate that American alligators do leave potentially diagnostic bite marks, including hook scores and bisected marks, but the marks were not as common as previous studies have reported. There was a total of 36 bones recovered from the enclosure of the alligators, 35 from the nine-year old enclosure and 1 from the adult alligator enclosure, and 412 tooth marks were observed on all bones. The most frequent bite mark observed on all bones were pits, occurring at a frequency of 46.0%. The least frequent bite mark observed on the bones were bisected marks, occurring at a frequency of 2.4%. The reason bisected marks and hook scores did not appear as frequent as previous studies have observed could be due to the fact that majority of the bones recovered were from the nine-year-old alligators and their bite is not as forceful as the adult alligators. Furthermore, the nine-year-old alligators have never been fed bone before the present study took place, and they lost interest in the long bones fairly quickly. This could be due to the fact that the long bones were large, had flesh, and were difficult for the young alligators to swallow whole. These long limb bones were utilized as a model for human remains and allowed for more accurate data collection. The

author observed a young alligator demonstrate the “death roll” maneuver when the fully fleshed articulated pig leg was placed into its enclosure.

While many individual tooth marks produced by mammalian carnivores and crocodylian species may be morphologically indistinguishable, the identification of bisected marks and hook scores is a clear indication of crocodylian species; these marks have not been observed in assemblages modified by mammalian carnivores (Capaldo 1995; Dominguez-Rodrigo and Piqueras 2003; Njau and Blumenschine 2006; Pobiner 2007, 2008; Selvaggio and Wilder 2001).

Future Research

Future research is also necessary to increase the understanding of alligator gnawing damage to bone and the effects on the postmortem interval. The present study focused on alligator bite marks to bone upon amply fleshed bone. The remains were not completely fleshed because the company elkusa.com does not supply fully fleshed white-tailed deer limb bones. To have access to more data, the author also used six fully fleshed pig hindlimbs. Additional research should be conducted utilizing fully fleshed articulated bones to determine the amount of damage alligators can inflict upon remains. Using fleshed bone could give a more accurate analysis of remains that may be disposed of in areas where alligators are most prevalent. For instance, feeding captive alligators a whole pig carcass or fully articulated white-tailed deer hind-limbs, commonly used as a proxy for humans, would provide a more in-depth analysis of alligator taphonomy.

Research is also necessary to understand how wild alligators would interact with the remains of a whole individual, to provide even more precise research within forensics. Wild alligators and captive alligators physically vary in size. Captive alligators are generally larger in size with a broad-shortened jaw, while wild alligators are smaller in size and have a narrow jaw (Erickson *et al.* 2004). Since forensic cases involving alligator postmortem damage to remains involve wild alligators, it is necessary to understand the behaviors and potential feeding behaviors of wild American alligators. The present study provides an analysis of alligator gnawing on bones, from which further methods of determining and classifying alligator bite marks can be utilized in future research.

APPENDIX A

A.1 Measurements of observed tooth marks on the ulnae/radii.

Bone	Tooth Mark Type	Length (all in mm)					Width (all in mm)				
Radius D	Scores (n=3)	3.3	3.2	2.2							
Radius E	Pits (n=2)	3.2	2.6				1.6	2.2			
Ulna F/ Radius F	Puncture (n=1)	3.0					1.7				
	Scores (n=3)	2.8	4.7	3.6							
Ulna G	Score (n=1)	5.3									
	Puncture (n=1)	2.2					1.5				
Ulna H/Radius H	Pits (n=15)	2.2	1.3	1.0	2.1	2.2	2.1	2.2	1.5	1.2	1.3
		2.8	3.2	2.2	1.9	1.7	1.7	1.4	1.8	1.5	1.1
		1.9	1.4	1.0	1.9	1.5	1.5	0.7	0.8	0.8	0.7
	Punctures (n=7)	4.3	5.1	3.6	3.2	3.1	3.6	3.4	3.0		
		3.7	3.1	4.6		2.7	2.4	3.3			
	Scores (n=35)	5.4	5.3	5.8	6.1	5.3					
		4.9	5.1	4.3	4.3	4.4					
		4.1	3.1	3.4	3.3	3.2					
		3.7	3.7	3.2	3.1	2.8					
		3.7	3.5	3.3	2.7	2.5					
2.1		2.2	2.3	2.6	2.3						
2.1		2.8	1.7	2.3	1.6						
Hook Score (n=1)	5.4					4.8					
Ulna I	Score (n=1)	5.3									
Ulna J/Radius J	Punctures (n=3)	2.7	2.5	1.8				2.4	1.9	1.3	
	Scores (n=5)	2.1	2.6	2.3	1.8	1.4					
	Hook scores (n=2)	4.4			3.7		2.6		3.8		
Ulna K/Radius K	Pits (n=1)	1.7					1.5				
	Puncture (n=1)	1.9					1.6				

A.2. Measurements of observed tooth marks on the humeri. Blank cells indicate that the width was not measured.

Bone	Tooth Mark Type	Length (all in mm)					Width (all in mm)					
Humerus A	Scores (n=3)	5.1		2.6		2.8						
	Pits (n=46)	3.1	3.6	3.9	3.5	3.3	2.3	2.2	2.7	3.1	2.6	
		3.4	3.3	3.8	3.1	4.2	2.1	2.5	2.7	2.7	2.5	
		3.3	3.0	3.0	3.6	3.9	2.4	2.3	2.6	2.9	2.5	
		3.2	3.1	2.9	2.0	2.0	1.6	1.5	1.7	1.6	1.6	
		2.4	2.0	3.6	2.3	2.1	1.6	1.8	2.4	1.7	1.5	
		2.4	2.6	2.7	2.0	2.0	1.5	1.9	1.9	1.8	1.8	
		2.2	2.1	2.2	1.8	1.3	2.0	1.6	2.0	1.5	1.0	
		1.9	1.7	1.2	1.6	2.3	1.5	1.6	1.0	1.3	1.8	
		1.4	1.5	0.8	0.9	0.8	0.9	1.1	0.7	0.7	0.8	
0.5	0.7	0.5	0.6	0.8	0.4	0.5	0.5	0.6	0.7			
Punctures (n=6)	6.3	4.1	5.7	3.5	7.2	29.1	3.7	3.3	3.8	2.5	4.9	17.1
Humerus B	Scores (n=4)	5.3		4.8		4.9		2.7				
	Punctures (n=6)	3.2	2.7	3.4	2.7	2.5	1.7	1.9	1.9	2.1	2.3	1.9
Humerus C	Puncture (n=2)	3.7			2.8			2.9			2.5	
	Scores (n=4)	5.6		4.8		3.4		3.7				

A.3. Measurements of observed tooth marks on the femora. Blank cells indicate that the width was not measured.

Bone	Tooth Mark Type	Length (all in mm)					Width (all in mm)				
Femur A	Hook scores (n=8)	19.1	15.0	11.9	12.3						
		10.4	6.1	6.5	5.6						
	Bisected marks (n=8)	13.8	11.2	9.3	8.1						
		7.8	7.3	6.7	1.5						
Punctures (n=3)	4.0	3.9	3.2			4.4	2.2	1.9			
Femur B	Scores (n=19)	10.4	7.7	6.4	5.5	5.4					
		5.1	5.8	5.4	5.0	5.3					
		4.9	4.7	2.1	2.8	3.0					
		3.9	4.1	2.4	2.0	2.8					
	Pits (n=6)	3.2	2.1	3.4			2.4	1.7	2.8		
		2.6	2.2	2.0			2.4	1.9	1.8		
Femur C	Pits (n=1)	10.3					9.7				
	Scores (n=9)	3.1	3.6	3.5							
		2.9	3.5	2.7							
		2.2	2.1	2.8							
Femur D	Punctures (n=1)	12.1					10.8				
	Pits (n=4)	7.6	3.4	3.1	2.7		6.9	2.8	2.9	2.3	
Femur E	Pits (n=19)	3.1	3.0	3.3	3.8	3.3	2.8	2.8	2.9	3.5	2.9
		3.0	2.5	2.5	2.3	2.6	2.7	2.1	2.0	2.0	2.0
		1.8	1.4	1.9	1.5	2.8	1.6	1.3	1.5	1.3	2.5
		2.6	1.5	1.6	1.2	1.3	2.2	1.2	1.5	0.9	0.7
	Punctures (n=1)	8.4					8.2				
	Scores (n=13)	5.4	5.5	5.8	5.2	4.8	3.5	4.3			
3.0		3.3	3.8	2.0	2.0	2.2	2.2				
Femur F	Score (n=1)	7.4									
	Punctures (n=1)	8.7					8.4				
Femur G	Punctures (n=1)	2.2					1.8				

	Tooth Mark Type	Length (all in mm)						Width (all in mm)								
		Scores (n=13)	7.2	7.8	5.1	6.4	6.3	5.8	5.5							
		5.7	4.5	4.1	3.9	3.0	3.0	3.2								
Pits (n=43)		3.0	3.1	3.4	2.9	2.4	2.8	2.5	2.7	2.3	2.1					
		2.6	3.6	2.3	2.7	2.2	2.3	3.2	2.0	2.4	2.0					
		3.4	2.8	2.8	2.5	2.5	2.8	2.5	2.5	2.2	2.4					
		2.1	2.5	2.5	3.2	2.6	2.0	2.2	2.3	2.8	2.2					
		2.0	2.6	3.8	3.9	4.1	1.7	2.2	3.5	3.4	3.9					
		3.7	3.0	3.5	1.1	1.7	3.5	2.8	3.2	1.0	1.5					
		1.3	1.2	1.2	1.7	1.0	1.0	1.0	1.0	1.5	0.5					
		1.8	1.9	1.9	1.5	1.5	1.5	0.5	0.5	1.1	1.2					
		1.2	1.4	1.0	1.2	1.3	0.8	0.9	1.0	0.6	0.8					
Hook score (n=2)	6.4			10.8												
Femur H	Pits (n=49)	3.4	2.0	4.3	3.2	3.0	3.1	2.1	3.8	2.9	2.5					
		3.7	3.0	3.5	3.8	3.6	3.5	3.2	3.4	3.5	3.4					
		3.3	3.6	3.7	3.2	2.1	2.8	3.5	2.9	2.8	2.0					
		3.8	3.2	2.1	2.5	2.7	3.4	2.6	2.4	2.1	3.0					
		2.7	2.8	2.3	2.6	2.4	2.3	3.0	2.1	2.5	1.5					
		2.1	2.5	1.7	1.4	1.1	1.8	1.9	1.6	1.0	1.0					
		1.0	1.2	1.5	1.3	2.0	1.7	1.0	1.4	0.8	1.6					
		2.5	2.9	2.0	2.7	2.9	1.6	2.5	2.3	2.5	2.5					
	Punctures (n=8)	3.8		3.1		3.5		2.0		3.4		3.3		3.2		1.8
4.3		3.0		2.7		2.4		4.1		2.9		2.6		2.0		
Scores (n=7)	7.4	5.7	5.6	4.0	3.3	3.7	3.5									
Furrows (n=2)	9.7			9.9												
Hook scores (n=1)	12.7															

A.4. Measurements of observed tooth marks on the tibiae. Blank cells indicate that the width was not measured.

Bone	Tooth Mark Type	Length (all in mm)					Width (all in mm)		
Tibia A	Scores (n=2)	6.7			4.9				
Tibia B	Pits (n=3)	3.5	3.8		2.0		3.0	2.8	2.2
	Scores (n=5)	9.5	11.6	5.5	5.9	8.1			
	Bisected mark (n=1)	7.7							
	Hook scores (n=1)	17.6							

A.5. Measurements of observed tooth marks on the innominate. Blank cells indicate the width was not measured.

Bone	Tooth Mark Type	Length (all in mm)						Width (all in mm)			
Innominate A	Scores (n=6)	28.0	18.0	10.2	9.2	4.7	13.2				
	Furrows (n=1)	24.1									
Innominate B	Pits (n=6)	3.3		3.2		3.1		2.4	2.7	2.0	
		2.3		1.4		1.8		1.4	1.4	1.1	
	Punctures (n=11)	5.9	8.3	3.4	6.9		4.6	3.9	2.6	5.0	
		4.9	3.5	2.7	5.0		2.8	3.4	2.2	2.2	
		2.6	3.7	2.3	2.8		2.3	3.2	2.1	2.1	
	Scores (n=4)	9.5	6.5	5.4	4.8						
	Furrows (n=1)	22.2									
Hook scores (n=3)	18.8		20.8		3.9						

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